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Autecology of Common Plants in British Columbia: A Literature Review

by
S. Haeussler[1], D. Coates[2], and J. Mather[3]

[1] Skeena Forestry Consultants
RR #2, Moncton Road
Smithers, B.C. V0J 2N0

[2] Ministry of Forests
Forest Sciences Section
Prince Rupert Forest Region
Bag 5000
Smithers, B.C.
V0J 2N0

[3] Skyline Forestry Consultants Ltd.
#200 - 156 Victoria Street
Kamloops, B.C. V2C 1Z7

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Forestry Canada
Pacific Forestry Centre
506 West Burnside Road
Victoria, B.C. V8Z 1M5
(604) 388-0600

or

B.C. Ministry of Forests
Research Branch
31 Bastion Square
Victoria, B.C. V8W 3E7
(604) 387-6719

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1 INTRODUCTION

The term autecology refers to the ecology of an individual organism. Plant autecology is the study of the ecological interactions between a plant species or population and its environment.

Resource managers require a basic understanding of the ecological characteristics of individual species and how they respond to management treatments. This publication summarizes the autecological characteristics of 35 vegetation species and provides information about how they respond to various silvicultural treatments now in use on forest lands. It contains valuable information for those who seek to manage vegetation either to control competing vegetation or to enhance browse, forage, and cover to meet wildlife, range, and other integrated resource management objectives.

Vegetation management is often carried out for silvicultural purposes. Many of the species described in this report compete with conifers. However, these deciduous trees, shrubs, and herbaceous plants have many important functions in natural ecosystems. These plants can act as forage and cover for wildlife and livestock; anchor species for reclamation of disturbed sites, erosion control, and streambank stabilization; ornamental and nurse crops; and crops in their own right. These values must be identified before silvicultural treatments are applied.

Many of the vegetation species in this publication are of great value to wild animals and livestock for food, cover, and/or nesting. On some areas, wildlife needs may require that certain vegetation species be left untreated for the long-term benefit of animals. Removal of vegetation may reduce biodiversity.

Information used in this report was gathered in an extensive search of ecological, silvicultural, and botanical literature pertaining to the selected species. Most of the literature originates in western Canada or the western United States. Some English-language literature from western Europe and further abroad is included for certain circumpolar species. For many of the species, there is little published information relevant to British Columbia. Personal communications (noted in text) and unpublished reports (indicated by footnotes) have therefore been used to supplement the literature.

2 EXPLANATORY NOTES

This section outlines the format used to present information about each of the plant species and provides some explanatory notes for each of the topics under discussion. The format is a modified version of the format developed for the "Biological Flora of the British Isles" series in the *Journal of Ecology* (see, e.g., Myerscough 1980) and subsequently adopted by the *Canadian Field-Naturalist* for its series "The Biological Flora of Canada" (Hall *et al.* 1979).

2.1 Description

This introductory paragraph gives a brief botanical description of the plant including its growth form or habit, and stem, leaf, flower, and fruit characteristics. The description and accompanying figure are not sufficiently detailed to enable the reader to identify the plant species. Readers seeking to identify plants are referred to plant identification handbooks produced by the Ministry of Forests, or to references cited at the end of the description.

2.1.1 Variation

A plant species is typically composed of a mosaic of populations, each of which differs in genetically-based morphological or physiological characteristics. Populations with distinct or consistent morphological variation may be designated as a subspecies (ssp.) or variety (var.). Taylor and McBryde (1977) was used as the standard reference for describing subspecies and varieties of the species in this publication.

2.2 Distribution and Abundance

This section and its accompanying distribution maps outlines the geographical distribution in British Columbia of each plant species. It indicates the abundance of each plant in biogeoclimatic zones and, in some cases, subzones. Biogeoclimatic zones and subzones are categories of the B.C. Ministry of Forests' ecosystem classification system (Pojar 1983). Zones are large geographic areas having a broadly homogeneous macroclimate and a characteristic combination of species. Zones are comprised of several subzones. Subzones are climatically less variable and geographically more confined than zones. The abbreviations used throughout the text to refer to biogeoclimatic zones and subzones are listed in Tables 1 and 2, respectively.

Information regarding the distribution of each species was obtained from published works (principally Hosie 1973; Hultén 1974; Krajina *et al.* 1982; Pojar *et al.* 1982; Angove and Bancroft 1983; and various Royal British Columbia Museum handbooks); from herbarium records on file at the B.C. Provincial Museum; and from discussions with vegetation researchers throughout the province.

TABLE 1. Abbreviations for biogeoclimatic zones

Abbreviation	Biogeoclimatic zone
AT	Alpine Tundra Zone
BG	Bunchgrass Zone
BWBS	Boreal White and Black Spruce Zone
CDF	Coastal Douglas-fir Zone
CWH	Coastal Western Hemlock Zone
ESSF	Engelmann Spruce – Subalpine Fir Zone
ICH	Interior Cedar – Hemlock Zone
IDF	Interior Douglas-fir Zone
MS	Montane Spruce Zone
MH	Mountain Hemlock Zone
PP	Ponderosa Pine Zone
SWB	Spruce – Willow – Birch Zone
SBS	Sub-Boreal Spruce Zone
SBPS	Sub-Boreal Pine – Spruce Zone

Sources: Pojar (editor) 1983 and Lloyd *et al.* 1990.

TABLE 2. Codes for biogeoclimatic subzones

Relative precipitation regime		Relative air temperature regime	
Abbreviation	Class	Abbreviation	Class
x	Very dry	h	Hot
d	Dry	w	Warm
m	Moist	m	Mild
w	Wet	k	Cool
v	Very wet	v	Very cool

Source: Lloyd *et al.* 1990.

2.2.1 Altitudinal range

Information about the altitudinal limits of plant species is scanty. The primary source of information was Lyons (1952) for shrubs and herbs and Fowells (compiler, 1965) for tree species. Species tend to have the broadest altitudinal distribution in the centre of their range, and tend to become confined to low elevations in the north and to higher elevations in the southern limits of their range.

2.3 Habitat

This section describes the ecological amplitude, or range of habitat conditions, which the plant species can endure. Species with a wide ecological amplitude can tolerate a wide variety of environmental conditions, while species with a narrow ecological amplitude are highly specialized for a particular ecological niche.

Because of the effects of competition from other plants, the observed ecological range of a species may differ significantly from the range of habitats it is capable of occupying (Barbour *et al.* 1980). The abundance or dominance of a species in a particular habitat does not necessarily indicate that the physical factors of that habitat are optimal for the growth of the species. Many species apparently adapted to the least favourable habitats will, in the absence of competition, grow far better in more favourable conditions and owe their ecological distribution to low competitive ability and high tolerance of extremes (Fitter and Hay 1981).

2.3.1 Climatic relations

This section describes the plants' adaptations to temperature, humidity, rainfall, snow, and wind. This section deals mainly with macroclimatic or regional climate conditions, but as Daubenmire (1974) points out, microclimate is of more immediate concern in autecology since a plant responds to the environment that envelops it. The local environment may be considerably modified from the macroclimate by local topography and surrounding plant cover.

Detailed characterization of the climatic relations of individual plant species is lacking in the literature. The comments in this section are largely subjective interpretations of the species' geographic and altitudinal distribution.

2.3.2 Site and soil conditions

Descriptive information about characteristic habitats is included in this category, along with details about landforms, parent materials, slopes, soil texture, and other soil profile characteristics.

2.3.3 Nutrient relations

This section describes the nutrient requirements of each plant species. There are large differences, both between and within a species, in the ability of a plant to absorb and use mineral nutrients. Optimum pH levels also differ between species that invade disturbed or young soils and those adapted to conditions in relatively undisturbed coniferous forests.

Of the mineral nutrients, nitrogen is probably the most important to plants. Nitrogen is frequently deficient in British Columbia forest soils (Freyman and van Ryswyk 1969; Hoyles 1979) and can be a major limitation to plant growth (Kramer and Kozlowski 1979). The nitrogen-fixing ability of alders can improve soil nutrient conditions (Tarrant and Miller 1963) and allows these species to invade heavily disturbed nitrogen-deficient soils.

Nitrogen fixation is just one effect of plants on the soil. Other impacts of plants on the soil are also discussed. For example, the litter of deciduous plants frequently contains higher concentrations of minerals and decays more rapidly than coniferous litter (Kramer and Kozlowski 1979). The rapid turnover of nutrients in deciduous foliage enhances nutrient cycling in the ecosystem. In addition, because deciduous litter has higher pH than coniferous litter it may reduce leaching losses from the soil in certain situations (Valentine *et al.* (editors) 1978).

Nutrient classes that appear in the text are listed in Table 3.

TABLE 3. Ecological nutrient classes

Trophotope	Description
Oligotrophic	Very poor nutritional status; very small supply of available nutrients
Submesotrophic	Poor nutritional status; low supply of available nutrients
Mesotrophic	Medium nutritional status; medium supply of available nutrients
Permesotrophic	Rich nutritional status; plentiful supply of available nutrients
Eutrophic	Very rich nutritional status; abundant supply of nutrients
Hypereutrophic	Saline nutritional status; excess salt accumulations

Source: Watts (editor) 1983.

2.3.4 Water relations

Moisture, more than any other single environmental factor, limits plant growth (Kozlowski 1972). This section describes the range of moisture conditions in which the plant is typically found, its drought tolerance, and its flood tolerance. The autecological importance of water is well documented in Daubenmire (1974) and Kramer and Kozlowski (1979).

Soil water classes used in this publication are listed in Table 4.

TABLE 4. Ecological moisture regime classes

Hygrotope	Description
Very xeric	Soil moist for negligible time following precipitation (ppt.)
Xeric	Soil moist for brief periods following ppt.
Subxeric	Soil moist for short periods following ppt.
Submesic	Water available for moderately short periods following ppt.
Mesic	Soil may remain moist for significant, but sometimes short, portions of the growing season. Available soil moisture reflects climatic inputs.
Subhygric	Soil wet for significant part of the growing season. Some temporary seepage and possibly mottling occur below 20 cm.
Hygric	Soil wet for most of growing season. Permanent seepage and mottling occur, and possibly weak gleying.
Subhydric	Water table at or near surface (<30 cm) most of the year. Gleyed or organic soils.

Source: Watts (editor) 1983.

2.3.5 Light relations

Light intensity, duration, and quality are key determinants of plant vigour and also have regulatory effects on various aspects of a plant's life history (USDA 1974; Lavender 1981). This section describes the shade tolerance of species, although, as Krajina *et al.* (1982) caution, generalizations about shade tolerance that do not take into account ecosystem conditions and the different stages of a plant's life cycle rarely provide meaningful information. In the shade, most species become suppressed and wane, and few produce seeds; in full light they grow more rapidly, produce fuller foliage, and usually produce abundant seed (USDA 1974). Photoperiod is instrumental in triggering many events in the plant's life cycle, particularly the onset of winter dormancy, but day length also affects the amount of photosynthesis possible and thus directly affects plant growth rates (Lavender 1981).

The spectral quality of light in the shade differs from full sunlight because shorter wavelengths are less able to penetrate the overhead canopy than longer, near infra-red wavelengths. Differences in spectral quality affect many plant functions (Lavender 1981). Long-wave radiation can penetrate beneath litter and humus layers and inhibit the germination of buried seed (Kenady 1978).

2.3.6 Temperature relations

Discussion of temperature relations includes information about the optimal temperatures for plant growth, the importance of temperature and thermoperiod in triggering phenological events, and the tolerance of the plant to heat and cold temperatures or frost. However, temperature relations of most selected species are poorly studied.

Both air and soil temperatures are ecologically important. Air temperatures in British Columbia are generally favourable to plant growth during late spring and summer, but soil temperatures at northern latitudes can severely restrict the potential for growth. Extremely high temperature at the soil surface can damage young plants (Lavender 1981), but such conditions are probably uncommon except in the southern interior or on some south aspects.

Most species become dormant well in advance of cold winter temperatures, and once dormant they are resistant to low temperatures (see, e.g., Smithberg and Weiser 1968). Plants are most susceptible to frost damage early in the growing season and during flowering and fruit set (Sharp 1974; USDA 1974).

2.4 Growth and Development

The vegetative growth of above- and below-ground plant parts is considered in this section. Both morphological and physiological aspects of growth and development are significant, but technical aspects of plant physiology are beyond the scope of this report. In addition, there is little information on this subject for the selected plants. Kramer and Kozlowski (1979) and Bidwell (1974) are good reference texts for basic information about the physiology of plant growth and development.

The life form of a plant (whether it is a tree, a tall or low shrub, or a herbaceous plant) has a major effect on its competitive abilities. Factors including longevity, size and structure of stem and root systems, leaf form, leaf area, and leaf longevity determine how well the plant will compete for limited site resources with other plant species (West and Tueller 1972).

All of the species discussed in this publication are perennials with underground parts (e.g., roots, rhizomes) that allow them to store reserves of energy through the dormant season, and permit rapid expansion of the foliage in the spring (Grime 1979). Many of the trees and taller shrubs compete successfully because their stature and long life span place them in the overstory, above smaller competitors. These species often have the added advantage of rapid juvenile height growth. Factors such as longevity, size and structure of stem and root systems, leaf form, leaf area, and leaf longevity determine how well the plant will compete for limited site resources with other plant species (West and Tueller 1972).

Many of the plants are also capable of lateral spread, by means of rhizomes, prostrate stems, or extensive horizontal root systems. This ability to develop clonal colonies with a high density of shoots and roots is a very effective means of occupying a site and pre-empting its resources (Grime 1979).

2.4.1 Phenology

Plant phenology refers to those periodic phenomena in the annual cycle of a plant that are controlled by climatic factors (Daubenmire 1974). Phenological events can be both morphological and physiological in nature and are controlled by predictable environmental factors such as photoperiod, temperature, summer drought, fall rains, and frost. In perennial plants, vegetative phenology includes such events as bud break, leaf expansion, shoot growth, leaf senescence and leaf fall, bud set, and winter dormancy. Reproductive or flowering phenology includes flowering times, fruit ripening, flower bud initiation, and seed dispersal. Conard (1983) outlines important aspects of shrub phenology and the role that they can play in forest vegetation management.

The timing of phenological events is an important part of a plant's competitive strategy (Grime 1979). For example, some plants such as salmonberry take advantage of the mild coastal climate to leaf-out early and gain a maximum vegetative advantage over associated plant species (Barber 1976). Plants that rely on sexual reproduction may time flowering events such that successful pollination (Heinrich 1976) or early seedling establishment (e.g., *Populus* spp.) is ensured.

2.5 Reproduction

The reproductive strategy of a plant is of fundamental importance in plant autecology and forest vegetation management. This section describes reproductive strategies including how a plant establishes itself on a site, how it increases in abundance following establishment, and how it persists through various stages of plant succession and habitat alteration.

2.5.1 Seed production and dispersal

This section describes the age of sexual maturity, the frequency and size of seed crops, the nature of the propagule (seed, fruit, or spore), and the method and efficiency of dispersal of each plant species.

Most species reviewed in this guide begin to produce seed between the ages of 2 and 10. Fruit and seed production rates are strongly affected by plant vigour, climatic factors, and biological agents. Most species disperse their seed from late summer to winter, although certain species have early-ripening seed.

Wind is an effective means of dispersal for light, small seeds, fruit, or spores. Seeds of other species are dispersed by gravity only. The seed of riparian species like willow and alder can be carried great distances by running water. Fleshy fruits are usually adapted for dispersal by birds and mammals (USDA 1974).

2.5.2 Seed viability and germination

Seed viability refers to both the germinative capacity of the seed and the length of time it can remain in a quiescent state before it loses its ability to germinate. The length of seed viability can vary from a few days to several decades or more. Many plants whose seeds remain viable for extended periods are known as "seed bankers" (Grime 1979; Rowe 1983). Seed of these species accumulates in the forest floor until environmental conditions become favourable for germination and subsequent plant growth.

The seeds of most North American plants are in a dormant state immediately following dispersal to prevent them from germinating too late in the year. The most typical form of seed dormancy is broken by several months of chilling (stratification) and the seeds germinate in the spring following dispersal (USDA 1974). Seeds that become ripe early in the growing season are usually capable of germination immediately following dispersal (see, e.g., Fowells (compiler) 1965; Zasada *et al.* 1983).

Another form of seed dormancy is found in seeds with a very hard seed coat. These seeds require acid treatment or physical abrasion (scarification) to germinate. Seeds with seed coat dormancy are often found in species with fleshy fruit and some lose their dormancy after they pass through the digestive tracts of animals (Sharp 1974). Still other seeds may require exposure to high (fire-induced) temperatures to overcome dormancy (Rowe 1983).

The requirements for successful seed germination are adequate moisture, favourable temperatures, adequate gas exchange, and — for some species — light (USDA 1974). Most seeds will germinate on a variety of moist seedbeds, but moist mineral soil is preferred by many species. Seed germination requirements are normally much less critical than conditions required for successful seedling establishment (Fowells (compiler) 1965; Barber 1976).

There is great variance among the plant species included in this report in the relative importance of regeneration from seed. Some species like red alder reproduce almost entirely from seed, while for other species like trembling aspen, seedling production is an insignificant part of the reproductive strategy. Certain species, like bigleaf maple and oval-leaved blueberry, are "seedling bankers" (Grime 1979). Like western hemlock and amabilis fir, they produce advanced regeneration which can persist beneath a forest canopy for many years, but does not grow beyond the seedling stage until released from overstory shade.

2.5.3 Vegetative reproduction

All of the plants included in this report reproduce vegetatively. Vegetative reproduction is the dominant form of reproduction in some, but not all, of the species in this report. Methods of natural vegetative reproduction include sprouting, suckering, layering, and rooting of stem or root fragments.

Sprouting is the dominant form of vegetative reproduction. It refers to production of new shoots from dormant or adventitious buds on stems or root collars. Suckering refers to the production of new shoots from laterally spreading roots or rhizomes at some distance from the parent plant. Suckers tend to become independent plants, and thus lead to the production of genetically identical colonies or clones (Gill and Healy (compilers) 1974).

There is some disparity in the literature in the use of the terms "sprouting" and "suckering." Many authors use "suckering" to describe the production of shoots from roots only, and use "sprout" to refer to rhizome shoots. The literature also includes a profusion of names for rhizome-like structures. Terms such as "rootstock", "underground stem", "stolon", and "runner" are variously used to describe prostrate branching structures that occur at or slightly beneath the soil surface and produce roots along their length.

Layering is a form of vegetative reproduction that occurs when stems come in contact with the ground surface and produce roots. Eventually a new plant can be formed.

Most perennial plants can be reproduced artificially from root or stem cuttings. The same situation can occur in nature when plants fragmented by disturbance become buried in a favourable rooting medium.

2.6 Pests

This section provides information about disease and insect pests.

2.7 Effects on Crop Trees

Plant species growing in association with coniferous crop trees may have both negative and positive effects on conifer growth. Competitive and beneficial effects are discussed separately in this section.

2.7.1 Competition

This section describes what is known about the importance of each plant as a competitor in different regions of British Columbia, and the nature of its competitive interactions with coniferous crop trees.

The following list outlines some negative effects of competing vegetation on crop trees (Conard 1983, 1984).

1. Moisture competition. Competing vegetation normally results in a net loss of moisture from a site.
2. Shading. Overtopping vegetation reduces light available to crop trees.
3. Nutrient competition. Most perennial plants cause net depletion of nutrients in the soil profile.
4. Reduced soil and air temperatures. Shading and insulation of the forest floor by foliage and litter can reduce crop tree growth.
5. Allelopathy. Some plants release chemicals which interfere with the growth and development of crop trees.
6. Attraction of pests. Non-crop vegetation may provide shelter or supplementary food to rodents, browsing animals, or insect and diseases that damage conifer stands.
7. Mechanical damage. Seedlings may be compressed under snow-pressed vegetation or damaged by wind-whipping.
8. Fire hazard. Shrubs and herbaceous vegetation may provide fuels that increase fire hazards.

2.7.2 Beneficial effects

This section describes the benefits of non-crop vegetation to crop trees. Benefits include:

1. Increased relative humidity and soil moisture. Evapotranspirative stresses to the crop tree may be reduced through shading and transpiration by surrounding vegetation, and by the mulching effect of plant litter.
2. Reduced temperature extremes. Shade from surrounding vegetation may prevent damage from excessively high temperatures or frost.
3. Improved nutrient relations. Non-crop vegetation can act as a site improver through nitrogen fixation or through deposition of rapidly-decomposing, nutrient-rich litter.
4. Reduced pest damage. Non-crop vegetation may act as an alternative food source, or discourage pests from entering conifer stands.
5. Reduced long-term competition. A cover of low-growing or short-lived plants may prevent the invasion of longer-lived, more aggressive competitors.

2.8 Response to Disturbance or Management

This section describes how cover, abundance, and plant vigour of each species may be affected by natural disturbance or management practices.

2.8.1 Forest canopy removal

Information describing how the plant species responds to partial or complete overstory removal through harvesting, thinning, or by natural means is summarized in this section. Most of the selected species respond favourably to the increased light resulting from canopy removal by developing a fuller crown and increasing flower and fruit production, provided evapotranspirative stresses do not become extreme. Some species increase rapidly in abundance through vegetative spread or seeding-in.

2.8.2 Fire

The response of each plant species to natural or prescribed fire is discussed. Processes by which vegetative recovery take place following fire are identified. The main processes are 1) sprouting or suckering from residual plant parts (usually underground rhizomes) that have survived the fire, 2) germination of seed buried in the forest floor, and 3) invasion by wind or animal dispersed seed and spores. Rowe (1983) gives a good summary of the adaptations of plants to fire.

Where information is available, the response of plants to fires of different severities is described. Fire severity is a function of weather, soil, and fuel conditions, and is defined by the amount of surface organic material removed, and the depth of heat penetration into the soil (Miller 1977; Rowe 1983). The degree of damage to, or stimulation of, underground organs and buried seed is usually directly related to the fire severity.

2.8.3 Cutting and grazing

Manual cutting of woody species is carried out either as a silvicultural treatment or to simulate the effects of browsing animals in wildlife studies. The response of plants to cutting, browsing, or grazing depends on their ability to reproduce by means of sprouts or suckers and is a function of season, frequency or severity of cut, height and angle of cutting, and the age of the plant (Gill and Healy (compilers) 1974; Harrington 1984; Hoyer and Belz 1984). Light browsing or single cutting treatments will stimulate growth of most sprouting or suckering species. Repeated cuttings, however, will eventually exhaust the carbohydrate reserves of all but the most resistant plants.

2.8.4 Herbicides

This section summarizes reports of herbicide applications to the selected species. The emphasis is on chemicals registered for forestry use in British Columbia, and, where possible, on studies conducted in British Columbia. No attempt was made to provide detailed descriptions of the conditions under which the herbicides were applied. Because of the large number of variables affecting plant sensitivity and herbicide efficacy (Newton and Knight 1981), readers are advised to consult the referenced articles for specific details.

Plant injury from herbicides is provided with a descriptive rating. The percent injury corresponding to each descriptive rating is listed in Table 5.

TABLE 5. Herbicide injury classes

Percentage injury[a]	Descriptive rating of injury
90 – 100	Very severe
60 – 90	Severe
25 – 60	Moderate
< 25	Light
0	No visible injury

[a] Injury: The amount of reduction in live canopy or foliage as compared to that in untreated plants of the same species.
Source: Conard and Emmingham 1984c.

2.8.5 Soil disturbance

This section summarizes the plant's known or expected response to natural or man-caused soil disturbance. It includes information pertaining to the plant's ability to colonize disturbed areas through germination of buried or newly-deposited seed, or to regenerate from root and stem fragments. Information is also provided on the effects of mechanical site preparation techniques used in silviculture on individual plant species.

2.8.6 Fertilization

Nitrogen fertilizers applied to the selected plant species generally improve vigour, growth rates, and fruit production (see, e.g., Freyman and van Ryswyk 1969; Nelson 1974). However, the plants vary in their ability to respond to additions of other essential elements (Nelson 1974; Watt 1976).

Fertilizers applied to improve the growth of crop trees may cause the vigour and cover of competing species to increase as well (Turner 1979). Increased vigour and shading of overstory trees may partially offset this response (Stanek *et al.* 1979).

2.9 Wildlife and Range

2.9.1 Food

This section summarizes use of the plant for food by ungulates, other mammals, livestock, and birds in British Columbia. The discussion of the plant as a food resource includes: its importance for wildlife and livestock, the principal species that feed on it, the plant parts consumed, season of foraging, and the plant's ability to recover from foraging. Singleton (1976) provides a useful summary of literature on the food habits of ungulates in the province. Information pertaining to food habits of other mammals as well as birds is very scattered in the literature, and highly variable within British Columbia. Information provided in this section should be supplemented with local knowledge of regional wildlife experts.

2.9.2 Other resources

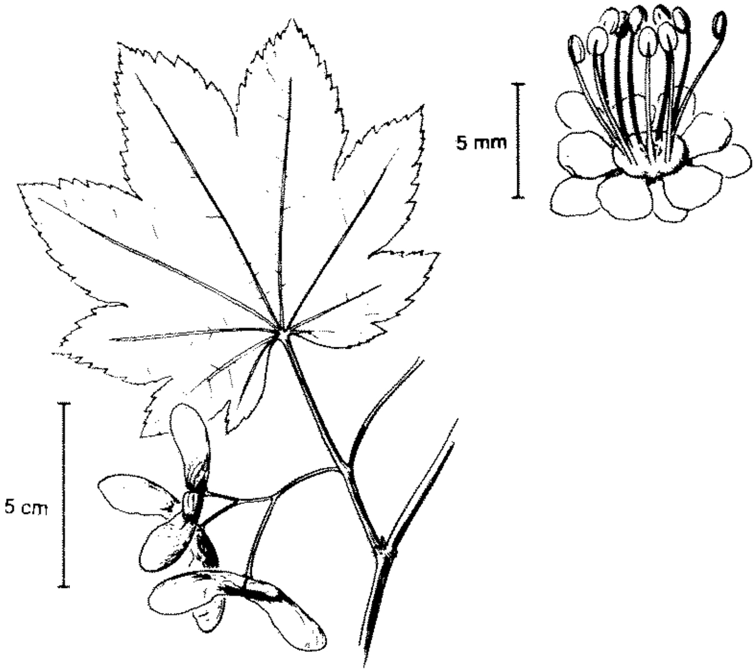
This section describes the value of plants for uses other than food. The limited amount of information in this section attests to the limited availability of data in the literature. It also reflects the difficulty in obtaining information that applies to specific plant species when wildlife tends to make use of vegetation complexes rather than individual plant species. High wildlife use of a plant species can reflect its abundance and availability, rather than its preferability over other species or complexes of species.

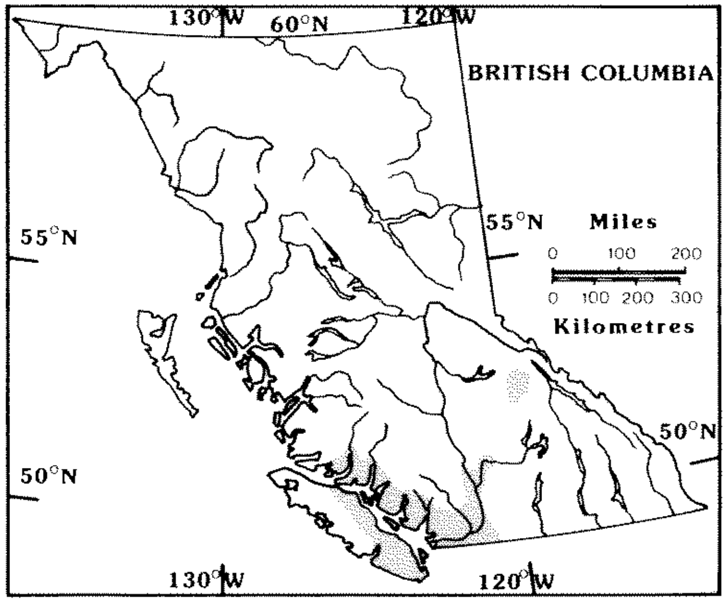
All shrub species described have the potential to provide security and/or thermal cover to wildlife. Cover is not necessarily plant species specific. More important is the maintenance of acceptable forage/ cover ratios during the planning and implementation of vegetation management prescriptions.

Information in this section should be supplemented with local knowledge of regional wildlife experts.

3 AUTECOLOGICAL CHARACTERISTICS OF SELECTED PLANT SPECIES

Acer circinatum
Pursh (vine maple)





Distribution of *A. circinatum* in British Columbia.

Acer circinatum Pursh **Vine maple**

DESCRIPTION

Vine maple is a deciduous, multi-stemmed shrub or, less commonly, small tree. It often grows in dense thickets interspersed with large gaps. It normally has a short, crooked trunk with arching limbs that support a low, broad, irregular crown. Plants reach 1–10 m in height, 7–25 cm in diameter, and up to 10 m in crown width. Stems are pale green to reddish brown and have many branches. Lateral buds are opposite, shiny, bright red, and either single or multiple. There is no terminal bud. Leaves are almost circular with 7–9 sharply toothed lobes. They are reddish when young, turning to bright green, then orange and scarlet in the fall. Male and female flowers occur on the same tree in loose, drooping, reddish-purple and white clusters. Fruits are yellowish-brown winged samaras (Lyons 1952; Hosie 1973; UBC Bot. Garden 1976).

Variation: There are no varieties or subspecies of vine maple described in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Vine maple is an abundant species in the forested regions of the Pacific Northwest Coast. In British Columbia, it is found as far north as Knight Inlet (51°N) on the mainland coast, as far inland as Manning Provincial Park, and along the Robertson and Salmon Rivers on Vancouver Island. It also occurs in wetter parts of the Interior, including Wells Gray Provincial Park (Lyons 1952; Hosie 1973; UBC Bot. Garden 1976). Vine maple grows in montane to submontane forests and is mainly found in the CDF, CWH, and IDF biogeoclimatic zones (Krajina *et al.* 1982). It is an early seral to late climax species and most commonly grows in the understory of Douglas-fir dominated forests (Bailey 1966; Stewart 1986).

Altitudinal Range: Vine maple grows from sea level to approximately 1000 m in coastal forests (Anderson 1969; UBC Bot. Garden 1976).

HABITAT

Climatic Relations: Vine maple occurs in rainy, subhumid to humid areas with warm, dry summers (Krajina *et al.* 1982). It grows in areas where total annual precipitation ranges from 66 to 665 cm and where mean annual temperature ranges from 5 to 11°C. It tolerates absolute minimum and maximum temperatures of -30 and 41°C, respectively (UBC Bot. Garden 1976).

Site and Soil Conditions: Vine maple grows on a wide variety of soils and moisture regimes, but prefers rich, moist, well-drained conditions (UBC Bot. Garden 1976). It is commonly found along streams, on river terraces and fluvial fans, and in depressions (Kirkwood 1902; Lyons 1952; Hosie 1973).

Nutrient Relations: Vine maple occurs on medium to rich sites but is most common on moderately rich sites. Its nutritional requirements are high for calcium, magnesium, and nitrogen, and it efficiently returns nutrients to the soil through litterfall (Krajina *et al.* 1982). Triska and Sedell (1976) found that vine maple leaf litter decomposed faster than litter of bigleaf maple, red alder, or Douglas-fir, due to a lower lignin content and higher nitrogen concentration. Vine maple's thin leaves also contribute to fast decomposition (T. Lewis, pers. comm., July 1989). The heavy annual litterfall and rich nutrient content of vine maple's leaves suggest that it contributes relatively more to nutrient cycling than do other understory species (Russell 1973).

Water Relations: Vine maple grows on submesic to subhygric sites, but is most common on hygric hygrotopes. It is very resistant to flooding (Krajina *et al.* 1982). Vine maple is capable of rapidly depleting soil moisture to a depth of 60 cm during July and August because of its extensive, vigorous root system and high transpiration rate (Drew 1968).

Light Relations: Vine maple is very shade tolerant (Krajina *et al.* 1982) but prefers Douglas-fir to hemlock or cedar canopies because of the greater light penetration. Growth of vine maple is greatest in canopy openings (Hosie 1973; UBC Bot. Garden 1976; Stewart 1986). Russell (1973) reports that vine maple biomass and stem frequency increase as overstory biomass decreases and light intensity increases. Vine maple exhibits two different growth strategies depending on light availability. It is short (1–2 m at 5 years) and compact in full sun and taller (2–3 m at 5 years) when shaded by surrounding brush (Brand 1978).

Temperature Relations: Vine maple is generally an indicator of warm sites though it can tolerate temperatures of -30°C. It does not grow in areas of frequent snowfall, which suggests that it does not tolerate heavy snow accumulation (Krajina *et al.* 1982).

GROWTH AND DEVELOPMENT

Vine maple exhibits a complex development cycle that has been studied in detail by Anderson (1967) and Russell (1973) in the Oregon Coast Range. It has the ability to adjust its growth and development to survive within the constraints of existing environmental conditions. Abundance of vine maple follows a bi-nodal distribution through succession in Douglas-fir forests. It is abundant in early succession (e.g., following clearcutting), reaches near extinction at the age of 40 years under dense coniferous canopies, and again increases in abundance as the overstory approaches senescence and openings in the canopy occur (Russell 1973). Longevity is generally 80 or 90 years (UBC Bot. Garden 1976); however, ages of up to 142 years have been reported in the central Oregon Coast Range (Anderson 1967). Anderson (1967) found that vine maple growing at high elevations in the Oregon Coast Range did not reach the old ages characteristic of low elevation vine maple plants. He attributed the shorter life span at high elevations to a shorter growing season and more severe environmental conditions.

Following disturbance, most vine maple plants develop vegetatively by sprouting or coppicing; very few originate from seed. During early seral stages, plants produce up to 40 even-aged stems per clump (Russell 1973). Early growth rates are rapid as a result of the large supply of water and nutrients from the established root system. Growth rates average 45–60 cm/year for about the first 6 years, after which they decline to 10–20 cm/year (B. D'Anjou, pers. comm., May 1989).[1]

In climax stands, vine maple reproduces primarily by layering and sprouting. During this stage, plants often produce only about 3 stems per clump and stems are less erect than those produced in earlier seral stages. However, J. Zasada (pers. comm., Sept. 1989) notes that 60-year-old vine maple stands can produce 40 stems per clump. The growth rate in climax stands decreases until it becomes almost zero. Russell (1973) reported heights of only 3.3 m at 130 years. Clumps that originate by layering depend on the parent tree for resources and therefore tend to have low root biomass relative to above-ground biomass. Once a root system is formed, the parent stem dies back. Clumps that originate by layering are made up of uneven-aged stems.

Phenology: Flowering occurs between March and June, when leaves appear or are about half grown. Fruit ripens from September to October and seeds are dispersed from September to January (USDA 1974; UBC Bot. Garden 1976).

REPRODUCTION

Seed Production and Dispersal: Seed crops are produced every year, but large crops occur sporadically (Anderson 1969; USDA 1974). Dissemination of seed is primarily by wind. This tends to be ineffective because little air movement occurs in the dense shrub layer in the understory, and the species often occurs in creek bottoms where wind patterns make upslope movement of seed difficult. Seed dissemination is most successful where the overstory has been removed.

Seed Viability and Germination: Vine maple plants originating from seed are reported to be very scarce (Russell 1973), but Zasada (pers. comm., Sept. 1989) has found that in Oregon, single stems are not uncommon and there is no evidence that they originated from "tip-layers". Anderson (1967) described seed germination as low (less than 5%), but more recent research in Oregon indicates that viability rates are higher than 5% (J. Zasada, pers. comm., Sept. 1989). In plots of known quality seed, a small amount of germination occurs the first growing season after sowing, and if seeds are protected from rodents, germination after 2 years is 50% or greater (J. Zasada, pers. comm., Sept. 1989). Predation is common and all unprotected seeds can be consumed by rodents (Anderson 1967; J. Zasada, pers. comm., Sept. 1989). Germination occurs in the first few years after dispersal, but it is inhibited by the tough samara wall

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[1] CRAFTS 1988.

(Anderson 1967). Fall stratification is required for germination; for maximum rates, seeds require 30–60 days of moist warm conditions followed by 90–180 days at 3°C (USDA 1974). Seeds can germinate through a litter layer.[2] Seedlings are uncommon under vine maple because of the dense understories of shrubs or moss. Survival of germinants is favoured by partial shade and a high proportion of organic matter (Anderson 1967).

Vegetative Reproduction: Reproduction of vine maple is almost exclusively by vegetative means (layering, coppicing, and rooting) (Anderson 1967; Russell 1973; UBC Bot. Garden 1976). Layering is the principal means by which vine maple invades unoccupied areas and reproduces. Layering results from stems becoming too long and massive to remain erect, or from mechanical force (e.g., snow) pushing the stems to the ground (Russell 1973). On steep slopes, layering seldom occurs uphill from the plant since generally only 10% of the stems lean upslope. Anderson (1967) states that rooting occurs when shoots arise from adventitious lateral buds on shallow roots but in Oregon no evidence has been found to support the idea of stem reproduction from roots (J. Zasada, pers. comm., Sept. 1989). Coppicing occurs when shoots arise from dormant or adventitious buds on the base of the main stem. Adventitious buds arise following damage by fire or logging (Anderson 1967).

PESTS

Vine maple is host to many defoliators which individually inflict very little damage. The most common defoliators in British Columbia are western winter moth (*Erannis vancouverensis),* western tent caterpillar (*Malacosoma pluviale*), and redhumped caterpillar (*Shizura concinna*) (L. MacLauchlin, pers. comm., Feb. 1989).

The most common pathogens are *Nectaria coccinea* (a stem canker), *Polyporus hirsutus* (stem decay), and *Polyporus versicolor* (stem decay) (H. Merler, pers. comm., April 1989).

EFFECTS ON CROP TREES

Competition: Vine maple is a common shrub and a major competitor in Washington and Oregon. In British Columbia, however, it does not occur extensively and it creates competition problems only in localized areas (T. Lewis, pers. comm., May 1989). Vine maple is a very strong competitor with conifers and other shrub species (Krajina *et al.* 1982; Beese 1986). It may interfere with Douglas-fir establishment because its initial growth is much faster (Krajina *et al.* 1982) and its root system depletes soil moisture and excludes the roots of other species (Drew 1968; Russell 1973). Chan and Walstad (1987) found that Douglas-fir sapling growth decreased as the amount of overtopping shrubs increased on a site dominated by vine maple and salmonberry in the Oregon Coast Range. Krajina *et al.* (1982) suggest that control of vine maple is necessary for up to 10 years until conifers are free-growing, after which vine maple can be left on the site for the beneficial effects of its leaves on the humus.

Allelopathy: Dense mats of litter under vine maple are believed to prevent other species from establishing (Steen 1966). Strong inhibitory phenolic extracts have been found in vine maple foliage and litter (del Moral and Cates 1971; Rice 1974; Tinnin and Kirkpatrick 1985). del Moral and Cates (1971) suggest that vine maple has an allelopathic effect on Douglas-fir and other shrubby species, and that western hemlock and western redcedar may have allelopathic effects on vine maple.

Beneficial Effects: Leaf litter of vine maple is believed to provide a rich supply of nutrients to the site. A moder humus form develops where vine maple litter is deposited (Krajina *et al.* 1982).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Vine maple is present in mature forests and, although it declines initially, it increases substantially in height and cover following overstory removal (Brand 1978). Vine maple re-establishes its dominance over the course of succession (Bailey 1966; Kellman 1969; Gashwiler 1970). Its roots usually survive the disturbance of logging and sprout soon after clearcutting, resulting in the same distribution of plants in seral forests as in the original forest (Bailey and Poulton 1968). In Oregon, excavation of dense patches of vine maple after disturbance showed that the plants originate from stems

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[2] CRAFTS 1988.

buried during harvesting, not from the roots (J. Zasada, pers. comm., July 1989). Vine maple rarely seeds-in to logged areas.

Fire: Vine maple has low to moderate tolerance of fire (Anderson 1969; USDA 1981) and can be killed by severe burns (Dymess 1973). The basal portion of the stem and root system survives all but the most severe burns and dormant buds form and sprout vigorously (Reid *et al.* 1938; USDA 1981). Regeneration of vine maple from seed is extremely uncommon on burned areas.

Several studies show that it initially decreases in cover following burning. Steen (1966) found that 9 years after a medium severity burn, vine maple had 12% cover, while on the unburned control, it had 18% cover. Dyrness (1973) found that 5 years after burning, vine maple was absent from severely burned areas, had 2% cover on lightly burned areas, had less than 1% cover on disturbed but unburned areas, and had 15% cover on an undisturbed control. Schoonmaker and McKee (1988) studied a chronosequence of burned sites in the Oregon Cascades and concluded that vine maple takes 15 years to recover to its pre-disturbance cover following logging and medium intensity burning.

Cutting: Manual cutting or physical damage due to logging, crushing, or slashing results in prolific basal sprouting of vine maple. Stems cut in both coastal British Columbia and the Oregon Coast Range have sprouted 90 cm in height in the first year following cutting. Vine maple can recover its pre-treatment height and crown volume 2 or 3 years after cutting (Roberts 1977; Kelpas 1978).[3,4]

Herbicides: Vine maple is effectively controlled with glyphosate (Conard and Emmingham 1984a; Boateng and Herring 1990). It is very susceptible to injury from glyphosate during late summer and mid-fall after growth has stopped.[5] Vine maple was 100% controlled with glyphosate applied at 1.6 kg a.i./ha as a late summer foliar spray at Lillooet Lake (B. D'Anjou, pers. comm., May 1989). Plants that are injured but not killed continue to decline in vigour 2 years after herbicide application (Kelpsas 1978).[6]

Vine maple is partially tolerant of hexazinone and is reported to suffer only light injury from foliar applications (Conard and Emmingham 1984a; Boateng and Herring 1990).

Applications of 2,4-D to cut surfaces have provided good control of vine maple in Oregon (Conard and Emmingham 1984b).

Several herbicides not registered for forestry use in British Columbia effectively control vine maple. They include:

1. Picloram: Foliar applications; early and late spring. Best control is obtained after full leaf development and while plants are actively growing. (Stewart 1972, 1974a; Vander Born and Malik 1984).
2. Picloram mixed with triclopyr (Conard and Emmingham 1984a; Boateng and Herring 1990).
3. 2,4-D amine mixed with triclopyr (Conard and Emmingham 1984a; Boateng and Herring 1990).
4. Triclopyr: Basal or cut surface treatment (Conard and Emmingham 1984b).
5. 2,4-D amine: Cut surface treatment (Conard and Emmingham 1984b).
6. Picloram mixed with 2,4-D amine: Cut surface treatment (Conard and Emmingham 1984b)
7. 2,4-D mixed with 2,4,5-T in diesel oil. Basal spray during dormant season (Hetherington 1964).
8. MSMA; early spring (Stewart 1972, 1974a).
9. MSMA mixed with 2,4,5-T (Stewart 1972, 1974a).

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[3] CRAFTS 1988.
[4] D'Anjou 1988c.
[5] Conard 1982.
[6] CRAFTS 1988.

Soil Disturbance: Vine maple seed rarely establishes on exposed mineral soil. Coppicing and rooting can be expected following mechanical site preparation (Anderson 1969; UBC Bot. Garden 1976; Kelpsas 1978). However, deep soil disturbance can eliminate vine maple (Kelpsas 1978).

WILDLIFE

Food: Vine maple is a highly important winter forage for black-tailed deer (Nyberg *et al.* 1986)[7] and is a common summer and fall forage for black-tailed deer (Rue 1978). Brown (1961) reported that black-tailed deer obtained 15% of its summer and fall diet from vine maple leaves and twigs in western Washington. In British Columbia, vine maple shoots are moderately important winter and spring forage for Roosevelt elk (Singleton 1976) and in the Oregon Coast Range they are the preferred forage of this animal (Bailey 1966). In the Oregon Coast Range, vine maple is also a preferred forage for mountain beaver (Bailey and Poulton 1968; Crouch 1968; Chapman and Feldhamer (editors) 1983), which can climb several meters to cut off small limbs (Harestad 1983). Mountain beaver has a very limited range in British Columbia, but it is abundant in the U.S. Pacific Northwest. Browsing stimulates vigorous sprouting of vine maple (T. Lea, pers. comm., Feb. 1989).

Other Resources: Vine maple communities are reported to provide excellent habitat for rabbits[8] and deer (Miller 1968) in the Oregon Coast Range.

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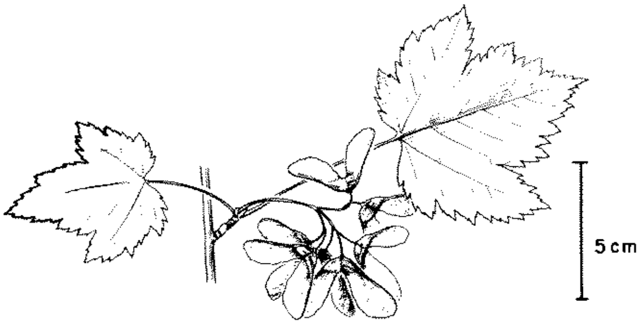
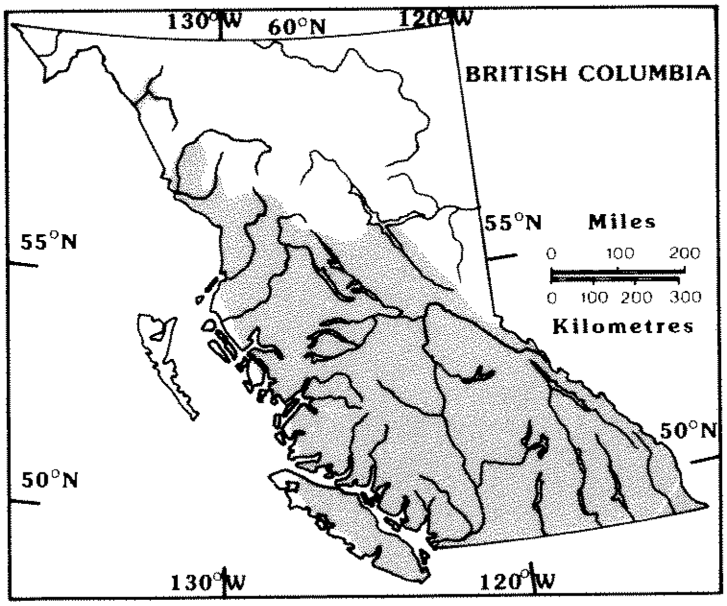
[7] Blower 1982.

[8] Newton and O'Dell 1973.

Acer glabrum
(Douglas maple)





Distribution of *A. glabrum* in British Columbia.

Acer glabrum Torr.

Douglas maple
(Rocky Mountain maple)

DESCRIPTION

Douglas maple is a deciduous small tree or shrub. It can reach 6–9 m in height and up to 30 cm in diameter but most often occurs as a multi-stemmed shrub 1.5–2 m tall. Stems are red with opposite branching; leaves are palmate with 3 to 5 toothed lobes, often reddish tinged. The imperfect flowers are small, greenish-yellow in drooping clusters. Male and female flowers can occur on separate trees. Fruit are paired, winged samaras, wrinkled, green to red in colour but becoming greyish brown with age (Viereck and Little 1972; Hosie 1973; Hultén 1974).

Variation: The Douglas maple of British Columbia is variety *douglasii* (Taylor and MacBryde 1977). Studies done in the United States refer to the Rocky Mountain maple (*Acer glabrum* var. *glabrum*) (Hultén 1974).

DISTRIBUTION AND ABUNDANCE

Douglas maple is found throughout most of British Columbia to approximately 56°N latitude. It is uncommon on the outer Coast and absent from the Queen Charlotte Islands (Viereck and Little 1972; Krajina *et al.* 1982). It is most abundant in the Interior of the province, especially in southern British Columbia, in the IDF and drier ICH subzones.

Altitudinal Range: Although most common in interior valley bottoms, Douglas maple grows from sea level to over 1200 m (Lyons 1952). It is generally absent from subalpine elevations.

HABITAT

Climatic Relations: Within British Columbia, Douglas maple does not tolerate climatic extremes. It is absent from areas of extremely wet coastal climate, from the boreal forest, from the semi-desert areas of the southern Interior, and from alpine and subalpine climates. Throughout central British Columbia, it prefers areas of moist, warm mesoclimate (R. Coupé, pers. comm., Nov. 1984) and is characteristically found on sunny south-facing slopes (Coupé *et al.* 1982).[9,10]

Site and Soil Conditions: In the mature forest of the SBS, northern ICH and drier CWH subzones, Douglas maple is characteristically found on well-drained colluvium or on shallow soils.[11,12,13] In the IDF and southern ICH zones, and in seral communities throughout British Columbia, it occurs on a much wider range of sites and soils (see, e.g., Mitchell and Green 1981). Along the coast, Douglas maple is commonly found on rocky cliffs, ledges, avalanche tracks, or on the border of openings such as meadows and bogs (Viereck and Little 1972; Hosie 1973). It is also abundant on alluvial terraces of coastal river valleys (J. Pojar, pers. comm., March 1985).

Nutrient Relations: Douglas maple is believed to have relatively high nutritional requirements. Krajina *et al.* (1982) state that it has high requirements for calcium, magnesium, nitrogen, potassium, and phosphorus, while Mueggler (1965) reports that it is associated with sites with high levels of potassium.

Water Relations: Throughout the province, Douglas maple grows over a wide range of moisture conditions. In wet zones (CWH and ICH) it is most common on dry sites; while in drier zones such as the IDF it is most common on moister sites (Angove and Bancroft 1983). Its best growth occurs on moist coastal bottomlands where it can become a medium-sized tree. Cline and Campbell (1976) studied the water relations of Douglas maple in northern Idaho where it was present on both moist, north aspects and dry, south aspects. During August, when evapotranspirative stresses were much higher on the south aspect, the south aspect maple had maximum conductances which were almost twice as high as those on the north aspect. The maple is apparently able to compete on both sites by adjusting its total leaf area, through

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[9] Coupé and Yee (editors) 1982.
[10] DeLong 1983.
[11] Coupé and Yee (editors) 1982.
[12] Yole *et al.* 1982.
[13] DeLong 1983.

stomatal control, and by shifting the water potential of its leaves on the south aspect to enable it to extract moisture from the soil.

Light Relations: Krajina *et al.* (1982) classify Douglas maple as having moderate shade tolerance. It occurs in relatively open forest and under full sunlight, but rarely in deep shade. It has been found at 4% of full light levels in the forests of southern Oregon (Emmingham 1972). Strong sunlight can be detrimental to young seedlings (Marchant and Sherlock 1984). Mueggler (1965) observed that it is a tall spindly shrub under a canopy, and a more dense, compact shrub in open sunlight.

Temperature Relations: Frost resistance is high, especially in the Interior (Krajina *et al.* 1982).

GROWTH AND DEVELOPMENT

There is no detailed information available on the morphological or physiological development of Douglas maple. Development of the species into a single-stemmed tree appears to be most common in the favourable environments of coastal and southern British Columbia, while in the Interior and on harsh coastal sites it is usually a multi-stemmed shrub (Hosie 1973; USDA 1974). Seedlings will grow rapidly during the first growing season if conditions are favourable (Marchant and Sherlock 1984). Maximum height growth is usually attained within 30–40 years of establishment (Mueggler 1965). Douglas maple has a wide-spreading root system with a mixture of deep and lateral roots (Hosie 1973; Marchant and Sherlock 1984).

Phenology: Flowering occurs between April and June. In coastal Alaska, flowering typically occurs in May and fruit matures in July and August, while in Montana and Idaho flowers open between mid-May and mid-June and fruit ripening extends from mid-July into September. Seeds are dispersed beginning in September and can remain on the stems until February or later (Viereck and Little 1972; USDA 1974; Schmidt and Lotan 1980; Shaw 1984).

In Montana and Idaho, leaf emergence can begin in early April and is complete by late May. Leaves are fully grown by mid-June at most locations. They begin to colour and die between late July and early September, depending on weather conditions, and leaf fall extends from early September to mid-October (Cline and Campbell 1976; Schmidt and Lotan 1980).

REPRODUCTION

Seed Production and Dispersal: Douglas maple begins to produce seed from an early age (USDA 1974). Crane *et al.* (1983) report that seeds were produced by the fifth year following a fire. There is a 1- to 3-year interval between large seed crops (USDA 1974). The winged seeds are dispersed throughout the fall and winter by wind (USDA 1974) and there are no reports of dispersal by animals.

Seed Viability and Germination: Douglas maple seeds remain viable for only a short period of time. Seeds remaining on the stem may slowly lose their viability during dry, frosty periods (Marchant and Sherlock 1984). Under ideal conditions seed can be stored for up to 3 years. High germination percentages (e.g., 85%) have been obtained under laboratory conditions. The seeds have embryo dormancy and require approximately 180 days of chilling before they will germinate (Shaw 1984).

Vegetative Reproduction: Douglas maple sprouts readily from root crowns following disturbance (Cholewa and Johnson 1983; Crane *et al.* 1983), but does not appear to spread by rhizomes or root suckers. Vigorous natural layering has been observed in the mountain maple (*Acer spicatum*) of eastern North America (Hosier 1974).

PESTS

No information.

EFFECTS ON CROP TREES

Competition: Douglas maple is not considered to be a significant competitor with conifers over most of its range (Krajina *et al.* 1982; R. Coupé and C. DeLong, pers. comm., Nov. 1984). However, it is viewed as a major competitor in the Kamloops Region (D. Lloyd, pers. comm., Nov. 1984). There are no studies of its competitive ability, but it is usually not an aggressive colonizer of clearcuts and, because it has a relatively open crown, it does not cause serious competition for light. Competition with conifers for moisture occurs in the dry climate of the IDF zone, and on dry sites in other subzones. Douglas maple competes with Douglas-fir and lodgepole pine in dry areas. Competition has caused moderate growth losses but not mortality (T. Lewis, pers. comm., July 1989). Because of its apparent nutrient-demanding status, it may also compete successfully with conifers for soil nutrients.

Beneficial Effects: Krajina *et al.* (1982) indicate that the litter of Douglas maple has a beneficial effect on humus, presumably because of the rapid decomposition recycling and of the high concentrations of nutrients contained in maple foliage. It may be beneficial to leave maple to provide shade for Douglas-fir on some harsh sites. However, the benefit of shade may be offset by competition for moisture on these sites.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Successional studies in the cedar-hemlock zone of northern Idaho (Mueggler 1965; Wittinger *et al.* 1977) indicate that the cover of Douglas maple increases slightly or not at all following canopy removal, and begins to decline 25 years following canopy removal. The shrub becomes broader and foliage becomes more dense following canopy removal. Eis (1981) showed a significant increase in cover of Douglas maple 6 years following logging on moist *Aralia – Dryopteris* sites in the SBS zone north of Prince George but did not indicate whether the increase was due to establishment of new seedlings or an increase in vigour of existing plants. Douglas maple cover and vigour were observed to remain unchanged following canopy removal in the ICHmw subzone (J. Wright, pers. comm., July 1989).

Fire: Several authors report that Douglas maple sprouts readily from the root crown following fire and increases in density by sprouting (Lyon 1966; Cholewa and Johnson 1983). Crane *et al.* (1983) observed that resprouting occurred the same year as the fire and, 5 years later, maple had increased 4 times over its original post-fire cover. Stickney (1981), however, reports that Douglas maple survival was low and percent cover remained well below preburn levels after 9 years. In western Montana, cover of Douglas maple was 11% on an unburned site and less than 1% 5 years after a severe burn (Bradley 1984). Differences in results among studies probably relate to fire severity.

Cutting: Resprouting following cutting is similar to burning response (Marchant and Sherlock 1984). Manual cutting results in vigorous sprouting in the ICHmw subzone in the Salmon Arm Forest District. Sprouts average 1–1.5 m/year in height growth, but have been observed to grow as much as 2.5 m/year (J. Wright, pers. comm., July 1989). Sprouts average 40–60 cm in height 1 year after cutting on medium sites near Penticton, B.C.[14] Three seasons after a 5.7 m tall stand of Douglas maple was cut to ground level in northern Idaho, clumps had recovered to 1.2–1.8 m in height. Cut stems produced up to 10 sprouts each (Miller 1985a).

Herbicides: Douglas maple is very susceptible to foliar applications of glyphosate in the ICHmw and ICHvk subzones near Salmon Arm and Revelstoke. An application rate of 2.1 kg a.i./ha has caused greater mortality than a rate of 1.4 kg a.i./ha (J. Wright, pers. comm, July 1989).[15] Minimal resprouting occurs one year after treatment. M. Newton (pers. comm., Dec. 1984) found that, in Oregon, glyphosate applied in the fall at 1.7 kg a.i./ha provides good control of Douglas maple. Boyd *et al.* (1985) documented 28 trials involving application of glyphosate to Douglas maple in the U.S. Inland Northwest. Top-kill varied from 0 to 100% after two growing seasons and tended to be highest at application rates above the maximum legal rate for British Columbia. Miller (1985b) indicated that in the U.S. Inland Northwest, glyphosate causes good top-kill of Douglas maple, but poor total plant kill.

Hexazinone tends to provide only partial control of Douglas maple. Mid-June broadcast applications of hexazinone in the ICH zone near Smithers resulted in fair control 1 year after treatment regardless of application rates (3 and 4.6 kg a.i./ha) or methods (spot gun, and spear attachment pushed 2 cm into the duff). Broadcast applications[16] of 1.1, 2.2, or 4.3 kg a.i./ha in early May near Burns Lake, B.C., did not cause significant injury to Douglas maple. On the same site, early May applications of both 4 and 8 mL

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[14] Noble-Hearle 1989.

[15] Dyke 1987.

[16] Newhouse 1988a.

of undiluted hexazinone at 2 m spacing resulted in about 30% injury to Douglas maple. At a spacing of 1.5 m, the injury was increased to 50%.[17]

M. Newton (pers. comm., Dec. 1984) found that, in Oregon, 2,4-D usually results in defoliation or top-kill followed by sprouting. In the U.S. Inland Northwest, however, 2,4-D ester has tended to result in unsatisfactory top-kill. Two years after treatment, top-kill for 10 trials ranged from 0 to a maximum of only 35%. Top-kill tended to increase as the application rate increased from 0.8 to 4.3 kg a.i./ha.

Soil Disturbance: Mechanical site preparation in the ICHmw subzone can reduce the abundance of Douglas maple. The species appears to be capable of germinating on mineral soil or LFH layers less than 5 cm thick (J. Wright, pers. comm., July 1989).

WILDLIFE

Food: Douglas maple is a preferred browse species for ungulates (Asherin 1974; Cholewa and Johnson 1983). It is important to deer especially in winter (Harvey 1981).[18,19] It is moderately important winter and spring browse for elk, moose, and bighorn sheep (Singleton 1976).[20] Browsing stimulates vigorous resprouting. (T. Lea, pers. comm., Feb. 1989).

Other Resources: Douglas maple provides nesting sites for birds.

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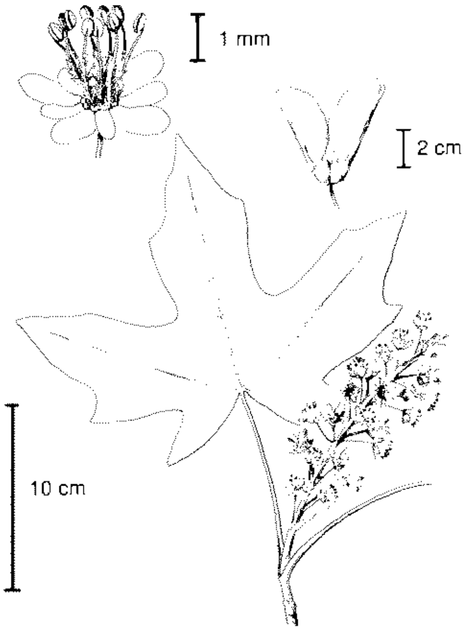
[17] Teskey and Masterson 1986c.

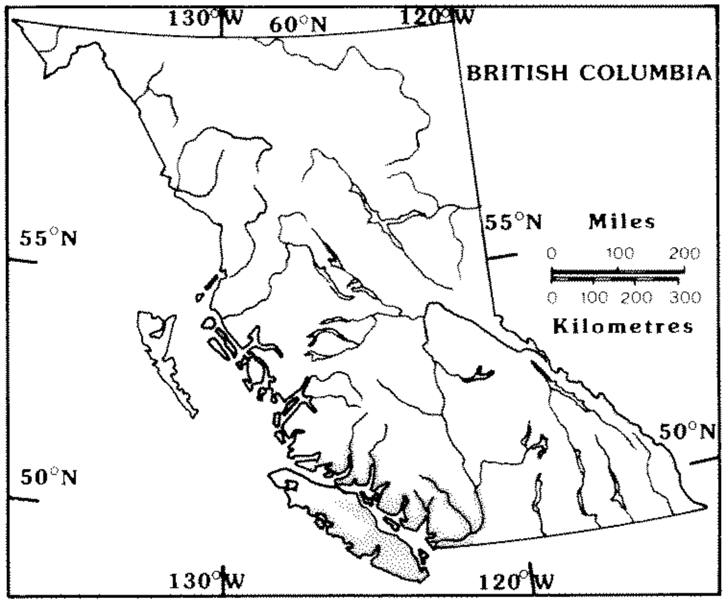
[18] Demarchi and Demarchi 1967.

[19] Miles and Weikle (undated).

[20] Balfour 1989.

Acer macrophyllum
(bigleaf maple)





Distribution of *A. macrophyllum* in British Columbia.

Acer macrophyllum Pursh.

Bigleaf maple
(broadleaf maple)

DESCRIPTION

Bigleaf maple is a large tree 15–25 m tall at maturity, with a broad, spreading crown. Twigs are stout with opposite branching. Leaves are large (15–30 cm) and palmate with deep lobes. The yellowish-green flowers are arranged in a raceme at the ends of the twigs. The fruit is a winged samara with paired, hairy seeds (Hosie 1973).[21]

Variation: There are no varieties or subspecies of bigleaf maple described in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Bigleaf maple in British Columbia is confined to Vancouver Island and the adjacent mainland coast as far north as Sullivan Bay at approximately 50°N latitude (Hosie 1973; Krajina *et al.* 1982). It penetrates inland up the Fraser Canyon to Lytton. It occurs only in the CDF, CWH, and subcontinental IDF biogeoclimatic zones, and is most abundant on southeastern Vancouver Island and adjacent areas of the CDF zone.

Altitudinal Range: Bigleaf maple is a low-elevation species and rarely occurs above 300 m (Fowells (compiler) 1965), but it has been observed at elevations above 350 m on southeastern Vancouver Island (Packee 1976).

HABITAT

Climatic Relations: Bigleaf maple is confined to the warmest, mildest climate in British Columbia (Krajina *et al.* 1982). The northern limit of the species is apparently defined by temperature, while insufficient moisture and humidity may combine with temperature to limit its extension towards the Interior. Its best growth occurs in a humid climate where mean annual temperatures are above 10°C and there is little annual variation in temperature (Fowells (compiler) 1965).

Site and Soil Conditions: Bigleaf maple is found on a variety of soils ranging from deep and loamy to shallow and rocky. Best growth is on fluvial sites and at the base of colluvial slopes (Fowells (compiler) 1965; Packee 1976), but it may also be found on morainal and marine soils, and often appears as pioneering vegetation following landslides. Hosie (1973) reports that it occurs most often on coarse, gravelly soils. Soils supporting good growth of bigleaf maple are usually Humo-Ferric Podzols, Sombric or Dystric Brunisols, and Regosols (see, e.g., Klinka *et al.* 1979; Klinka and Carter 1990).

Nutrient Relations: Best growth of bigleaf maple occurs in nutrient rich soils, and it has very high requirements for calcium, magnesium, nitrates, potassium, and phosphorus (Krajina *et al.* 1982). Levels of nitrogen, potassium and calcium in foliage, wood, bark, and litter are high relative to other northwestern tree species, while levels of phosphorus and magnesium are relatively low (Minore 1979).

Water Relations: Bigleaf maple most often grows where soils are moist, and best growth is on sites with abundant seepage or on fluvial sites along streambanks (Fowells (compiler) 1965; Hosie 1973; Packee 1976; Krajina *et al.* 1982). Minore (1979) classed bigleaf maple as intermediate relative to other Pacific Coast tree species with respect to moisture requirements for optimum growth. Its flood tolerance is rated as very high by Krajina *et al.* (1982), who observe that it occurs on floodplains.

Light Relations: In British Columbia, bigleaf maple is not normally found as an understory tree. Although shade tolerance is low to moderate (Krajina *et al.* 1982), it is the most shade tolerant deciduous tree in south coastal British Columbia (Packee 1976). Research in coastal Oregon (J. Tappeiner, pers. comm., Dec. 1984) indicates that tolerance seems to decrease with age, and best growth occurs where top light is available (Fowells (compiler) 1965). In Western Oregon, Fried *et al.* (1988) found that survival of seedlings after 2 years was highly dependent on canopy density, and was highest in clearcuts and very low under dense overstories.

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[21] Brand 1984.

Temperature Relations: The geographic distribution of bigleaf maple suggests that frost resistance is low, and that the species cannot tolerate frozen soil conditions (Krajina *et al.* 1982).

GROWTH AND DEVELOPMENT

Bigleaf maple is characterized by rapid growth for the first 40–60 years of its life. Maturity is reached at between 150 and 300 years of age and mature trees reportedly average about 15 m in height and 45 cm in diameter (Fowells (compiler) 1965), but trees may be more than 30 m tall and as much as 2.5 m in diameter. Under low light conditions, bigleaf maple develops a narrow crown and a long limb-free bole. Under open grown conditions its crown is broad and rounded (Hosie 1973). The tree has a wide-spreading root system (Packee 1976). This species is most often seen in cutovers as a multi-stemmed clump arising from a cut stump rather than as an individual of seed origin.[22] Sprouts and seedlings of bigleaf maple have quite different juvenile growth characteristics (M. Newton, pers. comm., Dec. 1984). Sprouts can grow 2–4 m in height in the first growing season. Their height growth is controlled by the number of sprouts and the size of the original stump. There can be 50 to 60 sprouts per stump. Within 30 to 40 years the clump can cover an area as large as 100 m^2 (Lauterbach and Warren 1982).[23,24] In contrast, early seedling growth is much slower than sprout growth because the seedling does not have an established root system and large carbohydrate reserves. Under ideal conditions, nursery seedlings grow very rapidly. They can attain 2 m in height in one growing season, but this size is seldom attained under natural conditions (J. Zasada, pers. comm., Sept. 1989). Seedlings established under a canopy of other species may have extremely slow rates of growth until released by removal of the overstory (J. Tappeiner, pers. comm., Dec. 1984). In western Oregon, Fried *et al.* (1988) observed that 8- to 10-year-old seedlings under mature Douglas-fir were only 25 cm tall. Suppressed trees are extremely persistent and can die back and resprout repeatedly under overmature conifer stands (M. Newton, pers. comm., Dec. 1984).

Phenology: Flowers and leaves emerge simultaneously from the same bud during April. Pollination occurs 2–4 weeks following bud burst. Fruits ripen between late August and October and are dispersed from October through January (Fowells (compiler) 1965; Hosie 1973; USDA 1974). In a western Oregon study, the peak period of leaf abscission was October 2–23. Abscission occurred rapidly following the first frost and was hastened by heavy rains (Campbell and Franklin 1979).

REPRODUCTION

Seed Production and Dispersal: Bigleaf maple first begins to produce flowers at about 10 years of age. Pollination of the flowers is by insects. Seed crops are produced every year and can be copious. Open grown trees begin to produce seed earlier in life and have larger seed crops than those growing in the shade. Seeds are dispersed throughout the fall and winter. Dispersal is primarily by wind, but small mammals and some birds may also be involved. The seed is one of the heaviest of northwestern tree species, but the large wings aid in effective dispersal (Fowells (compiler) 1965; Minore 1979).

Seed Viability and Germination: Little research has been done on the regeneration of bigleaf maple from seed. In Oregon, Fried *et al.* (1988) found that all bigleaf maple seeds not taken by predators either germinated within 1 year of dispersal or decayed. Germination apparently occurs on both mineral and organic seedbeds and survival depends on the presence of adequate moisture (Packee 1976). First-year survival rates of bigleaf maple seedlings have been reported to be significantly greater in clearcuts (77%) than in young (15%), old (29%), or pole-sized (50%) stands (Fried *et al.* 1988). Bigleaf maple seedlings in Oregon were significantly more abundant, taller, and older in small forest openings than in adjacent sites under a dense forest canopy (Sabhasri and Ferrel 1960).

The window for the most successful establishment of bigleaf maple seedlings appears to begin after canopy thinning and end before forbs and shrubs invade (Fried *et al.* 1988).

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[22] Brand 1984.
[23] Ibid.
[24] Roberts 1980.

Vegetative Reproduction: Bigleaf maple sprouts vigorously from dormant buds at the base of the stem following top kill or cutting of the parent tree (Fowells (compiler) 1965).[25,26] It does not produce suckers from rhizomes or roots and there are no reports of natural layering.

Reproductive Strategy: Researchers in Oregon, studying the establishment of bigleaf maple hypothesize that it is a "seedling banker" (Grime 1979). This regenerative strategy involves a bank of persistent seedlings that establish themselves under young coniferous or mixed stands, then persist in a stunted or etiolated condition until a disturbance occurs that creates conditions favourable for more rapid growth (J. Tappeiner, pers. comm., Dec. 1984). Seedlings of bigleaf maple are rarely found in Oregon clearcuts. Fried *et al.* (1988) found fewer than 20 one-year-old seedlings on a 16-ha clearcut and suggested that these probably originated from seedfall before clearcutting. There is some uncertainty whether this failure to become established is due to environmental conditions or whether deer browse of young seedlings is so severe that seedlings only become established at later stages of stand development when deer are less abundant (Fried *et al.* 1988).

PESTS

Principal diseases and insect pests are described by Fowells (compiler, 1965); Packee (1976); and Furniss and Carolin (1977). Minore (1979) rates bigleaf maple as being particularly resistant to laminated root rot (*Phellinus weirii*).

EFFECTS ON CROP TREES

Competition: Bigleaf maple is considered to be a very serious competitor with Douglas-fir on some of the most productive growing sites in British Columbia. It does not aggressively seed-in to clearcut sites, thus the primary source of competition is from plants already established on the site, especially those trees cut during logging. Bigleaf maple sprouts easily outgrow British Columbia conifers and because a single plant has the capacity to establish cover over a large area, the potential stocking by desired species can be greatly reduced.[27] No other individual of any plant species provides as much competition to Douglas-fir as a single sprouted stump of bigleaf maple (M. Newton, pers. comm., Dec. 1984). Its large leaves produce a deep shade that does not allow shade-intolerant species such as Douglas-fir to become established (Krajina *et al.* 1982) and the heavy leaf fall smothers young seedlings (Packee 1976). Although bigleaf maple is often outgrown in height by conifers (Fowells (compiler) 1965), this does not occur until relatively late in the rotation.

Beneficial Effects: Although bigleaf maple absorbs and retains large quantities of nutrients, its litter is believed to be valuable in supplying a rich supply of nutrients to a site. Fried (1985) suggests that the rapid cycling rates of bigleaf maple litter could benefit surrounding Douglas-fir trees by making bases more readily available to the tree roots instead of holding them in the forest floor. The mull humus which develops where maple litter is deposited is apparently beneficial to western redcedar (Krajina *et al.* 1982).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Plants already established on the site can be expected to respond to canopy removal with vigorous growth. Cut stumps sprout to produce a wide-crowned multi-stemmed shrub. Rapid seeding-in of cutover areas is not observed in coastal Oregon (Fried *et al.* 1988; D. Minore and J. Tappeiner, pers. comm., Dec. 1984). In a coastal British Columbia study (Mueller-Dombois 1965), spread of bigleaf maple tended to be confined to moist, nutrient-rich sites similar to those where the maple is normally found in mature forest.

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[25] Brand 1984.

[26] Pendl and D'Anjou 1984.

[27] Brand 1984.

Fire: Burning produces top-kill of bigleaf maple followed by rapid sprouting from dormant basal buds. Sprouts can grow 3–4 m per year (Kelpsas 1978; B.M. Geisler pers. comm., Jan. 1985). A severe prescribed burn completely eliminated bigleaf maple for at least five growing seasons on a site in the western Cascades of Oregon. Light burning produced no significant difference in cover from preburn conditions (Dyrness 1973).

Cutting: Manual cutting of bigleaf maple plants or coppices promotes rapid, vigorous sprouting. When sprouted maple clumps were manually cut back with axes, the coppices grew almost immediately.[28] Five-year-old bigleaf maple coppices cut with a machete in early September on southern Vancouver Island vigorously resprouted; there were 45 sprouts per stump 3 years after cutting.[29] Bigleaf maple cut during three different seasons averaged six sprouts per cut stem with the least sprout production occurring on the late summer cuttings.[30]

Manual cutting can significantly reduce the crown volume of bigleaf maple for at least 1 year.[31] However, CRAFTS[32] found that clumps regained more than half of their original crown volume during the first year after cutting. Crown volume has recovered within 3 years of cutting.[33]

In Oregon, bigleaf maple has regained about 75% of its original height during the first year after cutting.[34] In the CDF zone on southern Vancouver Island, bigleaf maple vigorously sprouted back to its original height 1–1.5 years after cutting (R. Muller, pers. comm., July 1989). Wagner (1984) found that manual cutting in March or April controlled bigleaf maple more effectively than it did red alder, vine maple, salmonberry, or elderberry.

Herbicides: Broadcast applications of most available herbicides will cause top-kill but roots are seldom killed because little chemical is transported downwards. The plant quickly responds by producing sprouts (Sund and Finnis 1978; Lauterbach and Warren 1982).

Bigleaf maple has been controlled with foliar glyphosate applications in British Columbia, Washington, and Oregon (Conard and Emmingham 1984b; Boateng and Herring 1990).[35,36] Complete spray coverage of the foliage of coppices seems to be essential to provide total kill of resprouts on stumps.[37] Substantially less resprouting occurs if glyphosate is applied to the cut surfaces of the sprout stems immediately after summer and fall cutting (Conard and Emmingham 1984b).[38]

In British Columbia, 2,4-D has been ineffective at controlling bigleaf maple (Boateng and Herring 1990). Similarly, aerial applications of 2,4-D in winter, spring, or summer in Washington and Oregon do not control bigleaf maple (Conard and Emmingham 1984a). However, application of undiluted 2,4-D amine to cut surfaces in summer or late summer causes moderate injury in Washington and Oregon (Conard and Emmingham 1984b).

Also, in Washington and Oregon, spring broadcast applications of amitrole have resulted in no control of bigleaf maple, and summer applications in moderate control (Conard and Emmingham 1984b).

Soil Disturbance: Large crawler tractors and backhoes were used to uproot stumps of bigleaf maple on Vancouver Island. Stump sprouting was minimal and sprouts were of very low vigour (B.M. Geisler, pers. comm., March 1985).

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[28] Pendl and D'Anjou 1984.
[29] Boateng and Ackerman 1988.
[30] Roberts 1980.
[31] CRAFTS 1988.
[32] CRAFTS 1987.
[33] CRAFTS 1988.
[34] CRAFTS 1987.
[35] Boateng and Ackerman 1988.
[36] CRAFTS 1987.
[37] Boateng and Ackerman 1988.
[38] CRAFTS 1987.

WILDLIFE

Food: Young shoots are browsed by elk[39] (Devereux 1988; A. Harcombe, pers. comm., Feb. 1989) and seedlings and saplings are favoured by black-tailed deer. Seeds are eaten by many small mammals and some birds (Fowells (compiler) 1965). Fried *et al.* (1988) reports that rodents can clip bigleaf maple seedling roots and pull entire seedlings down into burrows. Bigleaf maple can make a moderate contribution to the diet of mountain beaver, a mammal that has a very limited range in British Columbia but is abundant in the U.S. Pacific Northwest.

Other Resources: Bigleaf maple is an important cavity nesting tree for hairy woodpeckers in southern British Columbia[40] and it is a roosting site for pileated woodpeckers in Oregon (Mellen 1987). It provides daytime perches for bald eagles on the southern coast of British Columbia and in northwest Washington. The blunt top and stout branches allow eagles to perch high in the tree (Stalmaster and Newman 1979; T. Lewis, pers. comm., July 1989). Hollow maples are preferred den sites for racoons (Banfield 1974). Miller (1968) observed that black-tailed deer in Oregon use bigleaf maple communities for bed sites, especially in October.

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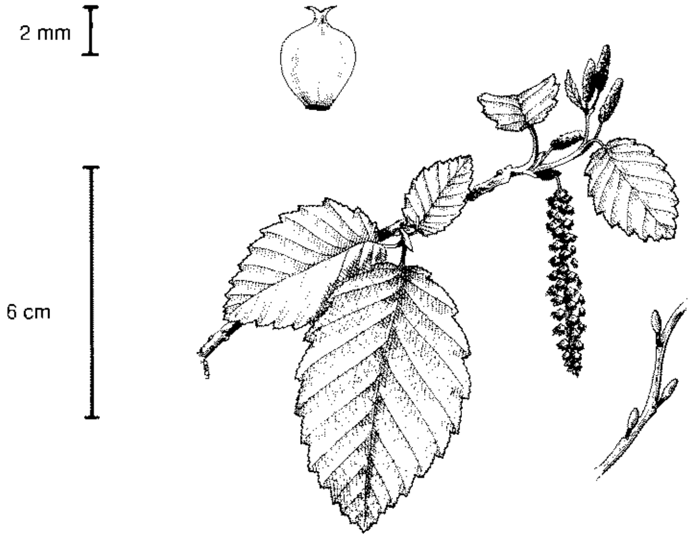
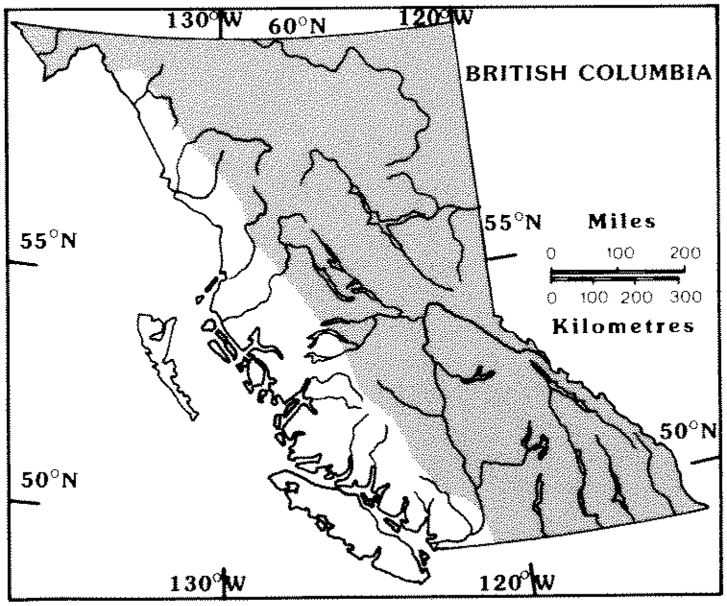
[39] Smith *et al.* (undated).
[40] Korol and Wallis 1983.

Alnus incana* ssp. *tenuifolia
(mountain alder)





Distribution of *A. incana* ssp. *tenuifolia* in British Columbia.

Alnus incana* (L.) Moench spp. *tenuifolia* (Nutt.) Breit. *(A. tenuifolia)

Mountain alder

(thin-leaved alder, speckled alder)

DESCRIPTION

Mountain alder is a deciduous small tree or coarse, multi-stemmed shrub up to 15 m tall. It looks similar to green and Sitka alder but is often taller and straighter. Stems have smooth greyish-yellow bark and twigs have club-shaped, stalked buds. Leaves are thin, oval, and non-sticky, with teeth of two sizes. Separate male and female catkins are produced on the same twig. Fruits are small nutlets with tiny wings, and are borne in cones (Hosie 1973; Brayshaw 1978; Furlow 1979; C. DeLong, pers. comm., Nov. 1984).

Variation: Mountain alder is very closely related to the speckled alder (*A. incana* ssp. *rugosa* or *A. rugosa*) of the Prairie Provinces and eastern Canada, and to the grey alder (*A. incana* ssp. *incana*) of Europe. Several varieties of this subspecies have been described, but they are poorly distinguished because the morphological variation is continuous rather than discrete (Hosie 1973; Brayshaw 1978).

DISTRIBUTION AND ABUNDANCE

Mountain alder is found throughout British Columbia east of the Coast Mountain Range. It occurs widely in all interior biogeoclimatic zones but is only locally abundant (Hosie 1973; Taylor and MacBryde 1977; Krajina *et al.* 1982; Angove and Bancroft 1983).

Altitudinal Range: Mountain alder ranges from 100 m in Alaska to over 3 000 m in Colorado and Arizona (Furlow 1979). In British Columbia, it ranges from Interior valley bottoms to high mountain elevations (Lyons 1952) but does not extend as high as Sitka alder (J. Pojar, pers. comm., March 1985).

HABITAT

Climatic Relations: Mountain alder requires cool climatic conditions throughout its range (Furlow 1979). The range of this species in British Columbia indicates that it is adapted to a wide variety of continental climatic conditions and can tolerate a broad range of temperature and precipitation.

Site and Soil Conditions: Mountain alder is most often associated with alluvial or streambank habitats (Hultén 1974; Brayshaw 1978). In Great Britain, *A. incana* is known for its ability to thrive on very cold, heavy soils (Hadfield 1968).

Nutrient Relations: The nutritional requirements of mountain alder are high. It is described as a calciphyte by Krajina *et al.* (1982) and is usually found growing in moderately rich to rich habitats (Pojar *et al.* 1982; R. Coupé, pers. comm., Nov. 1984). Wali (1969) found that near Prince George mountain alder is restricted to a very narrow range of site conditions with high rates of available calcium, magnesium, and nitrogen. Like other alders, mountain alder has the capacity to fix atmospheric nitrogen (Flescher *et al.* 1976). It fixes higher rates of nitrogen than Sitka alder and can produce amounts similar to red alder (Binkley 1981). On floodplain sites in Alaska, soil pH gradually decreased under a stand of mountain alder over a period of 20 years and there was a marked increase in potassium, calcium, magnesium, manganese, and phosphorus within 5 years of mountain alder establishment (van Cleve and Viereck 1972).

Water Relations: Throughout British Columbia, mountain alder is most common on wet sites (C. DeLong, R. Coupé, W.R. Mitchell, and D. Lloyd, pers. comm., Nov. 1984) and it seems to have higher moisture requirements than *A. viridis.* Flood tolerance is high (Krajina *et al.* 1982), but Knighton (1981) found that growth and root development of speckled alder (*A. incana* ssp. *rugosa*), which is also abundant on saturated soils, were severely reduced when water levels were at or above the root crown.

Light Relations: Mountain alder is shade tolerant (Krajina *et al.* 1982) and is frequently found growing in the shade of the understory. However, it is usually found where there is good exposure to sunlight (Lyons 1952). Sprouts may be more tolerant of shade than seedlings (Healy and Gill 1974).

Temperature Relations: Mountain alder has a high tolerance of frost (Krajina *et al.* 1982).

GROWTH AND DEVELOPMENT

Under favourable conditions, mountain alder can grow to 25 cm in diameter and 15 m in height (Hosie 1973; Furlow 1979). At high elevations it often becomes a scraggly, sprawling shrub (Lyons 1952). It frequently forms pure dense clumps in wet pockets and along streams.

Mountain alder is much less aggressive, in terms of its growth rate and its ability to invade new territory, than red alder and the European grey alder (*A. incana*) (Krajina *et al.* 1982).

Phenology: Male and female catkins of mountain alder expand before the leaves in spring. Flowering occurs during March and April in the northwestern U.S. and during May and June in the interior of Alaska. The cones ripen in late fall with seedfall occurring immediately following ripening. Leaves remain green until they drop in fall (Lyons 1952; Viereck and Little 1972; USDA 1974; Brayshaw 1978).

REPRODUCTION

Seed Production and Dispersal: Mountain alder produces abundant seed. The fruit is a small, single-seeded nutlet with a narrow wing. Dispersal is by wind and water (Hosie 1973; USDA 1974).

Seed Viability and Germination: Seed viability can be low: in some cases as many as 95% of seed produced have been found to be empty. The seed requires no treatment or chilling to break germination and can be expected to germinate immediately following dispersal if conditions are favourable (USDA 1974). In eastern North America, speckled alder requires saturated soil for seed germination, and seed is the primary source of new stands on freshly exposed, wet soil (Healy and Gill 1974).

Vegetative Reproduction: Like other alders, mountain alder can sprout from the root collar or stump if damaged. Both the European grey alder and the eastern speckled alder are reported to produce suckers at some distance from the main stem (Hadfield 1968; Healy and Gill 1974). Sprouting from exposed roots in streams has been noted, and submerged branches sometimes produce adventitious roots (Furlow 1979). Layering has also been reported in some alders and could be possible in mountain alder considering its sprawling branches and moist habitat. Cuttings of *A. incana* taken in Alaska could not be successfully rooted (Holloway and Zasada 1979).

Although this species frequently occurs in thickets, it is not known whether such groups of plants represent clones (Furlow 1979). Healy and Gill (1974) believe that in eastern North America, perpetuation and spread of established alder stands probably result mostly from sprouting or other vegetative means.

PESTS

In British Columbia, common insect pests include the alder flea beetle (*Altica ambiens*), the striped alder sawfly (*Hemichroa crocea*), the western tent caterpillar (*Malacosoma californicum*), and the poplar-and-willow borer (*Cyrptorhynchus lapathi*) (Gerber *et al.* 1980).

EFFECTS ON CROP TREES

Competition: On wet sites, mountain alder often forms dense thickets that compete severely with conifers, preventing germination or successful establishment of natural regeneration. Scattered individual trees usually do not pose a significant threat to planted conifers. Walker and Chapin (1986) found that in Alaska, mountain alder can inhibit growth of understory spruce seedlings by shading and root competition. In their study, the effect of competition outweighed the beneficial effects of nitrogen fixation. They also found that mountain alder inhibited seedling establishment because its dense litter layer prevented initial seedling germination and establishment.

Beneficial Effects: An important beneficial effect of mountain alder is its ability to improve soil nitrogen status. *Alnus incana* can fix between 43 and 360 kg/ha of nitrogen annually (Binkley 1981). The beneficial effect of nitrogen fixation on the growth of associated conifers should be most evident on nitrogen-deficient sites (Harrington and Deal 1982). Mountain alder may improve nutrient availability on forest sites (see, e.g., van Cleve and Viereck 1972).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Most published references dealing with the response of *A. incana* to disturbance or management refer to spp. *rugosa* (e.g., Healy and Gill 1974).

Forest Canopy Removal: Mountain alder increases in abundance after harvesting, especially on wet sites (Healy and Gill 1974; C. DeLong and W.R. Mitchell, pers. comm., Nov. 1984). In Alaska, density increased following summer and winter logging of an alluvial balsam poplar stand; increases were greatest on winter-logged areas (Zasada *et al.* 1981). Another Alaska study showed that growth of mountain alder significantly increased in response to overstory canopy removal, probably as a result of release from light limitation (Walker and Chapin 1986).

Fire: Where alders are present but suppressed, fire will tend to favour the alder over competing species (Healy and Gill 1974).

Cutting: Spring and winter cutting produces rapid sprout growth, while cutting in July and August produces fewer, slower-growing sprouts. Alder retains its vigour and sprouts heavily when subjected to repeated cutting at 4- to 5-year intervals (Healy and Gill 1974).

Herbicides: A broadcast application of glyphosate at 1.8 kg a.i./ha in early August in the SBSdw subzone in the Cariboo was severely damaging to mountain alder 14 and 16 months after treatment.[41]

Soil Disturbance: Mechanical treatments that expose areas of wet mineral soil provide a suitable seedbed for mountain alder. Sprouting from root crowns and stem bases of alders damaged during mechanical site preparation can be expected. In the Cariboo Forest Region, trials using a V-plow or straight blade to rip apart large areas of alder have been successful in setting back the alder sufficiently to establish a softwood crop.[42]

Fertilization: Laboratory experiments in Alaska showed that *A. tenuifolia* seedlings fertilized with NPK had similar growth to unfertilized controls (Walker and Chapin 1986).

WILDLIFE

Food: Mountain alder has low importance for ungulates in British Columbia (T. Lea, pers. comm., Feb. 1989), although small and large mammals will eat the twigs and foliage (Healy and Gill 1974). The catkins are readily consumed by squirrels (Harestad 1983). Snowshoe hare heavily browse mountain alder in Alaska (Hansen and Flinders 1969; Walker *et al.* 1986).

Other Resources: Mountain alder provides nesting sites for birds (Cannings *et al.* 1987).

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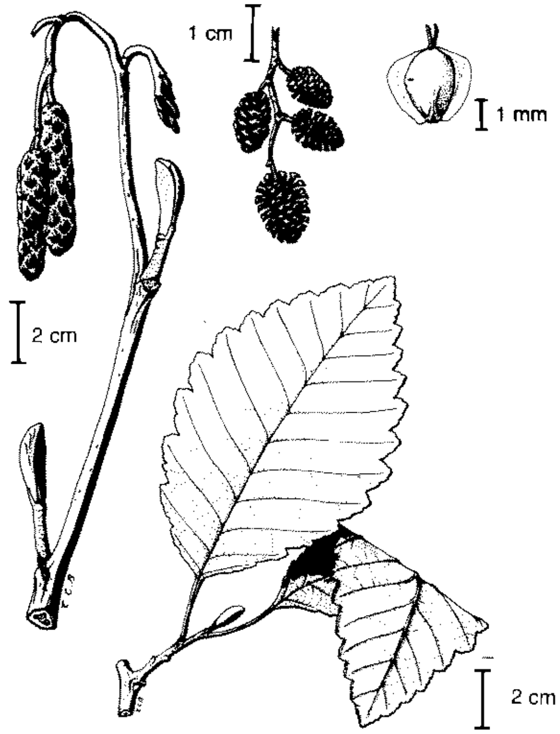
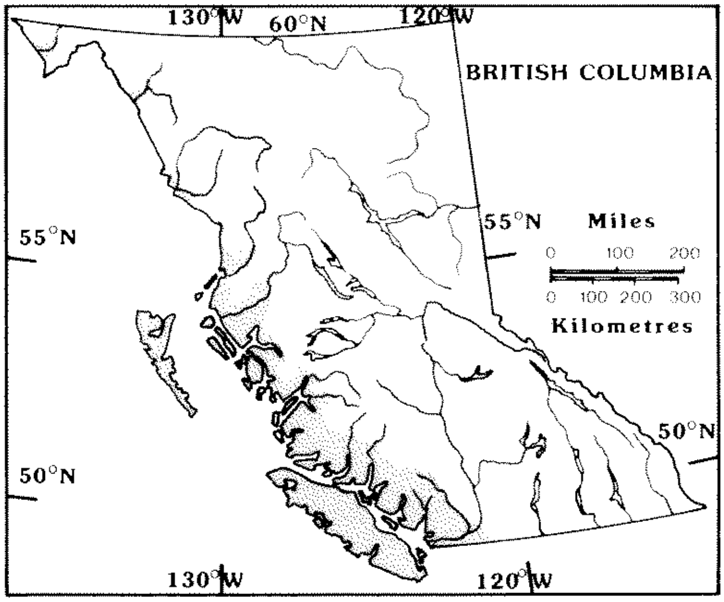
[41] George 1989.

[42] Perry 1983.

Alnus rubra
(red alder)





Distribution of *A. rubra* in British Columbia.

Alnus rubra Bong. Red alder

DESCRIPTION

Red alder is a medium-sized deciduous tree up to 25 m tall. Stems have smooth grey bark and twigs are reddish with club-shaped stalked buds. Leaves are oval and doubly toothed with an inrolled margin. Separate male and female catkins are produced on the same plants. The female catkins develop into small cones containing small, winged nutlets (Brayshaw 1978).

Variation: No subspecies or geographic varieties are described in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Red alder is the most abundant hardwood occurring along the northwest Pacific Coast. In British Columbia it is found along the entire length of the coast, including Vancouver Island and the Queen Charlotte Islands. It is restricted to within 200 km of the coast and only occurs inland of the Coast Mountains along major river valleys such as the Fraser and Skeena (Fowells (compiler) 1965). Red alder is abundant in the CWH and CDF biogeoclimatic zones and occurs at low elevations in the MH zone.

Altitudinal Range: Red alder primarily grows in low coastal valleys, ranging from sea level to approximately 1200 m (Fowells (compiler) 1965).

HABITAT

Climatic Relations: Red alder grows in humid to perhumid coastal climates characterized by mild, wet winters and warm, dry summers (Chester 1988), with annual precipitation ranging from 400 to 5600 mm. Most of the precipitation within its range occurs as rain during the winter. Red alder does not grow well on exposed, windy sites (Harrington 1987). The range of red alder appears to be limited, at northern latitudes and inland, by low winter temperatures (Fowells (compiler) 1965), but the factors controlling its distribution are not well understood. Harrington (1987) reports that annual summer precipitation below 150 mm may limit distribution. Red alder growth slows with increasing elevation (Fergerson 1978), but plants transported to Michigan, where the winters are quite severe, proved to be perfectly hardy (Furlow 1979).

Site and Soil Conditions: Red alder is found on a wide variety of soils and substrates ranging from well-drained gravels and sands to poorly drained clays or organic soils. The best stands are found on deep, well-drained loams, sandy loams, or silt loams of alluvial origin (Fowells (compiler) 1965). Red alder has been found to increase soil bulk density over time (Bormann and DeBell 1981). In the Oregon Coast Range, stands on toe slopes had the highest site index values, but those on mid-slope positions tended to attain the greatest basal area and density (Carlton 1988).

Nutrient Relations: Red alder has a major influence on the nutrient conditions of a site. It is well known for its ability to increase soil nitrogen through its symbiotic association with nitrogen fixing organisms and for its contributions to the organic matter content of a soil (Tarrant and Miller 1963; Binkley 1981; Bormann and DeBell 1981). Nitrogen fixation varies with season, environment, tree vigour, stand composition, age, density, and the inherent fertility of the site (DeBell *et al.* 1983; Chester 1988). Maximum nitrogen fixation occurs in late spring and summer when trees are at their maximum growth levels (Tripp *et al.* 1979; Wheeler *et al.* 1981). Maximum nitrogen fixation occurs when soil pH is between 4.5 and 7.0; nodule growth is inhibited at pH levels below 4.5 and above 9.0 (Elliot and Taylor 1981; Wheeler *et al.* 1981; Knoulton and Dawson 1983). Trees with the greatest leaf mass fix the most nitrogen (Monaco *et al.* 1982; Bormann and Gordon 1984).

Although nitrogen fixation per tree is higher for older trees than younger trees, young stands tend to be very dense and so generally fix more total nitrogen than older stands (Chester 1988). Bormann and Gordon (1984) found that per-tree nitrogen fixation decreased as stand density of red alder plantations in northwestern Oregon increased. Total nitrogen fixation of stands increased from 50 kg/ha per year at 1000 stems per hectare to a maximum of 80 kg/ha per year at 5000 stems per hectare, then fell back to 50 kg/ha per year at 10 000 stems per hectare. Nitrogen fixation rates for the forest floor and soil range between 35 and 80 kg/ha per year for pure red alder stands over a 40-year period (Chester 1988). Measures of nitrogen in the total ecosystem biomass range from 85 to 210 kg/ha per year over a similar time period.

Red alder affects soil nutrient status in other ways. As soil nitrogen increases in soils under an alder stand, there is a drop in soil pH and a concurrent decrease in exchangeable calcium and magnesium. The concentration of phosphorus and several other nutrients in foliage and leaf litter has been found to decrease with stand age (Bormann and DeBell 1981; DeBell *et al.* 1983, 1984).

The relationships described above suggest that the growth of red alder may be limited by the natural levels of phosphorus, calcium, or magnesium in the soil (DeBell *et al.* 1984), especially in light of its high nutritional requirements for these nutrients (Krajina *et al.* 1982).

Water Relations: Red alder tolerates poorly drained soil conditions and survives prolonged periods of flooding (Krajina *et al.* 1982). Among its associates, it is considered to be one of the most tolerant species of shallow water tables (Minore 1979). Although red alder may grow slowly on poorly drained soils, it grows faster than most conifers on these sites (Scott 1978). Based on growth during a combined flooding and recovery period, red alder was judged to be more tolerant of short-term flooding than black cottonwood (Harrington 1987).

Although red alder growth is generally reduced as waterlogging increases, families have been identified in which height is not reduced by a shallow water table. Genetic differences in growth response to soil waterlogging indicate that genetic selection programs could be used to manage for enhanced growth of red alder on wet sites (Hook *et al.* 1987).

Despite its tolerance of a wide range of soil moisture conditions (Krajina *et al.* 1982), red alder is uncommon on droughty soils, areas of low precipitation, and steep south- or southwest-facing slopes where it may be subjected to severe environmental stresses (Fowells (compiler) 1965). Moisture stress or flooding can reduce nitrogen fixation (Heilman and Ekuan 1982; Winship and Tjepkema 1984). Young red alder exhibits its best growth under well-irrigated conditions, and compared with Douglas-fir, red alder is more adversely affected by low soil moisture (Chan *et al.* 1988).

Light Relations: Red alder has low shade tolerance (Krajina *et al.* 1982; Dukes *et al.* 1988) and does not occur as an understory plant except on wet, productive sites where the mature forest has a very open canopy.[43] Although seedlings can survive in partial shade, establishment and subsequent growth are best in full sunlight. Chan *et al.* (1988) found that diameter and height growth of red alder were significantly reduced under low light levels (15% of normal sunlight) compared with normal sunlight. As dense natural red alder stands age, competition for light results in high mortality (Chan *et al.* 1988).

Temperature Relations: Growth is slowed in continuously hot or cool environments, regardless of available moisture (Newton 1978). Nitrogen fixation is inhibited at temperatures below 8°C or above 30°C and rates steadily increase as temperature increases from 16 to 28°C (Winship and Tjepkema 1984, cited by Chester 1988). Frost resistance of red alder is low (Krajina *et al.* 1982; Harrington 1987) and mortality and stem damage can occur during heavy frost and ice conditions (Webster 1987, cited by Chester 1988). Repeated frosts in late April and early May caused extensive damage to newly planted red alder seedlings in western Washington (Peeler and DeBell 1987). Older natural stands and plantations appear to be less susceptible to frost and are better able to recover from it than are planted seedlings.

GROWTH AND DEVELOPMENT

Red alder exhibits rapid early growth.[44] Of its associates, only black cottonwood and bigleaf maple sprouts can grow as rapidly during the juvenile stage. Where moisture is adequate, a seedling can grow to 1 m or more in the first year. However, Haeussler (1987) found that seedling growth on clearcuts in the central coast of Oregon was much slower, averaging only 2 cm after the first year and 12 cm after the second. Chester (1988) described first-year height growth as averaging between 14 and 40 cm.

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[43] Brand 1984.

[44] Harrington 1981.

Maximum annual height growth occurs at a very early age. Red alder near Haney reached 9 m in height and 9.5 cm in diameter by age 9 (Kunzli 1985). It is possible for a seedling to be nearly 10 m tall by age 5. Growth slows after the juvenile stage, with the decrease beginning much earlier on poor sites. Maximum annual productivity occurs between the ages of 10 and 15 years (Zavitkovski and Stevens 1972). Red alder is a short-lived tree, becoming decadent at 40 years and rarely living for more than 60 years.

In most situations, red alder grows as a single-stemmed tree; multi-stemmed shrubs are rare. Under low light conditions the crown is narrow, but in full light in the absence of competition, branches spread out from near the base to produce a broad, rounded crown.

Growth and yield of red alder are described in detail in Briggs *et al.* (1978). Chester (1988) compared the growth of red alder and conifers. On good sites, red alder trees are taller than Douglas-fir for the first 30 years and taller than western hemlock for the first 40 years. Red alder tree volume is greater than that of Douglas-fir for at least 60 years and greater than that of western hemlock for the first 40 years. However, the early mortality of red alder stands causes them to have significantly lower volume per hectare than coniferous stands after age 40. Stand density management guidelines have been derived for red alder by Hibbs (1987).

When a 14-year-old stand of red alder in the Oregon Coast Range was thinned, diameter growth doubled for the first 5 years after thinning.[45] At the increased growth rate, a 30-cm diameter tree could be grown in 29 years.

Phenology: Red alder flowers between late February and early May depending on latitude and climate (Kenady 1978). In coastal Alaska, flowering is in April and May (Viereck and Little 1972). Cone ripening takes place between August and September. Seed dispersal begins shortly after ripening and continues through fall and winter (Kenady 1978). On the south coast of British Columbia, seeds disperse between November and February and germination occurs in May (A. McGee, pers. comm., Feb. 1989).

REPRODUCTION

Seed Production and Dispersal: Red alder begins to produce seed at about 6–8 years of age with optimum production occurring at about age 25. It produces ample seed every year with bumper crops every 3–5 years. Dissemination of seeds is primarily by wind. The narrowly winged nutlets can be carried great distances, but they are notably more abundant close to their sources (Fowells (compiler) 1965; USDA 1974; Kenady 1978; Burns (compiler) 1983; Haeussler 1987; McGee 1988b).

Seed Viability and Germination: Red alder seed remains viable in storage for at least 3 years. However, seed probably remains viable for only 1 year in the field on the south coast of British Columbia (A. McGee, pers. comm., Feb. 1989) and in the Oregon Coast Range (Haeussler 1987). The short viability is likely due to the lack of a hard seed coat and susceptibility to decay and predator consumption (Haeussler 1987).

There is very little difference in germination percentage between stratified and unstratified seed. Seed germinates best after a period of water imbibition. Germination in nature is best on moist mineral soil in full sunlight. Litter and organic debris create microenvironments too dry for seedling survival, especially on south-facing slopes, xeric sites, and inland areas where summer drought is most intense (Newton *et al.* 1968). Haeussler and Tappeiner (1988) observed that mineral soil is not required for alder germination and survival in moist, humid environments, such as north-facing slopes. Infra-red light that penetrates through thick layers of vegetation or surficial soil layers strongly inhibits seed germination. This prevents seed from germinating until after a disturbance, when it is exposed to full sunlight. Seeds can germinate and seedlings can tolerate partial shade for several years but full sun is required for normal development (Fowells (compiler) 1965; Kenady 1978). Germination of seed on freshly exposed mineral soil is the primary method of regeneration in red alder.

Exposure of mineral soil and spring rainfall patterns are the most important factors affecting seed germination in the central Coast Range of Oregon. Seedling emergence on disturbed mineral seedbeds in clearcuts ranged from 7 to 65% of viable seed sown and on disturbed forest seedbeds from 23 to 57%. Emergence was limited by soil moisture in the clearcut but not in the undisturbed forest. Seedling emergence generally averaged below 10% on undisturbed organic seedbeds (Haeussler 1987).

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[45] Hibbs and Kromack 1989.

Seedlings that successfully germinate can suffer heavy mortality from herbivores and disease (e.g., damping-off fungi) in the spring, succumb to moisture stress in the summer, or be buried by leaf litter in the fall (Haeussler 1987; Carlton 1988). First-year seedling survival is favoured by shade, which protects seedlings from heat injury and drought, and by thin organic materials, which conserve moisture. During a 2-year period, no seedlings survived on two harsh sites in the Oregon Coast Range, and survival was only 3–30% on clearcuts and less than 2% in the forest on two coastal sites (Haeussler 1987). These Oregon results should apply to the CDF zone in British Columbia.

Vegetative Reproduction: Red alder sprouts vigorously from the root collar or stump when young. Sprouting declines with age, and stands less than 6 years old are the best choice for coppice regeneration (Chester 1988). Once alder reaches age 15, its capacity for vegetative reproduction is greatly diminished, and few trees will produce sprouts that live for more than 2 years (DeBell *et al.* 1984). Red alder does not sucker from the roots (Harrington 1984). Greenwood cuttings from young trees can be successfully rooted (Monaco *et al.* 1980). Vegetative reproduction allows recovery of individual damaged trees but is not a means of population growth in this species.

PESTS

Red alder is exceptionally free from disease, decay, and insect attacks for the first 30–40 years (Fowells (compiler) 1965; DeBell and Turpin 1983, cited by Chester 1988), but as the tree gets older, pest problems become increasingly common. *Fomes igniarius* induces white trunk rot in mature living trees (Carlton 1988). Chester (1988) suggests that this may be the most serious disease affecting red alder utilization. *Hypoxylon fuscus* induces white heart rot in older trees, and other fungi invade the dead and dying tissue.

Insect pests of red alder include flatheaded borers, bark beetles, sawflies, and tent caterpillars (DeBell and Turpin 1983, cited by Chester 1988). Tent caterpillars and sawflies are the insects that pose the greatest threat to red alder management. Tent caterpillars rarely cause mortality but can severely defoliate trees and thereby lead to growth reductions during prolonged infestations. Sawflies also defoliate red alder and are becoming more prevalent as the amount of alder in the province increases. Gara and Jaeck (1978) suggest that sawflies may become the most threatening insect pest of red alder. Bark beetles are currently a minor pest of red alder, but logging slash could increase population levels.

For more detailed information on the pests of red alder refer to Fowells (compiler, 1965), Gerber *et al.* (1980), and Burns (compiler, 1983).

EFFECTS ON CROP TREES

Competition: Red alder is a major competitor with young conifer plantations throughout its range in British Columbia. Competition problems are prevalent with Douglas-fir, which is both the most frequently planted conifer where alder occurs in the Vancouver Forest Region and is shade intolerant and therefore highly susceptible to light competition. Alder also competes seriously with Sitka spruce in the Prince Rupert Forest Region. Alder seedlings that establish in disturbed areas following logging form the primary source of competition. Sprouts that develop from stems cut during logging are a lesser source of competition for young conifers.

Most studies on the effect of alder competition on crop trees have involved Douglas-fir. Alder competition reduces height, diameter, and biomass of Douglas-fir (Cole 1984), and can cause significant mortality (Miller and Murray 1978). The extent of alder competition is related to the amount of site disturbance which influences the density of invading alder. If alder is widely spaced, Douglas-fir can receive enough light to become established before a complete alder canopy develops. Newton *et al.* (1968) concluded that Douglas-fir needs 3–8 years of free growth to remain above alder, regardless of site quality.

The rapid juvenile growth of red alder gives it a competitive advantage over Douglas-fir, and competition becomes more pronounced with time as the growth of alder outstrips that of Douglas-fir. Without chemical or mechanical control, equal-aged alder usually overtops associated Douglas-fir for about the first 25 years (Miller and Murray 1978). Red alder can establish this dominance very quickly. Cole and Newton (1987) found that 1 year after planting of similarly sized alder and Douglas-fir, growth of alder exceeded that of Douglas-fir and differences in height were accentuated over 5 years. Once Douglas-fir becomes suppressed under alder, its growth quickly slows and mortality often occurs within 5–7 years (Newton *et al.* 1968).

In contrast to the above, the presence of 1100 red alder stems per hectare in a Douglas-fir plantation on an average quality site in the Oregon Cascades had neither a negative nor a positive impact on the conifers. Delaying the release of Douglas-fir from alder until age 7, instead of age 3, did not reduce growth or mortality of the conifers through age 10. For alder densities lower than 1250 stems per hectare, alder control can be delayed on poor to medium sites until 6 to 8 years after planting Douglas-fir (Murray and Miller 1986).

Control of competing alder has resulted in significant growth increases in Douglas-fir. One year after red alder was controlled with herbicides, the volume of Douglas-fir trees was as much as 35% higher than where alder was untreated.[46] In the Oregon Coast Range, 7-year-old planted Douglas-fir seedlings grew significantly slower when overtopped by red alder and other hardwoods than when influenced by low encroaching vegetation (Howard and Newton 1984).

Chan and Walstad (1987) found that Douglas-fir sapling size generally decreased as the percentage of visible sky decreased and the amount of overtopping vegetation, particularly red alder, increased. The authors suggest that factors other than the percentage of visible sky (i.e., light), such as soil moisture, also affected conifer growth. Shainsky (1988) concluded that both moisture competition and light caused growth losses of red alder and Douglas-fir seedlings. In 5-year-old plantations, Cole and Newton (1986) found that increasing densities of red alder negatively affected Douglas-fir growth by competing for light and soil moisture. While light availability is the primary mechanism driving allocation of resources in Douglas-fir, resource allocation patterns and priorities in red alder are primarily driven by soil moisture availability (Chan *et al.* 1988).

A few studies have investigated competition between red alder and Sitka spruce. Overtopping red alder reduced survival and growth of 6- and 8-year-old Sitka spruce trees near Haney, B.C. (Kunzli 1986). Five years after control of 9 m tall red alder with herbicide on a productive floodplain site, Sitka spruce trees were 2.15 m tall compared to 1 m tall on an untreated control.[47]

Alder canopies that allow light to penetrate may suppress moderately shade-tolerant conifers like Sitka spruce, rather than kill them outright.[48] However, some 4–8-year-old alder stands allow very little penetration of light (B. D'Anjou, pers. comm., May 1989) and, as a result, can lead to conifer mortality.

Red alder competition can seriously hinder natural regeneration of conifers. Studies of red alder succession in the Oregon Coast Range show that natural regeneration under red alder is very rare. Alder stands often succeed to salmonberry or vine maple dominated communities rather than to conifers (Carlton 1988).[49]

Interactions between red alder and crop trees involve trade-offs between the negative effects of competition and the beneficial effects of soil fertility enhancement (Binkley 1984). For conifers to benefit from nitrogen fixation, red alder could be regenerated after conifers are well established. Red alder can successfully grow and fix nitrogen under thinned Douglas-fir stands, but it suffers heavy mortality and only minimal nitrogen fixation when grown under dense Douglas-fir stands (Helgerson *et al.* 1984). DeBell *et al.* (1983, 1984) have shown that available nutrients decrease under a canopy of red alder.

Grass-seeding can be used to exclude red alder for the benefit of conifer seedlings (McDonald 1986). Klinger (1986) reported significant reductions in the cover of red alder 5 years after seeding of two rhizomatous grass species.

For information on competition between red alder and black cottonwood, see Heilman and Stettler (1985), Pezeshki and Oliver (1985), and Pezeshki and Hinkley (1988).

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[46] Dunsworth 1987.

[47] Pollack and van Thienen 1986.

[48] Brand 1984.

[49] Hibbs and Cromack 1989.

Allelopathy: del Moral and Cates (1971) found that extracts of red alder foliage and litter inhibited growth of test plants in the laboratory, but there was no evidence that allelopathic interference was occurring under field conditions.

Beneficial Effects: The primary beneficial effect of red alder on the growth of crop trees is its ability to increase the nitrogen content of forest soils. Because nitrogen deficiency in the soil is the most common nutritional factor limiting Douglas-fir growth in the Vancouver Forest Region (Atkinson and Hamilton 1978), there is interest in growing alder to meet this nitrogen requirement. Red alder interplanted with Douglas-fir clearly increased height and diameter growth of the associated dominant conifers on a nitrogen-deficient site in southwestern Washington (Miller and Murray 1978). The authors recommended that 50–100 uniformly distributed alders per hectare be retained for nitrogen improvements. Miller and Murray (1979) suggest that nitrogen-fixing plants should supply 20–50 kg/ha per year of available nitrogen to the soil to be effective for silvicultural purposes. In a plantation on Vancouver Island, Douglas-fir stem growth increased by 2.5 times when growing in association with red alder, compared to that grown without alder (Binkley 1984).

Benefits of red alder should be expected to be greatest on soils that are deficient in total or available nitrogen and low in organic matter and clay (Miller and Murray 1978; Binkley 1982a).[50] Although red alder often increases yields of Douglas-fir on nitrogen-deficient sites, it may decrease Douglas-fir yield on good sites (Gholz *et al.* 1985). In addition to increasing soil nitrogen, red alder trees also increase soil organic matter content by their root debris and nutrient-rich leaf litter, and they decrease soil bulk density (Tarrant and Miller 1963; Bormann and DeBell 1981; Binkley 1984). Chester (1988) discusses the advantages of using red alder rather than nitrogen fertilizers to increase conifer yields.

Another potential beneficial effect of red alder in mixtures with conifers may be its ability to reduce losses from laminated root rot (*Phellinus weirii*) in Douglas-fir (Nelson *et al.* 1978). Overtopping red alder also appears to reduce the frequency of attack of spruce weevil (*Pissodes strobi*) on Sitka spruce saplings (Kunzli 1985). See Chester (1988) for a comprehensive discussion of the beneficial effects of red alder.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Red alder will rapidly invade clearcut areas especially if disturbance has created areas of exposed mineral soil (Hosie 1973; Kenady 1978). Removal of a forest canopy, by itself, does not generally cause an increase in seedling emergence. Germination rates are highest when both spring soil moisture is adequate and light availability is increased by canopy removal (Haeussler 1987).

Red alder regeneration may be reduced by the removal of alder seed trees before harvest. Bancroft *et al.*[51] suggest that the optimum period for removal of seed trees is 1 year prior to harvest. Advantages to 1-year pre-harvest alder seed tree control include loss of viability of alder seed in the forest floor within 1 year (usually) and inhibition of sprouting of cut alder stumps by overstory shade. In comparison to trees that are cut down and removed, chemically girdled trees may take more than a year to die and may produce viable cone crops before mortality occurs.

Fire: Red alder is generally one of the first trees to become established on burned-over areas (Hosie 1973). Although red alder can sprout near the root collar, seeding-in is the primary means of invasion following a fire. Red alder's nitrogen fixing capabilities allow it to establish quickly and grow on sites where burning has created a nitrogen deficiency. Ash from the burn contains high levels of many nutrients required for alder growth including calcium, magnesium, phosphorus, and potassium. Severe burns in the CDF and CWH zones on southern Vancouver Island have created mineral soil seedbeds and resulted in alder invasion 1 or 2 years after burning. In contrast, light burns on these sites can reduce alder invasion if the hydrophobic duff remains in place (R. Muller, pers. comm., July 1989).

Fire is rarely a damaging agent to established pure stands of red alder because of their extremely low flammability; in fact, red alder has been planted to act as a firebreak to protect adjacent conifers (Fowells (compiler) 1965).

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[50] Hibbs and Cromack 1989.

[51] Bancroft *et al.* 1988.

Cutting: Red alder will sprout from the stem following cutting, but it is not considered a strong sprouter compared with other species. Three years after cutting 7-year-old alder in February in the Washington Cascades, the tallest stump sprouts ranged from 3.7 to 4.9 m in height (Murray and Miller 1986). Coppicing experiments have shown the effects of tree age, cutting height, cutting angle, season of cut, and repeated cuttings on the sprouting vigour of red alder (DeBell *et al.* 1984; Harrington 1984; Hoyer and Belz 1984; DeBell and Turpin 1989). The major findings of these studies are as follows:

1. Sprouting vigour is greatest on trees aged 1–4 years. Vigour falls off dramatically after 15 years. Trees aged 15 years or older rarely have live sprouts 2 years after cutting.
2. The average number of sprouts per cut stem increases significantly as stump height is increased (e.g., 5 sprouts on stumps below 10 cm; 9 on 70 cm stumps). Sprouting is maximized on stumps taller than 10 cm and shorter than 60 cm.
3. Stumps with the cut surface facing south or west have the least mortality and are most likely to sprout, presumably because of light interception. Level cuts may have higher mortality and fewer sprouts than angled stumps, possibly because water is slower to drain off, causing faster decay.
4. Stems cut in January have the lowest mortality; stems cut during the growing season, especially in July or August, have the greatest mortality (e.g., 75–95%).
5. Numbers and height of sprouts may be reduced by cuts in June and July.
6. Trees cut for the first time in January at age 2, and every second year for 8 years thereafter, showed a significant reduction in sprouting vigour after every cut.

In British Columbia, D'Anjou and Pendl found that first year mortality increased from 20% following June cutting to 75% following September cutting.[52] The number of alder sprouts following cutting decreased as cutting was carried out from early to late in the growing season. Manual cutting in early spring effectively controlled red alder for at least 2 years in the CWH zone near Chilliwack.[53] Cutting in mid-summer also controlled alder; success was due to suppression of resprouts by shading of the stumps.

The cutting window for red alder in Washington and Oregon begins 50–70 days before bud break and lasts 2–8 weeks, depending on climatic conditions. Below-normal precipitation in winter and early spring may shorten the growth period because of resource limitations, and thereby shorten the cutting window.[54] Mortality rates are constant within the cutting window (DeBell and Turpin 1989).[55] Alder has been effectively controlled by girdling in every season. However, girdling of alder in the CWH subzone in the Queen Charlotte Islands has only been effective on trees greater than 15 years old and 15 cm dbh. Younger trees tend to resprout (S. Craven, pers. comm., June 1989). Girdles must be wide enough to prevent bridging of the cambium, which is particularly prevalent in summer girdled trees.[56] Girdled red alder may take more than 1 year to die, during which time a seed crop may be produced. To ensure seed control, Bancroft *et al.*[57] suggest girdling 2 to 3 years before harvest.

Herbicides: The response of red alder to foliar sprays of glyphosate has been variable, and ranges from moderate to very severe (Conard and Emmingham 1984a, 1984b; Boateng and Herring 1990). The variation is largely an effect of the age and size of alder (R. Whitehead, pers. comm., May 1989). Results from late August foliar sprays of glyphosate in the Campbell River Forest District indicate that at least 5 L/ha of glyphosate are needed to kill large alder (up to 15 m tall) (J. McLarnon, pers. comm., July 1989). Five years after a late summer foliar spray of 2.0 kg a.i./ha glyphosate on a productive Skeena floodplain, red alder cover and height was 2% and 2.8 m compared to 97% and 9.1 m on the control.[58] Many

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[52] D'Anjou and Pendl 1989.
[53] D'Anjou 1988e.
[54] Belz 1989.
[55] Ibid.
[56] B. Wilson, pers. comm., 1988, cited by Bancroft *et al.*
[57] Ibid.
[58] Pollack and van Thienen 1986.

treatments do not result in such effective long-lasting control. For example, control declined by the second growing season after a September application of 2.0 kg a.i./ha glyphosate in the CWHvm subzone on southern Vancouver Island.[59] Backpack spray applications of 2.0 kg a.i./ha glyphosate on various dates on a site in the CWH zone showed that the August 12 application was the most effective, the September 3 application was next most effective, and the June 4 and July 9 applications were ineffective.[60]

Spring through fall cut surface treatments with glyphosate or 2,4-D cause severe damage to red alder (Conard and Emmingham 1984b). Hack and squirt with a 50% solution of glyphosate in water, applied at 1 mL per cut at 1.1 m height effectively controlled 50 cm dbh red alder on a highly productive floodplain site.[61] Red alder is very sensitive to 2,4-D applied by broadcast spray or tree injection (Stewart 1974a, 1974b; Conard and Emmingham 1984a, 1984b; Boateng and Herring 1990). Cut stump treatment with 2,4-D amine in the fall significantly controlled red alder sprouts.[62] Thin-line treatment (application of concentrated herbicide directly to the bark on the lower part of the stem) of small red alder stems (diameter less than 2 cm) using 2.4–4.6 mL per stem of either 2,4-D ester in diesel or triclopyr in diesel at various dilution rates is very effective (Hibbs and Landgren 1987). May and June applications may be more effective than earlier applications.

Conard and Emmingham (1884a) rate red alder as very sensitive to triclopyr. Results from studies in British Columbia generally support this finding, though in some instances triclopyr has been only partially effective. For example, early and late spring applications of 3 kg a.i./ha triclopyr ester in the CWH zone near Chilliwack, resulted in only moderate control of red alder.[63] High mortality resulted from broadcast applications of triclopyr ester at 1.4 and 2.9 kg a.i./ha in mid-September in the Fraser Valley.[64]

Limited information indicates that hexazinone is ineffective in controlling red alder (Boateng and Herring 1990), but this may be due to thick organic layers on areas where the herbicide has been applied.[65]

Soil Disturbance: Red alder readily seeds-in to areas of exposed, moist mineral soil (Fowells (compiler) 1965) such as that created by scarification. McGee (1988b) suggests that, given adequate rainfall, scarification may expose buried alder seeds to the environmental conditions required for germination. A scarified site in the Vancouver Forest Region had a much higher cover of red alder than unscarified and burned sites.[66] Dense stands of red alder are almost invariably associated with soil disturbances such as roads, landings, and other forms of localized deep scarification (Newton *et al.* 1968; McGeough 1985; Alaback and Herman 1988).

Fertilization: Growth of young red alder may be substantially enhanced by applications of non-nitrogenous fertilizers. Phosphorus fertilizers produced the greatest response, but alder also responded to applications of calcium, magnesium, potassium, and sulphur in greenhouse and field studies (DeBell *et al.* 1984). Radwan (1987) found that the response of red alder seedlings to pure and mixed applications of calcium, magnesium, potassium, sulphur, cobalt, and molybdenum fertilizer varied according to soil type. Phosphorus produced the greatest growth increase, but other fertilizers were also found to have potential for increasing growth.

WILDLIFE

Food: Red alder is relatively important to wildlife in British Columbia. Deer and elk eat the foliage, buds, and twigs.[67] Red alder is moderately important browse for black-tailed deer, particularly in the summer and fall (McTaggart-Cowan 1945; Brown 1961; Singleton 1976; Rue 1978; Harvey 1981; Leslie *et al.* 1984).

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[59] Reynolds *et al.* 1988.
[60] D'Anjou 1988b.
[61] Pollack and LePage 1988.
[62] Dunsworth 1987.
[63] D'Anjou 1988b.
[64] D'Anjou 1986a.
[65] D'Anjou 1988e.
[66] Brand 1984.
[67] Ibid.

Many small mammals and some birds forage on red alder. Alder catkins are readily consumed by squirrels (Banfield 1974; Harestad 1983). Seeds are often eaten by deer mice in clearcuts and by shrews and red backed voles in uncut alder stands in the Oregon Coast Range (Haeussler 1987). Alder leaves are sometimes eaten by blue grouse (Zwickel and Bendell 1972).

Mountain beaver, a common mammal in the U.S. Pacific Northwest but not common in British Columbia, makes high use of alder year-round (Crouch 1968). Mountain beaver can climb several metres up alder trees to cut off small limbs (Harestad 1983).

Other Resources: Red alder contributes detritus to streams, which forms the basis of the food chain in many small streams. It maintains stability of streambanks and moderates stream temperatures, thereby maintaining the quality of fish habitats.[68] Chester (1988) indicates that since ungulates require diverse and varying habitats, red alder stands may provide important alternative habitats to second-growth forests in low snowfall regions. Brown (1985b) suggests that shrub to pole-sized red alder stands are primary breeding and feeding habitat for deer. In addition, pole-sized alder stands provide primary resting habitat for deer. Female black-tailed deer use thick stands of alder trees in November and December to avoid pursuing bucks (Miller 1968). Red alder in riparian zones is used by beaver for building dams.[69] Alder trees are also commonly used by bald eagles for daytime perching (Stalmaster and Newman 1979), and they are important cavity nesting trees for woodpeckers in southern British Columbia.[70]

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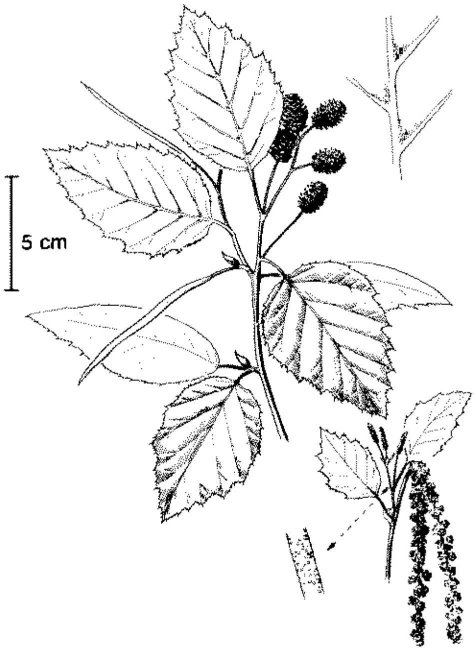
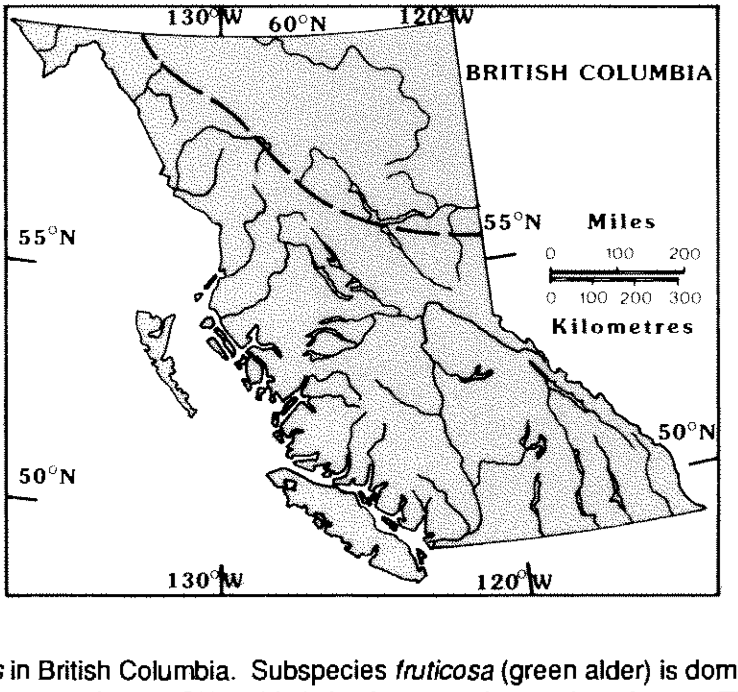
[68] Bancroft *et al.* 1988.

[69] Hibbs and Cromack 1989.

[70] Korol and Wallis 1983.

Alnus viridis* ssp. *sinuata
(Sitka alder)





Distribution of *A. viridis* in British Columbia. Subspecies *fruticosa* (green alder) is dominant north and east of the dashed line, while ssp. *sinuata* (Sitka alder) dominates to the south and west. There is a broad area of introgression between the two species.

Alnus viridis* ssp. *sinuata **Sitka alder**

(A. sinuata, A. sitchensis, A. crispa ssp. *sinuata)* (slide alder)

Alnus viridis* ssp. *fruticosa **Green alder**

(A. virides, A. crispa ssp. *crispa)*

These two alders are very similar, although their exact taxonomic relationship and designation may be in dispute. They are discussed together here to avoid repetition. Most of the available literature applies to Sitka alder. The information can probably be applied to green alder, as long as allowances are made for the latter's boreal habitat.

DESCRIPTION

Sitka and green alder are deciduous plants which grow either as tall shrubs or small trees. As a tree, Sitka alder has a slender trunk with an open crown and a shallow root system. On favourable sites, it can attain a height of 12 m and a stem diameter of 20 cm (Hosie 1973). Twigs are slender and reddish-brown and have buds without stalks. Leaves are oval with toothed leaf margins. Male and female catkins are borne in small clusters on the same twig and produce small, wide-winged nutlets (Brayshaw 1978; Furlow 1979; Harrington and Deal 1982).

Variation: Green and Sitka alder are known by a variety of scientific names. They are closely related and interbreed freely producing intermediate forms where their ranges overlap in northern British Columbia (Brayshaw 1978).

DISTRIBUTION AND ABUNDANCE

In British Columbia, Sitka alder is found as far north as the Yukon border and south to the American border. It occurs throughout the province except northeast of the Rocky Mountains where it is replaced by green alder. There is no area of the province where one of the two subspecies cannot be found (Brayshaw 1978; Krajina *et al.* 1982). Green alder is almost exclusively limited to the BWBS and SWB biogeoclimatic zones, while Sitka alder is found in every zone except the PP and BG (Krajina *et al.* 1982; Angove and Bancroft 1983).

Altitudinal Range: Sitka alder is predominantly found at middle to higher forested elevations in British Columbia. It has been found from 100 to 1500 m on Vancouver Island (Binkley 1981), but Harrington and Deal (1982) were unable to find any below 500 m in Washington. It is often found near the upper timberline in the mountains of British Columbia (Brayshaw 1978) and forms a subalpine to alpine scrub in the northwest of the province (J. Pojar, pers. comm., March 1985). Green alder is found from valley bottoms to timberline elevations in northeastern British Columbia.

HABITAT

Climatic Relations: Both Sitka and green alder are cold climate species. While green alder is clearly adapted to the harsh, boreal climate, Sitka alder is found in cool, moist situations and shady aspects at both high and low elevations within its range (Mueggler 1965; Hosie 1973; Tiedemann and Klock 1974). The springy branches of Sitka alder allow it to tolerate heavy snow loads and sustain only minor damage during avalanches (Lyons 1952; Marchant and Sherlock 1984).

Site and Soil Conditions: Sitka alder is a pioneer species and is able to colonize disturbed sites such as clearcuts, roadcuts, and skid trails where the mineral soil has been exposed. It also occurs on avalanche tracks, talus slopes and fresh alluvium, and behind retreating glaciers where it is one of the first species to invade. Sitka alder is also found in relatively stable environments within the forest and along streams. It occurs on a wide variety of parent materials and soil textures (Johnson 1968; Mitchell 1968; Viereck and Little 1972; Furlow 1979). Green alder is found on a similar variety of habitats within its range (Brayshaw 1978; Krajina *et al.* 1982; Foote 1983), but it is most often associated with sandy, gravelly, or rocky soil (Furlow 1979).

Nutrient Relations: The nutrient requirements of Sitka and green alder are high for calcium, magnesium, phosphorus, and potassium (Krajina *et al.* 1982), but growth is generally independent of the levels of nitrogen available on a site (Harrington and Deal 1982). Both alders are efficient nitrogen fixers with reported rates of nitrogen fixation ranging from 20 to 150 kg/ha per year (Crocker and Major 1955; Dalton and Naylor 1975; Carpenter *et al.* 1979; Binkley 1981, 1982b; Heilman and Ekuan 1982). Both alders fix less nitrogen than mountain alder. Sitka alder, depending on age, produces approximately the same as or less nitrogen than red alder (Binkley 1981, 1982b; Heilman and Ekuan 1982). The ability of Sitka alder to fix nitrogen allows it to invade sterile mineral soil that has been recently exposed by glaciers or avalanches and is very deficient in organic materials (Viereck and Little 1972; Krajina *et al.* 1982). Like red alder, it increases the soil nitrogen level and builds up the organic matter content of young soils. Binkley (1984) was able to demonstrate an increase in total and available nitrogen, and extractable phosphorus, calcium, and magnesium in the top 10 cm of mineral soil of a Sitka alder stand as compared to a non-alder stand in the same area. An increase in soil carbon under Sitka alder stands was also reported by Bollen *et al.* (1969) and Tarrant (1983). Both Sitka and green alder appear to have an acidifying effect on soil. Crocker and Major (1955) observed that recently deglaciated soils under green alder were reduced from a pH of 8.0 to pH 5.0 within 35–50 years. Mitchell (1968) found very low soil pH levels (as low as pH 3.3) under Sitka alder in Alaska.

Water Relations: Sitka alder prefers moist sites that are reasonably well drained but will grow on sites ranging from submesic to subhygric or possibly hygric. Although Krajina *et al.* (1982) report that Sitka alder is highly resistant to flooding damage, it is not abundant on very wet sites with a high water table (Pojar *et al.* 1982; Angove and Bancroft 1983). Green alder has similar moisture requirements and flood resistance to Sitka alder, and like Sitka alder it is described (Furlow 1979) as being adapted to somewhat drier conditions than most alders while still being associated with some source of moisture. Cline and Campbell (1976) describe Sitka alder in northern Idaho as being poorly adapted to drought. It is absent from exposed, sunny sites because it lacks the physiological adaptations that are needed to prevent moisture loss from the foliage.

Light Relations: The shade tolerance of Sitka and green alder is described as moderate by Krajina *et al.* (1982). Both subspecies are able to grow as shrubs in the understory of taller tree species and are abundant in seral forests (Johnson 1968; Foote 1983; Pojar *et al.* 1984) but thrive on overhead light and are unable to withstand the shading of a dense coniferous overstory (Viereck and Little 1972).

Temperature Relations: Both Sitka and green alder are very tolerant of frost. Krajina *et al.* (1982) note that green alder is susceptible to frost damage if not covered by snow, but Foote (1983) reports that in Alaska it is abundant on sites with very cold soil temperatures where the frost level is only 30 cm below the soil surface in mid-summer. Benecke (1970) found maximum nitrogen fixation of Sitka alder at soil temperatures of 25°C and no nitrogen fixation at temperatures below 5°C.

GROWTH AND DEVELOPMENT

Growth rates of Sitka alder vary considerably with site quality, climate, latitude, and elevation. Sitka alder on mild coastal sites grows much faster and taller than that growing in the Interior. In western Washington, height growth of Sitka alder slows rapidly on poor sites, but on better sites at low elevations it can continue to grow at a steady rate for at least 10 years. It takes approximately 3–4 years to reach 1 m in height and can reach 4 m by age 10 (Harrington and Deal 1982). In central British Columbia near Vanderhoof, Sitka alder typically reaches a mature height of only 3 m (C. DeLong, pers. comm., Nov. 1984). Height growth is decreased at higher elevations (Hultén 1974; Harrington and Deal 1982). For example, Sitka alder grew only 1 m in 10 years on a high-elevation site in Washington. It frequently develops crooked, upward curving limbs as a result of snowpress at higher elevations (Lyons 1952).

Green alder grows similarly to Sitka alder, except it is smaller and slower to develop, rarely growing into a small tree (Viereck and Little 1972; Brayshaw 1978). Three-year-old green alder seedlings reached a maximum height of 47 cm in Alaska (Zasada *et al.* 1983).

Phenology: Male and female catkins emerge before or with the leaves in spring. Flowering takes place in May and June in Alaska. Nitrogen fixation on the south coast begins in May, concurrently with leaf emergence, and peaks in July. The cones ripen from mid-September to mid-November, depending on latitude and elevation, and seed dispersal occurs immediately after that (Viereck and Little 1972; Brayshaw 1978; Binkley 1981; Marchant and Sherlock 1984).

REPRODUCTION

Seed Production and Dispersal: Sitka alder begins to produce seeds at about 6–8 years of age, with optimum production occurring at about age 25. It produces ample seed every year and has bumper crops every 3–5 years. Seed can be dispersed over long distances by wind or water (Fowells (compiler) 1965; USDA 1974; Kenady 1978; Burns (compiler) 1983).

Seed Viability and Germination: Zasada *et al.* (1983) found 40% viable seed in a sample of green alder seed from Alaska. There is no information on the viability of Sitka alder seed after storage. A lengthy period of chilling is recommended for best germination (Marchant and Sherlock 1984). The seed does not tolerate drying out (Zasada *et al.* 1983), and Sitka alder requires a moist mineral soil seedbed for germination (Viereck and Little 1972). Green alder germination begins early in the spring following dispersal and the majority of germination is complete by the end of June (Zasada *et al.* 1983). Germination of green alder seeds has been found to be greatest on sites that have been heavily burned (Zasada *et al.* 1983). Germination from seed on disturbed habitats is the primary form of reproduction of both green and Sitka alder.

Vegetative Reproduction: Both green and Sitka alder sprout from the stump if damaged or cut. Sprouting from exposed roots in streams has also been noted in Sitka alder (Furlow 1979). Vegetative reproduction can be important for the persistence and expansion of established colonies but is generally insignificant as a means of reproduction of new plants and invasion of new areas.

PESTS

Gerber *et al.* (1980) report that the alder flea beetle (*Altica ambiens*), the western tent caterpillar (*Malacosoma californicum*), and the poplar-and-willow borer (*Chrytorhynchus lapathi*) are common insect pests affecting Sitka and green alder in British Columbia.

EFFECTS ON CROP TREES

Competition: The low, bushy form and slow growth rate of Sitka alder make it a less serious brush problem than red alder (Binkley 1981, 1982a; Harrington and Deal 1982). In coastal British Columbia, it has minimal importance as a competitor compared with other vegetation complexes. However, in moist Interior areas, Sitka or green alder are often well established in the understory prior to harvest and can be a major competitor following harvesting (M. Tanner, pers. comm., Jan. 1985). They can form an extensive canopy which may shade out conifer seedlings such as Douglas-fir (Harrington and Deal 1982). Scattered alder plants are not a major obstacle to plantation establishment on cutblocks (C. DeLong, pers. comm., Nov. 1984), but they can form dense thickets. In areas with moderate to high snowfall, Sitka alder may physically damage overtopped conifers as a result of snowpress.

Beneficial Effects: The major beneficial effect of these alders for crop trees relates to their ability to increase the nitrogen content of forest soils. Viereck and Little (1972) indicate that alder acts as a nurse tree to Sitka spruce on sterile sites, improving soil conditions and adding organic matter and nitrogen (Crocker and Major 1955). The growth characteristics of Sitka alder make it a more desirable species for interplanting with conifers than red alder (Binkley 1981, 1982b; Harrington and Deal 1982). Sitka alder appears to benefit Douglas-fir growth only on very nitrogen-deficient sites; Douglas-fir did not react positively to Sitka alder on fertile sites (Binkley 1982a). Heilman (1983) reported an increase in the first 5 years of Douglas-fir seedling growth on coal mine spoils planted with Sitka alder. Seedling growth differences between the control and alder sites were not evident after more than 5 years. Harrington and Deal (1982) suggest that Douglas-fir should be established prior to interplanting with alder to ensure that the conifer is not suppressed. The benefit of increased nitrogen availability may be outweighed by the negative effects of light competition, particularly for shade intolerant conifers such as Douglas-fir.

Sitka alder is also a valuable species for slope stabilization and erosion control on steep slopes (Marchant and Sherlock 1984).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Increases in Sitka alder after clearcutting have also been observed in the SBS zone near Vanderhoof and Fort St. James (J. Pojar, pers. comm., March 1985) and in the wetter ICH subzones near Salmon Arm (J. Wright, pers. comm., July 1989). In north central British Columbia, invasion of Sitka alder after clearcutting can be slow. Eis (1981) reported that alder cover increased slightly over the first 6 years after logging with the greatest cover levels (10%) occurring on alluvial sites. In mature lodgepole pine forests of central Alberta, green alder had significantly lower cover 6–12 years following logging than under the mature canopy (Corns and LaRoi 1976). This may be due in part to the increase in competition from herbaceous plants after logging.

Fire: Sitka alder is often favoured by burning. Following a wildfire in northern Idaho, Sitka alder increased in density by seeding-in and sprouting from surviving root crowns after initial seral vegetation had already established (Stickney 1986). Mueggler (1965) found that broadcast burning in the cedar – hemlock zone of northern Idaho favoured Sitka alder establishment, especially on sites that had been repeatedly burned over a 30-year period. In the SBS zone of the Prince Rupert Forest Region, Sitka alder is also abundant in areas with a history of frequent fires (Pojar *et al.* 1984). These authors suggest that Sitka alder's ability to fix nitrogen makes it a favourable pioneer species on sites that have had much of the organic matter removed as a result of severe fires.

Regeneration of green alder following a broadcast burn of black spruce in Interior Alaska was moderately vigorous. Six years after burning, alders originating from seed were 152 cm tall, and those originating from sprouts were 195 cm tall (Zasada *et al.* 1987).

On some sites, established plants are relatively slow to recover from burning. For example, in cool, wet subzones of the Kamloops Forest Region, Sitka alder can take 5–7 years to recover from moderate to severe broadcast burns (M. Tanner, pers. comm., Jan. 1985).

Cutting: Nearly 100% of cut Sitka alder stems sprout after cutting (Marchant and Sherlock 1984). Sprout growth is usually moderate. First-year sprouts averaged 45–65 cm after cutting in various seasons at four locations in the southern half of the province (Simard 1989; D. Barron, pers. comm., May 1989; J. Wright, pers. comm., July 1989).[71] In the wetter ICH subzones near Salmon Arm, Sitka alder sprout growth is not affected by season of cutting (J. Wright, pers. comm., July 1989). Second-year sprout height averaged 125 cm after cutting in late July in the MSxk subzone (Simard 1989). Observations near Penticton, B.C., indicate that sprout growth on poor sites can be substantially lower than on medium sites.[72]

One year after cutting near Grand Forks, Sitka alder produced 3–20 sprouts per plant. The growth and number of Sitka alder sprouts has been found to be similar on clean-cut and shattered stumps (D. Barron, pers. comm., May 1989).

Herbicides: Broadcast applications of glyphosate at 1.26 to 2.14 kg a.i./ha have effectively controlled Sitka alder (B. Raymor and J. Wright, pers. comm., June 1989).[73,74] September broadcast applications of 2–6 L ha of glyphosate in the ESSFwc2 variant near Blue River did not control Sitka alder.[75] Poor success was attributed to the late application date. Drought stress can also cause poor control of the species (B. Raymer, pers. comm., June 1989; J. Wright, pers. comm., July 1989).

Application of 2,4-D amine to freshly cut Sitka alder stumps resulted in good control of sprouting the following year. Most treated stumps were killed; those that were not killed sprouted with reduced vigour compared with untreated stumps (S. Simard, pers. comm., 1990).

Soil Disturbance: Both Sitka and green alder are adapted to seed-in to areas of exposed mineral soil. These alders often colonize sterile, recently disturbed soil such as avalanches, recently exposed glacial deposits, and skid trails on logged sites (Johnson 1968; Viereck and Little 1972; G. Lloyd, pers. comm.,

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[71] Noble-Hearle 1989.
[72] Ibid.
[73] Ladd 1989.
[74] Noble-Hearle 1989.
[75] Simard 1988.

Jan. 1985). Sitka alder does not seed-in aggressively after mechanical site preparation on wetter ICH subzones near Salmon Arm (J. Wright, pers. comm., July 1989). Sprouting can be expected from root crowns and stem bases of alders damaged during mechanical site preparation. In the Cariboo Forest Region, trials using V-plows or straight blades to rip apart large clumps of alder have apparently been successful in setting back the alder sufficiently to establish a crop of conifers.[76]

Fertilization: Fertilization of green alder with nitrogen and phosphorus resulted in increased growth and increased tannin, nitrogen, and phosphorus concentrations in twigs (Bryant *et al.* 1987).

WILDLIFE

Food: Sitka and green alder have relatively low browse value for ungulates (Marchant and Sherlock 1984). White-tailed deer feed on the leaves and twigs of Sitka alder, and mule deer have been reported to consume small quantities of Sitka alder in the summer near Kamloops, B.C. (Willms *et al.* 1980). The tender young shoots are browsed by elk in British Columbia (Devereux 1988). Although Sitka alder is considered high-quality moose browse (Peterson 1978), it is rarely used in the province. Sitka alder is a major food for snowshoe hares (Hansen and Flinders 1969). Squirrels readily consume catkins (Harestad 1983) and birds eat cones, buds, and seeds (Healy and Gill 1974).

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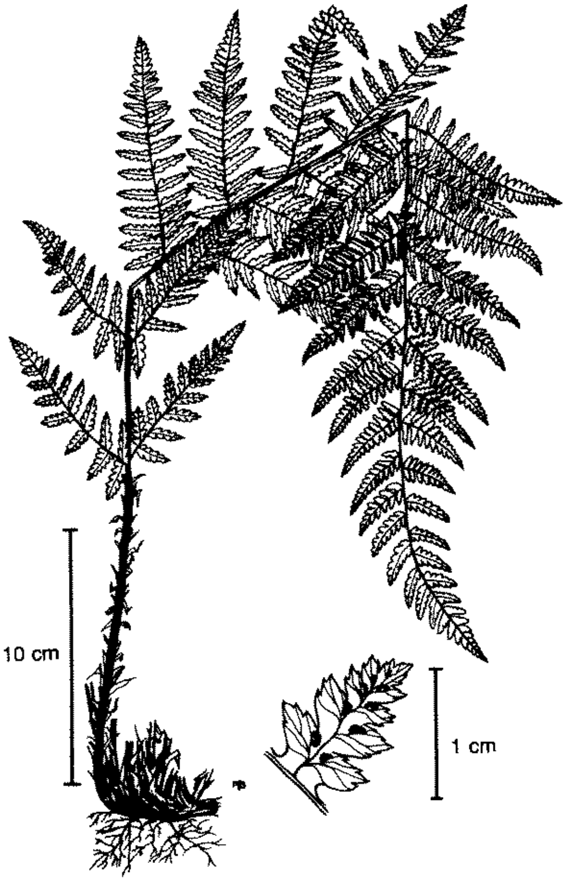
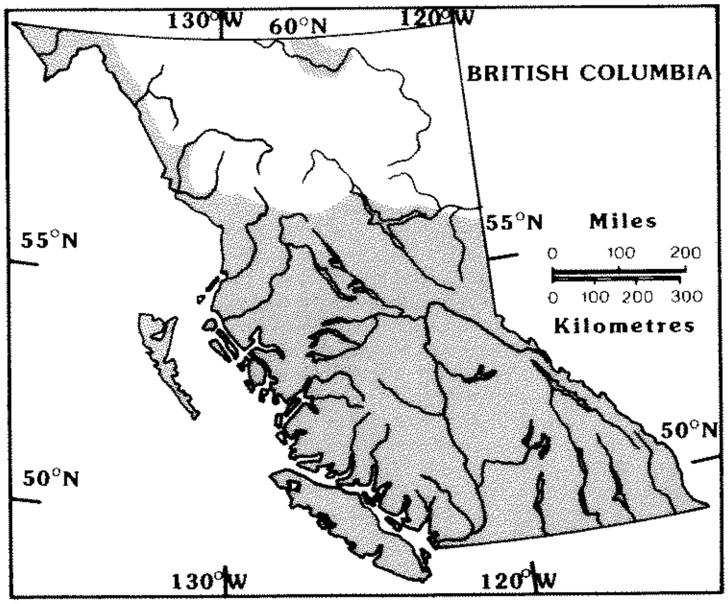
[76] Perry 1983.

Athyrium filix-femina
(lady fern)





Distribution of *A. filix-femina* in British Columbia.

Athyrium filix-femina (L.) Roth — Lady fern

DESCRIPTION

Lady fern has erect to spreading deciduous fronds up to 2 m tall arising from a stout, erect, or ascending rhizome clothed in brown scales. The frond has a succulent bipinnate blade that tapers at both ends, and a short, scaly stem that is prone to breaking or bending (Taylor 1973a).

Variation: Lady fern is a variable species of near world-wide distribution (Taylor 1973a). There are many geographical varieties of the species: the British Columbia version of this fern is described as ssp. *cyclosorum* (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Lady fern can be found throughout most of British Columbia and is one of the most common ferns in the province (Taylor 1973a). It has not been collected from northeastern British Columbia except for a location on the Liard River (A. Ceska, pers. comm., Nov. 1984). It occurs in all of the biogeoclimatic zones but is most abundant in the wet CWH and ICH zones and the SBSvk subzone. It is rare in dry areas of the southern and central Interior, including the PP and BG zones and the driest subzones of the IDF and SBS (Angove and Bancroft 1983).

Altitudinal Range: Lady fern occurs from sea level to subalpine and lower alpine elevations, to approximately 1200 m (Lyons 1952).

HABITAT

Climatic Relations: The distribution of lady fern in the province and elsewhere indicates that it can tolerate a broad range of temperatures, although it is uncommon in the extremely cold boreal zone. Its absence from the driest interior areas of the province suggests that it requires humid conditions during the growing season.

Site and Soil Conditions: Lady fern is found on a variety of moist to wet soils in forest and meadows, in riparian and floodplain habitats, and in rock crevices. It is also able to colonize a wide range of open semi-natural sites. Soils are often Gleysols or gleyed subgroups of other soils (Campbell and Franklin 1982; Comeau *et al.* 1982; Coupé *et al.* (compilers) 1982; Page 1982).

Nutrient Relations: In British Columbia, lady fern will grow on a wide range of nutrient regimes, but is most common on medium to very rich sites. (see, e.g., Klinka 1977b; Pojar *et al.* 1982).[77] Wali (1969) found that in the SBS zone near Prince George, lady fern occurred on sites with slightly higher than average levels of available nitrogen and a wide range of available calcium. According to Page (1982), lady fern avoids base-rich soils, except where these are overlain by acidic surface horizons.

Water Relations: Lady fern grows on moist to wet sites and is usually found on soils that have good drainage but permanent moisture (Page 1982). In climatically dry areas, it is restricted to hygric sites and floodplains, but in climatically wet areas it occupies a broader range of moisture regimes. In very wet subzones of the Interior Wet Belt (e.g., ICHvk, ICHhwk, SBSvk, ESSFvc, and ESSFwk) it occurs on submesic to hydric sites (Comeau *et al.* 1982).[78]

Light Relations: Lady fern has the ability to tolerate deep shade, but its best growth occurs in open woods or meadows where abundant sunlight and adequate moisture are available simultaneously. In shaded conditions, the lady fern blade is fairly flat, but with increasing light the pinnae (leaflets) become angled downwards (Page 1982). This appears to be an adaptation enabling the plant to optimize light interception in low light, and reduce evapotranspirative losses in full sunlight. In a laboratory experiment (Zimmer 1976), lady fern grew continuously and showed no apparent difference in growth rate under a wide variety of photoperiods. Warm white light from fluorescent tubes produced better growth than narrower spectrum light from mercury tubes.

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[77] Utzig *et al.* 1983.
[78] DeLong *et al.* 1984.

Temperature Relations: The dormant buds require at least 30 days of chilling between November and February for bud break to occur the following spring (Hill 1976). The minimum temperature for vegetative growth is near 5°C. Between 10 and 20°C, temperature does not significantly affect the rate of growth (Zimmer 1976). Lady fern fronds appear to be very sensitive to frost.

GROWTH AND DEVELOPMENT

Ferns have a well-developed vascular system with true roots, stems, and leaves; however, ferns have no flowers, and their life cycle differs significantly from that of flowering plants (Keeton 1972). The germinating spore develops into a tiny cluster of undifferentiated cells known as a prothallus that bears male and/or female reproductive organs. The prothallus depends on an adequate supply of moisture for growth because it has no vascular system. Free water is also essential during this stage of the fern's life cycle to ensure fertilization of the eggs by free-swimming sperm. The fertilized egg develops into the large, leafy spore-bearing plant (sporophyte). The lady fern sporophyte is a perennial plant in which most or all of the fronds die back each fall and persistence is by means of a fleshy underground rhizome. Most moderate-sized fern sporophytes take from 1 to 5 years to reach maturity and produce spores (Page 1979). At maturity, the lady fern frond averages between 30 and 150 cm in length and 10 and 30 cm in width, but can reach a height of 2 m.

Lady fern often exists in the forest understory as small individual plants; however, when it is large and vigorous it is most often found in nearly pure stands with minor herbaceous and shrub associates (Campbell and Franklin 1979; Page 1979). Schneller (1979) indicates that individual lady fern prothalli usually germinate together in densely packed colonies. Young prothalli may considerably influence the germination of spores and the development of other prothalli in their vicinity through the secretion of hormonal substances.

Phenology: Page (1982) notes that most lady fern fronds emerge in a single spring flush, but Schneller (1979) observes that the sporophyte continues to develop new leaves throughout the growing season. In Great Britain, lady fern fronds reach maturity by about late July (Page 1982). Although, spores generally become mature towards the end of the growing season, variation in development of individual fronds ensures that spore dispersal is spread over a lengthy period. In Scotland, spore production of most species begins in June and carries on until late September (Page 1979). The onset of fall senescence of lady fern fronds appears to be closely tied to the date of the first frost (Page 1982). In the western Oregon Cascades, this occurred in early October, and senescence proceeded at a fairly steady rate with only 25% of the fronds remaining by early November (Campbell and Franklin 1979).

REPRODUCTION

Spore Production and Dispersal: Most medium-sized forest ferns begin to produce spores at between 1 and 5 years of age, and production takes place regularly from year to year with little weather-induced fluctuation. Habitat, through its influence on plant vigour, is probably the major controlling factor of spore production (Page 1979). Lady fern reproduces more copiously than most other ferns (Frye 1934). Its spores are dispersed by gravity, wind, water, or animals. Fern spores are capable of travelling great distances, but dispersal of spores is often limited by the absence of air currents in undisturbed forest habitats. Airborne spores are often brought to earth during rainstorms (Page 1979).

Spore Viability and Germination: Fern spores in a dry, resting state are resistant to physical extremes. They can withstand intense radiation and very low temperatures but are reportedly very sensitive to temperatures above 55°C (Kato 1963; Miller 1968). Lady fern spores remain viable for about 3 years in storage. Spores that overwinter on the dead frond are often still viable in spring, and spores in soil remain viable for at least 1 year (Schneller 1979). However, their viability and speed of germination deteriorate with age (Page 1979). Spore germination rates ranged from 50 to 95% under experimental conditions (Schneller 1979).

Spores will generally not germinate until after a period of water imbibition (Page 1979). Lady fern spores most often germinate in unexposed places on bare soil or occasionally on decaying wood (Schneller 1979). They normally require light for germination (Weinberg and Voeller 1969), but hormones secreted by nearby prothalli can stimulate germination in the dark (Schneller 1979). The great majority of spores that land on the forest floor do not germinate.

Vegetative Reproduction: Vegetative reproduction in lady fern is achieved through division of the rhizome. The rhizome occasionally branches and in old plants may develop into large clumps with numerous closely packed crowns (Page 1982). However, unlike the bracken fern, lady fern does not form an extensive, laterally spreading rhizome. Although the species often forms large, uniform stands, these are populations of individual sporophytes rather than clonal colonies.

PESTS

Ferns are extraordinarily free of the damaging effects of insects and microbial pathogens (Page 1979). The annual shedding of fronds may serve as a protective mechanism against disease and insect infestations.

EFFECTS ON CROP TREES

Competition: Throughout most of its range, lady fern is not considered to be a major threat to the establishment of coniferous tree seedlings. However, because it is one of the largest herbaceous plants in British Columbia and because it often occurs in dense, pure stands, it can be a serious local competitor wherever it is abundant and vigorous. It is extremely abundant and a serious silvicultural problem in the SBSvk subzone east of Prince George (C. DeLong, pers. comm., Nov. 1984) and on hygric and wetter ecosystem associations in heavy snowfall areas of the ICH and ESSF in southeastern British Columbia (D. Lloyd, pers. comm., Nov. 1984).

In the CWH zone, lady fern is a dominant herbaceous plant on floodplain sites and skunk cabbage swamps, and it can be an important secondary competitor following logging. However, Brand did not consider it to be a significant competitor on 5 productive clearcut sites he studied in the CWH near Vancouver.[79] Vigorous growth of lady fern can shade out and crowd out young seedlings. Shading by lady fern dominated vegetation reduced spruce seedling growth in the SBS zone.[80] Smothering and mechanical damage caused by the shedding of fronds is considered to be of equal, if not greater, importance than competition for light and space (D. Lloyd, pers. comm., Nov. 1984).

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Lady fern does not usually appear to increase significantly following logging; it should probably be considered a serious potential competitor only if it is well established on a site prior to canopy removal. In the ICHwk and ICHvk subzones, lady fern has frequently been observed to increase in density and vigour 2–3 years after logging (J. Wright, pers. comm., July 1989). Lady fern can be expected to diminish in cover on those moist sites which are prone to drying out following logging. Eis (1981) did not report any increase in lady fern cover on 4 different site types 6 years following logging in the SBS zone north of Prince George. Brand noted that on recent clearcuts in the CWH zone near Vancouver, lady fern was initially found only on undisturbed patches, but it reappeared 3–4 years after logging, once other vegetation was well established.[81]

Fire: Light to moderate burns often increase lady fern cover. Severe burns are usually not achieved on lady fern sites. Lady fern exceeded its pre-burn cover within 4 years of burning a devil's club site in the SBSvk subzone (E. Hamilton, pers. comm., July 1989). C. DeLong (pers. comm., June 1989) also found that lady fern appeared to be stimulated by light burning on subhygric sites in the SBSvk subzone. In the ICHwk and ICHvk subzones, burns tend to control lady fern for 2–3 years, after which it recovers (J. Wright, pers. comm., July 1989).

Lady fern showed a slight decrease in cover following logging and prescribed burning in successional studies in Washington and northern Idaho (Mueggler 1965; Dyrness 1973).

Cutting: No information.

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[79] Brand 1984.

[80] Hamilton 1988.

[81] Brand 1984.

Herbicides: Broadcast applications of about 2.1 kg a.i./ha glyphosate between late July and early September have generally provided a high degree of top-kill in lady fern.[82,83,84] Complete recovery of the plant often occurs within two to three seasons of herbicide application (J. Wright, pers. comm., July 1989).[85]

Soil Disturbance: Mechanical site preparation has resulted in very successful control of lady fern for at least 4 years after treatment (J. Wright, pers. comm., July 1989).

WILDLIFE

Food: Lady fern is moderately important winter food for deer, elk, moose, and caribou.[86] Fiddleheads and mature fronds are readily eaten by black bear, grizzly bear, and deer during spring and summer (T. Hamilton, pers. comm., Jan. 1985).[87] Lloyd (1979) found that lady fern made up 8% of the spring and early summer diet of black bear and grizzly bear near Knight Inlet, B.C. The plant is also sometimes used by blue grouse (Zwickel and Bendell 1972).

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[82] Herring and Fahlman 1984.

[83] Pollack and LePage 1986b.

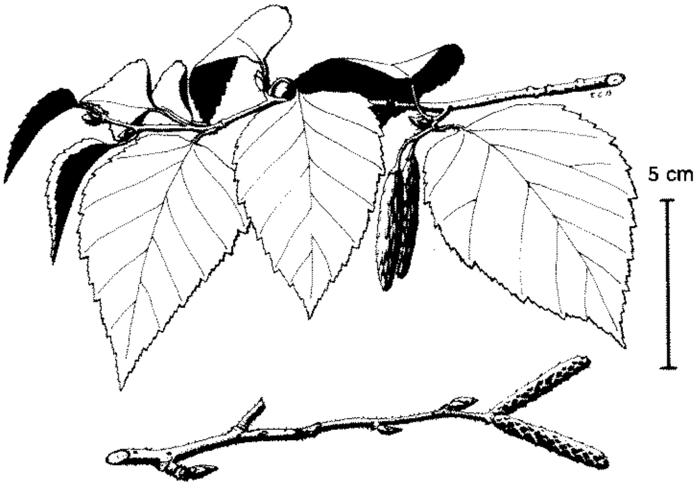
[84] Pollack and LePage 1988.

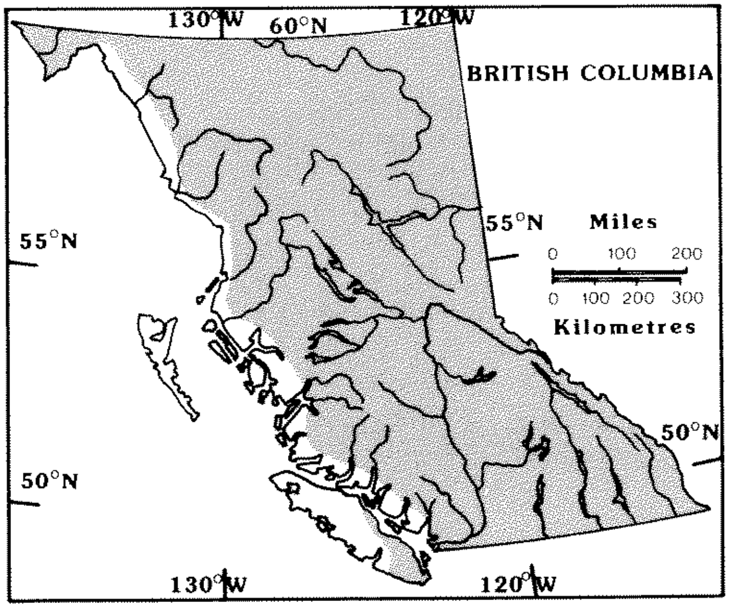
[85] Reynolds *et al.* 1988.

[86] Blower 1982.

[87] Pojar and Banner 1984.

Betula papyrifera
(paper birch)





Distribution of *B. papyrifera* in British Columbia.

Betula papyrifera Marsh.

Paper birch
(white birch, canoe birch)

DESCRIPTION

Paper birch is a deciduous tree to 30 m tall, often multi-stemmed. Bark colour varies but is characteristically white or cream, with conspicuous dark, horizontally elongated lenticels. It readily peels in sheets. Twigs are slender and pubescent or glandular, with fine, pointed buds. Leaves are variable in shape but generally ovate with single or double serrations. Separate male and female catkins are pendulous when mature. Female catkins release large quantities of small, wide-winged fruit (Hosie 1973; Brayshaw 1978).

Variation: Paper birch is probably the most variable tree species in Canada. Many geographic varieties have been described, some of which are difficult to recognize. It also hybridizes extensively with other birch species. Recognized varieties in British Columbia include: the common var. *papyrifera*, which occurs across Canada and is found in the Interior of B.C.; var. *commutata*, the coastal form found in the Fraser Valley, on southern Vancouver Island, and scattered along the coast; and var. *subcordata*, which results from the crossing of paper birch and water birch (*B. occidentalis*) (Dugle 1966; Taylor and MacBryde 1977; Brayshaw 1978). This discussion deals primarily with var. *papyrifera*.

DISTRIBUTION AND ABUNDANCE

Paper birch is one of the most widespread tree species in northern North America. It is found throughout British Columbia but is sporadic on the outer coast, absent in the Queen Charlotte Islands, and only found on the southeastern portion of Vancouver Island (Calder and Taylor 1968; Brayshaw 1978). Paper birch is common in most low- to medium-elevation biogeoclimatic zones in the Interior. It is common in the BWBS, SBS, IDF, and ICH zones, less common in the CWH, CDF, PP, and BG zones, and absent from the ESSF, MH, and AT zones. It is most abundant in warm, moist Interior valleys.

Altitudinal Range: Paper birch is found over a wide range of elevations but primarily occurs at low to moderate elevations. It does not occur in subalpine forests.

HABITAT

Climatic Range: Paper birch is adapted to a wide range of climates from humid to boreal and can tolerate wide variations in the patterns and amount of precipitation. It is tolerant of cold climates and grows to the northern limit of tree growth (Fowells (compiler) 1965). Across its entire range, the climate is generally characterized by short, cool summers and long, cold winters with long periods of snow (Fowells (compiler) 1965). In British Columbia, paper birch is especially abundant in areas of transitional climate, lying in the Coast/Interior ecotone or between the dry and wet belts of the Interior. It apparently cannot compete well in the perhumid climate of the outer British Columbia coast and is absent from most areas receiving extremely heavy snowloads.

Site and Soil Conditions: Paper birch is found on a wide variety of parent materials and on soil textures ranging from gravelly sands to loams and organic soils. It is most abundant on rolling upland terrain or on alluvial sites but is also found on open slopes, rock slides, bogs, and swamp margins. Best growth occurs on well-drained sandy or silty soils; or on soils derived from limestone (Fowells (compiler) 1965; Hosie 1973; Brayshaw 1978; Krajina *et al.* 1982; Marchant and Sherlock 1984).

Nutrient Relations: Paper birch is adapted to a wide range of nutritional conditions (Post *et al.* 1969). It prefers medium to rich sites but also occurs on sites that are nutrient poor or very rich (Klinka and Scagel 1984). Krajina *et al.* (1982) describe the nutritional requirements of birch as moderate to fairly high, especially for calcium and magnesium, although other sources report low requirements for calcium and phosphorus and moderate requirements for sulphur and nitrogen (Watson *et al.* 1980). Birch appears to prefer nitrates to ammonium as a nitrogen source since it grows much better where nitrates are readily available (Krajina *et al.* 1982). Paper birch grows on soils ranging from acidic to highly calcareous (Fowells (compiler) 1965). It has been observed growing on soils with a pH of 3.2–4.4 (Watson *et al.* 1980; Balsillie *et al.* 1978, cited by Marchant and Sherlock 1984).

Water Relations: Paper birch is described by some as having a high tolerance to flooding and poorly drained soils (Krajina *et al.* 1982; Marchant and Sherlock 1984). However, it has been found that flooding can severely affect birch seedling growth and physiology, indicating that it may be intolerant of flooding, at least in some situations (Tang and Kozlowski 1982; Norby and Kozlowski 1983). Birch seldom occurs on very wet sites (Fowells (compiler) 1965). In British Columbia it is most often found on sites ranging from subxeric or submesic to subhygric (Angove and Bancroft 1983; R. Coupé, pers. comm., Nov. 1985). Growth is best where the soil is moist but well drained.

Light Relations: The shade tolerance of paper birch is low (Fowells (compiler) 1965; Hosie 1973; Krajina *et al.* 1982). Paper birch is most abundant as an overstory tree in seral forests and only survives one generation because of its shade intolerance. It does not occur as an understory species and becomes restricted to openings as the forest matures (Hosie 1973). Although germination is best in the shade, subsequent seedling growth is favoured by full sunlight. Paper birch seedlings grown in full sunlight had larger roots and a higher root:shoot ratio than seedlings grown in partial shade (Marquis 1966).

Temperature Relations: Paper birch is very frost resistant and can easily tolerate frozen ground (Krajina *et al.* 1982). Seasonal growth often begins while minimum temperatures are below freezing (Fowells (compiler) 1965). In Alaska it grows in soils where the frost layer remains in the rooting zone throughout much of the growing season (Foote 1983). Paper birch often colonizes spoil piles which are subject to high temperatures (Watson *et al.* 1980), and in British Columbia it seems to be able to tolerate very high summer temperatures as long as sufficient moisture is available. Heninger and White (1974) found that paper birch seedlings grew well over a wide range of soil temperatures but that total seedling biomass was highest when seedlings were grown between 19° and 30°C.

GROWTH AND DEVELOPMENT

Paper birch does not exhibit the rapid early growth that characterizes other hardwood species such as black cottonwood and red alder. Paper birch seedlings average 10 cm in height after the first growing season (Fowells (compiler) 1965) and can reach a maximum of 40 cm on favourable sites in full sunlight (Marquis 1966). Grant and Thompson (1975) report that 3-year-old birch in British Columbia average 32 cm in height; in Alaska, a maximum height of 25 cm in 3 years was reported (Zasada *et al.* 1983). Fowells (compiler, 1965) reports that 4-year-old birch average 1 m in height. Growth of sprouts is considerably more rapid than that of seedlings. Sprouts can grow up to 60 cm in the first year and are twice as tall as seedlings after 4 years.

Birch reaches a maximum height of 30–40 m and a diameter of 50–100 cm at the base. The tree has a narrow, oval crown when it grows in the forest, but in openings the crown spreads out from near the base. Many trees develop a broad, multi-stemmed crown, particularly following disturbance. Paper birch is considered a short-lived species. Trees mature and cease height growth at 60–70 years and few live longer than 140 years. The tree has a deep, penetrating root system (Fowells (compiler) 1965; Hosie 1973; Ohmann *et al.* 1978; Marchant and Sherlock 1984).

Paper birch stands are characterized by a lack of birch in the smaller age classes (Foster 1984). Dense stands are found in nature, but little ingress of birch occurs once the stands are established (Foster and King 1986). Paper birch does not reproduce well in established forests and therefore only penetrates later stages of forest succession where gaps are created in the canopy following a disturbance such as blowdown (Hibbs 1982; Tang and Kozlowski 1982).

Solomon and Leak (1969) have provided site index curves for New Hampshire paper birch stands.

Phenology: Paper birch begins flowering in mid-April in southern areas and flowers during May and June in Alaska. Flowering takes place before the leaves expand. Height growth begins early in the growing season while temperatures are still quite cool. Diameter growth starts after maximum temperatures reach 21°C. The seed normally ripens during August and September, with dispersal beginning immediately after ripening and continuing through to the following January. However, seed dispersal as early as July 4 has been reported in Alaska. Opening of the mature female catkins is stimulated by low humidity and frost (Fowells (compiler) 1965; Zasada 1971; Viereck and Little 1972; Marchant and Sherlock 1984).

REPRODUCTION

Seed Production and Dispersal: Paper birch trees begin bearing seed at about 15 years of age, with the optimum seed-bearing age being 40 to 70 years. Paper birch trees produce good seed crops every 2–4 years. Seeds are winged nutlets that are dispersed by wind and water; they are often blown for long distances on crusted snow. Although the seed is light and travels easily, the majority of the seed falls within 100 m of the parent tree (Bjorkbom *et al.* 1965; Fowells (compiler) 1965; Zasada 1971; USDA 1974; Archibold 1980).

Seed Viability and Germination: The quality of paper birch seed is highly variable. In heavy seed years a high percentage of the seed is good (USDA 1974). Seed viability averaged 17% (range 1–42%) in 4 undisturbed Alaska stands. An estimated 200–400 paper birch seeds were required to produce a single 1-year-old seedling (Zasada 1971). Seed remains viable for up to 2 years but only if the moisture content is low. Seeds rapidly degenerate in moist conditions (USDA 1974). Exposure to a period of low temperatures significantly improves germination percentages (Nichols 1934). Germination normally takes place the spring following seed dispersal. Seeds tend to germinate as soon as temperatures exceed a threshold value following snowmelt, which allows them to take advantage of moisture from snowmelt as well as from spring and early summer rains (Zasada *et al.* 1983). Germination is best in the shade, on areas where the mineral soil and organic layers are mixed, where ample moisture is available, and where surface temperatures are moderate (Marquis 1966). Humus is satisfactory for germination but not as favourable as mineral soil or mixed soil and organic layers. Leaf litter is a poor medium for germination because germinants die of desiccation if their roots do not reach mineral soil (Tang and Kozlowski 1982). Best initial growth was observed on organic seedbeds (Marquis *et al.* 1964).

Vegetative Reproduction: Paper birch will sprout from the root collar and stump following cutting or fire (Fowells (compiler)1965; Hyvarinen 1968; Klinka and Scagel 1984). Prolific sprouting will occur when trees are young, but sprouting vigour decreases with age. Sprouting may occur at the base of standing live trees that have been subjected to increased exposure by disturbance (Fowells (compiler) 1965). Johansson (1985a) found that stumps cut in May–June sprouted less vigorously than those cut in other seasons. His findings generally agree with earlier results (Bjorkbom *et al.* 1965; Nordfors 1923, cited by Johanssen 1985a). No relationship has been found between stump height and number of shoots per stump. Paper birch can be propagated by cuttings treated with a growth-promoting substance (Fowells (compiler) 1965; Watson *et al.* 1980). Fragments are unlikely to root in nature. While vegetative reproduction is important for the persistence of individual trees following disturbance, regeneration from seed is the most important means of reproduction of the species (Lutz 1955).

PESTS

A large number of insect species attack paper birch at all stages of growth and over all parts of the tree (Conklin 1969). Insect damage to paper birch is described in detail by Fowells (compiler) 1965 and Conklin (1969).

The most important diseases affecting paper birch are usually associated with mechanically caused wounds on low-vigour trees and result in discoloration and decay of the wood (Shigo 1969). A disease termed "birch dieback" has been the subject of several studies in eastern North America. Trees die progressively from the top downward, resulting in lowered vigour, reduced growth, and dieback of twigs and branches which may ultimately lead to the death of the tree (Fowells (compiler) 1965; Hyvarinen 1968). A single factor causing birch dieback has not been determined, but trees growing on thin soils with shallow rooting are most likely to develop this disease, inferring a possible climatic influence (Pomerleau and Lortie 1962).

EFFECTS ON CROP TREES

Competition: Paper birch is sometimes considered to be an aggressive pioneer species (Watson *et al.* 1980), but it is not as serious a competitor as aspen in the Interior[88] and is too scattered on the coast to be a significant competitor. However, it can be a serious local competitor where there are concentrations of mature birch and where harvesting and silvicultural practices favour seeding-in. Crushing and smothering

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[88] Revel 1983.

beneath birch litter can significantly decrease growth and cause a high rate of mortality among spruce germinants. Gregory (1966) found that only an occasional white spruce can become naturally established beneath birch stands in Alaska. Vigorous growth and abundance of birch can cause localized threats to the survival and development of spruce seedlings in the Interior of British Columbia (Arlidge 1967). In the wetter ICH subzones of the Kamloops Forest Region, birch usually does not pose problems for regeneration establishment but may affect growth and survival several years after conifers are established (Mather 1988).

Beneficial Effects: Birch has potential as a crop tree, but no beneficial effects of paper birch on conifer growth are described in the literature. The deep rooting habit of the species, its relatively high demand for soil nutrients, and the rapid turnover of deciduous foliage suggest that soil organic matter content and associated levels of nutrients may be higher under birch than under a purely coniferous stand.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Following logging or disturbance, abundant seeding-in of paper birch will normally occur where seed trees are left standing and a suitable seed bed has been created. However, most seed is confined to within 100 m of standing trees (Archibold 1980), and felling birch seed trees would greatly reduce the number of paper birch seedlings (Arlidge 1967).

The sprouting vigour of mature trees cut during logging is variable and may depend to some extent on site conditions. Following canopy removal in the IDFmw and ICHmw subzones near Salmon Arm, height growth of birch is initially slow (30 cm/yr), but after 2 years the growth rate rapidly increases (J. Wright, pers. comm., July 1989). In Newfoundland, paper birch height exceeded the height of natural balsam fir by 73% on sites disturbed less than 10 years previously, but 20 years after disturbance paper birch was only 23% taller than balsam fir (Richardson 1979). Mortality of sprouts is usually high (Fowells (compiler) 1965).

Fire: Paper birch bark is thin and highly flammable, making this tree highly susceptible to fires of even moderate intensity (Lutz 1955; Fowells (compiler) 1965). Sprouting is common on trees damaged or killed by fire (Hosie 1973), but sprouts are less frequent on middle-aged and old trees than in young stands (Lutz 1955). Burning causes top-kill of coppices and saplings, but rapid regrowth from basal sprouts occurs following burning. Paper birch thrives in an environment with a regular fire history, and regeneration is frequently more common on burned areas than on unburned areas (Behrend and Patrick 1969). In the Kamloops Forest Region, broadcast burned sites have significantly less birch stems than mechanically site-prepared areas.[89] Birch mainly establishes on exposed mineral soil on burned sites and generally does not seed-in on burned LFH layers.

Cutting: Prolific sprouting from either the root collar or the stump usually occurs when young, vigorous trees are cut in the spring to stump heights of 15–30 cm (Fowells (compiler) 1965). Birch coppices grow at 1.5–2.5 m/yr following cutting in the ICHmw and IDFmw subzones near Salmon Arm. Coppicing occurs at all ages (J. Wright, pers. comm., June 1989).

Notch girdling or double-frill girdling of birch trees resulted in mortality or serious damage to 97% of trees 4 years after treatment (Crombie 1965); 21% of the stems sprouted following treatment. Single-frill girdling was ineffective, and addition of 2,4,5-T to the girdled area reduced suckering but was not considered necessary. P. Wadey (pers. comm., June 1989) found girdling to provide acceptable control when applied in any season in the Fort St. John District in British Columbia.

Herbicides: Glyphosate has effectively controlled paper birch in British Columbia when applied as a foliar spray, by hack-and-squirt or hypohatchet, and as a cut surface treatment. Information is unavailable on the effect of application rate and season in controlling paper birch. Although birch is highly susceptible to foliar applications of glyphosate, birch coppices have been observed to be more resistant to glyphosate than aspen or cottonwood. Birch of all ages is highly susceptible to cut surface treatments. For example, hack-and-squirt with 50 and 100% concentrations of 3.5 kg a.i./ha glyphosate in late October in the

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[89] Mather 1988.

Invermere Forest District resulted in 100% kill of birch. Mortality from hack-and-squirt occurs within 1 year of treatment (D. Mullet and J. Wright, pers. comm., July 1989).[90] Glyphosate applied by hypohatchet at a 20% solution and 2 mL per 7.5 cm dbh killed or seriously injured all paper birch trees in a New Brunswick study (Wile 1981).

Broadcast applications of hexazinone at 2.2–4.3 kg a.i./ha in May often provide good to excellent control of birch. Birch injury after 2 years is often about 50% at the lower application rate and 75–100% at the higher rates. A thick organic layer impairs hexazinone effectiveness, and variations in organic matter thickness over a site can lead to apparent inconsistencies in results, such as better control at lower herbicide rates than at higher rates.

Spot applications of hexazinone in May or June have effectively controlled birch. Higher application rates tend to be more effective than lower rates, but variations in organic matter thickness can offset this trend. Mid-June spot applications of 4 and 8 mL hexazinone per spot and six spots per tree to 40-year-old birch near Fernie resulted in 39% defoliation at the higher rate after one season. This is typical of the degree of control obtained on areas with thick organic layers.[91,92,93,94,95]

Pure hexazinone or pure triclopyr applied by hypohatchet at 2 mL per 7.5 cm dbh seriously injured all paper birch trees in a New Brunswick study (Wile 1981). In Maine, triclopyr (full or half strength) was effective in controlling paper birch using hack-and-squirt (Filauro 1982), and 2,4-D amine has caused moderate to severe injury to paper birch in British Columbia (Boateng and Herring 1990). Good control of paper birch was achieved with a foliar spray of 2,4-D ester at 3 kg a.i./ha in the Vancouver Forest Region (M. Scott, pers. comm, Nov. 1984).

Soil Disturbance: Paper birch readily seeds-in to areas of mineral soil exposed during logging or mechanical site preparation.[96] Soil disturbance that exposes mineral soil or mixes mineral and organic soil layers provides the best seedbed for germination of paper birch (Marquis *et al.* 1964; Marquis 1966; Horsley and Abbott 1970). Seedling growth also appears to be best where mineral soil is exposed (Bjorkbom 1972). In Maine, stocking was 2 to 3 times greater on mechanically site-prepared areas than on winter- or summer-logged areas that received no site preparation (Bjorkbom 1967). In the wetter ICH subzones of the Kamloops Forest Region, birch, as well as cottonwood and willow, rapidly increases in cover on exposed mineral soil created by mechanical site preparation. Up to 10 000 birch stems per hectare can establish on lower elevation sites (J. Wright, pers. comm., July 1989). On these sites, birch stocking is higher after mechanical site preparation than after burning or logging with no site preparation. Birch can attain 50–100% cover 5–10 years after disturbance.[97] In the SBS subzone near McGregor, exposed mineral soil resulting from scarification was rapidly covered with birch (and willow) which overtopped planted spruce trees after 13 years (MacKinnon and McMinn 1988).

Fertilization: Paper birch responds very favourably to fertilization treatments. Seedling response has been favourable under both field and laboratory conditions (Safford 1982). Seedling height and biomass have been significantly increased with the addition of an NPK fertilizer (Bjorkbom 1973a, 1973b; Safford 1982; Bryant *et al.* 1987). Bjorkbom (1973a) reported a 19-fold increase in seedling height after NPK fertilization. Seedlings appear to be more responsive to applications of nitrogen than phosphorus or potassium; application of phosphorus and potassium without nitrogen did not significantly increase growth. Bjorkbom (1973b) found that additions of potassium increased the potassium content of foliage but did not cause any significant growth response. Schmitt *et al.* (1981) found that direct applications of nitrogen and phosphorus dramatically increased the uptake of these elements by paper birch and resulted in higher

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[90] Ladd 1989.
[91] Teskey and Masterson 1985c.
[92] Teskey and Masterson 1986a.
[93] Teskey and Masterson 1986d.
[94] Teskey and Masterson 1986c.
[95] Newhouse 1988a.
[96] Perry 1983.
[97] Mather 1988.

concentrations of elements in live branches of fertilized trees compared with unfertilized trees (Schmitt *et al.* 1981). Fertilization of paper birch stands following thinning increased the diameter growth of remaining trees for a 10-year period (Safford and Czapowskyj 1986).

WILDLIFE

Food: Paper birch is highly palatable (Peterson 1978) and is important food for wildlife in British Columbia. It has medium importance to moose in all seasons (Singleton 1976) and is a moderately important winter browse for mule deer, Rocky Mountain elk, caribou, and mountain goat.[98]

Paper birch is a favourite food of snowshoe hares (Banfield 1974), which eat bark, twigs, and leaves in season (Wolff 1978). Buds, catkins, and new leaves are preferred foods of porcupines (Chapman and Feldhamer (editors) 1983). Squirrels feed on flowers and leaf buds in the spring. Paper birch is also an important food for beaver.

Paper birch sprouts vigorously following browsing (T. Lea, pers. comm., Feb. 1989). Repeated browsing by moose retarded the height growth of paper birch but increased the density of stems and amount of biomass in the 0–3 m height class (Risenhoover and Maass 1987). Miquelle (1983) investigated moose feeding and foliage regrowth in the boreal forest. Leaf regeneration was most prolific on plants defoliated in June and early July; less leaf regeneration occurred on plants defoliated after August 1. Regrowth leaves of paper birch were significantly smaller than primary leaves.

Other Resources: Many birds nest in paper birch in British Columbia, including woodpeckers, owls, hawks, sapsuckers, flycatchers, and vireos (Cannings *et al.* 1987).[99]

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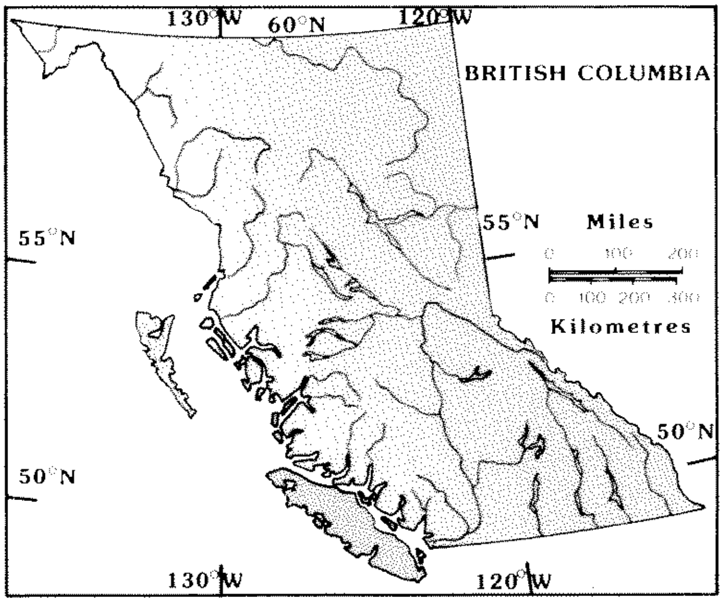
[98] Blower 1982.

[99] Korol and Wallis 1983.

Calamagrostis canadensis
(bluejoint)



Distribution of *C. canadensis* in British Columbia.

Calamagrostis canadensis (Michx.) Beauv.

Bluejoint
(marsh reed grass)

DESCRIPTION

Bluejoint is a perennial, tussock-forming grass with stems 60–120 cm tall and creeping rhizomes. The leaf blades are elongate, slightly drooping, and flat, 10–30 cm long and 4–8 mm wide. The inflorescence, or seedhead, is a drooping panicle that varies from narrow and rather dense to loose and open and often has a purplish tinge (Hubbard 1969; Hitchcock and Cronquist 1973).

Variation: Bluejoint is a widely distributed and exceedingly variable species (Hitchcock 1971) with various subspecies and varieties recognized by different authors. Taylor and MacBryde (1977) have broken out a separate species, *C. scribneri* (Scribner's reed grass), to describe varieties found in the central and northern Interior of British Columbia that have traditionally been considered part of *C. canadensis*. *C. scribneri* is included as part of *C. canadensis* in this discussion, and the name "bluejoint" is used to refer to the entire complex.

DISTRIBUTION AND ABUNDANCE

Bluejoint is found throughout British Columbia in every biogeoclimatic zone. It is more abundant and occurs over a wider range of sites in the Interior than on the coast. It is most common in the northern half of the province and at higher elevations in the south (Hubbard 1969; McLean 1979).

Altitudinal Range: Bluejoint is found from sea level to the alpine tundra zone.

HABITAT

Climatic Relations: Bluejoint is able to tolerate a very wide range of climates, as shown by its extremely broad geographic distribution within western North America. It seems to be particularly well adapted to a harsh northern climate since it reaches its greatest abundance and best development in Alaska and northern Canada (Mitchell 1974; Watson *et al.* 1980). It can tolerate very exposed conditions (Mitchell 1978) and is extremely winter hardy (Alaska Rural Development Council 1977)

Site and Soil Conditions: Throughout much of southern British Columbia, bluejoint is primarily a wetland species, occurring in swamps, marshes, wet meadows, and floodplains. In the SBS and particularly in the BWBS zone, it is common on both wetland and upland sites (Hubbard 1969; McLean 1979; Pojar *et al.* 1982). Bluejoint is found on both mineral and organic soils. In southeastern British Columbia, it occurs mainly on gleyed or organic soils (Comeau *et al.* 1982); in northern British Columbia and Alberta, it is found in openings on moist forest sites and along streambanks, and it commonly invades clearcuts and a wide variety of disturbed soils (Blackmore and Corns 1979; Watson *et al.* 1980; Eis 1981).

Nutrient Relations: Bluejoint is thought to have moderate nutritional requirements (Alaska Rural Development Council 1977). Comeau *et al.* (1982) report that in British Columbia it is found on sites ranging from very poor to very rich in nutrients. In Alaska, it grows in moderately to strongly acidic soils ranging from pH 5.5 to 3.5 (Mitchell 1974).

Water Relations: Bluejoint is characteristically a species of wet to moist sites, but it can survive a wide range of moisture regimes (Watson *et al.* 1980). Mueller-Dombois and Sims (1966) grew bluejoint under a range of moisture conditions in the laboratory and concluded that its dominance on wet to moist sites in Manitoba is attributable to its tolerance of, rather than preference for, such localities. It is very tolerant of flooding and saturated soil conditions (Alaska Rural Development Council 1977). Bluejoint seedlings had the lowest drought tolerance of the three grass species tested by Mueller-Dombois and Sims (1966), but once the root system is established drought tolerance is apparently good.

Light Relations: Bluejoint is most abundant and reaches its best development on open sites, but it will also tolerate partial shade (Watson *et al.* 1980). It appears to be adapted to grow very rapidly during the long daylight regime of early to midsummer in northern latitudes (Mitchell 1974).

Temperature Relations: The root system of bluejoint tolerates low soil temperatures (Younkin 1974, cited by Watson *et al.* 1980).

GROWTH AND DEVELOPMENT

Watson *et al.* (1980) reported that bluejoint establishes slowly, but in growth experiments by Sims and Mueller-Dombois (1968) it produced a continuous, dense sod of roots after just 1 year. The sod was 1–2 cm thick on a poor sandy soil and 4–8 cm thick on a loamy sand. The fine roots were intermingled with numerous rhizomes (Mueller-Dombois and Sims 1966). On logged sites, bluejoint can form continuous sods within only 3 or 4 years (Frisque *et al.* 1978, cited by Eis 1981). Once established, bluejoint can grow quickly. Mitchell (1974) reports that luxuriant stands in south central Alaska can grow to heights of over 150 cm in 6 weeks. In trials in the northern boreal forest reported in Watson *et al.* (1980), biomass and cover of bluejoint equalled or exceeded those of commercial grass species by the end of the first growing season. During the growing season, dead leaves make up approximately 50% of the total above-ground biomass in a stand of bluejoint (Sylvester and Wein 1981). The above-ground parts of bluejoint die back at the end of each growing season, producing a thick organic mulch.

Phenology: In south central Alaska, bluejoint completes its height growth by mid-July (Mitchell 1974) and is fully headed by mid-August (Mitchell and Evans 1966).

REPRODUCTION

Seed Production and Dispersal: Like other grasses, bluejoint is adapted for wind pollination and seed dispersal (Hitchcock 1971). The drooping panicle moves readily in the wind, and seeds are easily windborne. Bluejoint rapidly seeds-in to disturbed sites (Watson *et al.* 1980; Rowe 1983). Seed is produced annually, provided that environmental conditions are favourable, but seed yields are reportedly low (Younkin 1974, cited by Watson *et al.* 1980).

Seed Viability and Germination: Younkin (1974, cited by Watson *et al.* 1980) reported a germination rate of 90% in seed from Inuvik, N.W.T. Germination occurred without cold stratification. Mueller-Dombois and Sims (1966) also observed very high rates of germination after 3 days on both sandy and loamy sand soils when the soils were wetted to field capacity. Germination apparently will not occur under droughty conditions (Wein and MacLean 1973).

Vegetative Reproduction: Bluejoint is a rhizomatous grass species (McLean 1979), and once it has seeded-in to an area, further spread is primarily by rhizomes (Wein and Bliss 1973; Watson *et al.* 1980).

PESTS

No references to insect or microbial pests were found in the literature.

EFFECTS ON CROP TREES

Competition: Bluejoint is a significant competitor with crop trees in the BWBS, SBS, and ESSF biogeoclimatic zones and provides relatively minor localized competition on wet sites in other zones. It is a particularly important competitor in the boreal forest of the Prince George Forest Region where it is extremely abundant in clearcut areas. Root competition with young seedlings is considered to be the dominant mode of competition. Bluejoint roots in the same zone as young tree seedlings and produces a very dense, continuous sod (Sims and Muller-Dombois 1968). These authors showed that bluejoint reduced tree growth the most on moist, loamy soils where the grass was most vigorous. On the driest sites, root competition was minimized because young seedlings were able to get their roots below the shallow, poorly developed grass sod. Bluejoint can also shade out young seedlings, and the heavy litter causes snowpress and smothering (Arlidge 1967; Blackmore and Corns 1979; Eis 1981). Eis (1981) also noted that thick sods of grass prevent natural regeneration by conifers. Conifer seeds falling into the grass are suspended above the soil and the germinants desiccate as the grass dries out in spring. Bluejoint may reduce seedling growth in northern latitudes by preventing soils from warming up during the growing season. Mitchell (1974) notes that the thick layer of litter and mulch that develops under a bluejoint cover has a significant insulating effect on the soil.

Beneficial Effects: The high percentage of ground cover and dense root sod of bluejoint provides good control against surface soil erosion (Watson *et al.* 1980). Blackmore and Corns (1979) speculate that a light growth of bluejoint on a scalped area of soil may be beneficial in reducing frost-heaving of seedling conifers. No other beneficial effects of the species on tree growth are documented in the literature, but it undoubtedly increases soil organic matter content, particularly on heavily disturbed sites. A cover of bluejoint can also limit invasion of larger brush species that may have a longer-lasting and more serious impact on crop tree growth.

RESPONSE TO DISTURBANCE AND MANAGEMENT

Forest Canopy Removal: Bluejoint is favoured by forest canopy removal. Bluejoint increased significantly on three moist site types north of Prince George following clearcut logging (Eis 1981). On the alluvium site type it invaded all areas not covered by shrubs, and thick continuous sods had formed by the third or fourth year following logging. In the BWBSmw subzone near Fort St. John, bluejoint increased from 20% cover and 40 cm maximum height before logging to 70–90% cover and 130 cm maximum height within 3 years of clearcutting (P. Wadey, pers. comm., June 1989). Bluejoint invaded after a 65-year-old lodgepole pine stand was thinned in central Colorado (Crouch 1986).

Fire: Results from British Columbia, Alberta, Idaho, and Minnesota indicate that bluejoint increases following burning. In the SBS zone in central British Columbia, E. Hamilton (pers. comm., July 1989) found that increases were greatest on wet sites. In central Idaho, bluejoint increased after fires on wet to moist sites. Reproduction was both by wind-disseminated seed and sprouting from rhizomes (Crane and Fischer 1986). Rhizomes survived a fire and cover increased by 400% 12 years after burning in the arctic tundra (Wein and Bliss 1973). In northern Minnesota (Ahlgren 1960), bluejoint occurred widely the first year after burning and did not appear to be affected by fire severity. Reproduction was primarily by rhizomes, but some seedlings were established by windborne seed. Sylvester and Wein (1981) point out that fire spreads rapidly through stands of bluejoint because of the large volumes of fine, dry litter present. Live plant material is very resistant to burning but does not slow down the rate of fire spread.

Cutting and Grazing: Bluejoint is intolerant of heavy cutting (Mitchell and Evans 1966). Yields decreased by up to 20% when the grass was cut two to four times during the growing season and by 70% when cut seven times (Corns and Schraa 1962).

Herbicides: Glyphosate has controlled bluejoint in British Columbia. An early August application of 1.5 kg a.i./ha glyphosate near Fort St. John resulted in 98% kill of the species after one growing season, but the grass reinvaded the following year (P. Wadey, pers. comm., June 1989). Glyphosate applied in June, July, or August as a foliar spray at 2.2 – 4.5 kg a.i./ha has provided good to excellent control of bluejoint (Blackmore and Corns 1979).[100] Blackmore and Corns (1979) found that glyphosate applied in August at 2.2 kg a.i./ha gave better control than the same rate applied in June.

Broadcast applications of 1.1–6.5 kg a.i./ha liquid hexazinone have provided moderate to excellent control of bluejoint in British Columbia (Boateng and Herring 1990).[101] For example, 2 years after May applications of 1.1–2.2 kg a.i./ha liquid hexazinone near Dawson Creek, bluejoint cover had decreased from about 65 to 13%, and 2 years after application of 4.3 and 6.5 kg a.i./ha bluejoint cover had decreased from about 65 to 3% cover.[102] Hexazinone gridballs applied aerially at 4 kg a.i./ha in late May to a mesic BWBSmw site near Dawson Creek resulted in excellent control of bluejoint 5 years after treatment.[103] With increasing organic matter depths, control of bluejoint becomes less successful.[104,105]

Soil Disturbance: Bluejoint aggressively invades disturbed sites. Invasion is by seed or through rhizomes from adjacent areas (Watson *et al.* 1980). North of Prince George, bluejoint invaded most heavily on moist to wet compacted soils on roads, landings, and skid trails on the alluvium site type (Eis 1981). Arlidge (1967)

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[100] Expert Committee on Weeds 1984.

[101] Expert Committee on Weeds 1984-1988.

[102] Teskey and Masterson 1986b.

[103] Herring 1988a.

[104] Fahlman and Herring 1984.

[105] Teskey and Masterson 1986b.

found that within 2–3 years following scarification, bluejoint was a serious competitor on mounded microsites within wet depressional areas. In the Peace region of British Columbia, L. Herring (pers. comm., March 1985) has found that bluejoint spreads onto disturbed ground first by rhizome extension, and after that by seed. Heavy cultivation substantially controls established plants, but areas of newly exposed soil are rapidly reinvaded by adjacent, undisturbed plants. Intense 30 cm deep cultivation in the BWBSmw subzone near Fort St. John controlled bluejoint for only one growing season (P. Wadey, pers. comm., June 1989).

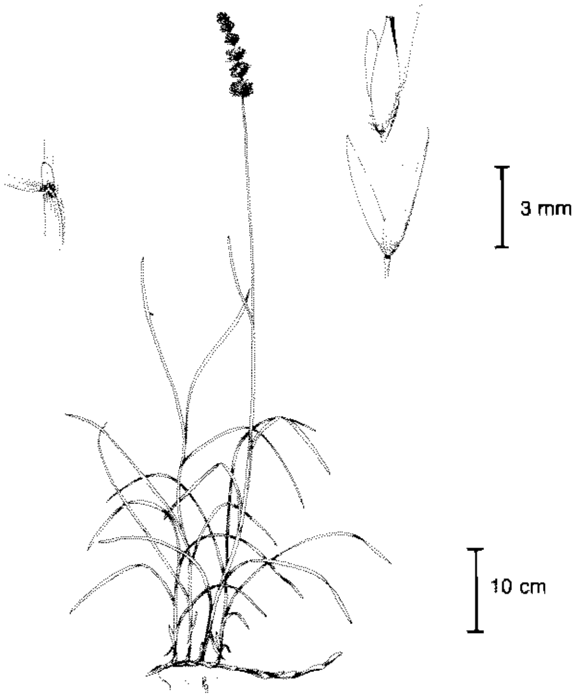
Fertilization: Fertilization with nitrogen, phosphorus, and potassium caused major increases in production of bluejoint in south central Alaska (Mitchell 1974; Laughlin *et al.* 1982). In the Northwest Territories, fertilization markedly stimulated flowering rates and increased vegetative growth (Hutchison and Hellebust 1978).

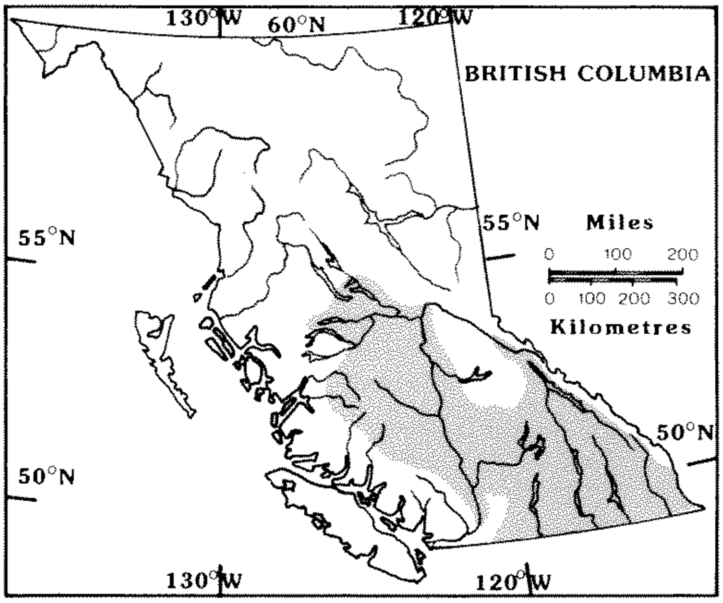
WILDLIFE AND RANGE

Food: Bluejoint generally has low importance to ungulates in British Columbia (T. Lea, pers. comm., Feb. 1989). It also has low to moderate importance as a winter and spring food of Rocky Mountain elk in the province (Singleton 1976), but is commonly used by elk in winter in Colorado (Hobbs *et al.* 1981). Wolff (1978) reports that bluejoint is used by snowshoe hares from October to March in Alaska, but makes up less than 2% of the diet. Bluejoint is moderately palatable but not highly favoured by domestic livestock. It withstands heavy grazing (McLean 1979).

Calamagrostis rubescens

(pinegrass)





Distribution of *C. rubescens* in British Columbia.

Calamagrostis rubescens Buck. **Pinegrass**

DESCRIPTION

Pinegrass is a slender, tufted grass, with creeping rhizomes. It is 60–100 cm tall when flowering but only 30–50 cm in the more common vegetative state. The stems have a reddish tinge at the base and a ring of hairs where the leaf meets the stem. The leaf blades are erect, flat or somewhat rolled, and are rough to touch. The inflorescence (seedhead) is a congested, narrow panicle 7–15 cm long, pale or with a purplish tinge (Hitchcock 1971; McLean 1979; Angove and Bancroft 1983).

Variation: This species is found only in western North America, from southern British Columbia to California. There are no varieties or subspecies described in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Pinegrass is found throughout the central and southern Interior of British Columbia. It is absent from the west side of the Coast Mountains and extends only as far north as Francois Lake and Fort St. James in the Interior. Pinegrass is the most abundant grass in forested areas of the southern Interior. It is most dense and widespread in the IDF biogeoclimatic zone where it dominates the understory. It is common in most SBS and MS subzones and also occurs at lower elevations in drier subzones of the ICH and ESSF zones and in moist areas of the PP zone (McLean 1979; Angove and Bancroft 1983). In the IDF zone, pinegrass often forms nearly pure stands, while in the other zones it tends to grow in mixtures with other plant species.

Altitudinal Range: Pinegrass ranges from the valley bottoms of the Interior to subalpine elevations, but is absent from the lower elevations of the PP zone. It is found between 600 and 1850 m in the Similkameen Valley (McLean 1970), while in the moister climate of northern Idaho it is most abundant in the 850–1000 m elevation band (Mueggler 1965).

HABITAT

Climatic Relations: The geographic distribution of pinegrass in British Columbia suggests that it favours a continental climate with warm, dry summers and can tolerate moderately cold — but not extreme — winter temperatures. It is not present in areas of high precipitation, and it is absent from the hottest, semi-desert areas of the southern Interior. Tiedemann and Klock (1974) observed that it was most abundant on south aspects in Washington, while Mueggler (1965) found no preference for aspect in northern Idaho.

Site and Soil Conditions: Pinegrass is found on a wide variety of well-drained sites. Ecosystems in which pinegrass is a characteristic dominant understory species have a wide variety of parent materials, slopes, and soil characteristics, but soils are most often well-drained, loamy to coarse textured Luvisols and Brunisols (see, e.g., Freyman and van Ryswyk 1969; McLean 1970; Mitchell and Green 1981).[106] In the ESSF zone of the Similkameen Valley, pinegrass is virtually absent on shallow rocky soils and is sparse on Podzolic soils (McLean 1970). Mueggler (1965) noted that pinegrass was frequently found on steeply sloping sites in the cedar–hemlock zone of northern Idaho.

Nutrient Relations: In southern British Columbia, as well as in the SBS zone, pinegrass occurs on sites ranging from very poor to moderately rich (Mitchell and Green 1981; Pojar *et al.* 1982).[107] Soils supporting a heavy growth of pinegrass are frequently low in nitrogen, and increasing the levels of nitrogen, nitrogen and sulphur, or phosphorus stimulates growth of pinegrass (Freyman and van Ryswyk 1969).

Water Relations: Throughout British Columbia, pinegrass tends to be associated with soils that experience at least moderate moisture deficits during the growing season. Pinegrass is tolerant of dehydration (Vogel 1985). The ecological moisture regime of sites with abundant pinegrass varies considerably depending on climate. In the IDF zone where it is most abundant, pinegrass occupies a range of moisture conditions from extremely xeric to hygric (Angove and Bancroft 1983). A growth chamber study showed that pinegrass adjusted to increased water stress by partially (but not fully) closing its stomata. The partially closed stomata allowed entry of CO_2, so that when pinegrass was under moisture stress, photosynthesis

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[106] Coupé and Yee (editors) 1982.
[107] Utzig *et al.* 1983.

could continue at a decreased level (Vogel 1985). Nicholson (1989) found that pinegrass played a major role in the water balance of a pinegrass-dominated clearcut in the IDF zone of south central British Columbia. Pinegrass roots extended throughout the soil profile and transpiration removed most of the soil water below 10 cm. Because of its extensive root system, pinegrass was found to be very responsive to changes in weather, such as an increase in available moisture due to rain. The ability of pinegrass to regrow following grazing in mid-summer depends on the availability of water in surface soil horizons (Freyman and van Ryswyk 1969).

Light Relations: Pinegrass is variously described as moderately shade tolerant (Crane *et al.* 1983) to very shade intolerant (B. Mitchell, pers. comm., Nov. 1984). Throughout its range in British Columbia, pinegrass occurs in the understory of fairly open forests of Douglas-fir and ponderosa and lodgepole pine, but under these conditions it rarely flowers. Flowers and seeds are produced in open situations such as burns and clearcut areas (McLean 1979; Crane *et al.* 1983). The shade tolerance of pinegrass appears to vary with elevation and accompanying moisture and temperature conditions. McLean (1970) reports that, between 600 and 900 m in the Similkameen Valley, pinegrass is present under Douglas-fir but declines when stands are opened up. In the ESSF zone between 1350 and 1850 m, pinegrass cover varies greatly with the amount of shade and is most abundant in stand openings on south aspects.

Temperature Relations: Pinegrass is fairly tolerant of frost and high air temperatures. During the growing season on pinegrass-dominated sites in the IDF and MS zones, frosts are common and maximum air temperatures of 33°C are not uncommon (Nicholson 1989; Simard 1989).

GROWTH AND DEVELOPMENT

In the understory of forest stands, pinegrass forms a loose, open turf connected by a system of creeping rootstocks or rhizomes (McLean 1979). Fine fibrous roots are produced at each node of the rhizome (Hitchcock 1971). The rhizome and root system develops into a continuous dense sod, with very dense roots in the top 5 cm of soil but also extensive development throughout the soil profile. It tends to be shallow in depth (occurring in the top 5 cm of soil) and may establish itself more slowly than the root system of a non-rhizomatous grass species such as orchard grass (Clark and McLean 1975). Pinegrass stands remain fairly stable over time if ground and overstory conditions are not changed.

Phenology: McLean and Tisdale (1960) collected flowers of pinegrass on July 16, early seed on August 5, and late seed on September 2 near Kamloops. The growth of pinegrass peaks in late spring (late May or early June) (Nicholson 1989; Stoute and Brooke 1985). The leaves of pinegrass begin to die in July. New tillers are initiated each spring and some new tiller development occurs during fall (Stoute and Brooke, 1985; Svejcar 1986). Vegetative growth of pinegrass is available for grazing in the Kamloops and Cariboo Forest Regions between early May and late October (McLean *et al.* 1971).

REPRODUCTION

Seed Production and Dispersal: Pinegrass seldom produces seed except in openings in forests or on recently burned or logged areas (McLean 1979; Crane *et al.* 1983). Following a wildfire in western Montana, pinegrass bloomed profusely the first post-fire growing season and in the succeeding 3 years (Crane *et al.* 1983). In northern Idaho, pinegrass produced seeds during the first decade following a wildfire (Stickney 1986). Seeds are produced in erect, spike-like panicles, and dispersal is primarily by wind as with other grass species (Hitchcock 1971).

Seed Viability and Germination: In germination studies carried out by McLean (1967), maximum germination of pinegrass was 38%. Neither stratification nor scarification of the seed is necessary to induce germination. The lack of a chilling requirement suggests that pinegrass may germinate whenever an adequate supply of moisture is available, and that fall germination is a possibility (Grime 1979).

Vegetative Reproduction: The primary method by which pinegrass establishes and regenerates is through the lateral extension of creeping rhizomes (McLean 1979; Crane *et al.* 1983).

PESTS

No information.

EFFECTS ON CROP TREES

Competition: The abundance and dominance of pinegrass in the south and central Interior of British Columbia, particularly in the IDF zone, gives it major importance as a competitor with conifer seedlings. Several studies have demonstrated significant increases in seedling growth following pinegrass removal. Three growing seasons after a dual application of 2.5 L/ha of glyphosate in early spring and again in the fall in the ICHdm subzone in the Nelson Forest Region, pinegrass was 70% controlled and there was no regrowth. Lodgepole pine that was planted 2 weeks after the spring herbicide application had 5 times greater volume, 2 times greater diameter, and 20 cm greater height than trees on the untreated control. Pine planted on an area that only received the spring herbicide application (40% control of pinegrass) had 3 times greater volume, nearly 2 times greater diameter, and 20 cm greater height than trees on the control. Although growth differences occurred, survival of planted trees was similar on the control and areas with either 70 or 40% pinegrass control (D. Barron, pers. comm., May 1989).

In first-year pine plantations in southern Oregon, cattle under constant herding removed pinegrass with an acceptable level of conifer damage (8%). Seven years of cattle grazing for one month a year improved tree height by 31% (50%) and improved diameter growth by 35% (Krueger 1983). Seventeen years of grazing for 1 month a year increased tree height by 50% and diameter by 56%.

Pinegrass competition is usually most severe on droughty sites, and root competition for moisture appears to be the dominant mode of competition. Competition for soil nutrients also occurs and the degree of competition between pinegrass and tree seedlings may be influenced by soil fertility (Clark and McLean 1975). Shading and smothering by pinegrass are of relatively minor importance.

Several studies have demonstrated that pinegrass competes with conifer seedlings for moisture. In a field study to determine the impact of vegetation and microclimate on survival and growth of planted Douglas-fir seedlings on a pinegrass-dominated clearcut in the IDF zone of south central British Columbia, Nicholson (1989) found that the risk of seedling death increased and growth was reduced in the presence of pinegrass. Removal of pinegrass and other non-crop vegetation reduced the moisture stress on seedlings and increased soil temperatures early in spring when Douglas-fir root growth occurs. Complete removal of pinegrass benefited seedlings more than partial removal. On a pinegrass-dominated site, Petersen and Maxwell (1987) found that needles of ponderosa pine seedlings were under high water stress when surrounding pinegrass cover was high and low water stress when there was negligible surrounding vegetation. Soil water content decreased in direct proportion to increasing amounts of pinegrass-dominated vegetation. A 4-year study in northwestern Montana by Petersen (1988) showed that ponderosa pine saplings had 4–5 times greater weight of foliage, above-ground wood tissue, and roots when grown in the absence of pinegrass than when grown with pinegrass. Ponderosa pine populations growing with pinegrass had many small individuals and relatively few larger ones, while pine growing at low densities of pinegrass had a less skewed distribution. This suggests that decreasing the density of pinegrass will increase the mean size of young pines.

Tree seedlings that have not yet established a good interlocking root system compete poorly with grass for available moisture.[108] Thus, seedlings that are established prior to grass invasion have a good chance of survival, whereas those established simultaneously with, or later than, the grass will grow poorly. An experiment by Clark and McLean (1975) suggests that pinegrass provides less competition to lodgepole pine than orchard grass (a commonly seeded, non-rhizomatous, forage species) because pinegrass is slower to develop its root system.

Beneficial Effects: There are several possible beneficial effects of pinegrass growing in association with coniferous trees. The rhizomatous growth habit and the dense network of fine roots provide excellent control of surface soil erosion. A cover of grass incorporates valuable, nutrient-rich organic matter into surface soil layers.[109] Pinegrass will take up nutrients that might otherwise be leached to below the seedling rooting zone following fertilization. By returning and recycling added nutrients, pinegrass may have a positive effect on site productivity (T. Whynot, pers. comm., Feb. 1989). Pinegrass can also

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[108] Clark 1975.

[109] Carr (undated).

exclude invasion of more competitive species. Clark suggested that a cover of pinegrass may help to reduce or prevent overstocking of lodgepole pine.[110]

RESPONSE TO DISTURBANCE AND MANAGEMENT

Forest Canopy Removal: Under forest stands, pinegrass occurs as a loose, open turf connected by creeping rhizomes. Increased light conditions (and disturbance) due to canopy removal often causes a dramatic increase in pinegrass and development of a continuous grass sod. Pinegrass cover averaged 45% under forest canopies and 65% on non-site-prepared clearcuts on submesic IDFdk sites in the Kamloops Forest Region.[111] Complete canopy removal in Douglas-fir forests in western Montana improved soil water and light availability and increased photosynthesis of pinegrass. In contrast, thinning Douglas-fir to 4.3 by 4.3 m spacing did not improve light availability or water stress and did not increase the cover of pinegrass. Thinning of dense ponderosa pine produced over a 40% increase in pinegrass cover in eastern Washington where spacings were greater than 5.5 m. No increase occurred after spacing to 4 by 4 m. In the Similkameen Valley, pinegrass decreases in abundance following logging at lower elevations in open Douglas-fir–fescue ecosystems, but it increases in abundance following canopy removal above 1200 m in the Douglas-fir–pinegrass type and in the subalpine fir forest (McLean 1970; McLean *et al.* 1971). This difference in response according to elevation may reflect the relative moisture and temperature stresses that the plant experiences following canopy removal.

Fire: Pinegrass survives fire well and sprouts profusely following this disturbance (Tiedmann and Klock 1976). It is common for pinegrass to produce seed for the initial years following fire. The roots of pinegrass are most dense within the upper 5 cm of soil, thus any fire which penetrates the duff layer can be expected to do extensive damage (McLean 1979). However, severe fires that burn roots and rhizomes still only provide short-term losses to pinegrass.

Light to moderate severity fires create a favourable environment for pinegrass development (Stickney 1986). Such fires provide poor control of pinegrass; cover of the grass rapidly increases after burning. Moderate severity burning under an immature ponderosa pine stand in the IDFxh subzone resulted in significant increase in pinegrass cover and seed production (J. Miles, pers. comm., July 1989). In western Montana, pinegrass increased steadily in abundance for the first 5 years following a fire, then maintained a cover well above preburn levels for at least 10 years (Stickney 1981). In the cedar–hemlock forests of northern Idaho, pinegrass was most abundant on sites that had received repeated burns over a period of 30 years (Mueggler 1965).

Cutting and Grazing: Environmental conditions, especially summer rainfall, affect the response of pinegrass to grazing or clipping, and year to year fluctuations in growth due to environmental availability can exceed effects of grazing (Stout *et al.* 1981). Grazing and clipping will control pinegrass, but the benefits of these treatments to conifer seedlings are probably outweighed by the effort required (R. Tucker, pers. comm., June 1989).

Stout *et al.* (1981) clipped pinegrass throughout the summer at three levels of intensity for 4 consecutive years. Clipping to 15 cm did not significantly affect stand vigour, but the 5-cm and 10-cm clipping treatments produced a steady decline in plant yield. The largest decrease in production occurred after the first year of treatment. After pinegrass growth is complete, herbage removal during July causes the greatest damage to the plant (Stout and Brooke 1985). Freyman and van Ryswyk (1969) found that pinegrass failed to regrow when clipped in mid-July due to depletion of surface water supplies. Research in Montana (Vogel 1985) indicates that pinegrass can withstand more severe clipping or grazing on clearcuts than under thinned or undisturbed forest canopies.

Clipping for several consecutive years tends to cause longer lasting control than a single treatment. Hall *et al.* (1987) predicted that clipping for 4 consecutive years to a stubble height of 5 cm would require a recovery period of 20 years after clipping ceased. Stout and Brooke (1987) compared the effects of clipping versus grazing on pinegrass yield and tiller production. Grazing and clipping were found to have

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[110] Clark 1975.

[111] Mather 1986.

similar effects on pinegrass yield after 1 year. However, grazing involved the removal of plant parts or the pulling-up of entire tillers with roots and tended to stimulate new tiller production whereas clipping did not. Clumps of pinegrass are easily pulled out by heavy grazing, and they are often partially replaced by other plant species (McLean 1979).

Herbicides: Broadcast glyphosate applications in a variety of subzones (e.g., IDFdk, MSxk, ICHdm) have provided good control of pinegrass for 2–3 years (D. Barron, B. Ivanco, R. Gray, S. Simard, and R. Tucker, pers. comm., April 1989). Information on the degree of control after more than three seasons is unavailable. Several trials clearly indicate that glyphosate is effective not only when applied in the active growing season (May and June) but also when applied in August. Summer applications may result in better kill than spring applications as herbicide translocation is slower and root kill is more complete.

Hexazinone successfully controls pinegrass. Hexazinone applied at 2.2 kg/ha provided good to excellent control of pinegrass for two growing seasons (Dimock *et al.* 1983). In the IDFdk subzone near Lillooet, June applications of 5 L/ha hexazinone to dense pinegrass provided 85% control in the first growing season. An application rate of 10 L/ha provided complete control (B. Bancroft, pers. comm., April 1989).

Other chemicals, all unregistered in British Columbia, have been tested for controlling pinegrass with mixed results (see Stewart and Beebe 1974; Dimock *et al.* 1983). Stewart and Beebe (1974) found that the mulch of dead grass present after spraying may have aided survival of planted conifers by conserving soil moisture and reducing high surface soil temperatures.

Soil Disturbance: Light to medium soil disturbance favours pinegrass. Lightly disturbed areas can be completely grown over within one season. Anchor chain drag scarification increase the cover of pinegrass significantly on some British Columbia clearcuts.[112] Patch scarifiers, such as the Leno, provide light to medium disturbance through exposure of mineral soil on patches about 50 x 100 cm in size. Pinegrass cover is reduced for about 2 years on these sites. Patch scarification was less effective than herbicides in controlling competition by pinegrass and seeded grasses in central Washington (Stewart and Beebe 1974).

Severe mechanical disturbance will destroy the roots of pinegrass which occur in the top 5 cm of soil. Pinegrass growth is retarded and the species is often controlled for 3–4 years by severe disturbance. However, even the most severe disturbance such as cutting and removing sods or 100% ripping result in complete reinvasion after 4 or 5 years (B. Ivanco, pers. comm., May 1989). Soil compaction caused by logging machinery can inhibit pinegrass invasion for 10 or more years, but it is also severely detrimental to conifer seedlings.

Fertilization: Freyman and van Ryswyk (1969) tested response of pinegrass to 100–200 kg/ha of ammonium nitrate, phosphorus, potassium, and sulphur. Nitrogen significantly increased growth and yield of pinegrass on all sites. Nitrogen combined with low levels of sulphur produced the greatest vigour, but high rates of sulphur caused some mortality of pinegrass. Phosphorus at 200 kg/ha, in combination with other nutrients, increased yields significantly. Fertilizer response was low when applied in mid-July because soil moisture was not adequate to permit absorption of nitrogen. T. Whynot (pers. comm., Feb. 1989) observed the effects of 50–150 kg/ha nitrogen fertilization 6 years after it was applied to a forest stand in the MS zone in the British Columbia Okanagan. Visual estimates indicated a pronounced increase in pinegrass vigour and abundance under the heavier application rates. Nutrient uptake of grass is favoured at the expense of conifers.[113] Thus, applications of fertilizer may have a detrimental effect on planted conifers because of the increased competition they face from vigorous pinegrass.

WILDLIFE AND RANGE

Food: Pinegrass is highly valuable forage for Rocky Mountain elk in the western United States and Canada from March until August and is valuable forage the rest of the year (Kufeld 1973). Pinegrass is also important early spring forage for mule deer (H. Armleder, pers. comm., 1989) and forage for cattle in the Interior of British Columbia.

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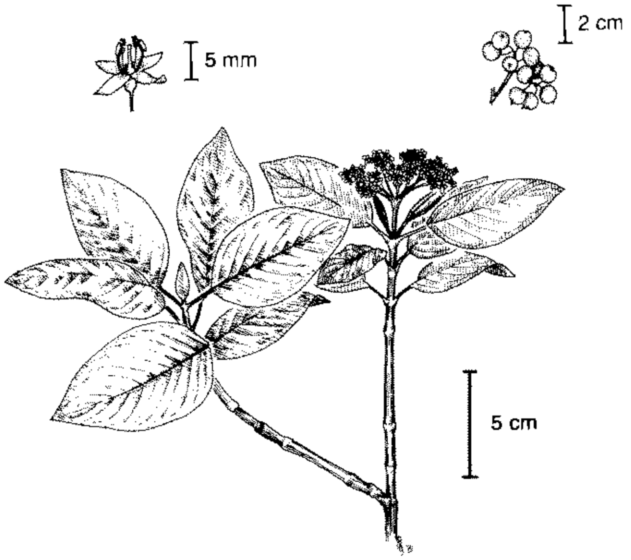
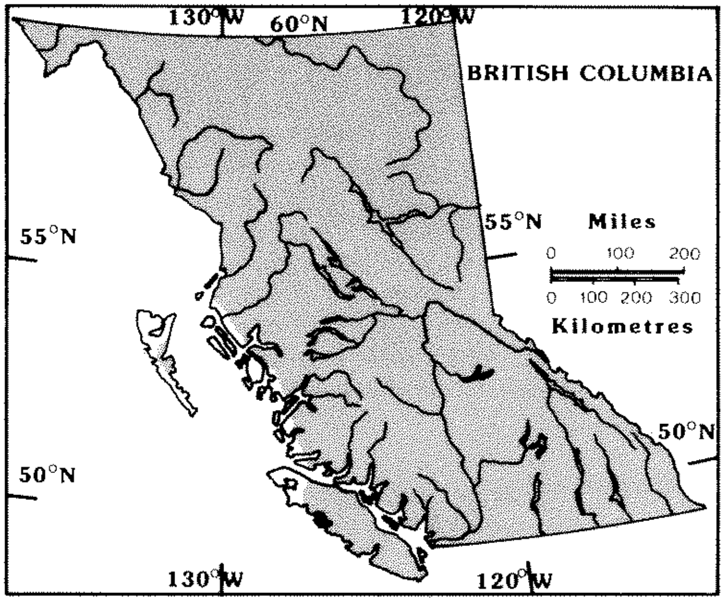
[112] Clark 1975.

[113] Ibid.

Cornus sericea
(red-osier dogwood)





Distribution of *C. sericea* in British Columbia.

***Cornus sericea* L.** **Red-osier dogwood**
(C. stolonifera)

DESCRIPTION

Red-osier dogwood is an erect or spreading deciduous shrub, 2–5 m tall, often bearing prostrate rooting (stoloniferous) branches. The stems are oppositely branched and have smooth bark that turns bright red during the dormant season. Leaves are elliptic to ovate, untoothed with prominent, curving veins. The small white flowers are found in a flat-topped terminal cluster. Fruits are a white to bluish drupe with a single nutlet (Rickett 1944; Viereck and Little 1972; McLean 1979).

Variation: This taxonomically confusing shrub is found across northern North America. It is sometimes treated as a single species with several varieties, and sometimes treated as several distinct species (Fosberg 1942). According to Rickett (1944), the shrub in British Columbia is taxonomically similar to the *C. sericea* or *C. stolonifera* of eastern North America, where most of the literature on this species originates.

DISTRIBUTION AND ABUNDANCE

Red-osier dogwood is found throughout British Columbia, both on the Coast and in the Interior. It occurs in all biogeoclimatic zones except the AT but is rare in the MH zone. It is most abundant in broad river valleys.

Altitudinal Range: Red-osier dogwood is primarily a low-elevation species, although it can occur near timberline (Lyons 1952). In the central Rocky Mountains it extends from 1370 to 3050 m in elevation (Watson *et al.* 1980).

HABITAT

Climatic Relations: The distribution of red-osier dogwood in North America appears to be restricted by high temperatures (Smithberg 1974). In British Columbia, however, local site conditions rather than climatic extremes appear most limiting to distribution. The cool and extremely wet climate of the outer north coast seems to be unfavourable to red-osier dogwood. In addition, although the species is found in northern Canada to the edge of the arctic tundra (Smithberg 1974), it does not appear to fare well in the high mountain climate of British Columbia.

Site and Soil Conditions: Red-osier dogwood is a characteristic species of swamps, low meadows, and riparian habitats; however it is also commonly found in open upland woods and forest margins (Smithberg 1974; Watson *et al.* 1980). In the dry Interior of British Columbia, it is restricted primarily to protected moist sites (McLean 1979). Red-osier dogwood is found on a wide range of soil textures and parent materials (Smithberg 1974; Alaska Rural Development Council 1977), but in British Columbia it is most characteristic of (and produces its best growth on) fluvial ecosystems with gleyed or regosolic soils (see, e.g., Haeussler *et al.* 1984; Pojar *et al.* 1984).[114]

Nutrient Relations: Wilde (1946, cited by Smithberg 1974) described ideal soil fertility conditions for red-osier dogwood as follows: pH 5.0–6.0; base exchange capacity 6.0 ME/100 g; total nitrogen 0.7%; nitrogen 17 kg/ha; phosphorus oxide (P_2O_5) 84 kg/ha; potassium dioxide (K_2O) 168 kg/ha; and replaceable calcium 1350 kg/ha. Red-osier dogwood is tolerant of alkaline soils and is found over a wide range of pH values, but plants on poor soils tend to grow more slowly and produce less fruit (Jewell and Brown 1929, cited by Smithberg 1974). In the SBS zone near Prince George, *C. sericea* has a narrow amplitude with respect to soil nutrient conditions, and it occupies sites with relatively high rates of exchangeable calcium and magnesium (Wali 1969).

Water Relations: Throughout its range, red-osier dogwood is associated with moist to wet soil conditions where it is not subject to significant moisture stress (Viereck and Little 1972; Smithberg 1974; McLean 1979). Conway (1949, cited by Smithberg 1974) states that red-osier dogwood is able to live with its roots immersed in water. Its presence as an understory species on river floodplains and in wetlands throughout much of British Columbia certainly attests to an ability to tolerate flooding.

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[114] Coupé and Yee (editors) 1982.

Light Relations: Rowe (1983) describes red-osier dogwood as semi-shade tolerant to shade tolerant, while Smithberg (1974) states that it is suppressed in shade and thus is never a dominant understory plant. In north central British Columbia, red-osier dogwood is a common understory shrub in relatively open mixed forest and may dominate under aspen or black cottonwood (see, e.g., Haeussler *et al.* 1984; Pojar *et al.* 1984), but it rarely displays the vigour that it has at forest margins and in openings. Sheppard and Pellet (1976) studied the effect of a range of light intensities on the growth of red-osier dogwood. Plants grown in full sun were dense and compact with many lateral branches and a high proportion of leaves, while those grown in 27% of full light were open and sprawling with fewer branches and leaves. Shaded leaves were larger, thinner, had less curl and less purple fall colouration than those grown in full light. Flowering was greatest at the higher light intensities. Above-ground biomass was greatest at 75% light, but the authors speculated that some moisture stress may have occurred in the 100% light treatment, and that similar stresses might not develop in the wet soils where the shrub is found in nature.

Temperature Relations: The temperature relations of red-osier dogwood have been studied in great detail. Soil temperature affects root and top growth, water usage, and nutrient relations (Barr and Pellett 1972). Optimum root growth occurs between 12 and 26°C, while shoot growth peaks at soil temperatures of 22–29°C. Heavy root mortality occurs at 37°C. Soil temperature has a significant impact on the percentage of phosphorus and potassium in above-ground tissues but no effect on percent nitrogen. Water use increases with soil temperature. Cold hardiness of red-osier dogwood is triggered by low temperatures, water stress, and short days (Chen and Li 1978; Bray and Brenner 1980). The degree of cold hardiness increases steadily as winter progresses, and by the beginning of December most provenances can withstand temperatures from -90 to -196°C. The date at which different provenances of dogwood become acclimated is closely related to the minimum winter temperature and length of growing season in their home territory (Smithberg and Weiser 1968). Once plants become fully dormant, temperatures of 5–10°C or lower are needed to maintain hardiness (Kobayashi *et al.* 1981).

GROWTH AND DEVELOPMENT

Under adequate environmental conditions, early growth of red-osier dogwood is rapid. An average plant can be 1 m tall and put on 1125 cm of branches by the end of the first growing season in the northeastern U.S. (Smithberg and Weiser 1968). Because layering and suckering occur readily, the plant is usually shrubby with many stems, but under intense grass competition, layering can be prevented and the species will remain single-stemmed. The form of the plant is also greatly affected by light conditions (see Light Relations). Under shady conditions the plant tends to grow into a tall scraggly shrub (Smithberg 1974). Red-osier dogwood varies considerably in height at maturity. In Alaska and Alberta its height typically ranges from 1 to 3 m (Viereck and Little 1972; Watson *et al.* 1980), while at more southerly latitudes, heights of 3 to 5 m are common (USDA 1974; McLean 1979). Heights of up to 9 m have been observed in British Columbia (B.M. Geisler, pers. comm., Jan. 1985).

Phenology: Red-osier dogwood flowers between May and June in the northeastern U.S. (Smithberg 1974), and in June and July in Alaska (Viereck and Little 1972). Fruits ripen between July and September at both locations. Second flushes of bloom are common in late summer in northeastern U.S. Vegetative phenological events were recorded in the Kimsquit valley on the central British Columbia coast during 1983 and 1984.[115] Flushing occurred during middle to late April and leaves were fully expanded by mid-May. The first leaves began to turn colour in early August and by mid-September most leaves were coloured. Most shrubs retained some leaves until mid-October.

REPRODUCTION

Seed Production and Dispersal: Red-osier dogwood typically bears its first fruit at 3–4 years of age, but yields are light for the first few years (Smithberg 1974). Good seed crops are produced every 1–2 years (Watson *et al.* 1980). The fruit are globular, white drupes with a single two-seeded stone or nutlet. Because the seed is heavy and encased in a fleshy fruit, dispersal is primarily by birds and other animals (Smithberg 1974; USDA 1974), and seeds tend to be located in caches or dropping piles rather than randomly distributed (Rowe 1983).

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[115] Hamilton 1984.

Seed Viability and Germination: The seeds remain viable for 4–6 years in cold dry storage. The seeds have a 60- to 90-day cold temperature requirement to break embryo dormancy and normally germinate the following spring (USDA 1974; Shaw 1984). However, this is a seed-banking species, and seeds can remain dormant for several years until conditions become favourable for germination (Smithberg 1974; Rowe 1983). Germination of the stored seed is favoured by light fires of short duration that partially remove the organic layer (Rowe 1983). Germination appears to be best when seeds are buried slightly beneath the soil surface (Watson *et al.* 1980).

Vegetative Reproduction: Red-osier dogwood develops into dense thickets through vegetative propagation. It is capable of producing stolons or prostrate above-ground stems that root at the nodes and send up new shoots. Smithberg (1974) indicates that this form of reproduction was observed most often on very moist or wet sites. The stolons can extend as far as 3 m from the parent plant (B.M. Geisler, pers. comm., Jan. 1985). Other forms of vegetative reproduction include layering of branches that come into contact with the soil; suckers that develop from dormant buds in the roots; and sprouts from old branches or stem bases. Cuttings of red-osier dogwood root very successfully (Marchant and Sherlock 1984).

PESTS

No information.

EFFECTS ON CROP TREES

Competition: Throughout British Columbia, red-osier dogwood can be a significant competitor with coniferous trees on subhygric to hydric sites that have a well-established, diverse brush community. These sites are often very productive for tree growth. Red-osier dogwood has an advantage of being established prior to harvest and can form a dense thicket. There is no published information about the effect of red-osier dogwood on the growth of crop trees.

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Limited data suggests that red-osier dogwood cover increases or remains the same following logging. Eis' study (1981) shows that 6 years following canopy removal, *C. sericea* was still present but had not become a dominant species on any of four different site types in the SBS zone north of Prince George. Harcombe *et al.* (1983) indicate that removal of the tree canopy will enhance red-osier dogwood, especially near wetter areas. Red-osier dogwood rapidly increased following juvenile spacing in the ICHmw subzone near Salmon Arm (J. Wright, pers. comm., July 1989).

Fire: Red-osier dogwood often occurs on sites that are too wet to burn. Rowe (1983) indicates that light fires stimulate germination of stored seed of red-osier dogwood. The shrub appears to increase in abundance after burning moist SBS sites (Hamilton 1988) or ICH sites.[116]

Cutting: Clipping produced a slight increase in total twig production of red-osier dogwood, but under heavy browsing its growth is retarded (Aldous 1952). Red-osier dogwood sprouted 60 cm in 1 year following manual cutting on a moderately productive site near Penticton.[117]

Herbicides: Red-osier dogwood is tolerant of August and September foliar applications of glyphosate, even when the herbicide is applied at the current maximum legal rate of 2.14 kg a.i./ha (Boateng and Herring 1990).[118,119,120] When plants are partially injured, they can recover in 2–3 years (J. Wright, pers. comm, July 1989). Pollack[121] found that red-osier dogwood increased in cover after late August foliar applications of 1.0, 1.5, and 2.0 kg a.i./ha glyphosate on an alluvial floodplain site in the ICHmc subzone near Hazelton.

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[116] Ketcheson *et al.* 1985.
[117] Noble-Hearle 1989.
[118] Herring 1984c.
[119] Ladd 1989.
[120] Dyke 1987.
[121] Pollack 1988.

Spot or broadcast applications of hexazinone have caused only light injury to red-osier dogwood in British Columbia (Boateng and Herring 1990). Canopy cover and height of red-osier dogwood were equal to or greater than pre-treatment levels 3 years after a mid-April application of 2 and 4 kg a.i./ha hexazinone in the CWH zone near Chilliwack.[122] Red-osier dogwood was unaffected by hexazinone gridballs aerially applied at a rate of 4.0 kg a.i./ha in late May near Dawson Creek.[123] Spraying with 2,4-D or paraquat prior to vegetative maturity caused tip-dieback, damaged foliage, and delayed spring budbreak and growth in Oregon (Crabtree and Fuchigami 1979). The effect of the herbicides was reduced when plants were sprayed following vegetative maturity. The authors recommended that the species be sprayed prior to the onset of vegetative maturity for maximum effectiveness.

Soil Disturbance: Soil disturbance tends to increase the cover of red-osier dogwood. Buried stem fragments of red-osier dogwood root readily without any special treatment in moist or wet soil. Plant parts are especially prone to rooting when they are cut during the dormant season (Smithberg 1974). Plants damaged during mechanical site preparation can be expected to sprout or sucker from roots and stem bases. Exposure of mineral soil may stimulate germination of buried seed.

WILDLIFE

Food: Red-osier dogwood is a very important food for British Columbia wildlife, particularly deer, moose, and birds (McLean 1979). The fruit and new shoots are the most frequently used part of the plant.[124] Red-osier dogwood is important winter browse for moose, Roosevelt elk, and mountain goat and is moderately important for Rocky Mountain elk, caribou, and coastal and Interior deer. Hatter (1948, cited by Peterson 1978) listed red-osier dogwood as one of the most palatable food plants for moose in central British Columbia. Moose browse on the twigs in the winter (Ritcey 1988) and leaves and new shoots in the summer (Harestad 1983).

Red-osier dogwood provides forage for bear, beaver, snowshoe hare, and many other mammals (Smithberg 1974; Harvey 1981).[125] The berries are consumed by black and grizzly bears (Hamilton 1987) and 93 bird species are known to feed on the fruit.

Red-osier dogwood sprouts and increases in density following browsing (T. Lea, pers. comm., Feb. 1989).

Other Resources: Red-osier dogwood provides nesting sites for many species of birds.

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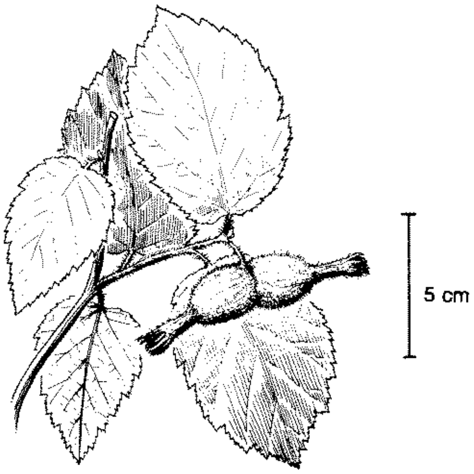
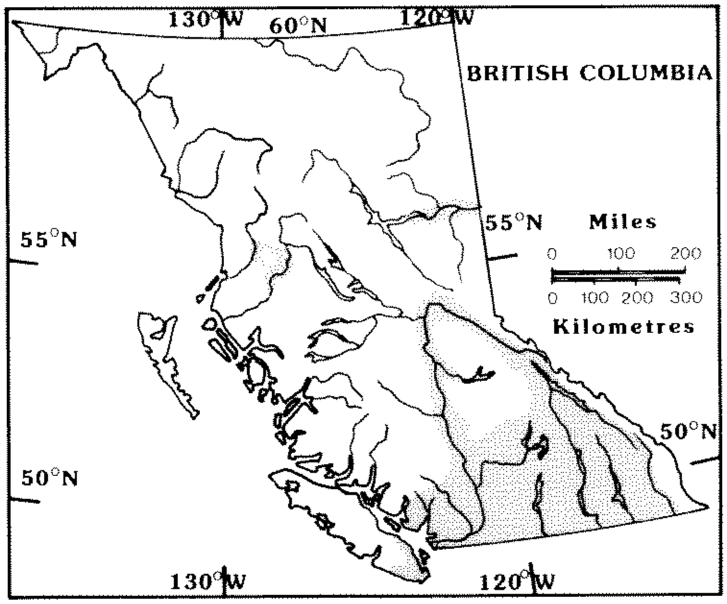
[122] D'Anjou 1988d.
[123] Herring 1988b.
[124] B.C. Min. Environ. (undated).
[125] Blower 1982.

Corylus cornuta
(beaked hazelnut)





Distribution of *C. cornuta* in British Columbia.

Corylus cornuta Marsh. **Beaked hazelnut**

(hazelnut, beaked filbert)

DESCRIPTION

Beaked hazelnut is a deciduous, multi-stemmed shrub up to 4 m tall. The shrub can be densely clumped or widely spreading. Twigs are brown to orange, with hairy buds. Leaves are soft and hairy, nearly round, and have sharply toothed margins. Flowers are inconspicuous with protruding stigmas. The fruit is a round nut enclosed in a hairy husk with a pronounced beak (Tappeiner and John 1973; Brayshaw 1978).

Variation: There are two varieties of *C. cornuta* in British Columbia. *Corylus cornuta* var. *cornuta* only occurs east of the Coast Mountains. It is replaced on the Lower Mainland and Vancouver Island by var. *californica*, a taller, clumped shrub with darker twigs and broader leaves. Introgression between the two varieties occurs in southern British Columbia (Taylor and MacBryde 1977; Brayshaw 1978).

DISTRIBUTION AND ABUNDANCE

Beaked hazelnut is found in major valleys throughout southern British Columbia and on southeastern Vancouver Island. Its distribution extends north to Prince George and McBride following the Fraser River, and there are populations in the Peace River valley and in the Coast/Interior transition in the Skeena and Nass valleys. It is found primarily in the ICH biogeoclimatic zone and drier CWH subzones, but also occurs to some extent in the IDF, southern SBS, and BWBS. Beaked hazelnut has a discontinuous distribution throughout its range in British Columbia and tends to be abundant only in localized areas. It is absent from subalpine areas and from the driest valleys of the southern Interior.

Altitudinal Range: Beaked hazelnut is found primarily at low elevations. It ranges from sea level to 800 m on the south coast, to 1200 m at Revelstoke (Lyons 1952), and to approximately 750 m in the Skeena Valley (Haeussler *et al.* 1985).

HABITAT

Climatic Relations: The range of *C. cornuta* in North America implies that this species is not well adapted to high summer temperatures nor to the extreme northern boreal climate (Stearns 1974). In British Columbia, beaked hazelnut tends to be found in rainshadow areas on the coast, in subcontinental or coast/interior transitional climates, and in moist, but not wet, climatic areas of the southern Interior. This distribution suggests that it is not adapted to a climate characterized by heavy rainfall, heavy snowfall, or drought. The var. *californica* apparently favours a mild, equable climate, while var. *cornuta* is adapted to more continental conditions.

Site and Soil Conditions: Throughout most of North America, beaked hazelnut is found in open woods, thickets, pastures, and clearings. It favours well-aerated, loamy soils over organic or gleysolic soils, and does poorly on heavy clay soils or excessively coarse sandy soils (Stearns 1974). Lyons (1952) states that beaked hazelnut is equally at home on exposed rocky sites and in shady glades. Beaked hazelnut is abundant and vigorous on fluvial parent materials in the Skeena–Nass area (Haeussler *et al.* 1985) and is common on open floodplain sites in Oregon (Hawk and Zobel 1974).

Nutrient Relations: Ecosystem associations in which beaked hazelnut is a dominant understory species tend to be moderately rich to very rich in nutrients (see, e.g., Haeussler *et al.* 1985).[126] Tappeiner and John (1973) estimated the nutrient concentrations and total nutrient content of *C. cornuta* understories in northern Minnesota pine stands. Compared to the overstory, hazelnut appeared to be rich in calcium, phosphorus, and magnesium. It contained from 2 to 22% of the nutrients in above-ground vegetation, even though it was only 5% of the above-ground biomass.

Water Relations: Beaked hazelnut favours well-drained moist sites and it does not grow well on wet, poorly aerated sites (Stearns 1974). Krajina *et al.* (1982) report that the species grows on mesic to hygric sites, and has a high tolerance of flooding.

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[126] Utzig *et al.* 1978.

Light Relations: Stearns (1974) indicates that beaked hazelnut requires 30% or more of full sunlight for best growth and will not germinate or grow well in dense shade. In British Columbia, hazelnut occurs primarily in the understory of open deciduous or mixed stands or in forest openings (Haeussler *et al.* 1985).

Temperature Relations: Krajina *et al.* (1982) indicate that frost resistance of hazelnut is probably high, but that it grows in habitats that afford some protection from frost. The var. *cornuta* undoubtedly has a higher frost resistance than var. *californica.*

GROWTH AND DEVELOPMENT

Hsuing (1951, cited by Stearns 1974) has conducted an in-depth study of the growth of seedlings and clones of *C. cornuta* in Minnesota. Most of the following information was taken from Hsuing's study and it probably applies well to the growth of beaked hazelnut in the Interior of British Columbia. Variety *californica* is known to have a different pattern of growth. It is a taller shrub, reaching 4 m or more at maturity, and does not expand by suckering (Brayshaw 1978; M. Newton, pers. comm., Dec. 1984).

Following germination from seed, hazelnut produces a deeply penetrating taproot. If growing conditions are favourable, a vigorous system of tap and lateral roots will develop. When the seedling is 7 to 12 years old, it starts to develop underground stems. The lateral roots and underground stems occur in the uppermost 20 cm of the soil, often at the boundary between humus and mineral soil. Tappeiner and John (1973) found that hazelnut has a relatively large proportion of its biomass (31–39%) underground.

Young plants grown from seed sprout from dormant buds only after damage to the main stem. Once the plant is well established, the rate of sprouting increases. Vigorous stems can reach heights of 60 cm or greater in 2 years. In Manitoba, untreated hazelnut grew from 1.2 to 1.6 m tall in 6 growing seasons (Waldron 1959). Individual branches can live for more than 18 years and the plant itself survives indefinitely. At 15–20 years the average height is 2.5 m, but as the stem becomes overmature, growth declines. Decadent stems often grow only a few centimetres per year.

The rate of spread of clones is slow but increases with age. A 6-year-old clone had 1–2 shoots and was 2 cm in diameter at the base. By 38 years of age it had 25 shoots and was 250 cm in diameter. Shoots become more vigorous as the clone expands with time.

Phenology: Male and female flowers are formed late in the summer on 1-year-old twigs and emerge before the leaves the following spring. Leaves emerge during March and April in the northeastern U.S. (Stearns 1974). In Oregon, male catkins were fully expanded but unopened by March 17 (Stewart 1974b). Fruits ripen during August and September in British Columbia (Brayshaw 1978). Stewart (1974a, 1974b) reports the following sequence of vegetative development for hazelnut in coastal Oregon: vegetative buds were swelling but closed on March 17; by June 16, three-quarters of the leaves were fully developed, and by August 11 all vegetative growth had ceased.

REPRODUCTION

Seed Production and Dispersal: Male and female flowers are produced on the same plant but are borne separately. Fertilized female flowers develop into round, hard-shelled nuts (USDA 1974). Production of flowers depends on weather, site, and light conditions. Late frosts can kill flowers and dry weather can affect fertilization (Hsuing 1951, cited by Stearns 1974). Production of fruit increases with stem age, peaking at 10–11 years and ceasing when twigs are approximately 18 years old. There can be large fluctuations in fruit production from year to year, and good crops occur approximately once in 5 years. Production rates vary from about 100 to 32 000 nuts per hectare with as many as 6 to 8 nuts per branch in good seed years (Stearns 1974). Dispersal of the heavy seeds is primarily by birds and small mammals such as squirrels and chipmunks.

Seed Viability and Germination: The seeds have poor viability in storage and must remain moist. Two to 6 months of chilling are required before germination can take place (USDA 1974). Germination rates are quite poor, averaging 30–60% in laboratory tests. Best germination occurs when nuts are covered to prevent drying out (Stearns 1974). Hsuing (1951, cited by Stearns 1974) obtained 30% germination in an upland soil, 56% on a black spruce–tamarack site, and 0% in a wet swamp in Minnesota. Survival of seeds is low because many nuts are destroyed by predators (Stearns 1974). Although few nuts actually produce seedlings, in good seed years regeneration by seed is an important method for hazelnut to invade new areas.

Vegetative Reproduction: Vegetative reproduction from underground stems is by far the most important means by which hazelnut colonizes a site (Ahlgren 1960; Buckman 1964). Horizontal stems radiate outward from the parent plant just beneath the litter layer. Rooting occurs along the length of the underground stem, and aerial shoots arise at scattered locations to produce new plants (Tappeiner and John 1973; Brayshaw 1978). In many areas of North America the clones of *C. cornuta* var. *cornuta* become larger and larger until they eventually grow together, forming a continuous shrub layer (Buckman 1964; Tappeiner 1971). *Corylus cornuta* var. *californica* apparently does not produce large clones but tends to remain as a compact shrub or small tree (Brayshaw 1978). Other methods of vegetative reproduction common to both varieties of hazelnut include vigorous resprouting of cut stems, layering of aerial branches buried in soil, and artificial rooting of cuttings (USDA 1974).

PESTS

No information.

EFFECTS ON CROP TREES

Competition: In British Columbia, hazelnut is not considered to be a major brush species because it tends to be abundant in valley bottom areas that are removed from forest production either by land alienation or domination by non-commercial hardwood species (R. Coupé and W.R. Mitchell, pers. comm., Nov. 1984). Many of these valley bottom sites where hazelnut occurs are highly productive and could be considered for conversion to coniferous species.

In other areas of North America, hazelnut is a very aggressive competitor and a major deterrent to successful regeneration of upland conifers. Dense aerial stems of hazelnut inhibit the establishment of natural regeneration of conifers and other shrub species (Tappeiner 1979). The primary impact of hazelnut on conifers is believed to be shading, caused by its aggressive growth and densely layered canopy which allows little light to penetrate (Waldron 1959; Buckman 1964). Available light may only be 2–7% of full sunlight beneath a dense canopy of hazelnut (Stearns 1974). The extensive and shallow root system can also cause severe competition for moisture in upper soil layers (Stearns 1974). Tappeiner and John (1973) also indicate that dense shrub layers of hazelnut tie up a significant component of total site nutrients in their above-ground biomass.

Beneficial Effects: Although hazelnut biomass may tie up a significant quantity of nutrients, these nutrients are recycled through the ecosystem, where they can become available to coniferous trees. Tappeiner and Alm (1972) showed that in jack pine stands with hazelnut present in the understory, total macronutrients present in the litter were nearly double the amount present in pure pine litter.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: The increased light reaching the forest floor after logging of spruce, or after mortality of decadent aspen, results in rapid expansion of established hazelnut colonies (Hsuing 1951, cited by Waldron 1959). Reduction of overhead competition increases stem vigour and stimulates both fruit and vegetative growth (Stearns 1974).

Fire: In most situations, hazelnut responds vigorously to fire. Above-ground parts are immediately killed, even after a light spring fire, but the shrub responds by sprouting prolifically from stem bases and sending up new aerial shoots. The original stand is replaced in stature and number of stems in only a few years (Ahlgren 1960; Buckman 1964; Wright 1972). Destruction of hazelnut from burning of underground stems and roots is unlikely under all but the most extreme conditions of fuel and weather (Johnston and Woodward 1985).

Repeated spring burning, done when the soil is moist, simply increases the number of stems present. The establishment of continuous colonies of hazelnut in some areas of British Columbia is probably the result of recurrent fires over a lengthy period of time. However, a series of mid-summer burns can cause hazelnut to decline in vigour and abundance by consuming the protective layer of humus and exhausting stored food reserves. If a stand of beaked hazelnut is in the early stages of development with scattered clones rather than a continuous canopy, the plant can be controlled with as few as two summer bums (Buckman 1964; Tappeiner 1979).

Cutting and Browsing: Heavy browsing by deer can stimulate hazelnut to produce basal sprouts or suckers (Steams 1974). A clipping experiment by Aldous (1952) produced similar results. Total twig production was increased for 3 years under heavy clipping but thereafter began to decline. Light clipping had little impact on growth. In Quebec, hazelnut stem density increased by 37–56% in an area winter browsed by moose for 5 years but remained constant where there was no browsing. Four years of browsing resulted in 3–4 times more browse than in the undisturbed area (Bedard *et al.* 1978).

Herbicides: Conard and Emmingham (1984a, 1984b) report that glyphosate applied in the spring, late summer, or fall causes severe or very severe injury to beaked hazelnut in Washington and Oregon. A summary of the limited number of trials from British Columbia indicates that glyphosate causes moderate injury to hazelnut (Boateng and Herring 1990). On the coast of British Columbia, a late summer broadcast application of 1.7 kg a.i./ha glyphosate reduced hazelnut cover by 90% and completely killed nearly half of the samples (B. D'Anjou, pers. comm., June 1989).

Winter or summer applications of 2,4-D produce heavy top-kill in hazelnut, but sprouting can be vigorous (Sutton 1958; Waldron 1959; Ahlgren 1960; Tappeiner 1979; Conard and Emmingham 1984a). Waldron (1959) found that resprouting was delayed for 2 years following a mid-summer foliage spray. Six years later there were 67–85% as many stems as on the control and stems were 30–60 cm shorter. Stewart (1974a) suggests that an early foliar spray may be the most successful application time for controlling resprouting in Oregon. On the other hand, Tappeiner (1979) found that Minnesota hazelnut was more tolerant in June that in July or August.

Some studies indicate that broadcast applications of hexazinone produce light injury to hazelnut in British Columbia (Boateng and Herring 1990). In western Washington and Oregon, summer applications of amitrole are reported to cause moderate injury to hazelnut (Conard and Emmingham 1984a).

Perala (1971) found that picloram was much more effective than 2,4-D or a 2,4-D/2,4,5-T mixture in reducing resprouting of hazelnut in Minnesota. Average recovery after 2 years was less than 10%. Aerial spraying was less successful than backpack spraying. Conifers were damaged by most applications and the site was invaded by grasses and sedges.

Soil Disturbance: Disk site preparation of a hazelnut brushfield in mid-summer turned up the underground stems and set growth back for several years (Eyre and Zehngraff 1948, cited by Ohmann 1982). As long as underground stems are not destroyed or removed during mechanical site preparation, hazelnut will sprout back and the number of aerial stems will be increased in the long run (Stearns 1974).

WILDLIFE

Food: In some locations, hazelnut is a preferred winter browse species for moose, mule deer, and white-tailed deer. However, the major part of the plant that is used is the fruit.[127] Hazelnuts are valued by many small rodents, particularly squirrels and chipmunks (Stearns 1974), which can consume tremendous quantities of the nuts (Stearns 1974; USDA 1974). Hazelnuts are also an important food of snowshoe hares (de Vos 1964; Hansen and Flinders 1969; Banfield 1974) where the range of the plant and animal coincide. The nuts, as well as the buds and catkins, are also consumed by some birds (Stearns 1974).

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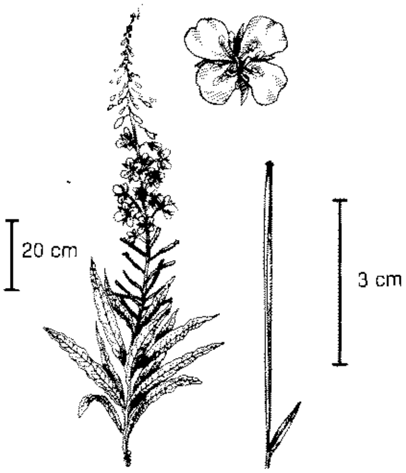
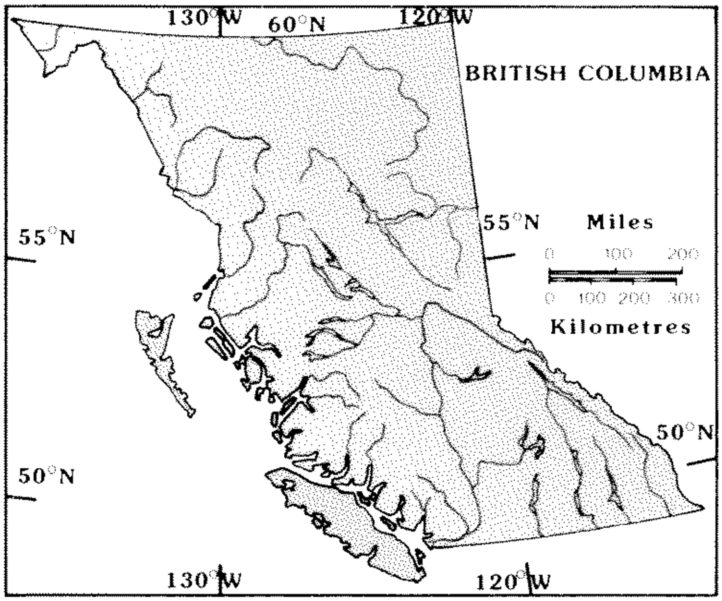
[127] B.C. Min. Environ. (undated).

Epilobium angustifolium
(fireweed)





Distribution of *E. angustifolium* in British Columbia.

Epilobium angustifolium L. **Fireweed**

(Chamaenerion angustifolium)

DESCRIPTION

Fireweed is a tall herbaceous perennial that forms extensive colonies through a spreading system of fleshy roots or "pseudorhizomes." The root system gives rise to erect, usually unbranched annual shoots 1–3 m tall. The untoothed, linear to lanceolate leaves are arranged spirally around the stem. Each stem has a large, showy terminal cluster of pink to purple flowers. The fruit is a narrow capsule up to 10 cm long that releases large numbers of plumed seeds (Mosquin 1966; Myerscough 1980).

Variation: Epilobium angustifolium is a completely circumpolar species with two recognized subspecies (Myerscough 1980) which both occur in British Columbia. The ssp. *angustifolium* is found in the northern boreal forests and at high elevations; ssp. *circumvagum* occurs at lower elevations in south and central British Columbia. The latter subspecies has larger leaves and is generally taller and coarser than ssp. *angustifolium*. There is considerable intergradation where these two subspecies overlap (Mosquin 1966; Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Fireweed is found throughout British Columbia and occurs in all biogeoclimatic zones wherever moisture is sufficient (McLean 1979). Fireweed is extremely common and abundant throughout the central and northern Interior, but it is less abundant on the outer coast (J. Pojar, pers. comm., Oct. 1984) and in the dry southern Interior (Angove and Bancroft 1983).

Altitudinal Range: In British Columbia, fireweed ranges from sea level to high alpine meadows. It has been found at elevations as high as 4000 m in the mountains of western North America (Mosquin 1966).

HABITAT

Climatic Relations: The extremely broad range of this species indicates that it can tolerate a wide range of climatic extremes. In northern climates the species appears to be confined to warm, sunny locales and south-facing slopes; towards the central portion of its range, including British Columbia, it occurs on a wide range of slopes and aspects; at the southern end of its distribution, in hot, dry climates, it favours cool, moist, shaded locales and high alpine and subalpine habitats (Myerscough 1980). Mosquin (1966) indicates that at the northern limits of the range of fireweed in Canada, the plants are frequently sterile.

Site and Soil Conditions: Fireweed tolerates a wide variety of site and soil conditions. It occurs at all elevations and on all slopes and aspects. It is most common on disturbed sites such as burned, mechanically site-prepared, and logged areas (Dyrness 1965; McLean 1979), and it also invades roadcuts, recently deglaciated terrain, and mine wastes (Watson *et al.* 1980). Fireweed also occurs in mature, usually seral, forests in the Interior of British Columbia. (see, e.g., Pojar *et al.* 1984) and is common in undisturbed alpine and subalpine meadows (Mosquin 1966). It occurs on both organic and mineral soils and on most kinds of parent material. It is found on a wide range of soil textures but is most common on sandy loam to loamy soils (Myerscough 1980).

Nutrient Relations: Fireweed can tolerate a wide range of pH values (pH 3–9) and nutrient concentrations (Myerscough and Whitehead 1967; van Andel 1976; van Andel *et al.* 1978; Myerscough 1980). It is frequently reported to be a nitrogen-demanding species or at least an indicator of nitrogen-rich habitats (Buesgen and Muench 1929, cited by Taylor 1932; Tamm 1956). However, experiments by van Andel (1976) suggest that, while the plant has great adaptability to high levels of nitrogen, potassium, phosphorus, and calcium, it does not appear to depend on them. These results from Europe correspond with observations and experimental results from western and northern Canada. Fireweed is frequently an invader of bare till and nitrogen-poor mining wastes, as well as sites with a post-fire "nutrient flush" (Watson *et al.* 1980). In the SBS zone north of Prince George, fireweed has been found on sites with an extremely wide range of available calcium (Wali 1969). Plants growing where the mineral nutrient supply is low may not produce flowers (van Andel and Vera 1977).

Water Relations: Myerscough (1980) reports that fireweed occurs most commonly on soils that are at least freely drained. This author notes that it occasionally occurs in waterlogged mires, but Etherington (1983, 1984) reports that fireweed is intolerant of waterlogged conditions. Over much of British Columbia it tolerates a wide range of moisture conditions (Pojar *et al.* 1982; Angove and Bancroft 1983), but on the coast and in the wetter ICH and ESSF zones in the southern Interior, fireweed is most vigorous and abundant on mesic and subhygric hygrotopes. Towards the northern limits of its range it may become less tolerant of excessive moisture and may be restricted to well-drained soils only (Myerscough 1980). Although fireweed tolerates rather dry sites, it does not germinate in droughty conditions (Watson *et al.* 1980).

Light Relations: As a plant associated with the pioneering stages of succession and most often seen on open ground, fireweed is presumably somewhat light-demanding (Watson *et al.* 1980). Flower buds form earlier in unshaded colonies than in shaded ones, and in deep shade the plant does not flower (Myerscough 1980). Plants have roughly equivalent growth rates in intermediate shade and full sun, but in deep shade growth rates are much reduced and seedlings are etiolated (Myerscough and Whitehead 1967).

Temperature Relations: The range of this species suggests that it is adapted to survive and grow under a variety of temperature regimes. Under experimental conditions, roots initiated growth at 4.5°C, while shoot growth occurred only at higher temperatures (Myerscough 1980). Emergent shoots tolerate some frost in spring but may later show minor tissue damage.

GROWTH AND DEVELOPMENT

Under favourable environmental conditions, fireweed seedlings grow at a comparatively rapid rate for the first 5 weeks from seed. Seedlings that germinate in late summer or early fall occasionally overwinter as a small rosette of evergreen leaves, but spring germinants may reach a mature height and produce flowers during their first year of growth (Myerscough 1980).

The seedling quickly develops an extensive root system. Shoot buds are produced along the length of the root system, giving rise to a colony of plants. These shoots expand late in the growing season and overwinter just beneath the soil surface (Myerscough 1980). In the spring, they emerge from the soil to form the erect annual shoots. Aerial shoots normally exceed 1 m in height at maturity, but height growth seems to be strongly correlated to environmental conditions. Best growth is generally observed on mesic and subhygric sites under full light conditions. Plant heights greater than 2 m are commonly attained. Van Andel (1975) observed up to 120 shoots per square metre and a maximum biomass of emergent shoots of 600–900 g/m^2.

Myerscough (1980) states that the fleshy underground roots of fireweed are most abundant at 5–20 cm below the soil surface and can penetrate deeper than 40 cm, but this does not appear to be the case in southern British Columbia, where McLean (1969) found most roots located between 1.5 and 5 cm beneath the soil surface. Pseudorhizomes can be in the mineral soil in the SBS and ESSF zones (E. Hamilton, pers. comm., July 1989). Lateral spread of a colony of fireweed averaged 1 m/yr in one direction (van Andel 1975). There is no information about how large a colony can become, but field populations have a longevity of several decades, and the roots can live for over 20 years (Moss 1936; van Andel 1975).

In many areas of the province, succession is too rapid for pioneer conditions favourable to fireweed to persist for as long as 20 years. In dry CWH subzones, for example, fireweed appears to reach its peak dominance in the second or third growing season following disturbance. Stands become noticeably less pure 5 years after disturbance and subsequent in-growth of shrubs and trees is rapid.[128] Fireweed tends to attain higher densities and persist longer on sites in the Interior compared to the coast of British Columbia (T. Lewis, pers. comm., May 1989). Once a forest canopy develops, fireweed generally dies out, but it can persist at low densities and vigour in the understory of open stands in the Interior (Mosquin 1966; Pojar *et al.* 1984).

Phenology: Roots begin growing before shoot buds below the surface begin to elongate. Aerial shoots begin to emerge between late March and early June at mid-latitudes, but most emerge in May. Leaves are full grown approximately 1 month later and maximum biomass is reached between the middle of June and the end of August. In the SBS zone near Prince George, B.C., fireweed reached half its maximum percent

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[128] Brand 1984.

cover by the beginning of June and was fully developed by mid-July or earlier. Its development was faster than that of lady fern or thimbleberry (DeLong 1988). At mid to high elevations, fireweed communities may not reach their maximum height until mid-summer (Douglas 1972). Aerial shoots begin to wither in late July or early August and all have died back by late September or early October (Myerscough 1980; Schmidt and Lotan 1980).

The flowering season extends from June to September because the inflorescence begins to flower at the base and continues to elongate during the summer, producing blossoms at the tip of the plant long after the basal fruits have ripened and released their seed (Clark 1976). In the intermountain U.S., seed ripening begins in late July (Schmidt and Lotan 1980). Seeds are released throughout the late summer until after the aerial shoots have withered in autumn.

REPRODUCTION

Seed Production and Dispersal: The plants can flower in their first year of growth from seed. Production of seeds is usually copious in temperate environments. There are an estimated 250–500 seeds in each capsule, and estimates of seed production for each live stem range from 20 000 to 80 000 or higher. The plumed seeds are dispersed by the wind and are very slow to settle (Salisbury 1961; Mosquin 1966; Myerscough and Whitehead 1966; Myerscough 1980). Seeds often reach high altitudes and commonly are dispersed in the order of 100–300 km (Solbreck and Andersson 1987). Fireweed accounted for 63% of the seed obtained in seed traps 1 year after fire at a northern Saskatchewan site (Archibold 1980). This represented 5.66 million seeds per hectare. At the northern limits of its range, fireweed may not produce ripe seeds regularly (Mosquin 1966; Myerscough 1980; Fredskild 1984).

Seed Viability and Germination: Seeds are capable of germinating immediately on release, but best germination rates often occur approximately 3 months after dispersal (Myerscough 1980). Most fireweed seeds germinate within a year of dispersal (Granstrom 1987), but germination can continue at reduced rates for up to 18 months (Myerscough 1980). Seeds most often germinate in late summer or early autumn following summer fires, or the following spring.

Seeds must be at or near the soil surface to germinate successfully. On the south coast of British Columbia and in the SBS zone, fireweed emerged from mineral soil and from depths of less than 5 mm in the forest floor (McGee 1988b; E. Hamilton, pers. comm., July 1989). Germination is most successful on moist, open sites with few initial plant competitors (van Andel and Rozema 1974). However, Granstrom (1987) noted that fireweed germinates freely in closed vegetation. In the laboratory, germination of fireweed was greater under either 50 or 80% shade levels than under no shade (McGee 1988b). Seed germination may be reduced by leachates from conifer leaves and litter (Jobidan 1986).

Germination is stimulated by light, a chilling period, and treatment of the seed in dilute acid (Myerscough 1980). Optimum temperatures for germination are between 15 and 30°C. Fireweed seed does not germinate under dry soil conditions (Myerscough and Whitehead 1966). Oberbauer and Miller (1982) found that no germination occurred when soil water potentials were below -3 bars. Increased nutrient availability may improve germination in laboratory experiments (Myerscough and Whitehead 1966). However, field experiments have not shown improved germination following nitrogen fertilization of established communities due to competition for water in these populations (van Andel and Rozema 1974).

Archibold (1980) found viable buried seed in soil cores taken immediately following a fire in northern Saskatchewan. He speculates that seed banking may account for the rapid invasion of fireweed on burned sites. In the SBS zone some fireweed seeds seem to work their way down through the soil to a depth where they can survive a burn (E. Hamilton, pers. comm., July 1989).

Vegetative Reproduction: Fireweed relies on large quantities of seed to colonize disturbed areas, but once it arrives on a site, expansion of the population is accomplished by vegetative reproduction. New shoots arise each year from buds located at the base of old stems, and on the horizontally spreading root system 2–8 cm below the soil surface. The root system is perennial and with each year it spreads further outward from the original seedling. New plants are created when they become detached from the parent plant through death of old roots or through disturbance. In an established colony of fireweed, vegetative reproduction occurs much more extensively than does reproduction by seed (Moss 1936; Myerscough 1980).

PESTS

Myerscough (1980) provides a comprehensive list of the many insects and diseases found on *E. angustifolium* in Britain.

EFFECTS ON CROP TREES

Competition: Fireweed is considered to be a species of low competitive ability because it is a pioneer of recently disturbed sites and will not invade sites with previously established vegetative cover (Mosquin 1966; Watson *et al.* 1980). However, in the early stages of stand development it can be an important competitor.

Fireweed is of more concern in the Interior than on the coast because it is ubiquitous there, it often dominates sites for a decade or longer, and it may overtop slow-growing seedlings for 10 or more years following establishment. On the south coast, fireweed can be outgrown by more competitive woody brush within 1–3 years.[129]

Fireweed cover establishes early in the growing season. DeLong (1988) found that fireweed had reached 30% of its maximum by May 26, and 90% of its maximum by July 12. In comparison, thimbleberry had attained only 2% of its maximum on May 26 and 68% on July 12. However, although fireweed is at its maximum level for a greater proportion of the growing season than thimbleberry, its narrow-leaved, single stalks do not create the extreme degree of light competition caused by the multi-layered, continuous canopy of well-developed thimbleberry plants.

Dense cover of fireweed may cause substantial reductions in the amount of light received by overtopped conifer seedlings. Light levels of less than 5% of full sunlight have been recorded under dense patches of fireweed (Comeau 1988).

Throughout British Columbia, fireweed can injure young seedlings through snowpress (J. Pollack, pers. comm., Jan. 1985).[130] Douglas-fir and western larch are particularly susceptible because young seedlings are flexible and spindly (D. Lloyd, pers. comm., Nov. 1984). However, widespread snowpress damage has also been observed in Engelmann spruce seedlings on mesic and subhygric sites in the ESSF zone. Reduced light levels beneath dense fireweed canopies results in the development of long spindly conifer stems which are more susceptible to snowpress damage. Physical damage due to fireweed appears to be greatest on wetter hygrotopes in subzones where rainfall and snowfall is high.

Competition between fireweed and conifers for moisture and nutrients has not been demonstrated in British Columbia. However, fireweed grows vigorously and may tie up nutrients. This may limit availability of nutrients, such as nitrogen and phosphorus, to other plants (van Andel and Nelissen 1979).

Beneficial Effects: A cover of fireweed may delay development of shrubby vegetation on cleared or burned areas (see, e.g., Stickney 1981), thus allowing planted conifers to gain dominance of a site. Fireweed's extensive root system helps to bind soil and reduce erosion (Watson *et al.* 1980). Invasion by fireweed undoubtedly increases the organic matter content of severely burned or otherwise disturbed sites. Nutrients are stored by fireweed and become available to conifers in subsequent years as the fireweed declines. This nutrient storage is particularly important on poor sites (T. Lewis, pers. comm., May 1989).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Fireweed aggressively colonizes logged areas (Mosquin 1966). Colonization is achieved primarily by seeding-in, but where fireweed already exists prior to canopy removal, it is able to expand by means of its spreading root system (McLean 1979; Myerscough 1980; Rowe 1983). The degree of ground disturbance caused by logging or site preparation influences the amount of fireweed invasion. In the ESSF zones in the southern Interior, virtually all summer-logged or site-prepared areas become dominated by fireweed immediately after disturbance. On the other hand, sites logged in the winter, when deep snow prevents disturbance of the ground vegetation and soil, often remain covered with the ericaceous vegetation that typically dominates the understory of Engelmann spruce–subalpine fir forests (J. Mather, pers. observ.).

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[129] Brand 1984.

[130] Ibid.

In Eis' study (1981) of four site types in the SBS zone north of Prince George, fireweed was absent from all sites prior to logging. He observed that fireweed's "first few seeds arrive in the fall of the first year following winter logging and germinate in the spring of the second year. Its presence is most noticeable during the third year after logging and . . . it appears in great numbers during the fourth year." Six years after logging, fireweed accounted for more than 60% of the herbaceous ground cover on the *Cornus*-Moss site and 50% on the *Dryopteris-Aralia* site, but it was less than 20% of the cover on the Devil's club site and was not a significant competitor on the Alluvium site. This study demonstrates that fireweed is able to exploit a vacant niche rapidly, but is unable to compete where vegetation is already well established. The *Cornus*–Moss type had a low diversity and cover of vegetation immediately after logging and fireweed readily became dominant. In contrast, shrubs and herbs were already well established on the Alluvium site and fireweed was unable to move in. Maximum cover of fireweed is usually achieved within 3–5 years of harvesting (Isaac 1940).

Fire: Fireweed is well known in western North America for its ability to invade recently burned areas (Mosquin 1966; Dyrness 1973; Watson *et al.* 1980; Cholewa and Johnson 1983; Foster 1986; Stickney 1986). Its light seeds rapidly colonize vacant ground created by burning. Following fire it can form dense, uniform stands over vast areas. Cover, density, and production of fireweed are usually greatest on areas that suffer the most intense burns (Ahlgren 1960; Mueggler 1965; Morris 1970). Vegetative reproduction is also a prominent means of fireweed invasion and expansion following burning (J. Zasada, pers. comm., Sept. 1989).

Fireweed cover generally increases to a maximum within a few years of burning and may then either decline or remain static (Kellman 1969; Miller and Miller 1974; Tiedmann and Klock 1976; Bartos and Mueggler 1981; Stickney 1986). In a burned western hemlock–Douglas-fir site in the western Cascades in Oregon, fireweed cover averaged 11% after 2 years, 33% after 5 years, 23% after 10 years, 17% after 15 years, and 3% after 20 years (Stickney 1986). Burned sites in the ICH and ESSF zones in the Interior of British Columbia commonly develop much higher fireweed covers; however, overall trends in fireweed development appear to be similar. The longevity of fireweed dominance in seral communities depends on the rate of development of other herb and shrub species (Stickney 1986).

McLean (1969) classified fireweed as moderately susceptible to fire because most of its fibrous roots are located within the upper 5 cm of the mineral soil surface. In some cases, fireweed rapidly loses vigour and will not survive under regimes of frequent burning (Myerscough 1980); however, it has a very low flammability and can suppress fire in early successional vegetation types where it is abundant. The plant acts as a heat sink because of its high moisture content, and because there is little standing dead fuel (Sylvester and Wein 1981).

Cutting and Grazing: There are no published reports describing the response of fireweed to manual cutting. Impact is expected to be short-lived and minimal unless cutting is repeated within a short period of time. Vigorous fireweed that was cut with hoes in late June on two rich mesic sites in the ICH zone near Clearwater was 10-65 cm in height after 60 days (J. Mather, pers. observ.). However, in the McBride Forest District, fireweed cut in early June did not recover at all after 40 days (D. Salayka, pers. comm., July 1989). Fireweed does not survive continued grazing (Myerscough 1980). One year after sheep grazing near Clearwater, fireweed had lost a tremendous amount of vigour and frequency. Plants on grazed plots were only half as tall as plants on the undisturbed control. Sheep can consume a large volume of fireweed before plantation damage occurs (G. Ellen, pers. comm., July 1989). Cattle will graze fireweed throughout the growing season, particularly when plants are in flower (McLean 1979).

Herbicides: Glyphosate severely injures fireweed, but the plant is not effectively killed and reductions in cover are not long-lasting. Broadcast applications of 1.4–2.1 kg a.i./ha in August and September have typically reduced fireweed cover by 60 to 100%. Pretreatment cover is almost always regained after 2 or 3 growing seasons. Initial regrowth may be stunted or deformed, but by the time the original cover is regained, plants tend to be healthy and vigorous with many thick, branched stalks (D. Barron, pers. comm., May 1989; B. Raymer, pers. comm., June 1989; J. Wright, pers. comm., July 1989).[131,132,133,134] Near Grand Forks,

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[131] Dyke 1987.

[132] Noble-Hearle 1989.

[133] Ladd 1989.

[134] Simard 1988.

D. Barron (pers. comm., May 1989) found significant differences in fireweed control between spring and fall applications of glyphosate. Spring applications resulted in complete recovery of fireweed after 1 year, while fall applications gave good control for at least 3 years.

Broadcast applications of hexazinone have resulted in poor to excellent control of fireweed after one growing season. Rates of about 1 kg a.i./ha of undiluted liquid hexazinone have tended to cause little damage (less than 20% defoliation). Rates of about 2 kg a.i./ha have also tended to give unsatisfactory control, though in Saskatchewan,[135] an application rate of 2.2 kg a.i./ha caused 82% defoliation after one growing season. Rates of 3–4.3 kg a.i./ha often result in good control; best control is achieved at the highest application rates.[136,137]

Spot applications of hexazinone have resulted in variable control of fireweed. Best control has tended to result from a rate of 8 mL per spot and 2-m spacing.[138] Information is lacking on the length of control provided by spot or broadcast applications of hexazinone; however, fireweed has completely recovered two seasons after low rates of application.[139] Hexazinone is ineffective on sites with deep organic matter. Humus depths greater than about 8 cm have greatly reduced the effectiveness of the herbicide.

Laboratory experiments have been carried out to investigate the impact of several other herbicides on fireweed. Soil-acting compounds which were found to kill fireweed include: bromacil, cyanazine, ethofusemate, lenucil, oxadiazon, oxyfluorfen, propachlor, and simazine. Foliar applications of 2,4-D amine, mecoprop, trichlopyr ester, paraquat, and pentschlor + chlorophan have been found to give effective control of fireweed (Turner and Richardson 1979; Bailey and Hoogland 1984).

Soil Disturbance: Fireweed rapidly seeds-in to exposed mineral soil (Watson *et al.* 1980). It also reproduces vegetatively from plant parts that have become detached from the parent plant during disturbance. Fireweed tends to reach higher densities on disturbed sites in the Interior than on the coast.

Severe mechanical disturbance involving complete removal of the forest floor and compaction reduces the height and density of fireweed but is likely to be detrimental to conifer regeneration. In the Gaspé Region of Quebec, Mosquin (1966) observed that fireweed was growing poorly on exposed subsoil but had very good vigour on adjacent sidecast mounds of humus and topsoil.

Fertilization: Fireweed may increase in abundance where fertilizers are used in silviculture (Reinikainen 1964, cited by Myerscough 1980). Germination is improved on fertilized sites lacking vegetation (Myerscough and Whitehead 1967), but when plant cover is well established on a site, fertilization may not increase germination of fireweed (van Andel and Rozema 1974).

Other: Areas seeded to grass can have lower cover and frequency of fireweed than unseeded areas (Hernandez 1973, cited by Watson *et al.* 1980; Crane *et al.* 1983).

WILDLIFE AND RANGE

Food: Fireweed has low to moderate importance for many wildlife species in British Columbia. Browsing is seldom heavy or extensive. However, this plant can be an important browse for deer in the province (Singleton 1976; Rue 1978; Willms *et al.* 1980; Harvey 1981). It has moderate to low importance in summer and fall for moose (Singleton 1976; Harestad 1983) and Roosevelt elk.[140,141] Fireweed is often grazed by elk in Montana (McLean 1979). Simpson and Woods (1987) found that caribou use fireweed in the spring near Revelstoke. Wolff (1978) observed that fireweed shoots made up 11% of snowshoe hares' diet in May but accounted for less than 3% of their diet the rest of the year.

Cattle will graze fireweed throughout the growing season, particularly when plants are in flower. Sheep can also be used to control fireweed (McLean 1979).

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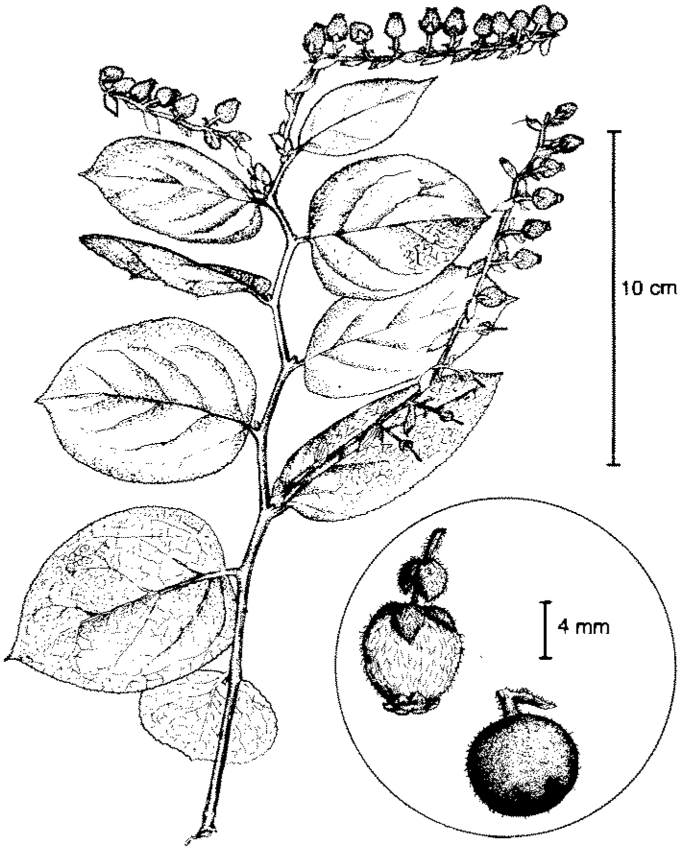
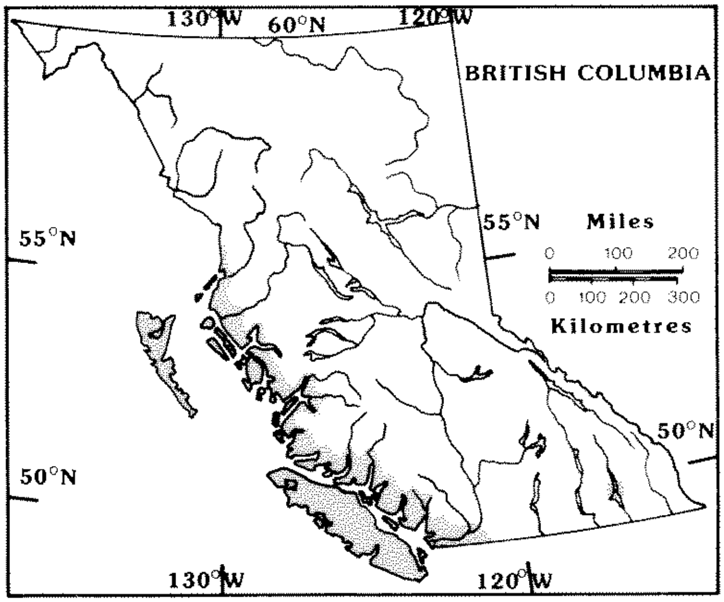
[135] Teskey and Masterson 1984b.
[136] Fahlman and Herring 1985.
[137] Teskey and Masterson 1984a,c; 1985b,c,d; 1986b,c.
[138] Teskey and Masterson 1986b.
[139] Teskey and Masterson 1985a.
[140] Smith *et al.* (undated).
[141] Balfour 1989.

Other Resources: The flowers are noted for their nectar production and are sought out by hummingbirds, bees, butterflies, and other insects. The fireweed complex provides habitat for many small mammals including deer mice, Oregon and Townsend voles, shrews, and chipmunks (T. Sullivan, pers. comm., April 1989).

Gaultheria shallon
(salal)





Distribution of *G. shallon* in British Columbia.

Gaultheria shallon Pursh. **Salal**

DESCRIPTION

Salal is an erect to nearly prostrate evergreen shrub, loosely to densely branched, and up to 2.5 m tall, sometimes forming impenetrable thickets. It has an extensive root system with spreading rhizome-like structures. The leaves are thick, leathery, and ovate, often with finely toothed margins. The pinkish, bell-shaped flowers are borne in terminal and subterminal, one-sided racemes. The fruit is a round, hairy, purplish-black, berry-like capsule (Szczawinski 1962; UBC Bot. Garden 1970).

Variation: No subspecies or varieties of salal are described in British Columbia (Taylor and MacBryde 1977). The presence of altitudinal ecotypes is possible but not probable, and the species apparently does not hybridize (Pojar 1974).

DISTRIBUTION AND ABUNDANCE

Salal occurs along the entire length of the B.C. coast in the CWH and CDF biogeoclimatic zones, seldom penetrating far inland. A single isolated population of the species is recorded from the Kootenay Lake area, but otherwise all records are from west of the Coast Mountains (Szczawinski 1962). It is extremely abundant in south coastal British Columbia but becomes less important on the mainland and inner islands of the north coast where it is rarely found at any distance from the shoreline.

Altitudinal Range: Salal is primarily a low-elevation species, becoming more restricted in elevation with increasing latitude. On the south coast it ranges from sea level to approximately 800 m (Lyons 1952), but on the north coast it rarely occurs above 100–200 m elevation.

HABITAT

Climatic Relations: The restricted range of salal suggests that it requires a humid to perhumid coastal climate with mild temperatures, little snow, and unfrozen soils in winter. In British Columbia, salal is most vigorous and abundant on Vancouver Island and adjacent coastal areas.

Site and Soil Conditions: Salal is a dominant understory plant in lowland coniferous coastal forests and is very abundant in open, shoreline habitats such as bluffs and rocky knolls (Calder and Taylor 1968). It grows on a wide variety of mineral and organic substrates including shallow rocky soils, sand dunes, glacial till, and peat. Soils supporting salal are most often Podzols, frequently with deep mor humus forms, but salal is also found on Brunisolic, Folisolic, and organic soils (see, e.g., Klinka *et al.* 1979).[142]

On poor, shallow soils the plants often exhibit a low mat-forming habit, while on better deeper soils they become vigorous upright shrubs (UBC Bot. Garden 1970; M. Newton, pers. comm., Dec. 1984). Best growth in cultivation occurs on moist sandy or peaty soil. Salal frequently grows on decaying wood, particularly old stumps, and in extremely humid environments it can be found as an epiphyte on living trees (UBC Bot. Garden 1970).

Nutrient Relations: Salal can survive and grow under a wide range of nutrient conditions (Sabhasri 1961). Throughout its range, it is noted for its abundance on nutrient-poor sites (see, e.g., Klinka 1977a)[143,144] Its abundance on these sites reflects a tolerance for nutrient-poor conditions but should not be construed as a preference for a low-nutrient environment. In fact, salal shows a definite growth response to additions of macronutrients, particularly of nitrogen (Sabhasri 1961; UBC Bot. Garden 1970). It does not grow well in limy soils (UBC Bot. Garden 1970).

Water Relations: Salal will survive and grow under a variety of soil moisture conditions but growth is most vigorous in moist conditions and the plant has poor vigour on shallow, droughty soils (Sabhasri 1961; Allen 1969; UBC Bot. Garden 1970; McMinn *et al.* 1976). In the Vancouver Forest Region, salal is found on soil moisture regimes ranging from very xeric to hygric sites. However, it tends to occur on the wetter sites in the driest CDF subzones, and it is most abundant on the driest sites in wet subzones of the CWH (Klinka 1977b).

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[142] Banner *et al.* 1983.
[143] Yole *et al.* 1982.
[144] Banner *et al.* 1983.

Light Relations: Salal grows well in partial shade but is uncommon and has very low vigour under dense forest canopies. Increasing light intensity by reducing overstory shade increases the vigour and growth rate of salal (Sabhasri 1961; Stanek *et al.* 1979; Koch 1983), but in most cases best growth is in light shade rather than in full sunlight (UBC Bot. Garden 1970; USDA 1974; Koch 1983). This may reflect evaporative stresses rather than an intolerance of sunlight (Koch 1983). Sabhasri (1961) reports that germination and survival of salal seedlings is not affected by low light intensities, but Schopmeyer (1974) found that partial shade is needed to successfully establish salal seed.

Although these field observations indicate that salal is at least a moderately shade tolerant species, Sabhasri's (1961) laboratory research suggests that the photosynthetic and respiration characteristics of salal are similar to those of plant species classed as shade intolerant. Actively growing plants are very sensitive to light conditions and significantly increased in photosynthetic activity and seedling growth with increased light intensities up to the maximum level tested (400 ft-candles). At low light intensities (100 ft-candles) respiration appears greater than photosynthesis. Maximum growth occurs under red light.

Messier *et al.*[145] found dramatic differences in salal leaf morphology under different light intensities. At 1.8% full sunlight (80% canopy cover), leaves were almost 3 times larger in area than they were in a clearing. However, in deep shade (0.3% full sunlight) leaves were similar in size to those in the clearing. Leaves growing in 0.3% full sunlight were less than half the weight and about half the thickness of those in the clearing.

Temperature Relations: The geographic range of salal suggests that it may be sensitive to frost. This suggestion is supported by Sabhasri's (1961) observation that a short period of freezing temperature in the middle of May killed nearly all germinants.

GROWTH AND DEVELOPMENT

In nature, early growth of salal seedlings is very slow (M. Newton, pers. comm., Dec. 1984). Once established, the plant adds considerable biomass each growing season, but actual height increment is slower than for many other shrub species. Vigorous salal may grow to a height of over 2.5 m (Szczawinski 1962), but most plants average 60–120 cm in height (Clark 1976). The average new shoot increment during a growing season in western Washington was 5 cm (Sabhasri 1961).

Leaves of salal normally live for 2–4 years and occasionally last as long as 6 years. Twigs survive for 16 years or more but only bear leaves during the first few years (Koch 1983). Individual plants survive for an indefinite period because of continued resprouting.

The root system of salal is very extensive. Plants expand outward by means of rhizome-like root structures. Shoots consisting entirely of new growth were found up to 2 m from the parent plant (Koch 1983).

The total weight of new leaves added to a site in western Washington during the growing season averaged 900 kg/ha, while the total weight of salal biomass was approximately 36 000 kg/ha. Total root biomass exceeded the weight of above-ground parts (Sabhasri 1961).

Phenology: Phenological development of salal is highly variable (Stewart 1974a). In Washington, vegetative buds burst in early April. Most rapid vegetative growth occurred from late April onward, peaking in early June (Sabhasri 1961).

Flowering can occur any time between March and July (USDA 1974) but commonly occurs during May and June in Alaska (Viereck and Little 1972). Near Vancouver, flowering took place between June 12 and July 4 in 1971 (Pojar 1974), while in western Washington, fruit set began by the third week of June (Sabhasri 1961). Fruits ripen between August and October and remain on the stem until December (USDA 1974).

REPRODUCTION

Seed Production and Dispersal: Pollination of salal flowers is by insects, primarily bumblebees and flies (Pojar 1974). The fruit is a many-seeded capsule with a fleshy outer calyx that forms a pseudo-berry. Fruits have

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[145] Messier *et al.* 1989.

an average of 126 seeds each. Heavy crops of fruit are produced on a regular basis, but fruiting was not observed by Koch (1983) under canopies with greater than 30.3% closure. Dispersal of the seeds is by birds and mammals that feed on the sweet fruit (Sabhasri 1961; USDA 1974).

Seed Viability and Germination: The fruits of salal are persistent and seeds remaining on the plant are viable for a considerable time following ripening. In cold, dry storage, the seed will remain viable for several years, but viability diminishes more rapidly under most natural conditions. The seeds do not appear to require chilling to induce germination. Schopmeyer (1974) reported that moist, acid conditions under partial shade are needed for the successful propagation of salal from seed. A germination rate of 27–35% has been obtained from fresh seed under lighted conditions (Sabhasri 1961; USDA 1974). Germination rates of about 60% were obtained in a British Columbia nursery (C. Messier, pers. comm., July 1989).

Even though large quantities of seed are produced and numerous germinants may appear, very few seedlings survive due to limitations of dispersal, seedbed conditions, and sensitivity to environmental extremes. Best germination was observed on decaying wood, but survival and seedling development on this seedbed was poor. In Oregon, salal is reported to germinate well both in clearcuts and under mature Douglas-fir stands, but establishment is most successful in the understory of young Douglas-fir stands. Seedling production is insignificant as a means of reproduction on most sites where salal is already established (Sabhasri 1961; Stewart 1978; Koch 1983; McGee 1988a; Nuszdorfer and Nuszdorfer 1988).

Vegetative Reproduction: Once salal is present on a site, further expansion is almost exclusively by vegetative means (Sabhasri 1961; Koch 1983; McGee 1988a) including layering and sprouting or suckering from roots and stem bases. Vegetative resprouting was an important mechanism for re-establishment of salal on the southern coast of British Columbia (McGee 1988b). Cuttings made from roots or stems readily form new roots and sprouts (Sabhasri 1961; Pojar 1974; Stewart 1974b; USDA 1974).

PESTS

Of the numerous diseases known to occur on salal, the most common and serious is the leaf spot fungus (*Mycosphaerella gaultheriae)*. The grey weevil also causes severe leaf damage to salal in southern British Columbia (UBC Bot. Garden 1970).

EFFECTS ON CROP TREES

Competition: Salal is a common and often serious competitor with coniferous tree species in low-elevation coastal British Columbia. Barker *et al.*[146] suggest that the understory of 100 000 ha of cedar–hemlock forests in coastal British Columbia is dominated by salal. Over most of its range, salal is a competitor primarily on mesic and drier ecosystems, but it may occasionally become abundant on moister and richer ecosystems. Salal is capable of gaining nearly complete occupancy of a site and, unlike most other brush species, is relatively insensitive to nutrient or water levels (Sabhasri 1961). Competition is most severe during the early stages of stand development (Long 1977) but may continue through the rotation, particularly if the canopy is open enough to allow a well-developed understory of salal to persist (Stanek *et al.* 1979)

Several studies have shown that salal can be successfully controlled with herbicides, burning, or mechanical treatments, and that conifers typically show a positive response to salal eradication by the second year after treatment. Two years after a herbicide application, the average diameter of Douglas-fir seedlings was 37% larger where salal was removed than on an untreated control.[147] On eastern Vancouver Island, reduction of salal cover by moderate and severe burns increased Douglas-fir height growth by about 40% while light burns increased height growth by only 12.5% (Vihanek 1985).

Salal is believed to provide serious competition for moisture on dry sites (Sabhasri 1961; Stanek *et al.* 1979). Price *et al.* (1986) showed that salal removal in the CDF zone increased Douglas-fir growth because of the higher soil water potential. However, salal is unlikely to compete with seedlings for water in the wetter CWH zone where soil water deficits are rare. During a typical summer drought, mechanical

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[146] Barker *et al.* 1987.

[147] Wellman and Harrison 1987.

removal of salal provided Douglas-fir with 14% more water than on adjacent areas without salal removal, and it increased conifer growth (Kelliher 1985). Douglas-fir stem diameter growth and colour were enhanced in the second growing season following salal eradication in the CWHdm subzone on southern Vancouver Island. The improved performance of Douglas-fir is likely due to greater soil moisture availability (B. D'Anjou, pers. comm., July 1989). Dunsworth obtained a 56% increase in stand volume in a 12-year-old Douglas-fir stand on eastern Vancouver Island 3 years following salal cover removal.[148] He attributed some of the growth increase to lower moisture stress. Removal of salal had no significant impact on a 25-year-old Douglas-fir stand.

Salal can have an impact on the nutrient budget of conifers (Germain 1985; G. Weetman, pers. comm., Nov. 1984). Barker and Weetman[149] found that 2 years after salal eradication on northern Vancouver Island there was a modest increase in nitrogen and phosphorus uptake in Sitka spruce, western hemlock, and western redcedar, and a modest increase in hemlock and cedar height growth (spruce growth response was not measured). The authors considered that effects of salal removal on nutrients are likely to be gradual, and that nutrient-stressed trees may respond particularly slowly to salal eradication.

Dense salal can lower soil temperatures and thereby reduce conifer growth by reducing root growth and mycorrizal infection (Parke *et al.* 1983) or by reducing the activity of the microflora. On northern Vancouver Island, however, temperature differences under different salal covers were small and may not be biologically significant.[150]

Allelopathy: A western Washington study (del Moral and Cates 1971) found no evidence of allelopathic chemicals in extracts of salal foliage and litter. Further research on the possibility of salal allelopathy is under way in British Columbia (L. Montigne, pers. comm., Feb. 1989).

Beneficial Effects: Sabhasri (1961) could not demonstrate any negative impact of salal on Douglas-fir growth in his test plots in western Washington. In fact, control plots had significantly better growth than those plots where salal was manually removed. He noted that salal roots could make an important contribution to the organic matter content of the soil, and speculated that the loss of organic matter and associated nutrients caused by removal of the salal may have contributed to the poor growth of the seedlings.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Several studies indicate that salal biomass is inversely related to overstory cover, and salal will increase in cover, vigour, and height when the overstory cover is either reduced or totally removed (Sabhasri 1961; Long and Turner 1975; Long 1977; Stanek *et al.* 1979; Black *et al.* 1980; Koch 1983; Gholz *et al.* 1985; Vales and Bunnell 1986, cited by Vales 1986). However, salal does not grow as rapidly as many other shrub species, and may take many years to become dominant above ground following clearcutting. Salal establishes itself relatively quickly below ground (C. Messier, pers. comm., July 1989).

Re-invasion of salal after logging occurs from rhizomes that were present in the undisturbed forest. Salal can only dominate clearcuts if it is not shaded out by the developing overstory.[151] Salal cover and height were measured under four coniferous stand densities.[152] Very open stands had 85% salal cover, open stands 75%, closed stands 45%, and very closed stands 1%. Differences in cover were caused by differences in light intensity. Salal height decreased with decreasing stand closure (increasing light). D. Harrison (pers. comm., May 1989) has also observed that overstory removal on northern Vancouver Island tends to increase cover and lead to reduced height of salal. Spacing on southern Vancouver Island in the CDF and CWH zones caused salal to increase in height after 1–2 years (R. Muller, pers. comm, July 1989). Messier *et al.*[153] report that thinning practices that reduce the overstory canopy to below 80% may create conditions favourable for salal growth.

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[148] Dunsworth 1986.
[149] Barker and Weetman 1986.
[150] Messier and Kimmins 1988.
[151] Messier *et al.* 1989.
[152] Messier and Kimmins 1988.
[153] Messier *et al.* 1989.

Fire: Light fires tend to increase salal cover above pre-burn levels. Fire stimulates resprouting from roots and stem bases (Sabhasri 1961). In the Fraser Valley, salal cover increased from less than 10% before burning to 35–50% after 3–4 years and 85% after 9 years (Lafferty 1980). Similar results have been obtained on northern Vancouver Island (C. Messier, pers. comm., July 1989).

However, even on lightly or moderately burned areas, above-ground parts of salal can be slow to recover to pre-burn levels (G. Dunsmore, pers. comm., Dec. 1984; B.M. Geisler, pers. comm., Jan. 1985). For example, moderate severity burns led to salal covers of 3% after 2 years, 1% after 5 years, 10% after 20 years, and 18% after 30 years (Schoonmaker and McKee 1988). Despite slow above-ground recovery, the below-ground environment is usually fully occupied by salal within 8 years of burning in cedar–hemlock sites in the CWH zone.[154]

Severe burns can reduce salal cover only if fire penetrates sufficiently deep to kill the roots. High severity burns on dry sites on eastern Vancouver Island have decreased salal cover by 80% compared to adjacent unburned areas. In contrast, low and moderate severity burns have decreased cover by only 40% compared to unburned areas (Vihanek 1985). In the CDF and CWH zones on southern Vancouver Island, severe burns have reduced sprouting of salal, while light burns have resulted in more intense sprouting (R. Muller, pers. comm, July 1989).

Cutting: Manual or mechanical cutting of salal can be expected to stimulate sprouting; the response may be similar to that following burning.

Herbicides: Conard and Emmingham (1984a) report that glyphosate causes light damage to salal. Salal was not damaged by glyphosate applied in September at 2 kg a.i./ha in the CWHwm subzone on Vancouver Island.[155] Moderate damage occurred 1 year after glyphosate was applied at 4 kg a.i./ha by backpack sprayer in late summer in the drier CWH subzone on eastern Vancouver Island (B. D'Anjou, pers. comm., July 1989).

Results from hexazinone applications are inconsistent. It is often described as ineffective at controlling salal (Newton and Knight 1981; Boateng and Herring 1990). However, an April ground application of 2 kg a.i./ha granular hexazinone for site preparation resulted in good control of salal near Chilliwack. Two years after herbicide application, salal biomass on the treated areas was about half that on the control.[156] A backpack application of 4 kg a.i./ha hexazinone in February–March on southern Vancouver Island in a dry CWH subzone caused a 45% reduction in salal cover.

Conard and Emmingham (1984a) report that spring and summer applications of amitrole caused no visible injury to salal and that 2,4-D caused light damage.

Triclopyr ester (Garlon®) has been more successful than other herbicides in controlling salal.

Triclopyr ester in diesel applied at 4 kg a.i./ha using backpack sprayers reduced salal cover by 78%.[157] Garlon® in diesel provided at least three seasons of salal control in a Douglas-fir–salal ecosystem on the east coast of Vancouver Island near Nanaimo.[158] Application of 4 kg a.i./ha triclopyr ester in diesel oil at 100 L/ha in early spring or late summer reduced salal cover by 60–90% in the dry CWH subzone on Vancouver Island. Salal cover was reduced by only 40% when 100 L/ha mineral oil were used as the carrier instead of diesel oil. Reducing the concentration of chemical by using 150 L/ha diesel instead of 100 L/ha had no effect on results. Although above-ground parts of salal were well controlled, living root dry weight was 89% of that in an untreated control, indicating that roots continue to survive despite good foliar control (B. D'Anjou, pers. comm., July 1989).

Soil Disturbance: Any form of soil disturbance that causes mechanical damage to salal but does not physically remove it from the site can be expected to stimulate resprouting. Pieces of stems and roots that are detached from the parent plant and buried in soil will root and form new plants (Sabhrasi 1961). Backhoe

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[154] Messier and Kimmins 1988.
[155] Reynolds *et al.* 1988.
[156] Wellman and Harrison 1987.
[157] Barker 1988.
[158] Dunsworth 1986.

site preparation (i.e., mixing organic and mineral soil layers) on a mesic CWHwh site in the Queen Charlotte Islands initially reduced salal cover, but within 3 years it was rapidly invading (S. Craven, pers. comm., June 1989). Heavy scarification in the CDF and CWH zones on Vancouver Island has resulted in very slow re-invasion of salal (R. Muller, pers. comm., July 1989).

Fertilization: Salal responds to applications of fertilizer, particularly nitrogen, with increased above- and below-ground growth and vigour (Sabhrasi 1961; UBC Bot. Garden 1970). However, while Osmocote® substantially increased hemlock growth, it had no effect on salal 2 growing seasons after it was applied to western hemlock seedlings at the time of planting in the CWH zone on northern Vancouver Island (Nuszdorfer and Nuszdorfer 1988). In forest stands, applications of fertilizer that result in an increase in the density of the tree canopy may cause a decline in vigour and cover of the salal understory (Long and Turner 1975; Stanek *et al.* 1979).

WILDLIFE

Food: Salal is an important wildlife food in British Columbia. It is valuable to black-tailed deer year-round but is particularly important in winter (McTaggart-Cowan 1945; Brown 1961; Jones 1975; Singleton 1976; Rue 1978; Harvey 1981; Nyberg *et al.* 1986; Chambers 1988).[159] Stems, leaves, blossoms, and fruit are consumed. Salal has been described as one of the 10 most important foods of black-tailed deer and has made up about 10% of its total diet (Brown 1961; Jones 1975). Salal is an important winter and spring browse for Roosevelt elk (Bailey 1966; Singleton 1976).[160,161] It has made up 36–47% of the February diet of Roosevelt elk.[162] Salal sprouts well after ungulate browsing (T. Lea, pers. comm., Feb. 1989).

Salal is browsed by some small mammals and birds. Its leaves and twigs are fairly important foods for mountain beaver (Banfield 1974), although this mammal has very limited distribution in British Columbia. King (1969) found that leaves and buds were important to ruffed grouse from March to late May at a Vancouver Island site and Zwickel and Bendell (1972) noted that incubating female blue grouse also consume salal.

Animals that consume salal berries play an important role in seed dispersal (Halverson (compiler) 1986). The berries are commonly eaten by grouse and other birds (Viereck and Little 1972). Adult blue grouse have shown strong selection for salal berries even when the plant has been available only in relatively minor amounts (King and Bendell 1982). The berries are an important food for blue grouse chicks from May to September on northern Vancouver Island. Salal berries have made up 19% of the early August diet and 45% of the late August diet of juvenile ruffed grouse on Vancouver Island (King 1969). Other animals eating the fruit include black bear, black-tailed deer, and red squirrel (USDA 1974).

Other Resources: Mountain beaver often use salal for the central portion of their nests (Martin 1971, cited by Chapman and Feldhamer (editors) 1983).

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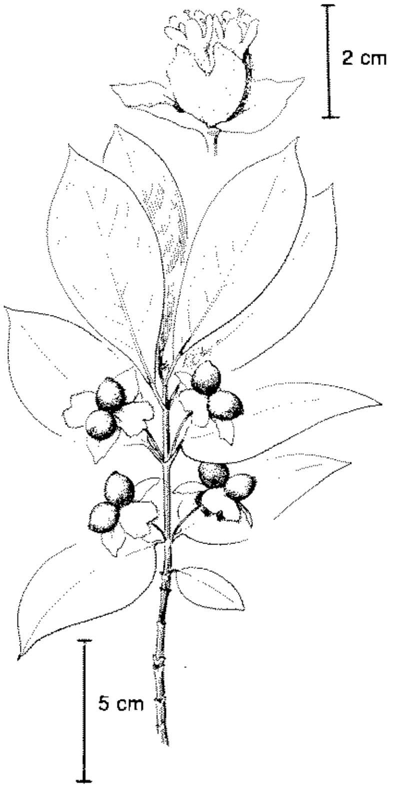
[159] Blower 1982.

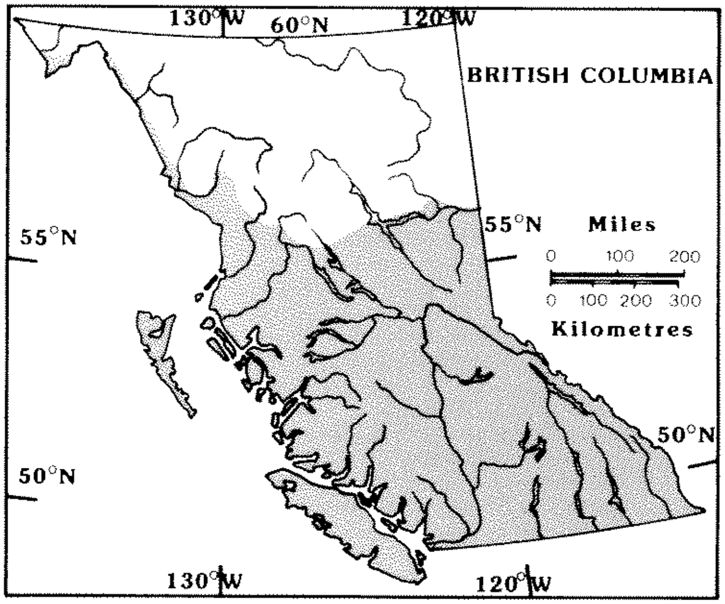
[160] Ibid.

[161] Smith *et al.* (undated).

[162] Ibid.

Lonicera involucrata
(black twinberry)





Distribution of *L. involucrata* in British Columbia.

Lonicera Involucrata (Richards.) Banks

Black twinberry

(twinberry, honeysuckle)

DESCRIPTION

Black twinberry is a straggling to ascending deciduous shrub 1–3 m tall. Stems have opposite branching and are four-sided when young. The leaves are elliptic to oblong, and untoothed. The yellow, tubular flowers occur in pairs above conspicuous green or purple bracts. The "twin" fruits are black to reddish round berries with few seeds (Viereck and Little 1972; Hultén 1974).

Variation: There are several forms of *L. involucrata.* The form occurring in British Columbia is the typical var. *involucrata* (UBC Bot. Garden 1979).

DISTRIBUTION AND ABUNDANCE

Black twinberry occurs throughout British Columbia to approximately 57°N latitude. It is common on the coast and in the Interior and is found in all forested biogeoclimatic zones, but it is absent from northern subzones of the BWBS. It is also present in the Peace River valley and scattered in specialized habitats in the Stikine–Iskut drainage, but it is apparently absent from the Fort Nelson and Liard River areas in the extreme north of the province (A. Ceska, pers. comm., Nov. 1984). As well, it is common in lowland areas of the Queen Charlotte Islands (UBC Bot. Garden 1979).

Altitudinal Range: Black twinberry is present from sea level to at least 1525 m in British Columbia (UBC Bot. Garden 1979).

HABITAT

Climatic Relations: The distribution of black twinberry suggests that it tolerates a wide range of climatic extremes but is not adapted to the extremely short growing season and harsh winter temperatures found in northern British Columbia and at high elevations. In various parts of its range, however, black twinberry appears to be prevalent in frost pockets or areas of cold air drainage (R. Coupé and A. Ceska, pers. comm., Nov. 1984).

Site and Soil Conditions: Black twinberry is a species of swamps, riparian habitats, alluvial soils, and moist woods (Lyons 1952; Viereck and Little 1972; Marchant and Sherlock 1984).

Nutrient Relations: Clark (1976) observes that black twinberry favours rich soil. Ecosystem associations in which black twinberry appears as a characteristic understory species typically have a medium to very rich nutrient status (Comeau *et al.* 1982; Pojar *et al.* 1982).[163]

Water Relations: Black twinberry is described as being a species of moist or wet soils (Lyons 1952; Viereck and Little 1972; Marchant and Sherlock 1984). In climatically humid areas such as the Interior Wet Belt it occurs on submesic to subhydric hygrotopes, whereas in climatically drier areas it tends to be restricted to hygric and subhydric sites (Comeau *et al.* 1982; Angove and Bancroft 1983).[164]

Light Relations: Black twinberry will tolerate semi-shade (Marchant and Sherlock 1984) but is most vigorous in open situations where sufficient moisture is available.

Temperature Relations: No information.

GROWTH AND DEVELOPMENT

Phenology: Black twinberry breaks bud in April in the Kimsquit Valley on the central British Columbia coast,[165] and between early and late May on the east slope of the U.S. Rocky Mountains (Schmidt and Lotan 1980). In the Rockies, leaves are fully grown by mid-June, and leaf-fall occurs between late August and late September. In contrast, at Kimsquit some leaves are fully expanded by mid-April. In early August, the first leaves begin to turn yellow and most shrubs retain some leaves until October.

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[163] Delong *et al.* 1984.

[164] Ibid.

[165] Hamilton 1984.

Flowering begins after the leaves open. In the Rocky Mountains, flowering occurs between late May and early July (Schmidt and Lotan 1980). On the British Columbia coast flowering can begin in April[166] and some plants can continue to flower until the end of August even as the fruits ripen (Clark 1976). Fruits ripen from mid-July to late August at low elevations in coastal British Columbia (Marchant and Sherlock 1984)[167] and throughout July only in the eastern Rockies (Schmidt and Lotan 1980).

REPRODUCTION

Seed Production and Dispersal: Each fruit has four to five seeds. Dispersal is primarily by birds and mammals (USDA 1974; UBC Bot. Gardens 1979); cedar waxwings are especially fond of the berries (Marchant and Sherlock 1984).

Seed Viability and Germination: Air-dried seeds can be stored for up to 15 years at 1–3°C without loss of viability, and for several years at warmer temperatures (USDA 1974; Marchant and Sherlock 1984). The lengthy period of viability suggests that black twinberry may be a seed banker; seeds remain buried in the forest floor until conditions become conducive to germination. The seeds have some embryo dormancy and require a chilling period of 45–60 days for satisfactory germination to occur. A scarification treatment of the seed coat also improves germination. High germination percentages (56–80%) have been obtained under artificial conditions (USDA 1974; Marchant and Sherlock 1984).

Vegetative Reproduction: Several *Lonicera* species sucker from a spreading root system (Jackson 1974), but there are no reports of this for *L. involucrata*. Artificial cuttings taken during the dormant season rooted well when a rooting hormone was applied (Marchant and Sherlock 1984).

PESTS

Marchant and Sherlock (1984) report that young plants are susceptible to leaf miner and that a leaf-deforming fungus which slows growth is prevalent in the southern Interior. The following diseases have been identified on *L. involucrata* in the wild in British Columbia: *Kabatia lonicerae* var. *involucrata* (leaf spot), *Microsphaera penicillata* (powdery mildew), *M. alni, Leptophaeria dumetorum,* and *Ophiobolus minor* (UBC Bot. Garden 1979).

EFFECTS ON CROP TREES

Black twinberry is a competitor of moderate, but not major, importance throughout most of its range in the province. It is primarily found as a component of a complex, vigorous brush community on moist productive ecosystems in many biogeoclimatic zones (C. DeLong, R. Coupé, and D. Lloyd, pers. comm., Nov. 1984; J. Pollack, pers. comm., Jan. 1985). Very little is known about its competitive ability or any negative or beneficial effects that it may have on coniferous tree growth.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Eis' study (1981) in the SBS zone north of Prince George showed that black twinberry was present and numerous on both the Devil's Club and Alluvium site types prior to logging. Six years after logging, black twinberry had become common on the *Aralia–Dryopteris* site type, had greater than 25% cover on the Devil's Club site type, and was the dominant species (40% cover) on the Alluvium site type. Twinberry had produced a small quantity of seed and had almost reached a mature height on the Alluvium site by the end of the first season following logging. Shrub density increased for several years following logging and was 120 cm high within 2.5 years. It took the shrubs 7 years to reach this same height on the Devil's Club site type.

Fire: On boreal sites, severe burns often eliminate twinberry, but light burns stimulate vigorous resprouting (Ahlgren 1960). In the oak fern community in seral SBSwk ecosystems, black twinberry was consistently present after burning. In the Queen's Cup ecosystem, it was more commonly killed by burning and resprouting and growth of the species was fairly slow. Black twinberry reached a maximum height of about 1.5 m after burning in the SBSwk subzone. Twinberry was 1.2 m tall within 2 years on burned SBSmk

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[166] Hamilton 1984.

[167] Ibid.

Horsetail sites and after 7 years on burned SBSmk Devil's Club sites. Burned sites in the SBSwk and SBSmk subzones with the greatest cover of twinberry were in the Horsetail association. Re-establishment from buried seeds did not occur during the first 10 years after burning in the SBSwk subzone (Hamilton and Yearsley 1988).

Cutting: No information.

Herbicides: Broadcast applications of glyphosate applied from mid-July to the fall have caused very severe injury to twinberry in British Columbia (J. Pollack, pers. comm., Jan. 1989; D. Barron, pers. comm., May 1989; Boateng and Herring 1990).[168,169] Broadcast applications of 1.5–2.1 kg a.i./ha have been effective.

Spot or broadcast applications of hexazinone have caused variable injury to twinberry in British Columbia (Boateng and Herring 1990). A fall application of 3.6 kg a.i./ha hexazinone in the SBS zone in the Prince Rupert Forest Region resulted in moderate control of twinberry in the third growing season.[170] Third-year canopy cover and height of twinberry were near or greater than pre-treatment levels following several methods of hexazinone application (granular and liquid; spot and broadcast; 2 and 4 kg a.i./ha) carried out in mid-April in the CWH zone near Chilliwack.[171]

Soil Disturbance: Twinberry increased in cover after intense mechanical site preparation in the SBSmk2 variant in the Mackenzie Forest District (D. Greenley, pers. comm., May 1989).

WILDLIFE

Food: Black twinberry is not a common browse species in British Columbia (T. Lea, pers. comm., Feb. 1989) but is a moderately important winter food for Roosevelt elk and moose.[172] The berries are the most common part of the plant eaten[173] and provide summer food for birds, black bears, grizzly bear, and other mammals on the coast (USDA 1974; UBC Bot. Garden 1979; Marchant and Sherlock 1984; National Wildlife Foundation 1987; Lofroth 1988). However, it can be unpalatable to snowshoe hares in Alberta (Keith *et al.* 1984, cited by Carreker 1985).

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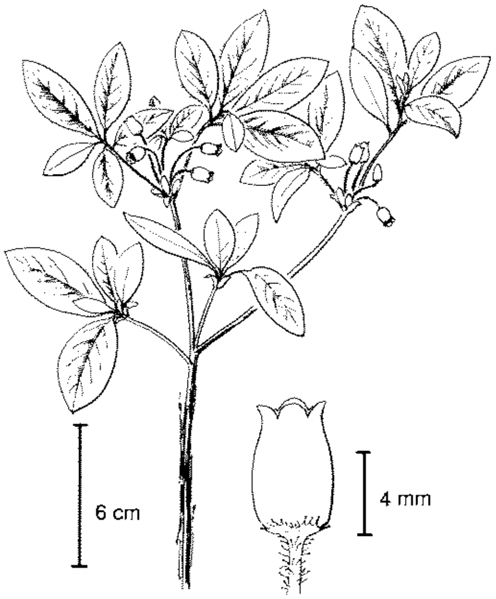
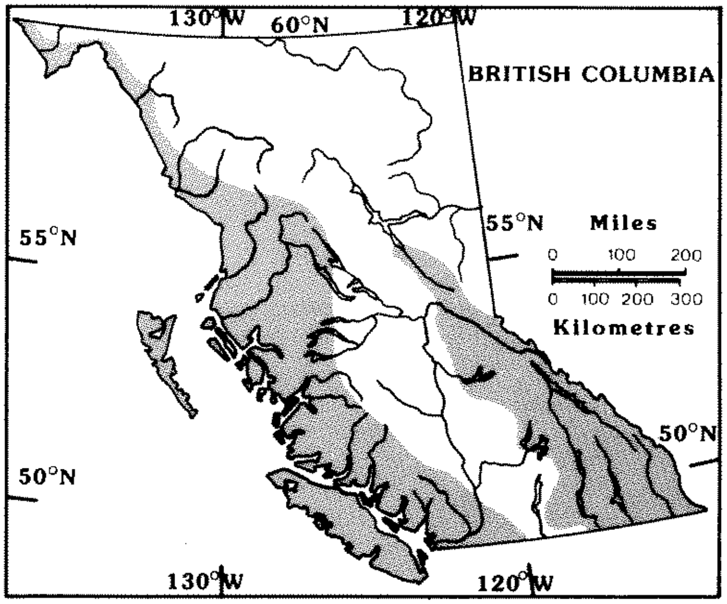
[168] Herring 1984a.
[169] George 1989.
[170] Newhouse 1988b.
[171] D'Anjou 1988b.
[172] Blower 1982.
[173] B.C. Min. Environ. (undated).

Menziesia ferruginea
(false azalea)





Distribution of *M. ferruginea* in British Columbia.

Menziesia ferruginea Sm. **False azalea**

(Rusty menziesia, Pacific menziesia)

DESCRIPTION

False azalea is an erect, spreading, deciduous shrub to 2 m tall with slender, widely forking, opposite branches. Young twigs are finely pubescent and older branches are smooth or have loosely shedding bark. Leaves are thin, oblong to obovate, up to 6 cm long, and slightly toothed along margins. Branches are opposite, but leaves appear to be arranged in whorls. Leaves sometimes have a distinct bluish colouration. The small, yellowish-red, bell-shaped flowers are borne in small terminal clusters on shoots of the previous year. The fruit is a thin-walled, reddish-brown ovoid capsule that splits along four partitions at maturity. The opened dry capsules often persist throughout the winter (Szczawinski 1962; Viereck and Little 1972).

Variation: Two subspecies of false azalea are found in British Columbia. *Menziesia ferruginea* ssp. *ferruginea* is found along the coast and in the central Interior, while ssp. *glabella* is found in southeastern B.C. only. The latter subspecies is differentiated from the former by its more rounded leaves and greater pubescence (Szczawinski 1962; Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

False azalea occupies coastal and mountain areas throughout the moist regions of British Columbia. It extends along the entire length of the province on the west side of the Coast Mountains and is also present in the Interior Wet Belt. It is rare, however, in the Interior Plateau and all of northern British Columbia east of the Skeena Mountains (Szczawinski 1962; Hickman and Johnson 1969). False azalea is present in many biogeoclimatic zones except the PP, BG, IDF, BWBS, and SWB, but it is abundant in only the CWH, MH, and ESSF zones.

Altitudinal Range: Along the coast, false azalea is common from sea level to the alpine tundra, although it is generally absent in the CDF and drier CWH zones of the south coast. East of the Coast Mountains, it tends to be found only at higher elevations, above approximately 900 m in the ICH and ESSF zones.

HABITAT

Climatic Relations: False azalea appears to require a fairly humid environment where only minor climatic moisture stresses are experienced during the growing season. This would explain why it occurs to sea level along most of the coast but retreats to more moist mountainous areas inland and along the Strait of Georgia. The dry central Interior of the province is described as "climatically unsuitable" for *M. ferruginea* by Hickman and Johnson (1969). These authors report that throughout western North America it becomes dominant in areas of high rainfall or persistent fog or mist. False azalea is also apparently unable to tolerate the extremely cold boreal climate of northeastern British Columbia. Evidence from other species suggests that adequate snow cover may be a critical factor in protecting false azalea from desiccation (Bowers 1960b).

Site and Soil Conditions: False azalea is well developed in mesic habitats but can occur on a wide variety of sites including shallow rocky and deep wet soils (Hickman and Johnson 1969).[174] Soils on which false azalea is typically found are predominantly Humo-Ferric or Ferro-Humic Podzols with a mor humus (see, e.g., Pojar (editor) 1983; Haeussler *et al.* 1984).

Nutrient Relations: In British Columbia, ecosystem associations on which false azalea is a significant understory component often have very poor to medium nutrient status (see, e.g., Klinka 1977b),[175] but it can occur over a wide range of nutrient regimes.[176] False azalea is typically found on sites with low pH (Brooke *et al.* 1970; Haeussler *et al.* 1984).[177] In the cedar–hemlock forests of northern Idaho, it is associated with soils low in potassium and with a high organic matter content (Mueggler 1965).

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[174] Banner *et al.* 1984.

[175] Ibid.

[176] Banner *et al.* 1983.

[177] Lloyd (compiler) 1984.

Water Relations: In moist climates, false azalea is most abundant on well- to moderately well-drained soils with a more-or-less mesic moisture status (Hickman and Johnson 1969; Viereck and Little 1972; Klinka 1977b). In very wet climates, both in the Interior and on the outer coast, false azalea can be very abundant on xeric sites (Angove and Bancroft 1983).[178,179] The species is also abundant in poorly drained coastal bogs (Hickman and Johnson 1969).[180]

Light Relations: False azalea is a common species of deeply shaded climax western hemlock forests (Szczawinski 1962; Viereck and Little 1972). Its ability to persist in these heavily shaded forest understories in which light intensities are typically 5% of full light (P. Alaback, pers. comm., Dec. 1984) indicates that it is very shade tolerant. However, the species usually displays its best vigour in the partially shaded conditions of forest openings among the tree clumps characteristic of the mature subalpine forests of the ESSF and MH zones (Brooke *et al.* 1970; Caza, pers. observ., 1987).

Temperature Relations: No information.

GROWTH AND DEVELOPMENT

False azalea can reach heights of 3 m at maturity (Viereck and Little 1972), but it is usually no more than 2 m tall (Clark 1976). The longevity of false azalea plants is not known, but other co-occurring ericaceous species may live over 100 years and Alaback's (1982) study indicates that plants survive at least 30 years in northern forests.

Phenology: In Alaska, false azalea flowers from late May through July. Leaves expand in early June at the time flowers open; they begin to senesce in mid-August and September at high elevations in the province (C. Caza, pers. observ., 1987). The capsule matures in July or August (Viereck and Little 1972).

REPRODUCTION

Seed Production and Dispersal: Numerous tiny seeds are produced in capsules, which open through natural dehiscence at maturity (Szczawinski 1962). Seed is dispersed by gravity and wind.

Seed Viability and Germination: No information.

Vegetative Reproduction: False azalea sprouts from root crowns and adventitious stem buds after destruction of above-ground stems (Miller 1977; Coates 1987). The species also appears to be capable of layering by forming roots from adventitious buds along stems (C. Caza, pers. observ., 1987). Layering is an effective means of growth and expansion at high elevations where heavy snow loads keep branches close to the ground. False azalea does not spread by means of rhizomes (Miller 1977).

EFFECTS ON CROP TREES

Competition: There have been no reports of dense, pure populations of false azalea, and the shrub is rarely the most abundant or aggressive member of shrub complexes (Miller 1977; Stickney 1980; Coates 1987). Nevertheless, false azalea is a member of the ericaceous shrub complex that is abundant on well-drained, usually more-or-less mesic sites along the coast of British Columbia and in moist mountainous areas of the Interior. The complex, common in the MH and ESSF zones, commonly includes *Rhododendron albiflorum* and *Vaccinium* spp. In coastal British Columbia, the *Vaccinium–Menziesia* shrub community is rarely a specific target of vegetation management efforts because it is perceived as having much less impact on the regeneration of conifers than the brush communities on productive low elevation sites. In contrast, in some areas of the southern Interior, such as the ESSF zone in the Kamloops Forest Region, the *Rhododendron albiflorum–Vaccinium* ssp.–*Menziesia ferruginea* complex is considered a major brush problem.

Although the complex in which false azalea occurs is very abundant and often dominates logged sites, research on its effects on the establishment and growth of crop trees is limited. Coates (1987) found that regrowth of false azalea after manual cutting or mechanical scarification is slow, indicating that conifer

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[178] Banner *et al.* 1983.
[179] Delong *et al.* 1984.
[180] Banner *et al.* 1984.

seedlings planted promptly after shrub reduction treatments are unlikely to be overtopped by the shrub. This suggests that it is relatively easy to maintain control of above-ground competition from false azalea. On ESSF sites where false azalea and its associates are left untreated, Coates (1987) suggests that shading is the most important mechanism of above-ground competition. Shading reduces light available to conifer seedlings and also reduces soil temperature throughout the growing season.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: The response of false azalea to overstory removal depends on the degree of ground disturbance. Logging on snow causes little destruction to mature false azalea in subalpine fir–Engelmann spruce forests. Summer logging damages false azalea, at least in patches, and commonly results in very slow recovery of the shrub and invasion of perennial herbs including *Epilobium angustifolium* and *Valeriana sitchensis*. In the cedar–hemlock forests of northern Idaho, there was no significant difference between the cover and frequency of false azalea on logged and unlogged sites (Mueggler 1965). On the central Oregon Coast, Alaback and Herman (1988) found that the percent cover of false azalea was greatest on heavily thinned plots and least in the undisturbed forest. Biomass of false azalea in early successional stands (up to 30 years) in southeastern Alaska was 3 times greater than the biomass in climax western hemlock–Sitka spruce forest (Alaback 1982).

Fire: False azalea is a fire-sensitive species (Stickney 1981). Miller (1977) speculates that it will sprout from the root crown after a burn but will not produce suckers. Fire appears to have totally removed this species from experimental plots in Washington and Oregon for up to 16 years (Morris 1970). In the ESSF zone in British Columbia, burning provides very effective control of false azalea for at least 10 years even though it is not completely killed (J. Wright, pers. comm., July 1989).[181] In western Montana, Stickney (1981) found that survival of false azalea was low and it was very slow to develop after fire, especially on areas which had been severely burned. On the other hand, Mueggler (1965) reported no significant difference in cover and frequency between burned and unburned areas in northern Idaho.

Cutting: False azalea does not respond vigorously to cutting. Stems cut in June on sites in the ESSFwc subzone regrew 2–75 cm by August of the same year. Average regrowth was 30 cm, or about 19% of the original height (C. Caza, pers. comm., July 1989). False azalea sprouted 40 cm in 1 year following a manual cutting treatment in the Penticton Forest District.[182] After false azalea was cut in early July at another ESSFwc site, new shoots averaged 1.3 cm in height by the end of the second growing season (Coates 1987). This represents slower growth on this site than that of associated shrubs (*Rhododendron albiflorum, Vaccinium membranaceum, Vaccinium ovalifolium*). Almost all new shoots arose from buds on existing stems rather than as sprouts or suckers from the soil. Height growth of false azalea was more vigorous in the second year after cutting than in the first. By the end of the second growing season, the tallest false azalea plant was 14.8 cm tall, or 13% of its pre-cut height. Mean crown area was 30% of the pre-cut level. Twenty-six percent of the original stems had new shoots after the first growing season. Stems with new shoots had an average of 5.6 shoots per stem, twice as many as any of the associated shrubs. A second cutting 1 year after the first did not affect regrowth vigour (Coates 1987).

Herbicides: False azalea was very susceptible to broadcast applications of 2.1 kg a.i./ha glyphosate applied in the ESSF and ICH zones in September near Revelstoke, Salmon Arm, Blue River, and Penticton (J. Wright, pers. comm., July 1989).[183,184] Control was effective for at least 2 years. Lower application rates are reported to cause partial control and more vigorous resprouting. For example, Simard[185] reported that September applications of 0.7 and 1.4 kg a.i./ha glyphosate resulted in 70% control after 2 years, with vigorous sprouting 2 years after the lowest application rate. In the same study, application of 2.1 kg a.i./ha provided 90% control and only weak sprouting after 2 years.

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[181] Mather 1986.

[182] Noble-Hearle 1989.

[183] Dyke 1987.

[184] Simard 1988.

[185] Ibid.

Soil Disturbance: In the ESSFwc subzone near Clearwater, scarification that removed tops or uprooted entire false azalea plants caused severe damage. Few new shoots were produced by surviving plants. Two growing seasons after treatment, there was no sign of new sprouts from the soil (Coates 1987).

WILDLIFE

Food: False azalea is seldom browsed and is generally considered unimportant to ungulates in British Columbia. However, it can be a moderately important browse for Columbian black-tailed deer and Roosevelt elk.[186] Although it is considered relatively unpalatable to Sitka black-tailed deer, the over-population of these ungulates on the Queen Charlotte Islands has depleted the species in many places.[187] In Alaska, false azalea was much more abundant outside deer enclosures than where deer were allowed to feed (Hanley 1987).

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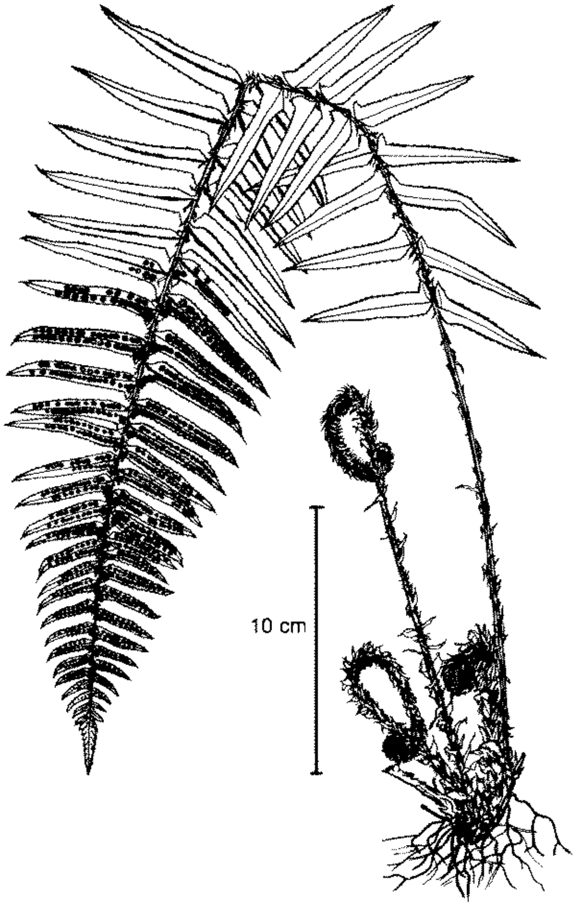
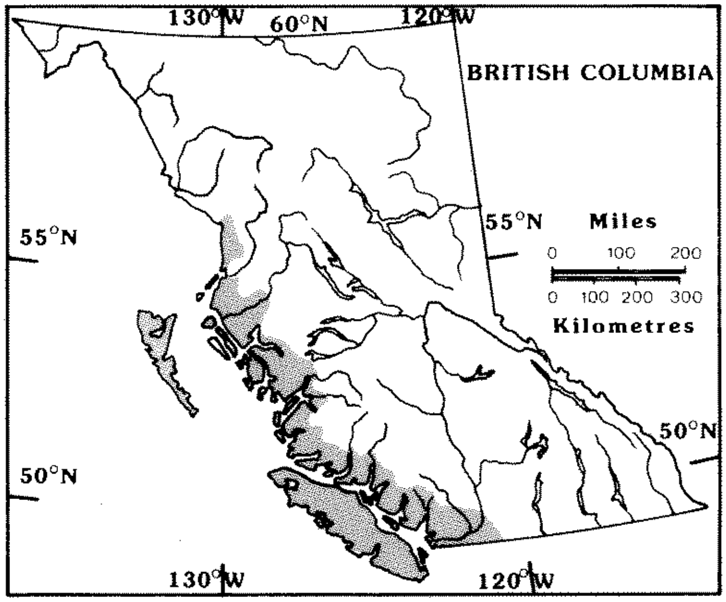
[186] Blower 1982.

[187] Pojar and Banner 1984.

Polystichum munitum
(sword fern)





Distribution of *P. munitum* in British Columbia.

Polystichum munitum (Kaulf.) Presl. Sword fern

DESCRIPTION

Sword fern is a large fern with stiff, erect fronds up to 1.8 m tall, rising from a stout, woody rhizome. The blades are evergreen, linear to lanceolate, with numerous toothed, sharp-pointed pinnae. The pinnae have a characteristic hilt-like projection near the base (Taylor 1973a; Wagner 1979).

Variation: Size and frond shape vary widely, particularly in response to environmental conditions (Taylor 1973a). A type of sword fern with a very narrow linear blade and closely crowded overlapping pinnae is common in exposed locations. There is some disagreement as to whether this fern represents an ecological form of *P. munitum* (forma *imbricans)* produced in response to extreme environmental conditions (Frye 1934; Taylor 1973a; Taylor and MacBryde 1977), or whether it is a distinct taxon (Wagner 1979).

DISTRIBUTION AND ABUNDANCE

Sword fern is widespread and common west of the Coast Mountains along the entire length of British Columbia, including the Queen Charlotte Islands. It is also found in the moist forests of the west Kootenays. In the U.S., the species extends inland to northern Idaho and Montana (Wagner 1979). Sword fern is abundant in the CDF and CWH biogeoclimatic zones and uncommon in the MH and ICH zones

Altitudinal Range: Sword fern is primarily a low elevation species in British Columbia. In southwestern British Columbia it is rarely found at elevations above 900 m (Brooke *et al.* 1970). On the north coast it is even more restricted in elevation, rarely found more than 100 m above sea level.

HABITAT

Climatic Relations: The geographic and altitudinal range of this species suggests that it requires a humid coastal climate with mild winters. It also occurs in areas of moist, relatively mild continental climate in Idaho and Montana and adjacent areas of British Columbia, but in these areas it tends to favour the shaded, moist northern aspects (Mueggler 1965). The evergreen frond of sword fern may be a limiting factor in its ability to survive in areas with cold winters.

Site and Soil Conditions: Sword fern will grow on a wide variety of parent materials including exposed bedrock, but the most luxuriant growth is found on deep loamy soils, especially those developed on fluvial parent materials (see, e.g., Klinka and Carter 1980).

Nutrient Relations: Sword fern grows best and is most abundant on fertile soils (Taylor 1973a; McMinn *et al.* 1976). Ecosystem associations with this species as a characteristic understory species are usually medium to very rich in nutrients (see e.g., Klinka 1977a).[188] When abundant and vigorous, sword fern is often considered to be an indicator of nutrient-rich sites.

Water Relations: Sword fern is characteristically found in moist or shaded locations, where drainage is good but little moisture stress is encountered. In the CDF zone of southern Vancouver Island, where summer moisture deficits are common, it is found only where seepage water augments the soil moisture supply (McMinn *et al.* 1976). In wetter climates it is less restricted by soil moisture supply. Ecosystem associations in which sword fern is abundant typically have a mesic to hygric moisture status (see e.g., Klinka 1977a).

Light Relations: Sword fern is apparently shade tolerant since it typically occurs in the understories of mature forests and favours shady sites or north aspects (Mueggler 1965; Taylor 1973a). In clearcut areas it often prefers protected, shaded locations.[189] This probably reflects sensitivity to high evapotranspirative losses rather than intolerance of light itself. When plants of *P. munitum* are subjected to increased insolation through removal of overstory shade, the fronds become dwarfed and more erect and the pinnae become crisped (Frye 1934; Taylor 1973a; Wagner 1979).

Temperature Relations: The evergreen frond of sword fern is presumably at least moderately resistant to frost.

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[188] Yole *et al.* 1982.

[189] Brand 1984.

GROWTH AND DEVELOPMENT

See *Athyrium filix-femina* for a simplified explanation of the fern life cycle. The growth and development of sword fern is probably quite similar to that of lady fern except that sword fern fronds are evergreen and thus persist for several years. At maturity the frond is 60–180 cm in length and approximately 25 cm wide (Taylor 1973a; Wagner 1979).

Phenology: Stewart (1976) reported that, in Oregon, sword fern fronds were partially unfurled on May 26. By July 28, the fronds were mature and spores were nearing maturity.

REPRODUCTION

Spore Production and Dispersal: Most medium-sized forest ferns begin to produce spores at between 1 and 5 years of age and spore production takes place very regularly from year to year. The vigour of the plant, as influenced by its habitat, is an important determinant of plant fertility. Most ferns similar in size to sword fern produce tens of millions of spores on each frond. The tiny spores are ejected into the air when mature and are carried away by gravity, wind, water, or animals. Evergreen ferns like *Polystichum* can retain some spores on the fronds over winter for dissemination the following spring. Fern spores are capable of travelling thousands of miles, but in forests there may be a lack of air currents to carry them aloft. Airborne spores are often brought to earth during rainstorms (Page 1979).

Spore Viability and Germination: Fern spores in a dry, resting state are resistant to physical extremes and can withstand intense radiation and very low temperatures. They are reportedly very sensitive to temperatures above 55°C (Kato 1963; Miller 1968). Under ideal conditions, fern spores remain viable for 2–4 years, but their viability and the speed of germination deteriorates with age (Page 1979). Spores usually germinate only after being soaked in water. Like most fern spores, the spores of sword fern germinate best when exposed to light, but sword fern is one of only a few fern species in which some germination will occur in darkness (Weinberg and Voeller 1969).

Vegetative Reproduction: Vegetative reproduction of sword fern can occur through division of its perennial, woody rhizome. The rhizome becomes somewhat branched with age (Wagner 1979) but is apparently not creeping. Although the species often occurs in pure, uniform stands, these stands probably represent populations of individual sporophytes rather than clones.

PESTS

No information.

EFFECTS ON CROP TREES

Competition: Sword fern is a dominant species of understory vegetation on some of the most productive growing sites for Douglas-fir and other conifers in British Columbia (Wagner 1979; Klinka and Carter 1980). However, it is not considered a serious or major competitor on the Coast since it interferes significantly with the regeneration and growth of conifers only in localized areas where it is extremely abundant or vigorous (Stewart 1976; M. Scott, pers. comm., Nov. 1984).[190] Reduction or elimination of sword fern from conifer plantations may reduce competition for moisture and light and may reduce the desirability of these plantations as habitat for tree-damaging mammals (Stewart 1976), but the magnitude and exact nature of the competitive effect have not been studied.

Allelopathy: del Moral and Cates (1971) studied the allelopathic potential of sword fern in western Washington; they found no evidence of inhibitory chemicals under either laboratory or field conditions.

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Limited evidence suggests that sword fern initially decreases in cover following logging (M. Scott, pers. comm., Nov. 1984; B.M. Geisler, pers. comm., Jan. 1985), but that it slowly

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[190] Brand 1984.

recovers (Lafferty 1972). Following logging of moist, productive sites in the CWH zone near Vancouver, sword fern, previously an important understory species, could only be found in shady spots under a protective canopy of bigleaf maple.[191] In contrast, 17 years after thinning of a spruce–hemlock stand on the central Oregon Coast, sword fern attained higher percent covers on heavily thinned blocks than on lightly thinned blocks (Alaback and Herman 1988). It seems likely that sword fern, like lady fern, is able to maintain its cover on sites where soils remain moist after logging, and that its cover is diminished on exposed and drier sites where evapotranspirative stresses are severe. The fronds often become dwarfed in size following exposure to dry air and strong light (Frye 1934; Wagner 1979).

Fire: Slashburning studies in the CWH zone near Vancouver show that sword fern is capable of surviving even a severe fire (Lafferty 1972), but on some sites it may be absent for the first few years following a fire or restricted to unburned patches only.[192] In the western Cascades of Oregon, Schoonmaker and McGee (1988) found that sword fern averaged 8% cover in undisturbed forests, 2% cover on 2-year-old burns, 10% cover on 5-year-old burns, and 19% cover on 30-year-old burns. Morris (1970) found that sword fern was equally abundant on burned and unburned clearcut areas from the third to the sixteenth seasons following burning in western Washington and Oregon.

Cutting: No information.

Herbicides: In western Washington and Oregon, glyphosate causes very severe injury when applied in late summer and moderate injury when applied in the fall (Conard and Emmingham 1984a). In British Columbia, glyphosate is reported to cause very severe injury to sword fern (Boateng and Herring 1990). Sword fern was significantly controlled but not eliminated one growing season after an early September broadcast application of 1.4 kg a.i./ha glyphosate near Campbell River on Vancouver Island (J. McLarnon, pers. comm, May 1989).

Broadcast applications of hexazinone have caused moderate injury to sword fern in British Columbia (Boateng and Herring 1990). D'Anjou (pers. comm., June 1989) found a 45% decrease in sword fern cover following a 4 kg a.i./ha hexazinone application.

Applications of 2,4-D in the winter or amitrole in the spring are reported to provide poor control of sword fern in western Washington and Oregon (Conard and Emmingham 1984a).

In Oregon, dicamba and bromacil effectively controlled sword fern when applied at any time between mid-May and mid-July (Stewart 1976).

Soil Disturbance: No information.

WILDLIFE

Food: Extensive use of sword fern is generally limited to periods when animal populations reach high densities (e.g., introduced Sitka deer on the Queen Charlotte Islands) and preferred foods are limited in distribution (Klein 1965).

Sword fern is a moderately important food for black-tailed deer year-round (Singleton 1976). Leslie *et al.* (1984) found that sword fern made up 13% of the annual diet and 70% of the winter diet of this deer at a site in Washington (Jones 1975).

Sword fern is an important winter food for mountain beaver in Oregon (Stewart 1976). In British Columbia, mountain beaver has a very restricted range and therefore consumption of sword fern by this mammal is limited to a small geographic area in the southwest of the province.

Black bears sometimes forage on this fern (Frye 1934; Pojar *et al.* 1984).

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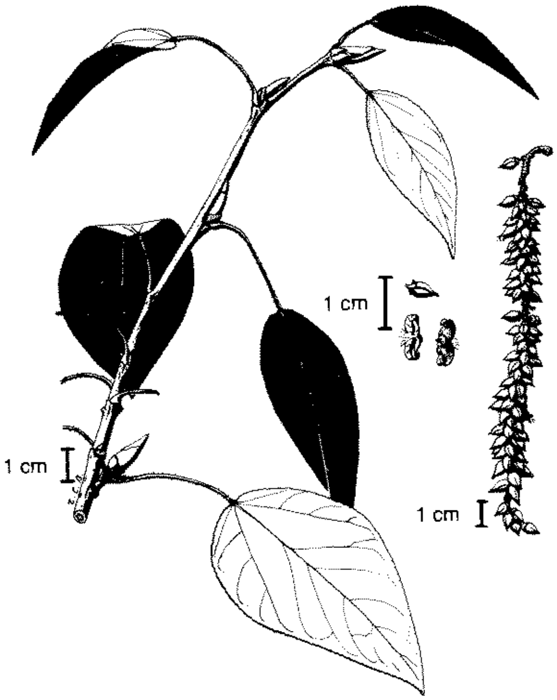
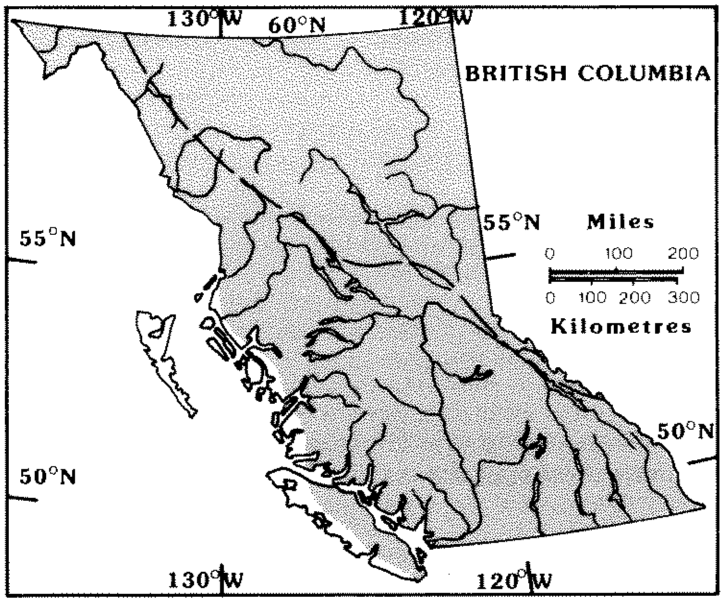
[191] Brand 1984.

[192] Ibid.

Populus balsamifera* ssp. *balsamifera
(balsam poplar)





Distribution of *P. balsamifera* in British Columbia. The dashed line indicates the approximate boundary between ssp. *balsamifera* (balsam poplar) to the north and east, and ssp. *trichocarpa* (black cottonwood) to the south and west. Specimens intermediate between the two subspecies are common where their ranges overlap.

Populus balsamifera L. ssp. *balsamifera* **Balsam poplar**

DESCRIPTION

Balsam poplar is a deciduous tree with a long straight trunk and an open crown, reaching 35 m in height and 60–80 cm in diameter. The bark is grey and deeply furrowed. The twigs are stout with large, pointed, resinous buds. Leaves are broadly lanceolate to ovate and untoothed. The fluffy seeds are produced on long drooping catkins (Hosie 1973; Hultén 1974).

Variation: No geographic varieties of balsam poplar are described in British Columbia (Taylor and MacBryde 1977). Balsam poplar hybridizes extensively with the closely related black cottonwood (*P. balsamifera* ssp. *trichocarpa*) and may hybridize with *P. tremuloides* in some areas (Hosie 1973; Hultén 1974).

DISTRIBUTION AND ABUNDANCE

Balsam poplar is found across Canada but is replaced by black cottonwood through most of British Columbia. In this province, it is restricted to areas adjacent to or east of the Rocky Mountains in the Peace River and Fort Nelson lowlands (Hultén 1974) and east of the Rocky Mountain Trench (Krajina *et al.* 1982). It extends westward in northern British Columbia to the Stikine Plateau. Balsam poplar is abundant in the BWBS zone, less common in the SWB zone, and occurs sporadically in some eastern subzones of the SBS, IDF, and ICH (Krajina *et al.* 1982).

Altitudinal Range: Balsam poplar grows from sea level in Alaska to 1650 m elevation in the Rocky Mountains (Fowells (compiler) 1965). It is primarily a lowland species (Hosie 1973; Zasada *et al.* 1981).

HABITAT

Climatic Relations: Balsam poplar is primarily a species of boreal climates, although it occurs in arctic to temperate climates. The boreal climate is characterized by frozen ground and snow cover for 6 or more months duration with the average temperatures below -3°C during the coldest month and rarely above 10°C in the warmest month (Krajina *et al.* 1982).

Site and Soil Conditions: Balsam poplar is most commonly found on moist upland and alluvial bottomland sites. It exhibits its best growth on moist, rich, bottomlands with deep soil. Where balsam poplar occurs together with black cottonwood, the cottonwood generally inhabits the alluvial sites, and balsam poplar the uplands. Balsam poplar rarely grows on dry, exposed sites. Soils supporting balsam poplar vary widely and include gravels, deep sands, clay loams, silts, silt loams, and shallow organic soils, but not deep peats (Fowells (compiler) 1965; Hosie 1973; Brayshaw 1978; Zasada *et al.* 1981).

Nutrient Relations: The nutrient requirements of balsam poplar are high; it does not tolerate acid mor humus forms in which nutrients are slowly released. Balsam poplar requires a good supply of calcium and magnesium and prefers nitrates to ammonium as a supply of nitrogen (Krajina *et al.* 1982). In the BWBS zone of northeastern British Columbia, it is most abundant on river terraces described as having a rich nutrient status.

Water Relations: An abundant supply of soil moisture is critical for good growth of balsam poplar (Fowells (compiler) 1965), but it does not tolerate brackish water. It is most often found on sites with a subhygric to hygric moisture status. Flood resistance of balsam poplar is possibly the highest among the trees growing in British Columbia (Krajina *et al.* 1982).

Light Relations: Balsam poplar has very low shade tolerance (Krajina *et al.* 1982). Best growth and development occurs in full sunlight; it will not grow in competition with other species unless it is in a dominant position (Fowells (compiler) 1965). Growth of shaded balsam poplar seedlings was significantly less than that of unshaded seedlings in a greenhouse experiment in Alaska (Walker and Chapin 1986).

Temperature Relations: The frost resistance of balsam poplar is very high; it can become established in areas of permafrost (Krajina *et al.* 1982). In the taiga of interior Alaska, balsam poplar grows on sites with low soil temperature, where surficial soil layers do not completely thaw until well into the growing season and frosts are common well into June (Foote 1983).

GROWTH AND DEVELOPMENT

Balsam poplar is characterized by rapid early growth that allows it to establish and maintain dominance above other vegetation. Rapid growth can be maintained for the first 40–50 years of life by which time it can reach heights of 25 m and diameters of 45 cm. Mature trees in southern Alaska average 35 m in height and 66 cm in diameter (Foote 1983); however, trees in eastern North America are typically smaller (Fowells (compiler) 1965; Hosie 1973). Balsam poplar is relatively short-lived in southern parts of its range but can live as long as 200 years in Alaska (Fowells (compiler) 1965; Foote 1983). It normally has a shallow root system (Hosie 1973), especially on wet soils or where permafrost is present at shallow depths.

On good sites, balsam poplar will outgrow aspen. The dominance of balsam poplar over aspen on some newly formed alluvial sites in Alaska may be more related to flood tolerance than to growth relations.

Phenology: Catkins flower between April and June before the leaves appear. The seed matures very early, from mid-May to mid-June when the leaves are about two-thirds grown. Seed dispersal occurs immediately after the seeds are mature. Flowering and seed maturation times appear to be regular from year to year within ecotypic ranges (Fowells (compiler) 1965; USDA 1974).

REPRODUCTION

Seed Production and Dispersal: Balsam poplar first flowers between 8 and 10 years of age (USDA 1974); it subsequently produces a good seed crop every year (Lutz 1955). The seeds have downy plumes and are readily distributed by wind (Fowells (compiler) 1965; Brayshaw 1978), but seed deposition is greatly reduced at distances greater than 100–200 m from the seed source (Zasada *et al.* 1981).

Seed Viability and Germination: Balsam poplar seed remains viable for only a few days following dispersal (Fowells (compiler) 1965). The seeds will germinate over a broad range of temperatures (J. Zasada, pers. comm., Sept. 1989), often immediately after arriving on a suitable seedbed (Lutz 1955). Thus, most germinants appear in mid-summer. In an Alaska study, more than 80% of total germinants appeared within 2 weeks of artificial seeding and seedlings continued to appear for 3–4 weeks (Zasada *et al.* 1983).

Young balsam poplar seedlings are extremely susceptible to drying, rain damage, and soil fungi. They require at least 1 month of abundant moisture to ensure survival (USDA 1974). Zasada *et al.* (1981) observed no seedlings establishing on organic and gravel surfaces at an alluvial site in Alaska following harvesting of a balsam poplar overstory, but regeneration by seed is very common on these river bottom sites (Zasada 1971). Lutz (1955) reports abundant balsam poplar seedlings wherever mineral soil is exposed and a seed source is available. Walker *et al.* (1986) found that, on an Alaskan floodplain, a litter–forest floor seedbed strongly inhibited germination and/or initial establishment of balsam poplar. Seedling density was increased by 5- to 10-fold once the litter and forest floor were removed. On upland sites, J. Zasada (pers. comm., Sept. 1989) found no germination except on severely burned microsites.

Vegetative Reproduction: Balsam poplar will regenerate vegetatively from root suckers as well as from stump sprouts and buried branch pieces (Lutz 1955; Zasada *et al.* 1981). Stump sprouts originate from either dormant buds or from callus tissue. Callus sprouts usually originate at the top of a cut stump, or form where a stump has been damaged during logging. Most root suckers grow from roots of approximately 1 cm in diameter that occur within the top 2 cm of the soil. Suckers also develop from exposed roots. Suckering is significantly less in gravelly soil than in silty soils and is greatest where the organic layer has been removed, exposing mineral soil. Branch parts must be well buried in the soil to produce aerial shoots (Zasada *et al.* 1983). Sucker regeneration is probably more important than regeneration from seed for balsam poplar in Alaska (Lutz 1955).

PESTS

Primary disease and insect pests of balsam poplar are discussed in Fowells (compiler, 1965).

EFFECTS ON CROP TREES

Competition: There are no quantitative data on the effect of balsam poplar competition on conifers. Its growth easily outstrips the growth rates of young conifers, especially when it is of sucker origin. White spruce is the primary crop species occurring in association with balsam poplar, and many of the most productive alluvial growing sites in the boreal forest are occupied by fairly pure stands of balsam poplar (Neiland and Viereck 1977; Foote 1983).

Allelopathy: Balsam poplar has been shown to have an allelopathic effect on the germination and early growth of green alder (Jobidan and Thibault 1981).

Beneficial Effects: There are no reports in the literature of beneficial effects of balsam poplar on the growth of coniferous trees. It plays an important role in stabilizing river banks and maintaining river islands, and it may be a valuable crop tree in northern British Columbia.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Trees cut or damaged during logging will sprout from the stump or sucker from the roots; seedling germination will likely occur on areas of exposed mineral soil (Lutz 1955; Zasada *et al.* 1981). Removal of the overstory canopy from a site in Alaska resulted in very large increases in balsam poplar growth (Walker and Chapin 1986).

Fire: Of the tree species in the northern boreal forest, balsam poplar is perhaps the most resistant to destruction by fire (Lutz 1955). Like aspen, balsam poplar is stimulated to produce root suckers following fire. In Alberta, the majority of balsam poplar suckering occurred during the second season following spring burning of a 15-year-old stand (Bailey and Anderson 1979). Density after 5 years was greater on burned areas than on unburned areas.

Cutting: In an Alaskan study (Zasada *et al.* 1981), more than 50% of mature balsam poplar cut during the summer, fall, and winter produced sprouts from callus tissue and dormant buds. Many stumps had more than 25 sprouts after the first growing season. Sprout survival on trees cut in the fall and winter was high, but less than 15% of the trees cut in the summer had surviving sprouts after 4 years. Stump sprouting was most pronounced on winter-logged areas, and sprouts originating from dormant buds were most common after winter logging. Cutting also stimulates suckering from the roots, but there are no studies documenting suckering response. In the Fort St. John Forest District, the response of balsam poplar to girdling has been similar to the response of aspen to this treatment. Girdling is apparently effective in all seasons (P. Wadey, pers. comm., June 1989).

Herbicides: Glyphosate applied either by backpack spray or aerially at 2.4–3.0 kg a.i./ha has provided good to excellent control of balsam poplar.[193]

Hexazinone applied as a liquid spray, by soil injection, or in granular applications also provides good control of balsam poplar. This herbicide is ineffective in areas with deep organic layers. Liquid hexazinone resulted in 100% control of balsam poplar 1 year after application of 2.2, 3.2, and 4.3 kg a.i./ha in late May in Saskatchewan.[194] Similarly, excellent control of balsam poplar occurred in Alberta 2 years after mid-August and late October applications of undiluted hexazinone liquid at rates of both 4 and 8 mL per spot and either 1.5- or 2-m grid spacing.[195] Liquid hexazinone applied around stem bases at 0.24 to 0.48 g/cm of dbh gave effective seed tree control of balsam poplars that were 70 cm in diameter and 30 m tall.[196] Hexazinone gridballs aerially applied at 4 kg a.i./ha in late May to a mesic BWBSmw site near Dawson Creek provided extremely good control of balsam poplar for at least five growing seasons. Less than 1000 stems per hectare emerged on the treated plots compared with over 32 000 stems per hectare on the controls.[197]

Balsam poplar is resistant to 2,4-D and was less sensitive than aspen when sprayed with 2,4-D in the dormant season. Rates of 2.2 kg a.i./ha had virtually no effect and a rate of 4.4 kg a.i./ha provided only marginal control (Bowes 1981). Similarly, increasing the concentration of 2,4-D from 0.25 to 6.75 % did

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[193] Expert Committee on Weeds 1984-1988.
[194] Teskey and Masterson 1986e.
[195] Teskey and Masterson 1986a.
[196] Newhouse 1988b.
[197] Herring 1988b.

not significantly increase the damage to balsam poplar in northeastern Saskatchewan (Waddington and Bittman 1987). In Alberta, mortality was high on first-year suckers sprayed with 2.2 kg a.i./ha as a mid-summer foliage spray, but spraying did not prevent further suckering from taking place the following year (Bailey and Anderson 1979).

Soil Disturbance: Exposure of mineral soil favours germination of balsam poplar seed and may promote root suckering by increasing soil temperatures. Branch fragments buried as a result of soil disturbance have a high likelihood of regenerating. (Lutz 1955; Zasada *et al.* 1981). Following heavy flooding, balsam poplar quickly sends out new roots into the freshly deposited silt layers (Neiland and Viereck 1977).

Fertilization: On a floodplain site in interior Alaska, balsam poplar fertilized with NPK had significantly higher dry mass and stem growth (in some plots) than unfertilized seedlings. However, balsam poplar seedlings were less responsive to fertilization than willow. An NPK fertilization in the greenhouse raised the shoot:root ratio of balsam poplar seedlings from about 2 to 4 (Walker and Chapin 1986).

WILDLIFE

Food: Balsam poplar is a moderately important winter food for mule deer and Rocky Mountain elk in British Columbia.[198] Snowshoe hares browse heavily on balsam poplar in Alaska (Walker *et al.* 1986), and the tree is a preferred food of beavers (Denney 1952, cited by Allen 1982). Squirrels feed on flowers and leaf buds in the spring (Harestad 1983). Balsam poplar sprouts after browsing (T. Lea, pers. comm., Feb. 1989).

Other Resources: Eagles use balsam poplar for perching, and cavity nesters make their home in this tree.

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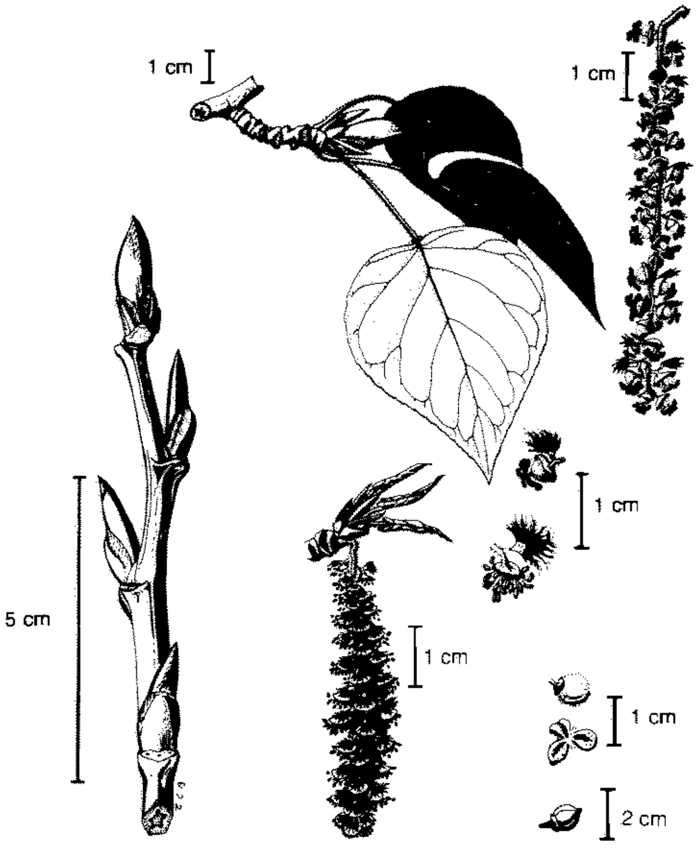
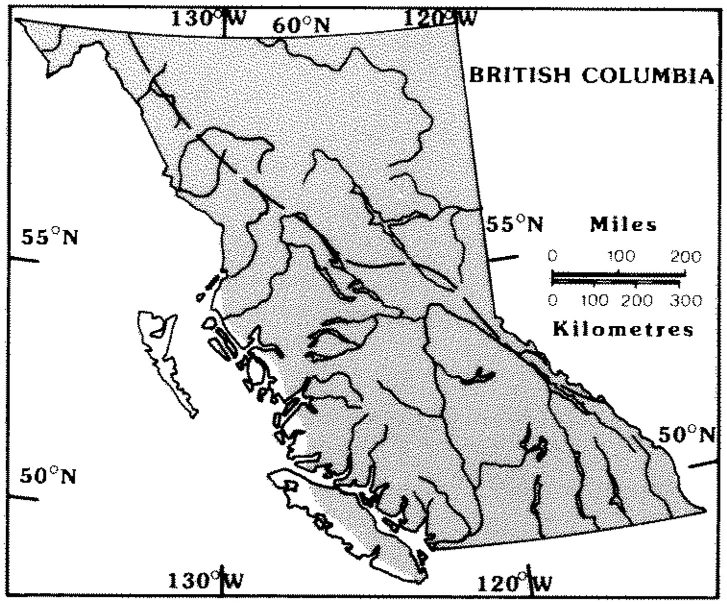
[198] Blower 1982.

Populus balsamifera* ssp. *trichocarpa
(black cottonwood)





Distribution of *P. balsamifera* in British Columbia. The dashed line indicates the approximate boundary between ssp. *balsamifera* (balsam poplar) to the north and east, and ssp. *trichocarpa* (black cottonwood) to the south and west. Specimens intermediate between the two subspecies are common where their ranges overlap.

Populus balsamifera L. **Black cottonwood**
ssp. *trichocarpa* (Torr. & Gray) Brays
(P. trichocarpa)

DESCRIPTION

Black cottonwood is a deciduous tree, up to 40 m high and 150 cm in diameter. The grey bark of mature trees is deeply furrowed; young bark is smooth. Twigs are stout and hairless, with large, resinous, pointed buds. Separate male and female flowers form long, drooping catkins which split to release seeds bearing cottony down. Black cottonwood differs from balsam poplar in having wider leaves and a three-valved rather than a two-valved fruit (Hosie 1973; Brayshaw 1978).

Variation: There are many intermediate forms between this subspecies and ssp. *balsamifera* where the ranges of the two overlap in northern British Columbia (Brayshaw 1978).

DISTRIBUTION AND ABUNDANCE

Black cottonwood is found throughout southern and central British Columbia to the edge of the Rocky Mountains. It is absent along the outer coast including northern Vancouver Island and the Queen Charlotte Islands. In northern British Columbia, it is present adjacent to the Alaska panhandle but is replaced by balsam poplar inland (Brayshaw 1978; Krajina *et al.* 1982). Throughout the province it is abundant in major river valleys. It is found in all biogeoclimatic zones except the SWB and AT.

Altitudinal Range: Although black cottonwood primarily grows in valley bottoms, it occurs from sea level to the lower limits of the MH zone on the British Columbia coast (Packee 1976) and has been recorded as high as 2100 m in elevation in the Selkirk Mountains of the Interior (Fowells (compiler) 1965).

HABITAT

Climatic Relations: Black cottonwood grows in climates ranging from relatively arid to humid, but it achieves its best development in areas of humid climate (Fowells (compiler) 1965). It is absent from the cool, perhumid areas of the outer British Columbia coast and is replaced by balsam poplar in the severe boreal climate of the northeastern province (Brayshaw 1978). It occurs marginally in subalpine climates (Krajina *et al.* 1982).

Site and Soil Conditions: Black cottonwood is characteristically associated with river banks, gravel bars, or low-lying land, but it also grows on the loams, clays, and rich humic soils of upland sites. Typical soils are young with little soil development. The largest trees grow at low elevations on deep alluvial soils, while the poorest growth is on newly deposited gravel (Lyons 1952; Roe 1958; Fowells (compiler) 1965).

Nutrient Relations: Nutritional requirements of black cottonwood are high. Like balsam poplar it requires a good supply of calcium and magnesium and does not grow well on acid mor humus forms where nutrients are released slowly (Krajina *et al.* 1982). A pH of 6–7 is required for optimum growth (Smith 1957, cited by Packee 1976). Black cottonwood commonly grows on deep alluvial soils that are among the richest, most productive growing sites in British Columbia.

Water Relations: Black cottonwood requires abundant, well-oxygenated water for optimum growth (Smith 1957, cited by Packee 1976). It is highly tolerant of flooding, and grows abundantly on sites that receive regular flooding, but it does not tolerate the brackish water that forms near the ocean or in stagnant pools following flooding. Fine sediment deposited by flooding tends to reduce soil aeration and inhibit cottonwood growth, whereas fast-moving water, rich in oxygen, speeds growth (Fowells (compiler) 1965; Krajina *et al.* 1982). Black cottonwood apparently has low tolerance of drought, and throughout most of its range is restricted to sites receiving supplemental moisture. There are reports (Shulte *et al.* 1987) that black cottonwood is incapable of closing its stomata, which would make it very poorly adapted to drought. In Washington, however, Pezeshki and Hinkley (1988) observed that while a long drought period during the growing season may significantly reduce red alder's growth, it may have less of an effect on black cottonwood's growth. In climatically dry areas it survives in protected valleys and canyon bottoms, where the roots can reach a permanent supply of soil moisture (Fowells (compiler) 1965).

Smith (1988) found that in a low-oxygen environment, rooted cuttings that were flooded for 6 weeks grew slower than unflooded seedlings. In a greenhouse experiment (Harrington, 1987), black cottonwood seedlings that were flooded a in low-oxygen environment for 20 days exhibited no differences in height growth in comparison to non-flooded seedlings. However, during the 20-day recovery period after flooding, the flooded seedlings had significantly slower height growth and put on significantly less root and leaf biomass than the non-flooded seedlings.

Light Relations: Black cottonwood is a shade intolerant species (Fowells (compiler) 1965; Krajina *et al.* 1982) that grows best in full sunlight. It does not survive in a forest understory.

Temperature Relations: While dormant, black cottonwood is one of the most frost-resistant trees in the northwestern U.S. (Minore 1979) although it can be killed or damaged by late fall frosts (Fowells (compiler) 1965). It is presumably less tolerant of cold temperatures than balsam poplar (Krajina *et al.* 1982).

GROWTH AND DEVELOPMENT

Black cottonwood exhibits rapid juvenile growth that outstrips that of its competitors, allowing it to establish and maintain a dominant position in a stand (Packee 1976). In Washington, Heilman and Stettler (1985) recorded average heights of 4-year-old pure black cottonwood stands at 10 m and average heights of black cottonwood grown with alder at 11 m. Exceptional trees can reach 13.7 m in height and 18 cm diameter in 7 years. By age 27, black cottonwood can exceed 36 m in height and 80 cm in diameter. It is the largest-growing deciduous tree in British Columbia. Maturity is normally reached in 60–70 years, but good growth can be maintained for as long as 200 years. Black cottonwood outlives red alder in mixed stands. Best growth occurs on coastal sites, with growth decreasing towards the north and in interior locations (Fowells (compiler) 1965; Hosie 1973).

The tree develops a long straight bole and is normally free of branches for most of its length. Young trees have a narrow, conical crown with upswept branches (Lyons 1952). The root system is shallow and wide-spreading (Hosie 1973).

In cutover areas, large numbers of sprouts are produced from cut stumps. With the possible exception of red alder, vigorous cottonwood sprouts are the fastest growing plants on recently logged coastal alluvial sites on the Skeena River (J. Pollack, pers. comm., Jan. 1985). Observations from the Pacific Northwest suggest that if black cottonwood can establish a deep root system it can outgrow all other species (Heillman and Stettler 1985; Hinkley *et al.* 1988, cited by Pezeshki and Hinkley 1988). According to Pezeshki and Hinkley (1988), if soil moisture is adequate, first-year growth of black cottonwood and red alder will be about the same.

Phenology: The flowers of black cottonwood appear from late March or early April through to late May on the coast; they can appear as late as mid-June in some areas of the Interior. Leaf emergence follows flowering. Fruits are ripe within a month of flowering, and seed dispersal is as early as late May and early July. Seed is shed between April and June on the coast (D. McLennan, pers. comm., July 1989). Trees of northern and inland provenances cease growth earlier in the growing season than provenances from south coastal areas (Fowells (compiler) 1965).

REPRODUCTION

Seed Production and Dispersal: Black cottonwood first produces seed at approximately 10 years of age. Good seed crops are produced annually. The downy seed is light and buoyant and can be transported for long distances by wind and water (Fowells (compiler) 1965; USDA 1974). The timing of seed dispersal coincides with the timing of flooding in many coastal rivers. Sandbars along rivers may be covered by seedlings in May and June (D. McLennan, pers. comm., July 1989).

Seed Viability and Germination: The viability of fresh seed is high but of short duration (Fowells (compiler) 1965). Cottonwood seed will readily germinate on a variety of favourable sites (Beals 1966), particularly where bare soil has been exposed or new soil laid down. Moist seedbeds are essential for high germination rates and seedling survival depends on favourably moist conditions for at least the first month (Roe 1958; USDA 1974). Mortality of seedlings is extremely high because precise moisture requirements must be met. Roots of developing seedlings must not dry out, thus successful growth depends on the ability of seedlings to follow retreating subsurface water levels as they subside after the summer flood (D. McLennan, pers. comm., July 1989). Seedling establishment is the primary means of reproduction of black cottonwood in the Cariboo Forest Region[199] and probably throughout British Columbia.

Vegetative Reproduction: Sprouting from the stump is the most common form of vegetative reproduction in black cottonwood, although minor root suckering also occurs (Roe 1958). Sprouts arise primarily from suppressed buds on the stump but can also originate in wound callus (DeBell and Alford 1972). Black cottonwood is also known to regenerate from broken stem or root fragments incorporated in moist mineral soil. An unusual form of vegetative reproduction has been reported by Galloway and Worrall (1979). Small shoots, complete with green leaves, abscise naturally and either root where they fall, or are transported some distance by water before taking root.

Artificial regeneration can be successfully obtained using stem cuttings of various lengths. For best results the cuttings should be collected from mid-December to mid-February from young saplings 2–3 m tall. Cuttings should average 1–2 cm in diameter and 25 cm to 3 m in length depending on the application (D. McLennan, pers. comm., July 1989). Early spring planting is recommended to capture soil moisture. Stine *et al.* (1981) report that survival of unrooted cuttings is as good as, or better than, survival of artificially rooted cuttings. However, other researchers (e.g., D. McLennan, pers. comm, July 1989) have observed the opposite effect. Rooted cuttings have exhibited more rapid juvenile growth than unrooted cuttings.

PESTS

Principal disease and insect pests are described by Fowells (compiler, 1965).

EFFECTS ON CROP TREES

Competition: Black cottonwood is a severe competitor with conifers because of its rapid height growth and early dominance of forested sites. Competition is most severe on extremely productive bottomland sites and will continue for the length of the rotation. Early competition comes from plants of both sprout and seed origin. Cottonwood plants may be extremely dense in the first few years of growth, but self-thinning will normally take place by age 5 as weaker trees are quickly suppressed by the more dominant plants (Roe 1958).

Beneficial Effects: D. McLennan (pers. comm., July 1989) described the following beneficial effects of black cottonwood on alluvial floodplains in British Columbia:

1. Black cottonwood can be a valuable crop tree. The short (20–30 year) rotation reduces the risk of losing the plantation to erosion of alluvial surfaces.
2. Black cottonwood can be regenerated relatively easily and it establishes rapidly, so that sites vulnerable to erosion are rapidly stabilized, which in turn reduces siltation of fish habitat, reduces plantation erosion, and stabilizes hydrolic regimes.
3. The relatively nutrient-rich litter is important for fish food chains.
4. Foliage provides summer shade to maintain cool water temperatures. Open canopies in the winter allow higher light penetration.

Near Haney, van der Kamp (1986) detected nitrogen fixation activity in the wetwood of black cottonwood. He suggested that wetwood of black cottonwood harbours nitrogen-fixing bacteria that may contribute to the total nitrogen input of forested ecosystems.

Allelopathy: A pot study (Heilman and Stettler 1985) indicated that black cottonwood leaf and litter material had an inhibitory effect on red alder seedlings. However, red alder seedlings grew normally in field soil collected from the cottonwood plots. This finding suggests that, at most, allelopathy is probably of minor significance under field conditions.

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[199] Perry 1983.

RESPONSE TO DISTURBANCE AND MANAGEMENT

Forest Canopy Removal: Black cottonwood is not found as an understory species beneath mature forest canopies. Following logging, seeding-in occurs from residual or nearby trees. Trees cut during logging sprout profusely and may produce some root suckers (Roe 1958). On northern Vancouver Island, D. Harrison (pers. comm., July 1989) has observed that black cottonwood cover increased through resprouting following forest canopy removal.

Fire: Black cottonwood is highly susceptible to fire and even light burns can cause considerable injury (Fowells (compiler) 1965). Cottonwood is apparently not a fire-adapted species, but there are no reports in the literature documenting its response to natural or prescribed fire.

Cutting: Young black cottonwood responds to cutting with vigorous sprouting. Repeated cutting on a 2-year cycle does not significantly affect sprouting vigour (DeBell *et al.* 1984). DeBell and Alford (1972) found that when 2-year-old trees were cut in February to a 30-cm stump, sprouts were abundant after two growing seasons. Most sprouts arose from dormant buds more than 15 cm above the ground level. When the same trees were cut to 15 cm in height 2 years later, they sprouted more slowly and some sprouts arose out of callus tissue. These adventitious sprouts were smaller and more susceptible to damage and decay than those arising from dormant buds. The authors speculated that if the first cutting height had been used for the second cutting, there would have been no decline in sprouting vigour. The same study found that sprouting vigour of eastern cottonwood (*P. deltoides)* was lowest when cutting took place early in the growing season, probably because food reserves were low after initiation of growth in spring.

Mid-summer cutting of 4-year-old black cottonwood in the CWH zone near Chilliwack resulted in effective control 2 years after treatment, as a result of the shading of cut stumps by salmonberry. On a nearby site that lacked shade, a mid-summer cutting treatment was followed by rapid resprouting (B. D'Anjou, pers. comm., Nov. 1989).

Herbicides: In British Columbia, Washington, and Oregon, excellent control of black cottonwood is obtained after summer or fall broadcast applications of glyphosate (Conard and Emmingham 1984b; Boateng and Herring 1990). D'Anjou[200] found that late spring broadcast applications can also be somewhat effective. When he applied glyphosate at 2.0 kg a.i./ha on various dates to a site in the CWH zone, he found that the August 12 and September 3 applications were most effective, the June 4 application was next most effective, and the July 9 application was ineffective.

Broadcast applications of hexazinone generally have caused moderate to severe injury to black cottonwood in British Columbia, while spot applications have provided severe to very severe injury (Boateng and Herring 1990). Excellent control of black cottonwood was maintained 4 years after a September application of 9–11 mL/spot of hexazinone on a mesic SBSmc site in the Prince Rupert Forest Region. The single herbicide appli-cation was anticipated to release the conifers to a free-growing condition (N. Endacott, pers. comm., July 1989). Black cottonwood suffered 80–95% defoliation and almost no resprouting one season after a mid-May application of hexazinone applied at 2 and 4 mL/spot on a 1 x 2 m grid in the Nelson Forest Region.

Broadcast applications of 2,4-D amine have resulted in light to moderate injury to black cottonwood in British Columbia. In Washington and Oregon, summer or late summer applications of 2,4-D amine to cut surfaces have severely injured black cottonwood (Conard and Emmingham 1984b).

Soil Disturbance: Logging disturbance or mechanical site preparation that exposes patches of moist mineral soil can create an ideal seedbed for germination and survival of black cottonwood seedlings (Fowells (compiler) 1965). Stem or root fragments incorporated into moist mineral soil can be expected to regenerate, and damaged trees will produce new shoots.

Fertilization: Fertilization increased black cottonwood growth in a 20-year-old stand on a floodplain in British Columbia that had medium nutrient status. However, no response occurred on two nutrient-rich floodplain

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[200] D'Anjou 1988a.

sites supporting 10- to 15-year old black cottonwood trees. In addition, black cottonwood did not respond to nitrogen fertilization on nutrient-rich sites on the Fraser River. Phosphorus added below the soil surface at the time of planting had increased growth and survival of black cottonwood whips (D. McLennan, pers. comm., July 1989).

WILDLIFE

Food: Black cottonwood is a moderately important source of food to wildlife in British Columbia. It is an important browse for Roosevelt elk in winter,[201] a moderately important winter and spring browse for moose (Singleton 1976), and a moderately important browse for white-tailed deer.[202] Black cottonwood sprouts vigorously after browsing (T. Lea, pers. comm., Feb. 1989).

Black cottonwood is a preferred food of beaver on Vancouver Island (Sadoway 1986) and probably elsewhere. Squirrels feed on the flowers and leaf buds in the spring (Harestad 1983). Damage by small mammals, especially voles or meadow mice, can be severe on young trees growing on grassy or herb-covered sites. Rabbits and hares can clip twigs and girdle around stem bases (D. DeBell, pers. comm., Dec. 1984). Brewer (1980, cited by Cade and Sousa 1985) noted that ruffed grouse feed on buds and catkins during winter in Washington.

Other Resources: Black cottonwood is important for daytime perching of bald eagles in winter. Stalmaster and Newman (1979) found that bald eagles spent 44% of their perching time on black cottonwood. In southern British Columbia, black cottonwood is an important cavity nesting tree for woodpeckers.[203] Many other birds nest in black cottonwood including owls, hummingbirds, starlings, sapsuckers, flickers, veeries, orioles, grosbeaks, and vireos (Cannings *et al.* 1987).

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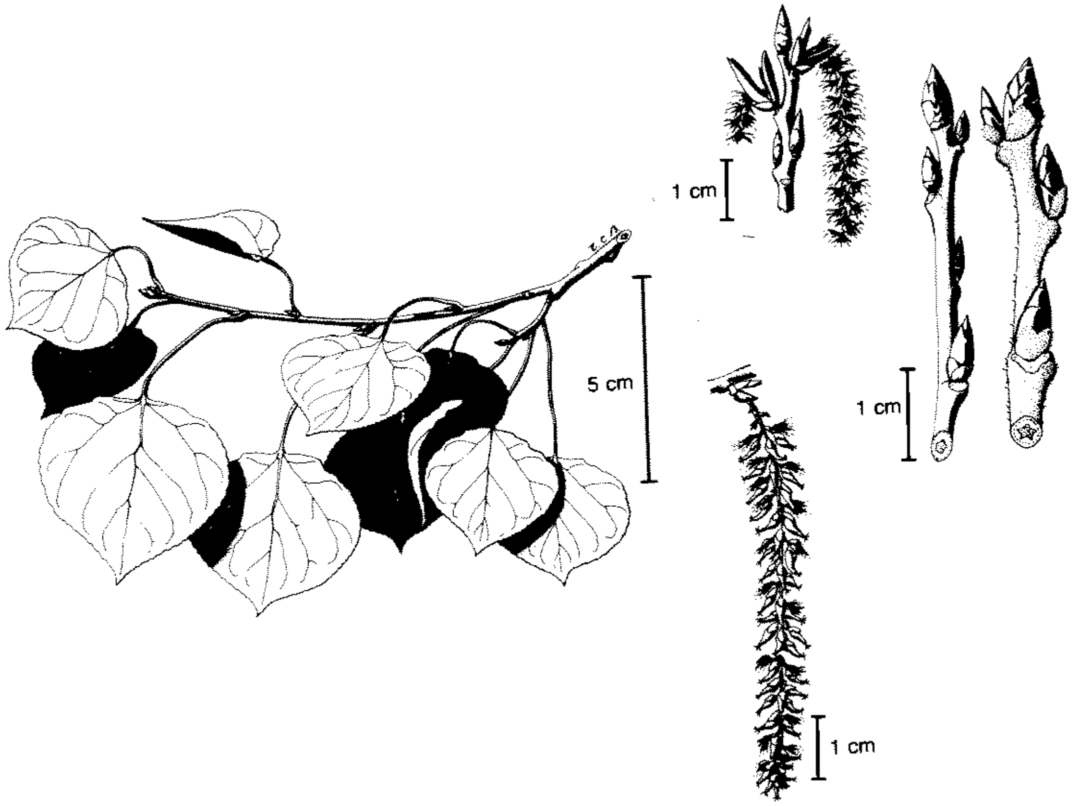
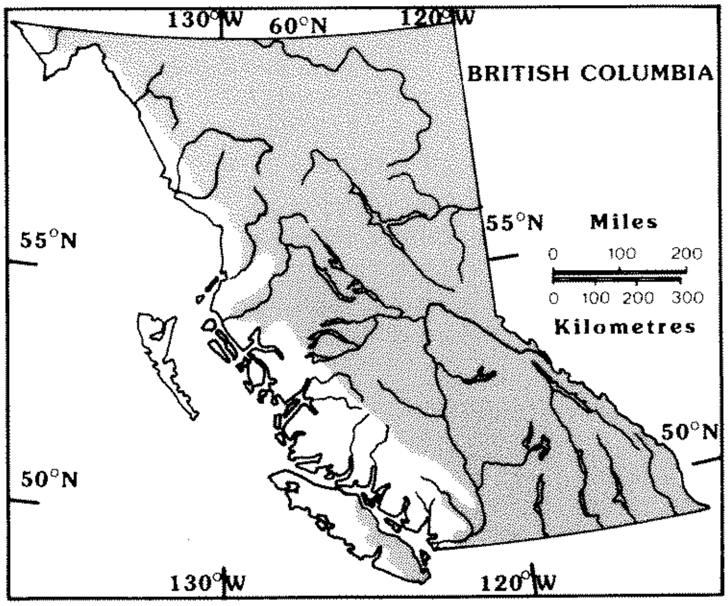
[201] Blower 1982.
[202] Ibid.
[203] Korol and Wallis 1983.

Populus tremuloides

(trembling aspen)





Distribution of *P. tremuloides* in British Columbia.

Populus tremuloides Michx.

Trembling aspen
(quaking aspen)

A comprehensive review of literature pertaining to the autecology and management responses of trembling aspen is provided by Peterson *et al.* (1989).

DESCRIPTION

Trembling aspen is a small to medium-sized deciduous tree with a narrow dome-like crown that forms extensive clones by means of root suckering. It is commonly 6–12 m tall but can reach 25 m in height. The bark, whitish to greenish-grey with characteristic black scars, is smooth but becomes furrowed at the base with age. Twigs are slender, reddish or grey, with long, pointed buds. Leaves are nearly round with a pointed tip, rounded teeth, and a flattened stalk that causes them to tremble in the breeze. The long, drooping male and female catkins appear on separate trees. Female catkins release many tiny, cottony seeds (Viereck and Little 1972; Brayshaw 1978).

Variation: Aspen is the most widely distributed native tree in North America (Brisette and Barnes 1984). Three poorly defined local varieties are recognized in British Columbia. The variety *vancouveriana* is found on Vancouver Island and adjacent coastal areas; var. *aurea* appears in the Cariboo Region to the Rocky Mountains; and the typical var. *tremuloides* is widely distributed throughout the British Columbia mainland (Taylor and MacBryde 1977; Brayshaw 1978). Because the species forms extensive, genetically identical, male or female clones, marked phenological or behavioural differences between adjacent clones can be easily observed (Fowells (compiler) 1965; Steneker and Wall 1970; Brayshaw 1978).

DISTRIBUTION AND ABUNDANCE

Aspen occurs throughout British Columbia, east of the Coast Mountain Range. Variety *vancouveriana* is scattered throughout the Georgia Strait area, but northwards, aspen occurs only sporadically on the coast where it has migrated westward along major river valleys. It is extremely abundant in the central and northeastern parts of the province, especially in the BWBS, SBS, and IDF biogeoclimatic zones, where it forms extensive stands (Brayshaw 1978; Krajina *et al.* 1982).

Altitudinal Range: Trembling aspen extends from valley bottoms to approximately 1200 m in the Interior and is occasionally found near sea level on the coast (Lyons 1952). In interior Alaska it is confined to elevations below 900 m (Viereck and Little 1972).

HABITAT

Climatic Relations: The broad geographic distribution of this species indicates that it is adapted to a wide variety of climates. Cold continental and boreal climates appear to be more favourable than the humid, equable coastal environment, and the species is almost absent in cool perhumid areas. Towards the southern limits of its range in the U.S., it tends to be found at higher elevations in the mountains only, and in dry climates it may be restricted to protected habitats (Fowells (compiler) 1965). In northern British Columbia and at high elevations it is most abundant on sunny, south aspects.

Site and Soil Conditions: Aspen can inhabit a wide range of sites, including shallow rocky soils, loamy sands and wet clays, but it is predominantly a species of well-drained uplands. Best growth is on moist but well-drained and porous, loamy soils; rockiness greatly limits stand development (Fowells (compiler) 1965; Steneker 1976; Bums (compiler) 1983). In British Columbia, trembling aspen occurs dominantly on Luvisolic soils.

Nutrient Relations: Aspen is tolerant of poor soils and exhibits its best growth on nutrient-rich substrates, especially calcium-rich soils derived from limestone (Fowells (compiler) 1965; Krajina *et al.* 1982). However, studies in Wisconsin indicated that soil nutrient levels were of little importance in determining aspen site index (Fralish 1972). Aspen is regarded as a soil improver, particularly after fire (Fowells (compiler) 1965). It has high levels of potassium in its foliage, wood, bark, and litter relative to other northwestern tree species (Minore 1979), and it redistributes great quantities of nutrients (especially calcium, magnesium, and nitrogen) to the surface soil layers through its litter (Fowells (compiler) 1965;

Krajina *et al.* 1982). Biogenic cycling of calcium by trembling aspen is believed to maintain the Luvisolic soils of the Fort Nelson area in a relatively productive state by retarding acid leaching (Valentine *et al.* (editors) 1978).

Water Relations: Aspen is abundant on sites ranging from xeric to hygric in moisture status, but best growth is found on sites with abundant moisture (Krajina *et al.* 1982; Angove and Bancroft 1983). Fralish (1972) indicates that soil moisture is the most important factor affecting the relative growth of aspen, and water tables between 1.0 and 2.5 m in depth are preferred, especially in coarse- and medium-textured soils. Aspen can survive long periods of flooding (Krajina *et al.* 1982).

Light Relations: Aspen is a shade-intolerant species that requires full sunlight for growth (Lutz 1955; Krajina *et al.* 1982). When overtopped by larger trees, it deteriorates and eventually dies (Mueggler 1984). Strong light is needed to stimulate production of root suckers and ensure their continued, vigorous growth. Higher light intensities increase production of roots in young suckers (Fowells (compiler) 1965; Johansson and Lundh 1988). At less than 10% full sunlight, sucker density is less than 10% of that on a clearcut (Mueggler 1984).

Temperature Relations: Frost resistance in aspen is high, and the species survives easily in frozen ground having no snow cover (Krajina *et al.* 1982). In the taiga of Alaska it is dominant on sites where the permafrost layer comes to within 20 cm of the soil surface (Foote 1983). Foliage is susceptible to late spring frosts (Strain 1966). Soil temperature is very important in the production of root suckers. Direct heat must reach the forest floor and temperatures must be 20–30°C for maximum production of root suckers (Fowells (compiler) 1965; Steneker 1976). Root cuttings from 10-year-old aspen exposed to different temperatures (10 and 25°C) and light intensities produced the most and largest suckers at 25°C and high light intensities (Johansson and Lundh 1988).

GROWTH AND DEVELOPMENT

Aspen is characterized by rapid early growth and a relatively short life-span. Although individual trees may live as long as 200 years, stands generally reach an advanced state of decay between 55 and 90 years. The tree develops a slender, limb-free trunk and a small crown. The wide-spreading roots typically extend 1.0 to 1.5 m into the soil but can penetrate to as deep as 2.2 m and may extend as far as 14 m from the stem base. Root development can be greatly hindered in rocky soils (Lutz 1955; Fowells (compiler) 1965; Maini 1972; Hosie 1973).

Aspen is most often seen in cutover or recently burned areas as small clumps of trees, each consisting of large numbers of root suckers (Schier and Campbell 1978). Sandberg (1951, cited by Schier and Campbell 1978) found that competition between the suckers usually reduces most clumps to a single stem by the fifth year and almost all to a single stem by the tenth year. Vigorous suckers may grow as much as 2 m in their first year, but subsequent height growth will average 30–60 cm annually (Steneker 1976). Seedling growth is much slower. Fowells (compiler, 1965) reports that growth in the first year averages 30 cm, while in Alaska, 3-year-old seedlings reached a maximum height of 27.5 cm (Zasada *et al.* 1981).

Phenology: Flowering takes place before the leaves appear in early spring (usually April or May). All trees within a clone develop their flowers simultaneously, although separate clones flower at different times. Male clones flower before females clones. The fruits mature as the leaves expand and are normally ripe during May or June, about 4–6 weeks after flowering. Seed dispersal takes place shortly after ripening is complete, typically in the first few weeks of June. Within ecotypic zones, flowering period and time of seed maturity appear to be quite regular and differences in flowering time apparently depend on current temperatures (Fowells (compiler) 1965; Steneker and Wall 1970; Viereck and Little 1972; USDA 1974; Brayshaw 1978). Leaf phenology is also identical for all trees within the same clone. Earliest and latest flushing clones within a given area may be 1–3 weeks apart in their phenological development, giving a patchwork appearance to an aspen stand, and making delineation ot individual clones easy. There may also be several weeks difference in the timing of leaf fall among different clones (Steneker and Wall 1970).

In a provenance study located in Michigan (Brissette and Barnes 1984), clones from western North America initiated shoot growth earlier in spring than clones from Michigan, indicating that, under native conditions, the western families are adapted to initiate growth at lower accumulated degree-days. Clones from northern latitudes or high elevations also ceased growth much earlier than the Michigan clones because they are genetically adapted to the photoperiods and growing season temperatures of their native habitats.

REPRODUCTION

Seed Production and Dispersal: Aspen begins to flower between 10 and 20 years of age. Flowers are typically unisexual, with male and female trees occurring in separate clones, but a small percentage of both male and female trees bear perfect flowers. The ratio of male to female trees is approximately 3 to 1 in natural populations in the eastern U.S. Pollen is wind-dispersed between clones. Female trees produce an adequate seed crop annually, with good seed crops every 4–5 years. The tiny cottony seeds can be carried several kilometers by wind (Fowells (compiler) 1965; Maini 1972).

Seed Viability and Germination: The viability of fresh fertile seed is high (Fowells (compiler) 1965), but seeds remain viable for only 2–3 weeks after maturity (Strothman and Zasada 1957). Reproduction does occur from seed (Maini 1972) but is rare, primarily because the short period of viability rarely coincides with environmental conditions that are sufficiently moist to allow seedling establishment (Barnes 1966). Peterson *et al.* (1989) indicate, however, that seedling establishment may be more important in relatively cold northern soils than is generally believed. Germination rates of 90–100% are possible if conditions are suitable (Mueggler 1984). Seed germination and seedling survival are best on moist mineral or humus seedbeds with moderate temperatures, good drainage, and little competition from other vegetation (Steneker 1976; McDonough 1979; Mueggler 1984). Germination is optimum between 10 and 21°C and temperatures in excess of 27°C are detrimental (Mueggler 1984). Regeneration from seedlings is of minor significance as a means of reproduction in western North America (Fowells (compiler) 1965; Steneker and Wall 1970).

Vegetative Reproduction: The dominant form of regeneration in aspen is through suckers or adventitious shoots that develop from the extensive lateral root system (Steneker 1976; Schier 1981; Schier *et al.* 1985). Meristems that begin in the cork cambium during secondary growth either develop into buds and then elongate into shoots or, more frequently, stop growing after the bud forms (Schier *et al.* 1985). Suppressed buds do not sprout as vigorously and may remain inhibited, while newly initiated meristems develop into suckers. Sprouts from the root collar or stump are uncommon but do occasionally occur (Maini 1972) in saplings and younger stems (Mueggler 1984). Root suckers in Alaska appeared up to 25 m away from a fire-killed mature aspen, with the majority of the suckers occurring within 10 m of the stem base (Lutz 1955). However, Schier (1981) provides evidence that suckering from lateral roots does not appear to depend on distance from the parent plant tree or root age. Suckers normally originate from roots in the upper 10 cm of soil but can appear on roots as deep as 28 cm (Kemperman 1978; Schier and Campbell 1978).

Sucker development on aspen roots appears to be suppressed by auxin transported from the aerial parts of the tree (i.e., apical dominance). When movement of auxins into roots is halted or reduced by cutting, burning, girdling, or defoliation of trees, auxin levels in the roots decline. In addition, cytokinins can no longer move out of the roots, resulting in an increase in the ratio of cytokinins to auxins, which promotes suckering (Mueggler 1984; Schier *et al.* 1985).

Suckers are dependent on the parent root carbohydrate reserves until they emerge from the soil surface and can photosynthesize. Low levels of carbohydrate reserves in the parent root can limit the density of suckers. This is particularly true of deep-rooted clones, because the suckers require more energy to push up to the soil surface. Carbohydrate reserves can be exhausted and sucker production drastically reduced by repeated destruction of new suckers by browsing, cutting, burning, or herbicide spraying (Mueggler 1984; Schier *et al.* 1985).

A few suckers will arise every year, even in undisturbed stands, but strong light and heat must reach the forest floor to stimulate vigorous suckering (Fowells (compiler) 1965). High temperatures increase cytokinin production in the roots and may also lower auxin concentrations in roots by speeding its degradation. Thus, high temperatures increase the cytokinin to auxin ratio and stimulate suckering (Mueggler 1984; Schier *et al.* 1985). The temperature range for suckering is 18–35°C, with 24° being optimum (Peterson *et al.* 1989). Light is not essential for sucker initiation, although increased light intensity increases sucker density and growth.

Suckering produces extensive clones of genetically identical trees. Clones as large as 81 ha in size have been identified in western North America (Kemperman and Barnes 1976), but most clones are much smaller. Trees of different clones vary significantly in their suckering ability, phenology, growth rates, form, and disease susceptibility (Steneker and Wall 1970; Maini 1972; Mueggler 1984).

Age does not seem to affect suckering capacity, provided that the stand is not breaking up as a result of decay and old age (Steneker 1976). In deteriorating stands, sprouting is inhibited because the shrinking root system results in a low cytokinin:auxin ratio. If root density has declined appreciably, regeneration following cutting or burning will be sparse or patchy (Mueggler 1984). Barring (1988) provides some evidence, however, that the roots of the closely related European aspen (*Populus tremula*) may remain alive for a long time after the disappearance of parent trees, enabling the species to form suckers continuously.

PESTS

Aspen is highly susceptible to various forms of decay and periodically suffers from major insect infestations. Young suckers without at least one injury due to insects or pathogens are rare (Peterson *et al.* 1989). Principal disease and insect pests are outlined by Fowells (compiler, 1965).

Galls, lesions, and shoot dieback are very common in young aspen stands and increase with decreasing site quality (Perala 1984). However, most injuries heal within a few years and do not contribute to suppression or mortality. *Hypoxylon mammatum* is a prevalent and lethal canker disease of young aspen. Peak infections occur at about 7 years of age and stem infections kill saplings within 2 or 3 years. White trunk rot *(Phellinus tremulae)* is the most important cause of decay in aspen stands older than 20 years (Perala 1984). *Armillaria mellea* infections of aspen stump roots have increased with succeeding short-rotations of aspen stands in Ontario (Stiell and Berry 1986). The high incidence of *Armillaria* probably contributed to the observed decrease in the number and size of aspen suckers, and similar *Armillaria* infections may reduce the productivity of short-rotation stands.

EFFECTS ON CROP TREES

Competition: Aspen is considered to be a serious competitor with coniferous trees throughout most of the interior of British Columbia, especially in the BWBS zone, where it is particularly well established. However, aspen rarely exceeds 10% cover within 15 years of site disturbance in the wetter ICH subzones in the Kamloops and Nelson Forest Regions. It is not considered to be a hindrance to establishment, survival, or growth of conifers in these productive subzones.[204] It rarely seeds-in to clearcuts, thus competition results from the suckers of trees already established prior to harvesting. The numbers of young suckers produced can be immense: a single tree in Alaska reportedly produced 36 230 suckers within 3 years (Lutz 1955). Aspen density and the rapid growth of young suckers provide young conifers with severe competition for root and crown space (Lees 1966). Suckers have the advantage of an established root system and always grow more rapidly than coniferous seedlings when open-grown (Jones 1974).

Conifers growing beneath an understory of aspen are also subject to significant mechanical damage (Kittredge and Gevorkantz 1929). "Whipping" damage is particularly severe at approximately 55–75 years when understory trees begin to pass through the increasingly decadent aspen overstory (Lees 1966).

Beneficial Effects: Aspen is considered to be a site improver where burning or other forms of disturbance have reduced soil nutrient levels, because it returns large quantities of nutrients to surficial layers through its litter (Fowells (compiler) 1965; Krajina *et al.* 1982).

Aspen stands of present or potential value occur on many NSR and non-commercial brush areas in the province. Some of these stands may be best managed for pure hardwood or mixed wood production.

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[204] Mather 1988.

Nutrient losses due to harvesting will be minimized if rotations are greater than 60 years and if whole-tree harvesting occurs during the leafless season, so that the foliage component of the nutrient pool is not removed from the site (Peterson *et al.* 1989).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Trembling aspen rapidly increase following overstory removal. However, it has been observed (J. Wright, pers. comm., July 1989) that much fewer suckers are produced in the drier ICH subzones than in cooler zones such as the MS and SBS (J. Wright, pers. comm., July 1989). Even where there are only a few scattered aspen residuals in a conifer stand, aspen root suckers will generally dominate regeneration after logging as long as aspen root density is adequate (Schier *et al.* 1985). Trees cut or damaged during logging will produce prolific suckers. Even trees that remain undamaged after logging will produce suckers because the root system is stimulated by the increased light and heat on the forest floor (Fowells (compiler) 1965). Suckers can grow up to 2 m in height during the first growing season following overstory removal (Steneker 1976). In the Penticton Forest District, 1-year-old suckers average 40 cm in height on moisture-deficient sites and 95 cm in height on sites with moisture available all year.[205] Sucker densities in the first year after harvest can reach 225 000 stems per hectare, but regardless of the first-year density, stands self-thin and usually stabilize in the range of 20 000–25 000 stems per hectare (Peterson *et al.* 1989).

Fire: Trembling aspen is adapted to an environment with recurring fires. High severity fires kill aspen, promote prolific sprouting, and maintain the seral aspen stage (Brown 1985b; Jones and DeByle 1985). Almost all even-aged aspen stands in the western U.S. appear to be the result of severe fire (Jones and DeByle 1985). Low severity fires thin aspen stands; aspen suckers and fire-tolerant conifer species (e.g., Douglas-fir and ponderosa pine) fill in canopy gaps.

Most suckers arise in the first year following a burn (Bailey and Anderson 1979; Zieroth 1984). The rapidly growing aspen suckers dominate burned sites before shrubs or trees that regenerate from seed are able to compete successfully. Brown (1985b) found that within about 4 years of burning, sucker density decreases and stabilizes as a result of competition-induced mortality. Burned areas typically produce more suckers than unburned areas because burning increases light intensity reaching the forest floor, and high soil temperatures in the rooting zone stimulate suckering (Horton and Hopkins 1965; Rouse 1986). A temperature threshold of 16°C for sucker initiation may exist (Hungerford 1988). The release of nutrients associated with burning may stimulate the growth rate of suckering during the first year after a fire (Fowells (compiler) 1965). High cytokinin:auxin ratios promote aspen suckering. These high ratios result when fire kills phloem tissue and leaves, thus preventing the downward flow of auxins and the upward flow of cytokinins (Brown 1985b).

Aspen suckering is common on burned sites in the SBS zone and is particularly prolific on dry sites that have abundant aspen prior to harvest (Hamilton 1988; Hamilton and Yearsley 1988). Root suckers can reach over 2 m in height within a few years and attain 10–20% cover in 16 years following burning of submesic and mesic sites.

Repeated burning is thought to promote suckering and result in denser stands (Fowells (compiler) 1965), but the regenerative capacity of aspen roots is not unlimited. A study by Buckman and Blankenship (1965) found that repeated spring burns eventually caused a significant reduction in sucker density. Jones and DeByle (1985) suggest that frequent fires may adversely affect site quality for aspen.

Cutting and Grazing: Cutting at any time of the year results in rapid regrowth of root suckers. In the ICHmw subzone in the Salmon Arm District, suckers average 0.5–1 m in height after one growing season (J. Wright, pers. comm., July 1989). Many suckers were 1 m tall 2 years after cutting with chainsaws and brush saws in the SBSmk subzone near MacKenzie (D. Greenley, pers. comm., July 1989). Suckers appear immediately after cutting treatments carried out during the growing season, or early in spring after a dormant season cutting (Fowells (compiler) 1965; Steneker 1976; Mueggler 1984). Factors that may influence sucker production include light availability, temperature, site quality, stump height, and cutting season (Johansson 1985b).

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[205] Noble-Hearle 1989.

Cutting during the active season tends to minimize the number of suckers (Fowells (compiler) 1965; Sutton 1984), but Stenecker (1976) found that the effect of cutting season was negligible 2 or 3 seasons after treatment. Similarly, Bella (1986) found that initial differences in stand density on summer and winter cut areas diminished significantly within 5 years of treatment. Although winter cutting usually results in more suckering than summer cutting, Bella (1986) found the opposite effect after cutting 70- to 80-year-old aspen stands in east central Saskatchewan. This apparent discrepancy is explained by the fact that the winter-logged area had more slash than the summer-logged area, hence soil warming was inhibited on the winter-logged area.

When suckers are extremely numerous after clearcutting, the number of suckers rapidly declines over time due to self-thinning and other damaging factors including insects, browsing, and snowpress (Schier *et al.* 1985)

In a study examining the effect of repeated harvesting (cutting) at rotations ranging from 1 to 20 years, Stiell and Berry (1986) found that the shortest rotation at which sucker production can be physiologically maintained is about 10 years. Reduced growth in short rotations may be due to depletion of root stores by the frequent removal of photosynthesizing tops.

Cut trees can produce more than twice as many suckers as girdled trees, and sucker growth from cut trees is superior (Schier 1978). Bancroft indicates that complete girdling is recommended to kill aspen effectively and that mortality may occur in 1–3 years.[206] He recommends girdling in the spring to obstruct the full growing season's supply of carbohydrates to the roots.

Moderate browsing causes vigorous sprouting of aspen, but intense browsing can severely damage or kill aspen sprouts. Although sheep are more destructive than cattle, aspen sprouts are out of reach of sheep sooner than of cattle (Brown 1985a). Trembling aspen showed severe signs of lost vigour 1 year after spring and early summer sheep grazing near Clearwater (G. Ellen, pers. comm., Aug. 1989).

Herbicides: Broadcast applications of 2–3 kg a.i./ha glyphosate have provided good to excellent control of trembling aspen (Sutton 1984; P. Wadey, pers. comm., June 1989; J. Wright, pers. comm., June 1989). Both Sutton (1984) and Mihajlovich and Switzer[207] found that fall applications were generally much less effective than summer applications. Length of control following aerial applications of glyphosate is variable. One year after a late August broadcast spray of 3.0 kg a.i./ha near Dawson Creek, the treated area had 400 aspen (and balsam poplar) shoots per hectare compared to 22 300 aspen (and balsam poplar) shoots per hectare on an untreated control.[208]

Hack-and-squirt treatments with glyphosate are highly effective. Hack-and-squirt may be most effective on stems smaller than 40 cm dbh.[209] A mid-July hack-and-squirt treatment in the SBSmk subzone with a 50% solution of glyphosate and water 1 year prior to harvest eliminated 90% of aspen root suckering. This treatment was considerably more effective in reducing suckering than a post-harvest cut stump application.[210] Near Penticton, hack-and-squirt was effective at one hack per 3 cm dbh with 1 ml of 50% glyphosate injected.[211] Another study found that undiluted glyphosate applied by hack-and squirt in August at 1 mL per 3–5 cm dbh resulted in complete aspen top-kill.[212] Fall applications of 1.6 kg ai/ha glyphosate with brush saws equipped with herbicide applicators has been severely damaging to aspen in a dry IDF subzone in the Cariboo.[213] Bancroft suggests that tree injections of glyphosate be applied in late summer or fall to ensure movement of the chemical to the roots.[214] He recommends a 3-year period between tree injection treatments and harvest of the coniferous component of the stand to control aspen suckering.

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[206] Bancroft 1989.
[207] Mihajlovich and Switzer 1984.
[208] Herring 1984a.
[209] Noble-Hearle 1989.
[210] DeLong 1988.
[211] Noble-Hearle 1989.
[212] Bancroft 1989.
[213] George 1989.
[214] Bancroft 1989.

Broadcast or spot applications of hexazinone control aspen providing organic soil layers are not deep. Excellent control of aspen was maintained 4 years after September applications of 9–11 mL per spot hexazinone on a mesic SBSmc site in the Prince Rupert Forest District (N. Endacott, pers. comm., July 1989). Hexazinone applied in four spots within 30 cm of tree bases at 1 mL per 10 cm dbh resulted in 70% kill after 1 year.[215] Liquid hexazinone applied around stem bases at 0.24–0.48 g per 1 cm of dbh controlled aspen seed trees in the Prince Rupert Forest Region.[216] Spot gun applied hexazinone caused 90–100% defoliation of aspen within 2 years of treatment on a variety of sites in British Columbia.[217]

Air or ground application of 2,4-D at 2.2 kg a.i./ha will kill all above-ground tree parts, but it will not prevent suckering (Bowes 1981; Harniss and Bartos 1985). However, 2,4-D applied at 4.4 kg a.i./ha kills aspen and results in minimal suckering. Basham (1982) found that after being sprayed with 1.4 kg a.i./ha of 2,4-D, surviving aspen had reduced height and diameter growth, but within 6 years they had resumed normal growth rates. To stimulate aspen regeneration, Harniss and Bartos (1985) recommend herbicide application soon after aspen leaves are fully expanded. For conifer release, they recommend herbicide application 1–3 weeks before aspen leaf fall.

Bancroft reports that one study found that pure 2,4-D amine applied by hack-and-squirt in August at 1 mL per 3–5 cm dbh resulted in complete aspen top-kill.[218] He suggests that tree injections of 2,4-D be applied in late summer or fall to ensure movement of the chemical to the roots.

Soil Disturbance: Site preparation methods that expose areas of mineral soil, such as scarification and discing, will increase suckering by increasing soil temperatures and light penetration in the rooting zone (Fowells (compiler) 1965; Jones 1974). Rows of suckers often appear along plowing furrows prepared for conifer regeneration (Fowells (compiler) 1965). A high level of cultivation that eliminates the aspen root system is needed for effective control. Deep plowing techniques that tear up the tree roots will reduce suckering. For example, 30 cm deep cultivation significantly reduced suckering of aspen in the BWBSmw subzone in the Fort St. John Forest District (P. Wadey, pers. comm., June 1989). Soil compaction as a result of silvicultural or harvest operations may reduce suckering because root buds, from which suckers are formed, are near the soil surface where compaction is greatest.

To retard aspen growth for the benefit of conifers, scarification should be carried out after the suckers have completed at least one season's growth (Basham 1988). In contrast, to attain sucker density and stocking for the development of a mature aspen stand, scarification should be carried out within 1 year of harvest. Basham (1982) found that scarified 3-year-old aspen suckers had significantly lower stem volumes after treatment than unscarified suckers, primarily due to damage to root systems. Scarification wounds on root systems were responsible for significantly more internal decay and stain on scarified than unscarified suckers. Susceptibility to windthrow and breakage due to decay is expected to be higher in scarified than unscarified aspen.

Hamilton and Yearsley (1988) observed no differences in the abundance of aspen after mechanical site preparation compared to burning in the SBS zone.

Fertilization: Nitrogen fertilization significantly increases aspen foliar biomass and leaf area (Coyne and van Cleve 1977). Aspen volume increased by 6–11% five years after application of various combinations of nitrogen, phosphorus, and potassium in Saskatchewan (Weetman *et al.* 1987). Safford and Czapowskyi (1986) found that nitrogen fertilization increased both growth and mortality of aspen 10 years after application, possibly by increasing competition and self-thinning. However, lime decreased mortality of nitrogen-fertilized aspen, possibly by reducing the activity of *Armillaria mellea*.

WILDLIFE

Food: Trembling aspen is important for ungulates, small mammals, and birds in British Columbia. It is common winter and summer food for moose, mule deer, and white-tailed deer, and a year-round food

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[215] Bancroft 1989.

[216] Newhouse 1988b.

[217] Teskey and Masterson 1985d.

[218] Bancroft 1989.

source for Rocky Mountain elk (Banfield 1974; Singleton 1976; Rue 1978; Harvey 1981).[219] Mule deer feed on the bark (Fowells (compiler) 1965; McLean 1979; Zieroth 1984; Sampson 1989). Aspen leaves are a preferred summer food of porcupines (Banfield 1974) and these animals also eat the buds and catkins (Chapman and Feldhamer (editors) 1983). Aspen is preferred by beaver (Denney 1952, cited by Allen 1982; Banfield 1974), although Jenkins (1981, cited by Allen 1982) indicates that the apparent preference may be a reflection of higher availability of aspen over other tree species. Trembling aspen is important to snowshoe hares, particularly in winter (Hansen and Flinders 1969; Banfield 1974; Wolff 1978). It is important winter food throughout the range of ruffed grouse, and Cade and Sousa (1985) report that in Minnesota, one mature male trembling aspen provides 8 or 9 days of food for one grouse. Aspen buds and twigs provided 55% of the winter diet of ruffed grouse in Alaska (McGowan 1973, cited by Cade and Sousa (1985) and 35% in Alberta (Doerr *et al.* 1974, cited by Cade and Sousa 1985).

Other Resources: Aspen clones provide cover and edge habitat for big game (Zieroth 1984) and aspen stands with dense understories are important habitat for snowshoe hares. Aspen provides habitat and nesting sites for many game and song birds. Ruffed grouse are associated primarily with forests in which trembling aspen is the dominant species (Gullion and Svoboda 1972, cited by Cade and Sousa 1985; Cannings *et al.* (1987), and breeding blue grouse have a preference for aspen clones (Aldrich 1963, cited by Schroeder 1982). Trembling aspen is an important nesting tree for many birds in British Columbia, including woodpeckers, owls, herons, sapsuckers, flickers, flycatchers, nuthatches, orioles, and finches (Keisker 1986; Cannings *et al.* 1987; Sadoway 1988).[220]

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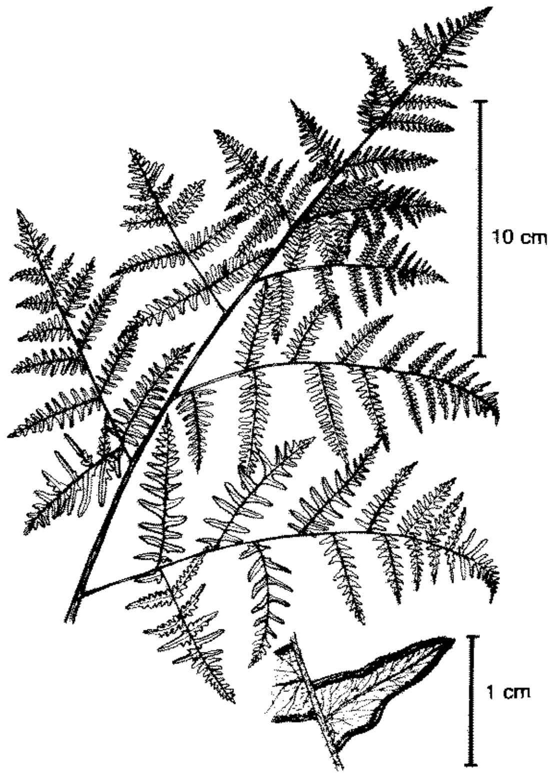
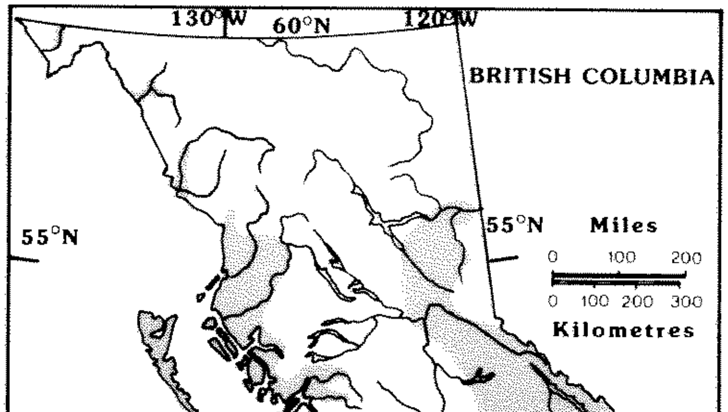
[219] Blower 1982.
[220] Korol and Wallis 1983.

Pteridium aquilinum
(bracken)





Distribution of *P. aquilinum* in British Columbia.

Pteridium aquilinum (L.) Kuhn Bracken

DESCRIPTION

Bracken is a large weedy fern with fronds that arise singly from an extensive creeping underground rhizome. The fronds are approximately 1–2 m tall with a stout, straw-coloured stipe (stem) and a triangular-shaped blade. The blade is 3 times pinnately compound; the final leaf divisions (pinnules) are leathery above and densely woolly beneath. The spores are borne in sori along the edge of the underside of the leaf (Taylor 1973a; Cody and Crompton 1975).

Variation: Bracken is a worldwide species with many geographic varieties. The western bracken found in British Columbia is described by Taylor and MacBryde (1977) as *Pteridium aquilinum* ssp. *aquilinum* var. *pubescens*. The biology, ecology, and control of bracken have been widely studied in Britain and elsewhere. British information on the autecology of bracken should apply well to var. *pubescens* in North America (Cody and Crompton 1975; D. Minore, pers. comm., Dec. 1984), but subspecies from New Zealand and other (sub)tropical areas behave differently since there is often no dormant season (Fletcher and Kirkwood 1979).

DISTRIBUTION AND ABUNDANCE

Bracken is one of the most widely distributed and successful vascular plants in the world (Page 1976). In British Columbia it occurs along the entire length of the coast and to approximately 56°N latitude in the Interior. It is most abundant in the CDF zone and adjacent drier subzones of the CWH on the south coast, and in the ICH and IDF zones in southeastern British Columbia. Over the rest of the province its distribution is sporadic and poorly documented. Bracken usually occurs in pure stands of clumpy distribution. In general, bracken is not abundant in areas where the natural vegetation is undisturbed by man (Page 1976).

Altitudinal Range: Bracken has been found at over 1800 m in the Alps (Fletcher and Kirkwood 1979) and as high as 3250 m in the Colorado Rockies (Page 1976). In British Columbia, however, it is rarely seen at high elevations (Taylor 1973a).

HABITAT

Climatic Relations: Around the world, bracken has successfully adapted to climates ranging from dry mediterranean to wet tropical (Gliessmann 1976), but it is not present in hot and cold desert regions. The northern limit of its range is set, at least partially, by winter cold, and also by a minimum requirement for growing degree days above 5.6°C (Page 1976). Cody and Crompton (1975) summarize climatic conditions where bracken occurs in Canada as having mean temperatures ranging from as low as -15°C in winter to as high as 21°C in summer and precipitation ranging from 61 to 165 cm annually. However, precipitation is undoubtedly higher at some locations on the west coast of Vancouver Island where bracken exists. Bracken is not found in British Columbia over most of the boreal forest, nor in the driest areas of the province. It is most abundant in areas of humid climate, relatively mild winters, and a lengthy growing season.

Site and Soil Conditions: Throughout its range, bracken is associated with a wide variety of disturbed habitats such as old fields, burned areas, roadsides, bomb sites, and recent lava deposits. Bracken favours sites where mechanical disturbance was high or burns were deep (T. Lewis, pers. comm., May 1989). It is also found on undisturbed open forest and woodlands, in swamps and peat bogs (Cody and Crompton 1975; Fletcher and Kirkwood 1979). In Canada, bracken is found on Podzolic and Brunisolic soils (Cody and Crompton 1975). A study in Michigan (Hellum and Zahner 1966) indicated that best development occurs on deep glacial outwash sands of medium productivity, and poorest growth is on outwash sands of low productivity.

Nutrient Relations: Bracken is characteristically found on subacidic to acidic, nutrient-deficient soils. Its absence on nutrient-rich sites is apparently due not to an intolerance of high levels of nutrients, but rather to lack of opportunity or an inability to compete successfully with rich-site vegetation (Hellum and Zahner 1966; Watt 1976; Fletcher and Kirkwood 1979). Nitrogen, phosphorus, potassium, and calcium are important for the growth of the sporophyte, and it responds well to fertilization, especially with potassium and nitrogen (Watt 1976; Fletcher and Kirkwood 1979). In northern Idaho, bracken is significantly associated with soils having high levels of potassium (Mueggler 1965). However, nutrient status seems to be less important for growth of bracken than other environmental factors.

Carlisle *et al.* (1967) studied nutrient cycling in an oak woodland in Britain and concluded that *Pteridium* plays an important role in the woodland nutrient cycle. It contributes a significant percentage of soil nutrient inputs through its litter and through foliar leachate. It is particularly important in potassium cycling, contributing 31.4% of the total potassium falling on the site. Other research indicates that the nutrient level of bracken litter is low relative to other species (e.g., 1% potassium, 0.0065% phosphorus), but the quality of the litter depends greatly on habitat conditions and frond vigour (Fletcher and Kirkwood 1979). Bracken produces prodigious quantities of litter and the rate of litter accumulation can exceed the rate of natural decay. Where this happens, the roots and rhizomes move upward in the soil so that the plant becomes progressively more dependent on nutrients contained within its own debris, and less on underlying mineral soil (Watt 1976).

Water Relations: In Canada, bracken grows on both moist and moderately dry sites, but its growth responds favourably to an abundant supply of soil moisture (Cody and Crompton 1975). On dry, shallow soils, fronds are sparse and short, and photosynthetic efficiency is much reduced as the plant adopts drought avoidance measures such as stomatal closure. It favours slightly shaded habitats such as woodlands and hollows where it is protected from drought and exposure. Growth is poor on waterlogged sites, presumably because of a lack of oxygen. The rhizome system is typically very shallow on such sites, but there are reports that bracken can survive in wet, poorly aerated soil by obtaining oxygen through the hollow stems of dead fern fronds (Watt 1976; Fletcher and Kirkwood 1979).

Light Relations: Bracken is considered to be semi-shade tolerant to shade tolerant (Rowe 1983). It is adaptable to a wide range of light intensities, but is most often a colonizer of open land (Fletcher and Kirkwood 1979). In southwestern Oregon it was found at all light levels above 3% of full light, but it only reached 75% or more of ground cover at 60–100% of full light (Emmingham 1972). Germination and satisfactory vegetative growth will occur under a wide range of light intensities, but spore production decreases significantly in the shade (Page 1976). Hellum and Zahner (1966) report that open- and shade-grown forms of the frond are somewhat different.

Temperature Relations: The fronds and rhizome buds of bracken are highly sensitive to frost, and frost is a major factor limiting the latitudinal and altitudinal distribution of the species (Fletcher and Kirkwood 1979; Grime 1979). Late spring and early fall frosts may determine the length of the plant's growing season. Fronds that emerge early in the spring are frequently killed by frost, and it is a major factor in fall senescence. Once fronds have safely emerged, heat requirements for growth are moderate (Watt 1976).

GROWTH AND DEVELOPMENT

Bracken is a highly successful and persistent plant because of its remarkable ability to develop from a single sporeling into a vast long-lived colony. The fern life cycle has been briefly outlined for *Athyrium filix-femina*. In *P. aquilinum*, the mature fern sporophyte is actually an extensive clone with a massive underground system of stems.

Once the sporeling develops from the fertilized fern prothallus, it multiplies rapidly in size. By the second season of growth, there can be 45 fronds produced, by the third season as many as 126, and by the fourth season there can be 297 fronds (Conway 1952). What is visible above ground, however, is merely a small fraction of the growth that is occurring underground.

The majority of the biomass of bracken exists as a system of creeping underground stems or rhizomes (Stanek *et al.* 1979). The rhizome system occurs on two levels. The lower level is situated deep beneath the soil surface (approx. 50 cm) and is responsible for storing food reserves and for lateral expansion of the colony. The upper level of rhizomes is located just beneath the soil surface. It produces numerous short shoots which give rise to the fronds and also has a network of fine roots for nutrient uptake (Cody and Crompton 1975; Fletcher and Kirkwood 1979).

Rates of growth of the rhizome vary from 5 to 200 cm per year. On average sites in Finland the rhizome spreads about 30 cm annually (Cody and Crompton 1975). Individual rhizomes as old as 72 years have been found, measuring 26 m in length from the young advancing front to the dying fronds at the rear of the colony (Watt 1940). Colonies have been known to survive for over 650 years (Fletcher and Kirkwood 1979).

Buds are formed on the ends of the underground short shoots in fall. Only a small percentage of these buds emerge in spring to form fronds. The majority of buds remain dormant, acting as a reserve to replace those fronds that are damaged or destroyed (Cody and Crompton 1975; Fletcher and Kirkwood 1979).

The rhizome system acts as a sink for carbohydrates. During the active growing season, developing fronds draw on these food reserves, and carbohydrate levels in underground stems are low. By mid-summer the fronds begin to produce photosynthate, and carbohydrate levels are restored to high levels by September (Fletcher and Kirkwood 1979).

Phenology: Bracken emergence times are strongly controlled by spring temperatures (Hellum and Zahner 1966). In north temperate climates, frond emergence begins between March and early May, with maximum frond extension taking place mid-May. If any emerging fronds are killed or injured during this time, replacement fronds will reappear up to mid-July (Cody and Crompton 1975). The growth rate of fronds following emergence is not related to the date of emergence. Thus, late-emerging fronds will be small at maturity compared with those emerging earlier (Hellum and Zahner 1966). Spores can be ripe as early as July 22 in British Columbia, but sporangia on any one frond do not mature simultaneously. Peak spore production occurs in late August and early September in Britain (Page 1976; Fletcher and Kirkwood 1979). Leaf senescence begins in August and is brought on by late summer drought and fall frosts. In the Pacific Northwest states, all fronds are dead by late October or early November (Gliessman 1976).

REPRODUCTION

Spore Production and Dispersal: Reproduction of bracken is by means of spores produced in sporangia on the underside of the pinnules (Cody and Crompton 1975). Spores can be produced by the second season of growth following germination (Fletcher and Kirkwood 1979). Approximately 64 spores are produced per sporangia (Conway 1957), so a single, well-developed frond may produce as many as 300 million spores. Not all fronds are spore-bearing and spore production varies enormously from locality to locality. During dry weather the spores are released by means of a natural dehiscence mechanism. The light spores are readily distributed by wind and can travel great distances. Spores are often brought to earth in the first fall rainstorm following the dry weather of late summer (Page 1976).

Spore Viability and Germination: Fern spores have remarkable viability and resistance to environmental extremes (Page 1979). Some fern spores have remained viable for as long as 48 years (Cody and Crompton 1975). Bracken spores have no dormancy requirements and can germinate within a few weeks of dispersal, but it is likely that most spores overwinter and germinate during moist spring weather. The spores will germinate in light or in darkness (Weinberg and Voeller 1969), and on a wide variety of substrates. Germination is frequently on disturbed habitats, and bare, sterile soil with a pH of 5.5–7.7 is ideal. It is rarely observed in the field and never occurs in an established bracken colony or under closed vegetation of any kind. The primary role of spores is to allow the species to invade new habitats — not to maintain the colony within an established territory (Cody and Crompton 1975; Page 1976; Fletcher and Kirkwood 1979).

Vegetative Reproduction: In Canada and elsewhere, vegetative reproduction is the primary means by which bracken regenerates and expands in size within an established territory. When portions of an existing colony are destroyed, the colony will regenerate itself by rapid resprouting of dormant buds. New clones are created when the underground stem is broken off from the parent plant by decay or soil disturbance. Even extremely small fragments of stem will reproduce rapidly by producing new side branches (O'Brien 1964; Cody and Crompton 1975).

PESTS

Cody and Crompton (1975) have produced a detailed summary of the major insect and microbial pests of bracken in Canada. One reason for the remarkable success of bracken is that toxic chemical constituents in its foliage provide immunity against insect predators.

EFFECTS ON CROP TREES

Competition: Bracken has the ability to dominate a wide variety of vegetation types. Associated plants are severely inhibited and often excluded from the interior of bracken stands (Gliessman 1976). In the Pacific Northwest states, bracken has been shown to prevent natural regeneration and retard growth of coniferous trees (Dimock 1964; Stewart 1976; Ferguson and Boyd 1988). After 7 growing seasons, trees planted where bracken was eliminated were nearly twice the height of trees growing in bracken-dominated spots (Boyd and Znerold, in preparation, cited by Ferguson and Boyd 1988). In British Columbia, bracken may cause mortality among coniferous seedlings. Douglas-fir is the most seriously affected conifer in coastal B.C. (T. Lewis, pers. comm., April 1989). The dense fern canopy, heavy litter, and extensive root and rhizome system of well-established bracken creates a competitive environment for young conifers. Damage from above-ground vegetation includes shading, smothering, and mechanical damage (Gliessman 1976; Stewart 1976). Mechanical damage is most severe in areas of heavy snowfall and on sloping sites where all stems fall in the same direction (M. Newton, pers. comm., Dec. 1984). The root and rhizome system competes directly with seedlings for moisture and nutrients; conifers may also be prevented from developing an adequate root system by the heavy layer of bracken litter (Cody and Crompton 1975; Gliessman 1976).

Allelopathy: Bracken is one of the better-known examples of a plant that produces toxic or growth-inhibiting chemicals to reduce competition from other plants. Aqueous extracts of dried bracken reduced radicle growth of cucumber seedlings to about 60% of that of controls (Tinnin and Kirkpatrick 1985). Stewart (1976) was able to demonstrate inhibition of germination and growth in thimbleberry and salmonberry, but Douglas-fir was relatively unaffected. Allelopathic effects on Douglas-fir and other conifers have not been unequivocally demonstrated. Gliessman (1976) believes that allelopathy is the primary mechanism by which bracken excludes its competitors in the Pacific Northwest. Toxic chemicals are apparently released during early spring from litter, rhizomes, and roots (Gliessman 1976). Extracts from mature fronds do not contain inhibitory chemicals (del Moral and Cates 1971).

Beneficial Effects: Nicholson and Paterson (1976) examined the ecological implications of intensive bracken control in Britain and concluded that eradication of bracken would cause no significant negative impacts on the ecosystem. Nonetheless, in areas where no understory vegetation exists beneath the bracken, it can play a significant role in preventing soil erosion (Martin 1976). In some situations, the shading effect of bracken can be beneficial to other plants by creating a moister environment, free of drought stress (Gliessman 1976).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Bracken usually dies back or loses vigour as a forest canopy closes in. Removal of the forest cover creates suitable habitats for bracken invasion, particularly if areas are denuded of understory vegetation that might compete with bracken (Fletcher and Kirkwood 1979). Spores dispersed to logging sites germinate on disturbed ground and colonies quickly develop where bracken was previously lacking. Where bracken was in the understory before logging, colonies develop through vegetative reproduction from rhizomes. In the CWH zone near Vancouver, bracken is able to expand quickly and increase substantially in dominance after canopy removal. Vigour, as measured by height, cover, and leaf area index, is significantly enhanced.[221] In the CDF zone on southeastern Vancouver Island, light thinning of Douglas-fir caused understory bracken biomass to increase by 3.8 times, while heavy thinning increased biomass by 8 times (Stanek *et al.* 1979).

Fire: Bracken is a fire-tolerant species whose reproductive strategy is adapted to periodic intensive fires. It is not only favoured by fire but actually promotes fire by depositing a thick layer of highly inflammable litter on the ground every autumn (Isaac 1940). It is similar to fireweed in that it produces abundant wind-dispersed disseminules that allow it to invade a recently burned site at some distance from the parent population (Keeley 1981). Sterile burned soil is an ideal substrate for spore germination (Page 1976). Once established, bracken is favoured by extremely hot fires that kill other species whose roots and

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[221] Brand 1984.

rhizomes are less well protected beneath the soil (Fletcher and Kirkwood 1979). Bracken vigorously produces new fronds following a fire (Tiedemann and Klock 1974; Cody and Crompton 1975; Rowe 1983), and its rhizomes spread quickly to take advantage of vacant niches (Fletcher and Kirkwood 1979). Bracken has become dominant in many areas along the Pacific Coast that have been subjected to repeated fires (Isaac 1940).

Cutting: Single manual cutting treatments are generally ineffective at controlling bracken. However, in Oregon, cutting a 10-year-old stand of bracken provided better first-year control than application of the herbicide asulam to the same stand. Repeated cutting at relatively short intervals over a period of several years can provide successful control. Timing of treatment is very important. The first cut should be made before the frond is fully expanded and the second should follow about 6 weeks later. In western Scotland, cutting 3 times a year completely eliminated bracken after 4 years, but cutting twice a year for 7 years was less effective.

Consecutive cutting treatments deplete rhizome food reserves, resulting in reduced height and density of fronds. Eventually food reserves are exhausted. The rhizome is rarely killed, however, and the potential for regeneration still exists. Special tools have been devised to "bruise" rather than cut the fronds, but opinion is divided on which treatment is more effective (Cody and Crompton 1975; Fletcher and Kirkwood 1979).

Herbicides: Virtually every herbicide known to man has been tested against bracken at one time or another. The history of these efforts is recounted in Fletcher and Kirkwood (1979) and Chavasse and Davenhill (1973). Effectiveness of different chemicals is extremely variable and regrowth is usually rapid. All of the chemicals that are currently registered for forestry use in British Columbia provide only short-term control of bracken because they do not kill the extensive underground system. The object of chemical investigations is to find a herbicide that will translocate into the extensive rhizome system and destroy the dormant rhizome buds. Effects produced on fronds are a secondary consideration, since any death of fronds will only stimulate more new fronds to emerge. The mode of action of herbicides on bracken is explained in detail by Fletcher and Kirkwood (1979).

Most literature cites asulam as the most effective herbicide for killing bracken without causing significant damage to crop species. A summary of data from 15 asulam trials in the U.S. Inland Northwest indicates that top-kill the second and third years after treatment is usually 80–90% (Boyd *et al.* 1985). Asulam is applied between July and September when fronds are fully emerged. Asulam applied by backpack sprayers to 2.5 m high bracken provided good control in the Port Alberni area (S. McRuer, pers. comm., April 1989).

Glyphosate may be marginally more effective than asulam in controlling bracken in certain situations (Martin 1976). In Washington and Oregon, late summer applications of glyphosate are very effective (Wendel and Kochendorfer 1982; Conard and Emmingham 1984a), whereas fall applications cause only moderate injury. A summary of 11 trials from the U.S. Inland Northwest indicates top-kill is usually 80–100% in the second growing season after application of 1.1–6.5 kg a.i./ha glyphosate. The amount of top-kill was similar after all application rates (Boyd *et al.* 1985). Near Prince George, glyphosate applied aerially in July at 2.25 kg a.i./ha controlled 70% of the bracken after the first growing season.[222]

In western Washington and Oregon, winter applications of 2,4-D are reported to cause moderate injury to bracken, while spring and summer applications tend to cause lighter injury (Conard and Emmingham 1984a). A late summer spray of 2,4-D ester at 2.2 kg a.i./ha in the U.S. Inland Northwest caused 50% top-kill by the second growing season (Boyd 1984, cited by Boyd *et al.* 1985).

Soil Disturbance: Where soil and topography will allow, repeated deep plowing is the best method of bracken control (O'Brien 1964; Fletcher and Kirkwood 1979). Rotary cultivation is also effective but is equally restricted by terrain and slash conditions. In areas of high summer rainfall, plowing and discing treatments may be less effective (O'Brien 1964).

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[222] Herring 1984b.

Fertilization: Roots and rhizomes of bracken respond to additions of nitrogen, phosphorus, potassium, and calcium by increasing the number of new fronds and rhizome branches initiated (Watt 1976). Where Douglas-fir was present as an overstory above bracken, fertilization led to a decline in bracken biomass because it promoted growth of the tree canopy and reduced understory light (Stanek *et al.* 1979). The amount of nitrogen fertilizer tied up in bracken biomass was small and was not considered to be critical to tree growth.

Other: Biological control of bracken has been investigated but does not at present appear to be feasible because the plant is susceptible to so few diseases. Cattle and pigs in fenced areas can be extremely effective in reducing frond density. Trampling by cattle is widely used as a means of control in agricultural areas.

In West Germany, sheets of gypsum board, fiberglass, and roofing paper have been used as a mulch to suppress frond growth around spruce trees (Fletcher and Kirkwood 1979).

WILDLIFE

Food: Bracken fern is an important food source for white-tailed deer, mule deer, and black tailed deer (Harvey 1981). Bracken has made up 3–7 % of the April diet of Roosevelt elk on Vancouver Island.[223] Edwards and Ritcey (1960) reported that caribou feed on bracken from October to December in Wells Gray Park in the Interior of British Columbia.

Bracken is a very important food for mountain beaver, a common mammal in the Pacific Northwest, that occupies a very limited range in British Columbia (Banfield 1974; Voth 1960, cited by Chapman and Feldhamer (editors) 1983; Harestad 1983). The fronds are a major food source for blue grouse from spring until fall on Vancouver Island (Fowle 1960; King 1969; Zwickel and Bendell 1972; King and Bendell 1982).

Other Resources: Mountain beavers often use bracken fern for the outer shell of their nests (Martin 1971, cited by Chapman and Feldhamer (editors) 1983).

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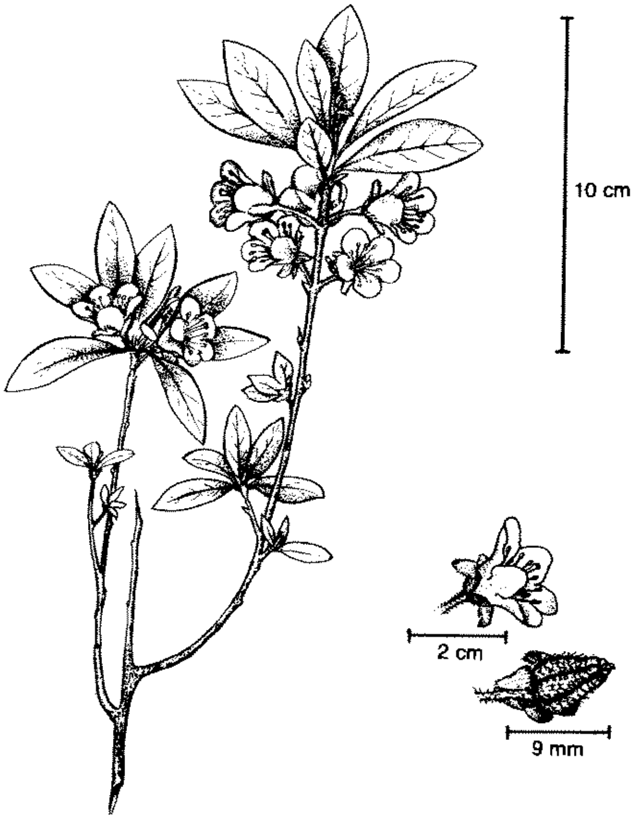
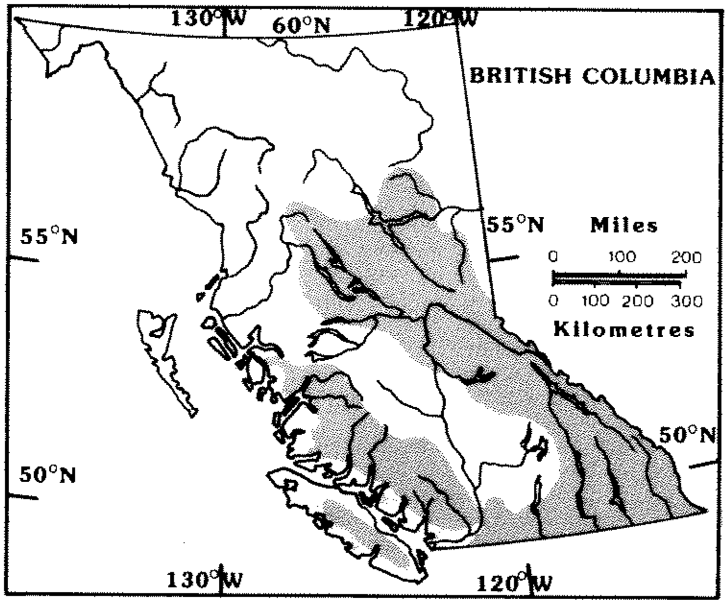
[223] Smith *et al.* (undated).

Rhododendron albiflorum
(white-flowered rhododendron)





Distribution of *R. albiflorum* in British Columbia.

Rhododendron albiflorum Hook. **White-flowered rhododendron** (mountain misery)

DESCRIPTION

White-flowered rhododendron is an erect, slender-branched, deciduous shrub 1–2 m tall with shedding bark. Leaves are thin and narrow and covered in loose reddish hairs. Flowers are white and showy, up to 2 cm long, and are borne in clusters of 1 to 4 blossoms below the whorls of the leaves. The fruit is an ovate capsule (Szczawinski 1962).

Variation: No subspecies or varieties are described in British Columbia (Szczawinski 1962; Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

White-flowered rhododendron is found in mountainous areas throughout British Columbia to 57°N latitude, but its distribution is very scattered north of approximately 52°N. It is most abundant in the mountains of Vancouver Island, in the southern Coast Range, and in mountainous areas of southeastern British Columbia (Szczawinski 1962). *Rhododendron albiflorum* is most abundant in the MH and wetter ESSF biogeoclimatic zones but also occurs in the AT, upper CWH, and ICH zones. It is rare in the SBS zone.

Altitudinal Range: In the Coast Range, white-flowered rhododendron occurs mainly above 750 m (Lyons 1952) but may be found as low as 250 m on the west coast of Vancouver Island (Clark 1976). In the central Interior it occurs above 1200 m on the east side of the Fraser River and in the North Thompson–Shuswap area of the Interior of British Columbia (R. Coupé, pers. comm., Nov. 1984).[224] Rhododendron is replaced by herbs including *Valeriana sitchensis* in forests above approximately 1700 m elevation in the ESSF zone in the southern Interior of British Columbia (J. Mather, pers. observ.).

HABITAT

Climatic Relations: White-flowered rhododendron grows in subalpine climates that are characterized by a short growing season and abundant snow. It is most abundant in climatically wet to moist areas where summer moisture deficits are uncommon. Rhododendrons are not drought tolerant and can only survive in cold climates where there is adequate protection from the drying effects of temperature and wind. Evidence from other species suggests that adequate snow cover may be a critical factor in protecting the plant from winter desiccation (Bowers 1960). Southern distribution may be limited by summer drought. Northern and altitudinal range may be limited by low temperatures.

Site and Soil Conditions: Rhododendron grows on a wide range of site types: in mature, open forest, on cutovers after logging, and in subalpine meadows (Mitchell and Green 1981).[225] Douglas (1972) observed that in the open subalpine forests of the western North Cascades, tree islands produced a very favourable environment for development of *R. albiflorum*. In British Columbia, parent materials on sites with *R. albiflorum* are often colluvial or morainal deposits and are frequently shallow to bedrock. Soils are typically Humo-Ferric Podzols, occasionally Dystric Brunisols, and have a mor or mor-moder humus (see, e.g., Mitchell and Green 1981; Klinka *et al.* 1982).[226] Shaw (1984) showed that *R. ponticum* in Britain was associated with sites of high humidity and rainfall, northern aspects, steep slopes, and coarse, rocky soils that did not dry out in summer. Available evidence suggests that *R. albiflorum* may have similar site preferences in British Columbia (Coates 1987).[227]

Nutrient Relations: Rhododendron is abundant on ecosystems ranging from very poor to very rich in nutrients (see, e.g., Klinka 1977a; Mitchell and Green 1981).[228] Most species are well known to favour acidic soil (Szczawinski 1962; Clark 1976). In British Columbia, *R. albiflorum* has been reported as a significant

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[224] Lloyd (compiler) 1984.
[225] Caza and Kimmins 1987.
[226] Coupé and Yee (editors) 1982.
[227] Lloyd (compiler) 1984.
[228] Coupé and Yee (editors) 1982.

species on soils with pH 4.0–5.5 (Brooke *et al.* 1970; Mitchell and Green 1981).[229] Yarie (1978) found that a shrub understory dominated by *R. albiflorum* on xeric sites in the MH zone of the province played an important role in forest nutrient cycling. Understory vegetation returned a significant proportion of nutrients to the ecosystem each year, mainly in a single pulse during the first autumn snowfall. Understory vegetation also had a significant effect on the quantity of nutrients present as throughfall precipitation reaching the ground.

Water Relations: Rhododendrons do not occur in arid regions of the world, and members of the genus are generally only found in environments with abundant soil or atmospheric moisture (Bowers 1960). In British Columbia, *R. albiflorum* is found only in those zones and subzones with high annual precipitation. However, within these areas, it can be found on sites ranging from xeric to subhygric, though its best development is on mesic sites (Angove and Bancroft 1983).[230]

Light Relations: White-flowered rhododendron is probably moderately shade tolerant. In the open mature forests of the subalpine, *R. albiflorum* is most frequently associated with conditions of semi-shade (Peterson 1965; Douglas 1972). It is abundant in partially shaded forest understories but does not grow well under dense forest canopies (W.R. Mitchell and D. Lloyd, pers. comm., Nov. 1984). The response to different light regimes has been studied in several other species of rhododendron by Nilsen (1986a, 1986b) and Davis and Potter (1987).

Temperature Relations: Horticulturists classify *R. albiflorum* as being tolerant of low temperatures (Bowers 1960). According to M. Burke (pers. comm., 1988), *R. albiflorum* is killed above ground at temperatures below -40°C.

GROWTH AND DEVELOPMENT

White-flowered rhododendron can reach heights of up to 2.5 m in favourable environmental conditions. Leaves expand rapidly in the spring at high elevations in British Columbia. Evidence from other species of rhododendron suggests that the growth and development of individuals of *R. albiflorum* may vary significantly among environments. Rhododendrons as a group are surface-rooting plants (Bowers 1960). Longevity of white-flowered rhododendron plants is not known, but plants of other species in the genus may live over 100 years (Plocher and Carvell 1987).

Phenology: In the subalpine environment, flowering occurs in late spring after leaf expansion in June. Shoot expansion occurs rapidly at the beginning of the growing season and at higher elevations, leaf senescence can begin as early as August (Lyons 1952). The growing season in its high-elevation habitat is short, extending from June to August (Szczawinski 1962). Unlike most species of *Rhododendron*, *R. albiflorum* has deciduous leaves which turn spectacular shades of red and orange with the arrival of the first snows (Clark 1976).

REPRODUCTION

Seed Production and Dispersal: Virtually no information about the reproductive biology of *R. albiflorum* has been published. Seeds of members of the genus *Rhododendron* are typically minute (4–13 million/kg) (USDA 1974). The fruit of *R. albiflorum* is naturally dehiscent and the seeds have winged margins (Szczawinski 1962), indicating that seed dispersal is probably by wind.

Seed Viability and Germination: The viability of the seeds of some species of *Rhododendron* has been found to vary under natural conditions, but it is not generally greater than 1 year (Cross 1981) unless conditions are very dry, in which case seeds typically remain viable for about 2 years. Most rhododendrons require light for germination, but seeds have no chilling or scarification requirement (USDA 1974). White-flowered rhododendron apparently does not produce large numbers of seedlings, since seedlings are rarely observed in the wild and are not abundant in clearcut areas (R. Coupé and O. Steen, pers. comm., Nov. 1984).

Vegetative Reproduction: White-flowered rhododendron can spread by means of rhizomes (D. Coates, pers. comm., Dec. 1989). It is capable of resprouting from the root crown and adventitious stem buds. It also

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[229] Lloyd (compiler) 1984.

[230] Caza and Kimmins 1987.

regenerates by layering, which is useful for expansion in subalpine environments where snowloads and snow creep on slopes keep lower branches pressed close to the ground.

PESTS

No information.

EFFECTS ON CROP TREES

Competition: *Rhododendron albiflorum* is a major species of an ericaceous (*R. albiflorum, Vaccinium* spp., *Menziesia ferrugina*) shrub complex in the ESSF and MH zones throughout much of southern British Columbia. This shrub complex dominates mesic and drier ecosystems in many high-elevation clearcut areas.

White-flowered rhododendron has an open habit and does not produce a deep canopy, but its longevity and shade tolerance may provide it with a strong competitive ability (Lyons 1952). Recent research in the ESSFwc subzone has shown that a well-developed rhododendron canopy can reduce light levels below the saturation point for Engelmann spruce and lodgepole pine, and maintain soil temperatures below critical thresholds for water and nutrient uptake (Coates 1987). Regrowth of rhododendron is slow after manual cutting or scarification; therefore, as long as conifer seedlings are planted promptly after the shrub reduction treatment, trees are unlikely to be overtopped by the shrub. Competition for soil nutrients may also limit tree growth, and in some cases it is possible that *R. albiflorum* competes for moisture (Coates 1987).

Allelopathy: del Moral and Cates (1971) showed that *R. albiflorum* has allelopathic potential in western Washington. Leaf — and especially litter — extracts inhibited growth of test plants in the laboratory, and field sampling showed that subordinate vegetation is markedly reduced beneath the rhododendron canopy.

Beneficial Effects: On droughty, exposed sites, rhododendron may provide some shade and reduce evapotranspiration in young seedlings.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: The response of white-flowered rhododendron to canopy removal depends on the degree of site disturbance and the season of logging. When logging is done on snow during the winter rhododendron is not damaged and it slowly increases in cover. In contrast, summer logging disturbs the soil and tends to cut and uproot rhododendron plants, resulting in replacement of the shrub by perennial herbs such as *Valeriana sitchensis* and *Epilobium angustifolium.* Rhododendron populations on logged sites are usually residuals from the pre-harvest forest which have escaped destruction during harvesting, rather than being established after logging.

Fire: Burning consistently sets back white-flowered rhododendron for 10–15 years on ESSF sites in the Kamloops Forest Region (J. Wright, pers. comm., July 1989).[231]

Cutting: Rhododendron does not respond vigorously to cutting (Coates 1987). After an early July cutting in the ESSFwc subzone near Clearwater, new rhododendron shoots averaged only 2 cm in height by the end of the growing season. This represents slower growth than that of black huckleberry and oval-leaved huckleberry, and slightly faster growth than that of false azalea. Rhododendron's first-year height growth was only 2% of its precut height. Crown diameter regrowth was less than 1% of the pre-treatment level. Almost all new shoots arose from buds on old stems rather than as sprouts or suckers from the soil. Height growth of rhododendron was more vigorous in the second year after cutting than in the first. By the end of the second growing season, the tallest rhododendron plant was 12 cm high, or 11% of its precut height, but it was still shorter than spruce and pine seedlings planted at the time of cutting. Mean crown area after the second growing season was 49% of precut levels. Sixty-three percent of the original stems had new shoots after the first growing season, and stems with new shoots averaged 3.4 shoots per stem. Three years after cutting, clipped rhododendron appeared to have more leaves per unit length of stem than unclipped plants (S. Lindeburgh, pers. comm., May 1989).

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[231] Mather 1987.

Herbicides: White-flowered rhododendron is highly susceptible to foliar applications of 1.4–2.1 kg a.i./ha glyphosate in the ICHvk, ESSFmw, and ESSFwc subzones. Translocation of glyphosate through the plant is poor. If one-half of the plant is sprayed, that half dies while the other half remains unaffected. Killed portions either do not resprout or resprout weakly. Treatments are reported to be effective for at least 3 years (D. Barron, pers. comm., May 1989; J. Wright, pers. comm. July 1989).[232,233]

Soil Disturbance: In the ESSFwc subzone near Clearwater, scarification that removed the tops or uprooted entire rhododendron plants caused severe damage after one growing season. A few new shoots were produced by surviving plants. Two growing seasons after scarification, there was no sign of new sprouts from the soil (Coates 1987).

Mechanical site preparation has consistently reduced rhododendron to a minimal level for 10–15 years on ESSF sites in the Kamloops Forest Region (J. Wright, pers. comm., July 1989).[234]

WILDLIFE AND RANGE

Food: Rhododendron albiflorum generally is unpalatable to livestock and ungulates (Nilsen 1986b). It is rarely browsed and its response to browsing is unknown (T. Lea, pers. comm., Feb. 1989). King (1973) found that blue grouse used small amounts of rhododendron on a subalpine area on Vancouver Island.

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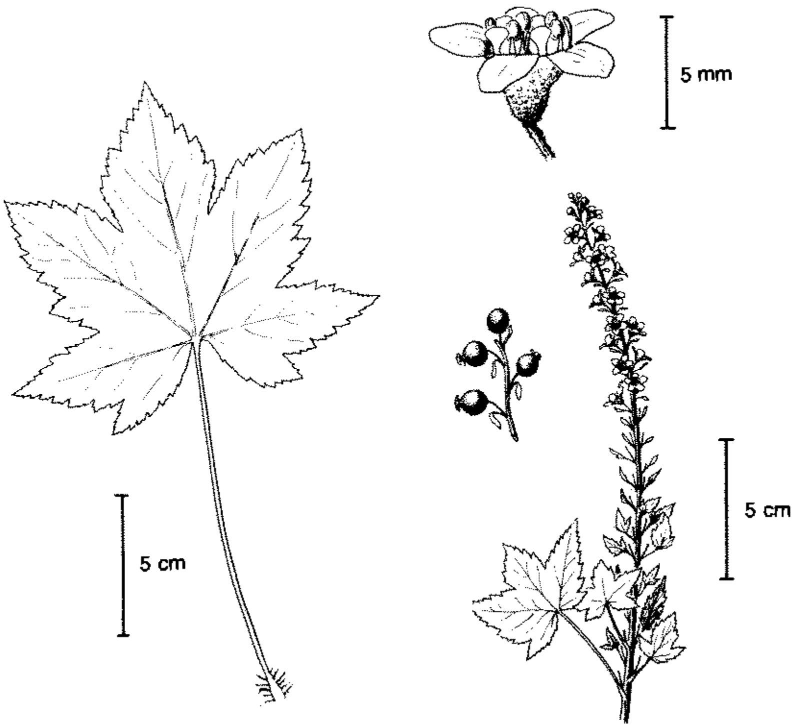
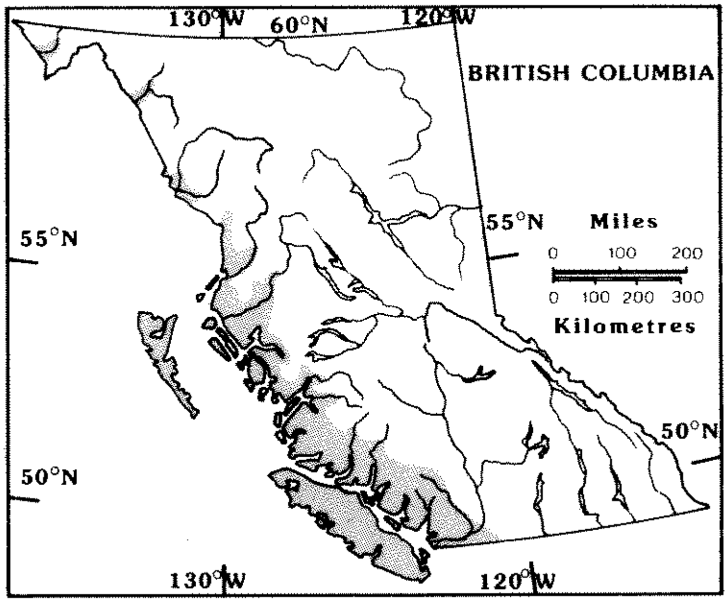
[232] Dyke 1987.
[233] Simard 1988.
[234] Mather 1987.

Ribes bracteosum
(stink currant)





Distribution of *R. bracteosum* in British Columbia.

Ribes bracteosum Dougl. — Stink currant (blue currant)

DESCRIPTION

Stink currant is an erect to spreading deciduous shrub, 1–3 m tall. The twigs are coarse and unarmed, with large red buds and often shredded bark. Leaves are large and palmate with 5 to 7 pointed, toothed lobes and yellowish glands on the undersurface. Flowers and fruits are borne in long, erect racemes. The flowers are small, white to greenish, and the fruit is a spherical berry with a glandular surface and a whitish bloom. The plant has a distinctly "skunky" odour (Viereck and Little 1972; Hultén 1974; Clark 1976).

Variation: No varieties or subspecies of *R. bracteosum* are described in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Ribes bracteosum is found along the entire length of the coast of British Columbia, including Vancouver Island and the Queen Charlotte Islands (Calder and Taylor 1968; Viereck and Little 1972; Hultén 1974). It is found occasionally in moist areas on the east side of the Coast Mountains in southern and central British Columbia but is never abundant (H. Roemer, pers. comm., Dec. 1984). Stink currant is most abundant in the CWH biogeoclimatic zone but is also found in the CDF and MH zones and is scattered in moister areas of some interior zones.

Altitudinal Range: Stink currant is primarily a low-elevation species, occurring near sea level along the coast (Lyons 1952). However, it does ascend to at least 1200 m in the MH zone of south coastal British Columbia (Brooke *et al.* 1970).

HABITAT

Climatic Relations: The geographic range of stink currant suggests that it is a species of humid to perhumid climates with generally mild winter and summer temperatures.

Site and Soil Conditions: Throughout its range, stink currant occupies riparian or alluvial habitats or moist woods (Hultén 1974; Clark 1976; Campbell and Franklin 1979). In Alaska, it is frequently a pioneer of avalanche tracks, roadsides, windfall areas, and other disturbed sites where mineral soil has been exposed and the humus layer has had an opportunity to break down (Taylor 1932; Viereck and Little 1972). Soils on sites with abundant *R. bracteosum* are most often Regosols or Orthic Dystric Brunisols.[235,236]

Nutrient Relations: The preference of this species for alluvial habitats suggests that it has quite a high demand for nutrients. Ecosystem associations in which *R. bracteosum* is a characteristic understory species are most often classified as having a rich to very rich ecological nutrient regime.[237,238]

Water Relations: In British Columbia, stink currant is typically associated with mesic to hygric sites that receive abundant supplies of well-aerated water through flooding or seepage flow (see, e.g., Brooke *et al.* 1970).[239,240] In the Cascade Range of Oregon, *R. bracteosum* is almost always found near permanent water sources (Campbell and Franklin 1979). Summer drought probably prevents this species from colonizing hillsides adjacent to the riparian zone.

Light Relations: Stink currant is most vigorous on open sites that receive abundant light but are not subjected to moisture stress (Taylor 1932; Viereck and Little 1972). In the forest it is typically found under open tree canopies or along streambanks where some sunlight is available.

Temperature Relations: No information.

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[235] Yole *et al.* 1982.
[236] Banner *et al.* 1983.
[237] Yole *et al.* 1982.
[238] Banner *et al.* 1983.
[239] Yole *et al.* 1982.
[240] Banner *et al.* 1983.

GROWTH AND DEVELOPMENT

There is no published information on the growth and development of stink currant. The form of the shrub is typically scraggly, and under favourable conditions it can reach over 3 m in height (Clark 1976). The average height is 1.5–2.5 m.

Phenology: In the Kimsquit Valley on the central British Columbia coast, leaves emerged by late April and were fully expanded by June.[241] In coastal Alaska, stink currant flowers during May and June and fruit ripens between late July and August (Viereck and Little 1972). Fruit dispersal was during August in the western Oregon Cascades (Campbell and Franklin 1979). Leaf senescence and abscission occurred between late July and mid-November in Oregon and at Kimsquit. Stink currant was one of the first species in the riparian community to begin losing its leaves, but the rate of abscission was slower than for most other species (Campbell and Franklin 1979).

REPRODUCTION

Seed Production and Dissemination: The fruit is a glandular berry that is dispersed almost entirely by birds and mammals during summer and fall (USDA 1974).

Seed Viability and Germination: Seeds of most species of the *Ribes* genus require a long period of chilling and in some cases an acid scarification treatment before germination can occur; however, each species seems to have its own unique germination characteristics. Germination typically occurs in the spring of the year following ripening of the seed, after the seed has passed through the intestines of the bird or mammal vector. The best seedbed for germination of *Ribes* seed appears to be moist mineral soil that is well supplied with humus (USDA 1974).

These general comments on *Ribes* seeds seem to correspond well with field observations of *R. bracteosum.* Propagation by seed is believed to be the most important form of reproduction in this species (M. Newton, pers. comm., Dec. 1984). Species of the genus *Ribes* are known to be seed bankers (Rowe 1983).

Vegetative Reproduction: Most species of *Ribes* can be readily propagated using cuttings taken during the dormant season (USDA 1974). *R. bracteosum* apparently does not spread by means of root or rhizome suckers, but it will sprout back from the root crown if damaged. Natural layering may also occur (M. Newton, pers. comm., Dec. 1984).

PESTS

Stink currant is an alternate host for *Cronartium ribicola*, the white pine blister rust (Foster and Wallis 1974).

EFFECTS ON CROP TREES

Competition: Stink currant is a common member of the complex brush community found on alluvial ecosystems along the coast of British Columbia. These brush communities pose some of the most serious vegetation management problems in the province because they occupy the most productive sites for coniferous tree growth and because competition to conifers is extremely severe.[242] *Ribes bracteosum* is not considered to be a major competitor in these coastal brush communities on the south coast (M. Scott and G. Kennah, pers. comm., Nov. 1984);[243] however, on the central and north coasts, it is one of the more abundant species on alluvial sites and can be a significant competitor (B.M. Geisler, pers. comm., Jan. 1985).

Stink currant does not grow or spread rapidly compared with other seral shrub species found on coastal alluvial sites (M. Newton, pers. comm., Dec. 1984), but where it is established prior to logging, or where planting is delayed for several years following disturbance, the species can impede conifer regeneration. Its large, palmate leaves can produce a dense, multi-layered canopy which allows very little light to penetrate. Competition on these moist, rich ecosystems is probably primarily for light.

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[241] Hamilton 1984.

[242] Macadam *et al.* 1984.

[243] Brand 1984.

Because it acts as an alternate host to the white pine blister rust, stink currant is an important limiting factor to the regeneration of western white pine on the south coast.

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

There is little information regarding the response of stink currant to common silvicultural practices or other forms of ecosystem disturbance. Stink currant undoubtedly increases in size and vigour following canopy removal, as long as removal of shade does not impose significant drought stress. It resprouts following cutting or fire but does not spread aggressively by vegetative means (M. Newton, pers. comm., Dec. 1984). Scarification of alluvial sites that produces a moist, mineral soil seedbed will favour germination of seeds (USDA 1974). Glyphosate at 2.0 kg/ha was successful in controlling stink currant in the Prince Rupert Forest Region (J. Pollack, pers. comm., Jan. 1985).

WILDLIFE

Food: R. bracteosum is not an important food source for most ungulates in British Columbia and is seldom browsed (T. Lea, pers. comm., Feb. 1989). The fruit is the most common part of the plant consumed[244] and is eaten by many bird species. The fruit is important to bears (Hamilton 1987). The plant is a moderately important food source for black-tailed deer and Roosevelt elk in the winter (Singleton 1976).[245]

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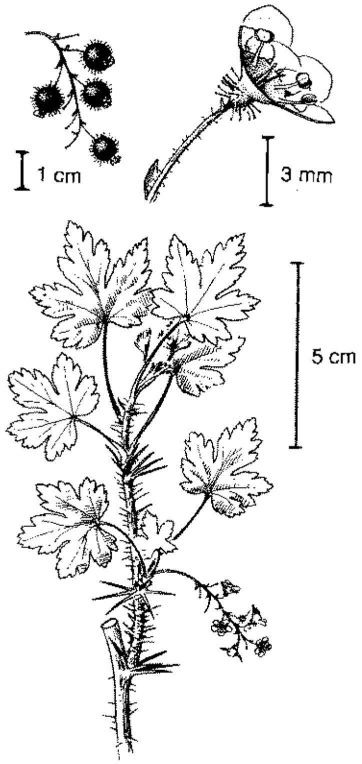
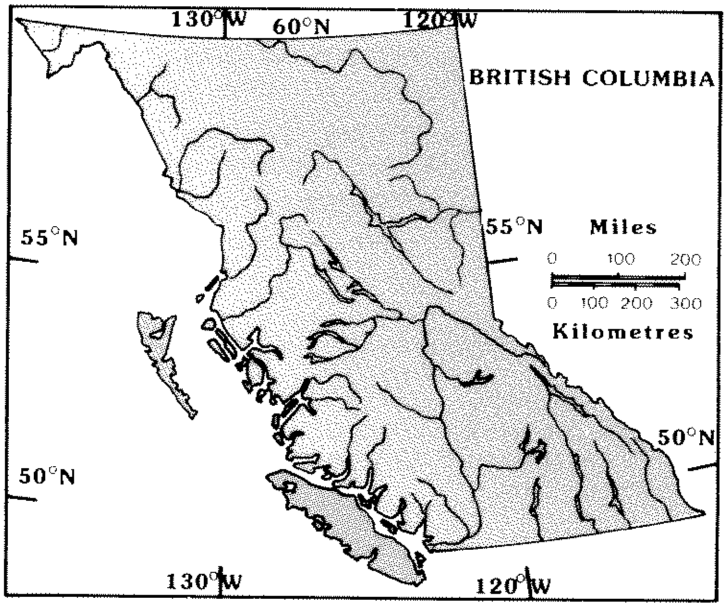
[244] B.C. Min. Environ. (undated).

[245] Blower 1982.

Ribes lacustre
(black gooseberry)





Distribution of *R. lacustre* in British Columbia.

Ribes lacustre (Pers.) Poir

Black gooseberry
(Black swamp gooseberry)

DESCRIPTION

Black gooseberry is a spreading to erect deciduous shrub, 1–1.5 m tall. It grows as individual plants or in extensive low thickets of weakly upright, straggly stems. Young stems are yellowish-brown with large nodular spines and many sharp prickles, while older branches are almost smooth. Leaves are small with a deeply dissected maple leaf shape. They have 5 lobes with coarse double serration. Flowers are saucer-shaped and clustered in drooping racemes of 6 to 15. The fruit is a densely glandular to bristly, purple-black berry with stalked glands (Viereck and Little 1972; Clark 1973; Porsild 1979; Angove and Bancroft 1983).

Variation: There are no varieties or subspecies of *R. lacustre* described in the British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Black gooseberry is found on riparian habitats, alluvial sites, and moist woods on mountain slopes throughout British Columbia (Taylor and MacBryde 1977). It occurs in all biogeoclimatic zones except the PP and BG.

Altitudinal Range: Black gooseberry occupies mountain slopes to over 1800 m (Lyons 1952) and frequently reaches subalpine elevations (Clark 1973).

HABITAT

Climatic Relations: The geographic range and preferred habitat of black gooseberry suggests it is a species of cool, moist conditions.

Site and Soil Conditions: Black gooseberry is most often found on Brunisols, Humic Gleysols, Gleyed Humic Regosols, or Cumulic Regosols (Mitchell and Green 1981).

Nutrient Relations: Black gooseberry characteristically grows on ecosystem associations with medium to very rich nutrient regimes (Eis 1981; Mitchell and Green 1981; D. Lloyd, pers. comm., March 1989).

Water Relations: Black gooseberry typically occupies alluvial or riparian habitats and moist to wet forests. However, it is also found in clearcuts where there is a growing season moisture deficit (Clark 1973). *Ribes lacustre* occurs on subhygric to hygric sites in the IDF and MS zones and submesic to hygric sites in the wetter subzones of the ESSF and ICH (D. Lloyd, pers. comm., March 1989).

Light Relations: Noste and Bushey (1987) report that *Ribes* spp. are shade intolerant. However, Hamilton and Yearsley (1988) found that *R. lacustre* is moderately shade tolerant in the SBS zone in central British Columbia. The shrub is most vigorous in canopy openings (D. Lloyd, pers. comm., March 1989).

Temperature Relations: No information.

GROWTH AND DEVELOPMENT

No information specific to *Ribes lacustre* was found.

Phenology: In coastal Alaska, *Ribes lacustre* flowers in June (Viereck and Little 1972). The USDA (1974) reports that in North America, flowering occurs between April and July and the fruit ripens in August. Black gooseberry often does not bear fruit in the ESSF zone, probably because of the very short growing season (D. Lloyd, pers. comm., March 1989).

REPRODUCTION

Seed Production and Dissemination: Black gooseberry can first bear seeds at the age of 3–5 years. Good seed crops occur at 2–3 year intervals. The berry is dispersed during summer and fall by gravity and by birds and mammals (USDA 1974).

Ribes lacustre is a seed banker (Rowe 1983; Kramer and Johnson 1987). Kramer and Johnson (1987) report a maximum viable seed bank density of 567 seeds per square metre under mature stands of Douglas-fir and grand fir in west central Idaho. Over 80% of the seeds were located in the top 5 cm of mineral soil.

Seed Viability and Germination: Seeds are viable for long periods of time, particularly if they are stored in sealed containers (USDA 1974; Noste and Bushey 1987). Seeds of most species of the *Ribes* genus require a long period of chilling and, in some cases, fire or acid scarification before germination can occur (USDA 1974). Germination of *R. lacustre* was 48% following chilling at 0°C for 120–200 days in a nursery. Considerable germination of *R. lacustre* can also be obtained by alternating diurnal temperatures between 25°C and 10°C, and soaking for 5 minutes in 2–10% sulfuric acid solutions. In nature, germination typically occurs in the spring of the year following seed ripening, after seed has passed through the intestines of a bird or mammal. The best seedbed for germination of *Ribes* seed appears to be moist mineral soil that is well supplied with humus (USDA 1974).

Vegetative Reproduction: Most species of *Ribes* can be readily propagated using cuttings taken during the dormant season (USDA 1974). Rhizomatous extension is limited (Stickney 1986). *Ribes lacustre* can reproduce by layering (D. Lloyd, pers. comm., March 1989).

PESTS

Ribes spp. are preferred hosts to California tent caterpillar (*Malacosoma californicum* Packard), but damage is generally minor. Other insect pests in British Columbia include aphids and the fourlined plant bug (*Poecilocapsus lineatus*) (Furniss and Carolin 1977; L. MacLauchin, pers. comm., March 1989).

The most common pathogen of *R. lacustre* is *Cronartium ribicola* (white pine blister rust)(H. Merler, pers. comm., April 1989). Prickly gooseberry is also the primary host to willow rust (*Melampsora ribesii-purpureae* Kleb.); willows are the secondary host. Initially the rust kills only the infected leaves, but after several years of infection all current foliage dies and growth is reduced (Hunt 1978). Other foliar rusts that infect prickly gooseberry are *Puccinia caricira* and *Puccinia commutata* (Hunt 1978; H. Merler, pers. comm., April 1989). Westcott (1971) provides a comprehensive list of the many diseases that are found on *Ribes* spp. in the United States.

EFFECTS ON CROP TREES

Competition: Ribes lacustre is a common member of brush complexes found on moist and alluvial ecosystems throughout British Columbia. These brush complexes pose serious vegetation management problems because they occupy sites with high productivity for coniferous forest growth and because competition with conifers for light can be severe. *Ribes lacustre* by itself, however, does not reach levels which are considered seriously detrimental to conifer regeneration. The species generally does not occupy more than 10% cover of logged sites (see, e.g., Hamilton and Yearsley 1988).

No information is available on the individual impact of *Ribes lacustre* on conifer establishment and growth. However, some studies have investigated competition between conifers and complexes that contain prickly gooseberry. On an alluvial site in British Columbia, Eis (1981) found that the cover of a shrub complex, which included *Ribes lacustre*, rapidly increased after logging and within 3 years competition was so intense that spruce height growth was less than 2 cm and mortality of spruce seedlings was severe. Practically all conifer seedlings died within 5 years of logging.

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Because black gooseberry is a seed banker and prefers sun to shade, it typically increases in cover following forest canopy removal. However, it seldom attains a high percent cover. For example, in the SBS zone, it rarely exceeds 10% cover following canopy removal (Hamilton and Yearsley 1988). *Ribes lacustre* invaded a submesic to mesic site with a moss seedbed and increased in abundance on alluvial and poorly drained (hydric to subhydric) sites following clearcutting near Prince George (Eis 1981).

Fire: Black gooseberry is fairly resistant to fire kill. Following light fires that only top-kill plants, sprouting from surviving rhizomes and root crowns, which are located beneath the soil surface, sometimes occurs. However, fires that remove the organic layer will often kill the root system (Fischer and Clayton 1983; Noste and Bushey 1987).

Germination of on-site, dormant seeds occurs immediately after fire (Noste and Bushey 1987; Hamilton and Yearsley 1988). Severe fires that destroy this on-site seed do not prevent black gooseberry from increasing in cover (Fischer and Clayton 1983). Seeds are carried into severely burned areas by birds that prefer sparse vegetation (Daubenmire 1974). Consequently, prickly gooseberry can invade a site or increase in cover, even after a severe fire (Fischer and Clayton 1983).

Several studies report invasion or cover increases of *Ribes lacustre* following prescribed burning, but the species by itself does not reach levels which are seriously competitive to conifer regeneration.

Cutting: Species in the genus *Ribes* have the ability to sprout from root collars following cutting, but no studies have investigated the specifics of their sprouting behaviour.

Herbicides: The maximum legal rate of glyphosate (2.14 kg a.i./ha) has effectively controlled *Ribes lacustre* in British Columbia when applied in the summer or early fall. For example, in the ESSF zone in the southern Interior, *Ribes lacustre* was killed after an early August application of 2.1 kg a.i./ha glyphosate (D. Lloyd, pers. comm., March 1989). Plants were severely defoliated 2 years after a foliar spray of 6 L/ha (2.1 kg a.i./ha) glyphosate in September in the ESSFwc subzone near Blue River. However, at application rates of 2 and 4 L/ha, plants were resprouting after 2 years.[246] Miller (1985b) reduced the cover of *Ribes lacustre* by 61–80% with 4.7 L/ha glyphosate in the U.S. Inland Northwest. Black gooseberry was relatively tolerant of a mid-July broadcast application of 2.25 kg a.i./ha glyphosate made near Prince George.[247]

Hexazinone may provide good control of prickly gooseberry if organic layers of the soil are not deep. *Ribes lacustre* was mildly affected by late June applications of hexazinone at 4 mL per spot in a 1 x 2 m grid in the SBSmw subzone near Quesnel. Recovery from the mild injury occurred the season after the herbicide application.[248]

In Washington and Oregon, fall foliar applications of 2,4-D in oil and water have moderately injured *Ribes* spp., while fall foliar applications of triclopyr in oil and water have severely injured *Ribes* spp. (Conard and Emmingham 1983).

Soil Disturbance: Ribes lacustre has been observed to increase in abundance the first few years following mechanical disturbance, then declines after about 10 years when taller vegetation begins to shade it out (Hamilton and Yearsley 1988). Black gooseberry increased 2 years after moderate intensity windrowing in the SBSwk subzone near Mackenzie (D. Greenley, pers. comm., May 1989) but remained absent for at least 2 years after mechanical site preparation in the ESSF zone in the southern Interior of British Columbia (D. Lloyd, pers. comm., March 1989).

WILDLIFE AND RANGE

Food: Black gooseberry is typically unimportant to wildlife or livestock (Noste and Bushey 1987) but is used to some extent by several species. Most species feed on the fruit rather than the leaves or stems.[249] *Ribes* spp. has moderate importance to black-tailed deer and Roosevelt elk in winter and to mule deer and moose in the summer and fall. The fruit has low food value to bears (Noste and Bushey 1987) but is a favourite food of squirrels and skunks (Banfield 1974; Chapman and Feldhamer (editors) 1983). Many birds eat the berries.

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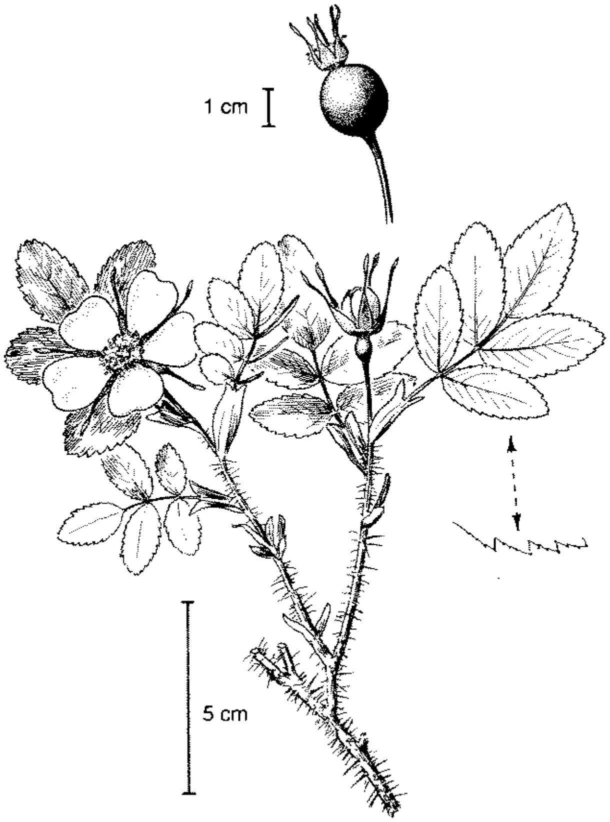
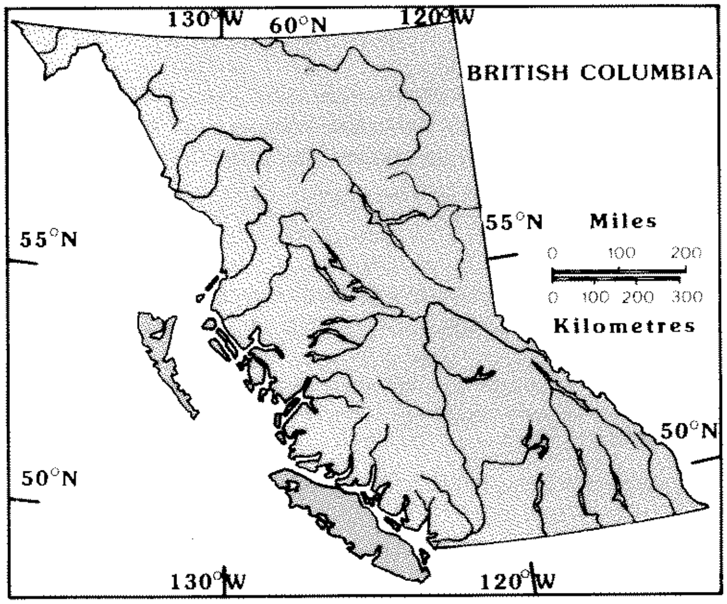
[246] Simard 1988.
[247] Herring 1984b.
[248] George 1989.
[249] B.C. Min. Environ (undated).

Rosa
(roses)





Distribution of *Rosa* in British Columbia.

Rosa spp. L. **Roses**

DESCRIPTION

Rose is a deciduous, perennial shrub with erect or trailing stems, 0.5–2.5 m tall. Stems usually have bristles, prickles, and/or thorns, but flowering branches are often unarmed. Roots are deep and fibrous. Leaves are odd-pinnately compound, with 3–11 serrate or doubly serrate, elliptic leaflets. Leaflets may be glabrous or have few to numerous hairs on the upper or lower surface. Flowers are fragrant, pinkish to rose-colored, usually large, and borne singly or occasionally in twos or threes at the ends of lateral branches or main shoots. Seeds are small, bony achenes borne in fleshy, berry-like purplish or reddish hips. Hips remain on the plants long after they ripen (Lewis 1959; Viereck and Little 1972; Taylor 1973b; Gill and Pogge 1974; UBC Bot. Garden 1978; Angove and Bancroft 1983; Halverson (compiler) 1986).

Variation: The genus *Rosa* is a taxonomically complex genus, due to within-species variation of some conspicuous characteristics, and frequent hybridization between species where their ranges overlap. There are at least 100 species of rose in the northern hemisphere (Taylor 1973b), 18 of which are native to North America, and 6 of which occur in British Columbia (Taylor and MacBryde 1977; UBC Bot. Garden 1978). There are also 2 European species (*R. canina* and *R. rubiginosa*) which have become naturalized near Vancouver and Victoria. Silviculturally, these two species are unimportant, and so are omitted from this discussion.

DISTRIBUTION AND ABUNDANCE

The following table lists the six native roses and describes their distribution in the province (Taylor 1973b; Taylor and MacBryde 1977; UBC Bot. Garden 1978).

Scientific name	Common name	Distribution in B.C	Habitat
R. acicularis	Prickly rose	Interior B.C, from Hope eastward except very arid areas. ESSF, BWBS, SBS, ICH, MS, IDF, PP, BG zones	Open woods; thickets; hills; banks
R. gymnocarpa	Baldhip rose	Southern B.C., south of latitude 56°N. CWH, CDF, ICH, SBS, IDF, PP, BG zones	Moist and dry woods; rock outcrops
R. nutkana	Nootka rose	Coast and Interior; south of latitude 56°N. CWH, CDF, ESSF, SBS, ICH, IDF zones	Thickets; open woods; rich soil
R. pisocarpa	Clustered wild rose	Southern coastal B.C. and Vancouver Island. CWH, CDF, IDF, PP zones	Thickets; woods; riparian
R. woodsii	Woods' rose	Dry Interior areas ESSF, ICH, SBS, IDF, PP zones	Grassland; riparian
R. arkansana	Low prairie rose	Northeastern B.C. BWBS zone	Open woods

Altitudinal Range: Most rose species occur from sea level to moderate elevations. Exceptions are baldhip rose, which occurs from sea level to about 1800 m (UBC Bot. Garden 1978), and woods' rose, which occurs from about 1000 to 3300 m (Blauer *et al.* 1975).

HABITAT

Climatic Relations: The altitudinal range of roses suggest that they favour moderate climates. However, baldhip and woods' rose will grow in alpine environments, which suggests they can tolerate a cold, snowy climate with a short growing season. Woods' rose seldom is found where the average annual precipitation is less than 260 mm.

Site and Soil Conditions: Wild roses tolerate a wide range of soils except those that are very wet or acidic. Most species thrive on moderately fertile, well-drained clay loam, sandy loam, or sandy soils (Smithberg and Gill 1974). In the southern Interior, roses most often occur on Eutric or Melanic Brunisols, occasionally occur on Gleyed Luvisols, and are usually found on a mor moder humus form (Mitchell and Green 1981).

Nutrient relations: Roses tolerate a wide range ot nutrient conditions (D. Lloyd, pers. comm., March 1989), but most grow best in moderately fertile, loamy soils. Roses prefer soils with pH values ranging trom 5.6 to 7.0 and have a low tolerance for extremely acidic conditions (UBC Bot. Garden 1978). Nootka rose prefers fairly rich soils while baldhip rose is found on thin soils over rocky exposed sites (Lyons 1952; UBC Bot. Garden 1978). In the IDF and BG zones, Nootka and prickly rose typically grow on medium to rich sites, while baldhip rose is found on poor to medium nutrient regimes (Mitchell and Green 1981).

Water Relations: Roses are adapted to a broad range of moisture conditions. However, they tend to favour moist, well-drained soils. Moisture adaptations vary between species of rose. For example, woods' and clustered wild rose prefer riparian ecosystems, while baldhip rose prefers dry rock outcrops (Lyons 1952; UBC Bot. Garden 1978).

Light Relations: Reports of shade tolerance ot *Rosa* spp. vary from moderately tolerant (Viereck and Little 1972; Blauer *et al.* 1975; UBC Bot. Garden 1978; Morgan and Neuenschwander 1988b) to intolerant (Gill and Pogge 1974; Smithberg and Gill 1974; D. Lloyd, pers. comm., March 1989). Roses grow more vigorously and produce more fruit when growing in full sunlight than in shade (Smithberg and Gill 1974). In the southern Interior of British Columbia, roses under forest canopies do not usually flower (D. Lloyd, pers. comm., March 1989). However, germination of rose is not inhibited by shade, suggesting some tolerance to overstory closure (Pratt *et al.* 1984).

Temperature Relations: The range of most rose species in the province suggests that they prefer moderate temperatures, although baldhip and woods' rose apparently are adapted to alpine conditions (Blauer *et al.* 1975; UBC Bot. Garden 1978). Prickly rose germinants grow vigorously at low temperatures, which enables the species to establish in a wide variety of habitats (Densmore and Zasada 1977).

GROWTH AND DEVELOPMENT

Rose germinants produce large root systems, drawing from large carbohydrate reserves in the hip and seed (Densmore and Zasada 1977). Maximum height is attained within 10 years (Mueggler 1965). Dense thickets can form. Roses continue to expand and increase in cover as the overstory canopy closes (Viereck 1983).

Phenology: Flowering generally occurs from late spring to mid-summer. However, it varies considerably according to elevation and exposure. Prickly and low prairie roses flower from June to August (UBC Bot. Garden 1978). Nootka, baldhip, woods', and clustered wild roses flower between May and August (Lyons 1952; UBC Bot. Garden 1978). Hips ripen in late summer and early fall and persist on the plant until winter or later (Smithberg and Gill 1974; Densmore and Zasada 1977).

REPRODUCTION

Seed Production and Dissemination: Most rose species first flower and produce seed when they are 2–5 years old and good seed crops are usually produced every 1–2 years (Gill and Pogge 1974; UBC Bot. Garden 1978; Hungerford 1985). Few to many seeds (achenes) are produced in hips. Baldhip rose has 7–14 achenes per hip (Gill and Pogge 1974). Seeds are dispersed mostly by birds and mammals, which can transport the seeds considerable distances. Germination of seeds may improve after passing through the gut (Smithberg and Gill 1974).

Rose is a seed banking species (Noste and Bushey 1987). Density of viable *Rosa* spp. seeds averaged 33 seeds per square metre in the top 10 cm of mineral soil under a canopy of ponderosa pine in east central

Washington (Pratt *et al.* 1984). Seed density decreased with increasing soil depth. Seed bank density of baldhip rose was only 2 seeds per square metre in the forest floor and top 2 cm of mineral soil beneath an overstory of western redcedar in northern Idaho (Morgan and Neuenschwander 1988a). Seeds of baldhip rose were absent from the seed bank under Douglas-fir and grand fir, even though the plant was an important component of the understory vegetation (Kramer and Johnson 1987).

Seed Viability and Germination: Germination of rose seeds is very difficult. Dormancy length varies among species; the average is between 12 and 15 months (UBC Bot. Garden 1978). Germination cannot occur until the seed coat is weakened by decay or opened chemically or mechanically (Smithberg and Gill 1974). Densmore and Zasada (1977) report, however, that prickly rose pericarps do not prevent imbibition of moisture nor do they offer resistance to embryo growth.

Treatments which have broken seed coat dormancy and shortened germination time include scarification (Smithberg and Gill 1974; UBC Bot. Garden 1978). After 2–3 months of cold or warm stratification, seeds of prickly rose can easily be opened along the suture (Densmore and Zasada 1977). Cold stratification at about 5°C for varying lengths of time has been recommended for many species of rose (Gill and Pogge 1974). These authors report germination capacities of 43% for baldhip rose and 63% for Nootka rose after varying lengths of cold stratification at approximately 5°C. In Alaska, Densmore and Zasada (1977) obtained 57% germination of prickly rose after cold scarification for 360 days. However, they obtained over 90% germination after a dual treatment of warm (25°C) stratification for 118 days and cold (5°C) stratification for 3 months. Dual warm–cold stratification treatments have achieved germination rates between 24% and 63% for most of the province's roses (UBC Bot. Garden 1978; King 1980).

In Alaska, prickly rose seeds take 2 years to germinate. Seeds develop and mature the first growing season and they are dispersed prior to snowmelt by mammals and birds that eat the fruit and defecate the seeds. Few seeds germinate in the spring. They warm stratify the summer after they mature, cold stratify the following winter, and germinate shortly after snowmelt (Densmore and Zasada 1977).

Vegetation Reproduction: Roses reproduce vegetatively by layering, rooting from stem cuttings, suckering from root crowns, and sprouting from rhizomes (Hungerford 1985; Noste and Bushey 1987). They are most easily propagated from semi-ripe (taken in August) or dormant (taken in fall or winter) cuttings. Densmore and Zasada (1977) found that prickly rose spread vegetatively over wide areas by rhizomes. Twenty-four percent of rose germinants under a ponderosa pine stand in east central Washington originated vegetatively (Pratt *et al.* 1984).

PESTS

The principal forest insect pests are California tent caterpillar (*Malacasoma californicum*), rose leaf hopper (*Edwardsiana rosae*) (L. MacLauchlin, pers. comm., Mar. 1989), and a subspecies of western tussock moth (*Orgyia vetusta* ssp. *gulosa*) (Furniss and Carolin 1977). Western tent caterpillar (*Malacosoma pluviale*) is also a common pest to roses (Ruppel 1968).

Rose is affected by many pathogens. The most common ones are *Sphaerotheca macularis* and *S. pannosa* var. *rosae* (powdery mildews) (H. Merler, pers. comm., April 1989). A detailed list of diseases affecting roses is provided by Westcott (1971).

EFFECTS ON CROP TREES

Competition: Rose is a common member of the dense complex shrub community found on subhygric to hygric sites in the IDF and PP zones in the southern Interior of British Columbia. The complex is composed of *R. acicularis*, *R. gymnocarpa* or *R. nutkana*, and common snowberry, red-osier dogwood, water birch, trembling aspen, and black cottonwood. It is thought to compete seriously with coniferous seedlings in these subzones (D. Lloyd, pers. comm., Mar. 1989).

Allelopathy: Roses may have considerable allelopathic activity, since they have been found to inhibit neighbouring plants and cause soil toxicity (Rice 1974).

Beneficial Effects: The thicket-forming roses may help control erosion. Most species are also suitable for landscaping (Gill and Pogge 1974).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Rose often decreases in abundance immediately following disturbance while invading herbaceous species dominate; it regains its pre-disturbance level after several growing seasons. Forest canopy removal generally does not result in a dramatic increase in rose cover, or development of extensive patches of the species. Rather, canopy removal often stimulates the development of shrub complexes with rose making up less than 10% of the total cover. Baldhip rose remained relatively low in cover for the first 10 years following logging of a western hemlock–Douglas-fir stand in the Oregon Cascades, but cover increased after canopy closure at 20–30 years, indicating rose's tolerance for shade (Schoonmaker and McKee 1988). In the cedar–hemlock zone of northern Idaho, rose also showed an initial decrease in cover following overstory removal. Subsequent development was more rapid and a higher cover was attained in the grand fir and western redcedar habitat types than in the western hemlock type possibly because of differences in light availability (Wittinger *et al.* 1977; Irwin and Peek 1979). Irwin and Peek (1979) found that height growth of baldhip rose after logging was related to the basal area of the remaining overstory; height growth decreased as basal area increased.

In some instances rose cover is unaffected by overstory removal. Cover and frequency of prickly rose was unchanged following removal of a trembling aspen–white spruce overstory (de Vos and Bailey 1970) and a lodgepole pine overstory (Corns and La Roi 1976). Similarly, rose was unaffected by opening size in Douglas-fir stands in the Oregon Coast Range (Sabhasri and Ferrell 1960) and cedar–hemlock stands in northern Idaho (Mueggler 1965). Rose cover remained unchanged 5 years after thinning of lodgepole pine stands in central Colorado (Crouch 1986).

Fire: Roses are moderately fire resistant and are usually favoured by light burns (Wright 1972; Noste and Bushey 1987). Roses can persist after light to moderate fires because of their ability to sprout from undamaged or buried root crowns and rhizomes and germinate from on-site or transported seeds (USDA 1981; Viereck 1983; Crane and Fischer 1986; Noste and Bushey 1987). However, the shallow root crowns of rose are susceptible to injury (Noste and Bushey 1987) and consequently plant abundance can decrease following severe fires.

Prickly rose appears to be moderately tolerant of typical burns on mesic and wetter sites in the SBS zone but is diminished by burns on drier SBS sites (Hamilton 1988), probably because burns are likely to be more severe on drier sites. Sprouting of prickly rose from underground parts was rapid and abundant on lightly burned areas in northeastern Minnesota but was relatively infrequent on severely burned areas (Ahlgren 1960). Stark and Steele (1977) recorded the response of baldhip rose to light, medium, and hot burns under a mature unlogged larch–Douglas-fir forest in Montana. Third-year cover of baldhip rose was below pre-burn levels after light and medium burns, and the species was absent after the hot burn.

Light and moderate fires often do not cause a significant increase in rose cover. For example, burning had little effect on the abundance of baldhip rose in northern Idaho (Mueggler 1965) and Nootka rose in Washington and Oregon (Isaac 1940). In other cases, rose cover has decreased immediately after wildfire, gradually increased, and then declined as the canopy closes (Reid *et al.* 1938; Yerkes 1960; Lyon 1971; Foote 1983; Hamilton 1988). This appears to be a characteristic response of rose to burning.

Rose has sometimes been eliminated, or cover has gradually declined, following burns that are not severe. Competition from other species may at least partially explain this result. Wittinger *et al.* (1977) found that baldhip rose progressively decreased in cover for at least 15 years while most other species on the site increased following logging and burning of western hemlock and grand fir sites in northern Idaho. Baldhip rose was fairly widely distributed in an old-growth Douglas-fir stand in the Oregon Cascades but was not present for at least 6 years following logging and a burn of varying intensity. Multiple burns can significantly reduce the cover of rose (Mueggler 1965; Noste and Bushey 1987).

Concentrations of nitrogen, potassium, magnesium, and manganese in the foliage of baldhip rose increased during the first growing season and decreased in the second and third growing seasons following light or moderate burns in the southern Rocky Mountain Trench of British Columbia (Demarchi and Lofts 1985).

Cutting and Grazing: Manual cutting of rose in July stimulated sprouting during the same growing season in the MS zone near Kamloops, B.C. (S. Simard, pers. observ.). Rose recovered to its pre-treatment height and cover within 5 years of cutting in Idaho (Hann 1986).

In an aspen parkland in western Canada, yield of rose was significantly lower following cattle grazing in early July compared with late August. The earlier grazing resulted in a decline in vigour because root carbohydrates are low early in the season (Fitzgerald and Bailey 1984). Nootka rose was the only shrub species to increase in cover following grazing by livestock in Douglas-fir stands in the northern Rocky Mountains of the United States (Cholewa and Johnson 1983).

Herbicides: Spring and fall foliar applications of glyphosate result in severe to very severe injury to rose, (Conard and Emmingham 1983; Boyd *et al.* 1985). In British Columbia, foliar applications of glyphosate have resulted in moderate injury (Boateng and Herring 1990). For example, in the ICHmc subzone near the Skeena River, late August application of 2.0 kg a.i./ha glyphosate provided a moderate reduction in rose cover for 1 year.[250] The plant fully recovered in the second year and increased above pre-treatment cover in the third year.

Spot and broadcast foliar applications of hexazinone in spring and fall have resulted in serious injury to *Rosa* spp. (Boyd *et al.* 1985; Boateng and Herring 1990). Foliar applications of hexazinone at rates of 3.2 and 4.3 kg a.i./ha in May caused over 85% defoliation of rose in Alberta.[251] In the same study, a rate of 2.2 kg a.i./ha caused about 50% defoliation.[252] Hexazinone applied during late July in Alberta, using liquid spot (4 and 8 mL at 2.0- and 1.5-m spacing), liquid broadcast (1.1, 2.2, and 4.3 kg a.i./ha), and granular broadcast (1.1 and 3.4 kg a.i./ha) resulted in complete control of rose.[253] In the SBS zone near Smithers, spring applications of hexazinone have been reported to control rose better than fall applications.[254]

Spring and fall foliar applications of 2,4-D can seriously injure roses (Boyd *et al.* 1985). An application of 3.4 kg a.i/ha 2,4-D in the U.S. Inland Northwest reduced rose cover by 61–89% (Miller 1985b). A site preparation treatment of 2,4-D applied at 4.5 kg a.i./ha resulted in 38% kill of rose in Idaho (Hann 1986); and 2,4-D ester applied at 2.75 kg a.i./ha in early August had no effect on woods' rose in northern Alberta.[255]

Spring and fall foliar applications of 1.7–3.0 kg ai/ha triclopyr have resulted in very serious injury to roses (Miller *et al.* 1983; Boyd *et al.* 1985; Miller 1985b).

Picloram applied alone at 1.1 kg a.i./ha or in combination with 2.2 kg a.i./ha of 2,4-D amine provided excellent control of prickly rose in aspen parkland in Saskatchewan (Bowes 1976). A 9:1 mixture of 2,4-D and picloram effectively controlled rose in grasslands in northeastern Saskatchewan (Waddington and Bittman 1987).

Soil Disturbance: Rose has the ability to sprout from rhizomes and root crowns damaged during mechanical site preparation. Rose sprouted with moderate vigour 1 year following mechanical site preparation in the IDF zone (F. Russell, pers. comm., Mar. 1989). It increased in cover after intense mechanical site preparation in July in the SBSmk subzone in the Mackenzie Forest District (D. Greenley, pers. comm., June 1989). In the lower Rocky Mountain foothills of Alberta, cover of prickly rose in scarified clearcuts stabilized to levels the same as in mature stands within 6 years of disturbance.

WILDLIFE

Food: Roses are a preferred browse of ungulates in British Columbia (McLean 1979). They are browsed by elk, deer, moose, caribou, and bighorn sheep in all seasons (F. Russell, pers. comm., Mar. 1989). Plants having few or no prickles are generally preferred, but even heavily prickled plants sometimes receive substantial use (Blauer *et al.* 1975). While rose hips are seldom highly preferred, they are important because they persist on the tree all winter.

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[250] Pollack and LePage 1986b.
[251] Teskey and Masterson 1984c.
[252] Ibid.
[253] Expert Committee on Weeds 1988.
[254] Ibid.
[255] Mihajlovich and Switzer 1984.

Roses can be one of the most important winter foods for black-tailed deer in southern British Columbia (Nyberg *et al.* 1986), but in most cases the plant has low or medium importance for this ungulate (Singleton 1976).[256] Rose has medium importance as a winter food for white-tailed deer and typically has moderate importance as a year-round food for mule deer (Singleton 1976).[257] Willms *et al.* (1980) found that rose made up 16% of the adult and 43% of the fawn mule deer summer diet in the IDF zone near Kamloops.

Rose hips, twigs, and foliage are used by many birds and mammals other than ungulates (Gill and Pogge 1974). Rose hips are a favourite food of squirrels (Banfield 1974). Mice and coyotes also feed on hips, while porcupines and beaver browse the leaves (Banfield 1974; Noste and Bushey 1987). Pika readily eat the shoots in summer (Banfield 1974; Harestad 1983). In Alaska, *R. acicularis* is an important food source for rodents, grouse, and snowshoe hares (Densmore and Zasada 1977). Wolff (1978) found that rose leaves made up 6% of the diet of snowshoe hare from June until September, and less than 1% the rest of the year. Blue grouse eat leaves and rose hips (Munro 1919; Zwickel and Bendell 1972). Fowells (compiler, 1965) noted that they frequently used rose seeds as grit from July until September. Rose hips are eaten by bears, but they apparently have low food value (Noste and Bushey 1987).

Other Resources: Rose thickets are used for nesting and escape cover by birds and mammals (Gill and Pogge 1974). Birds that nest in roses in the Okanagan include hummingbirds, flycatchers, veeries, and goldfinches (Cannings *et al.* 1987).

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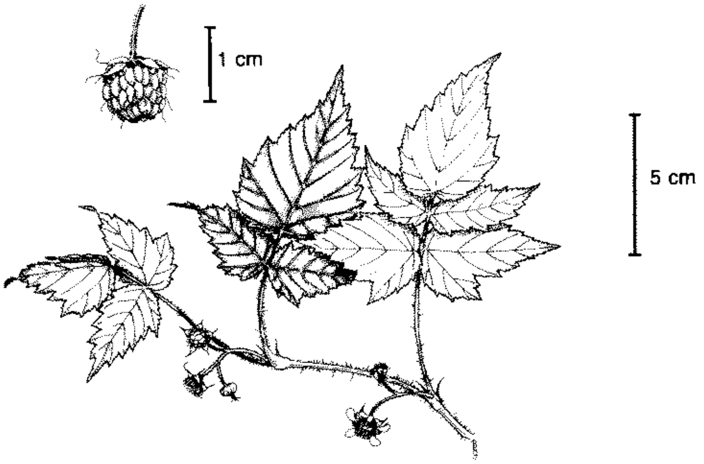
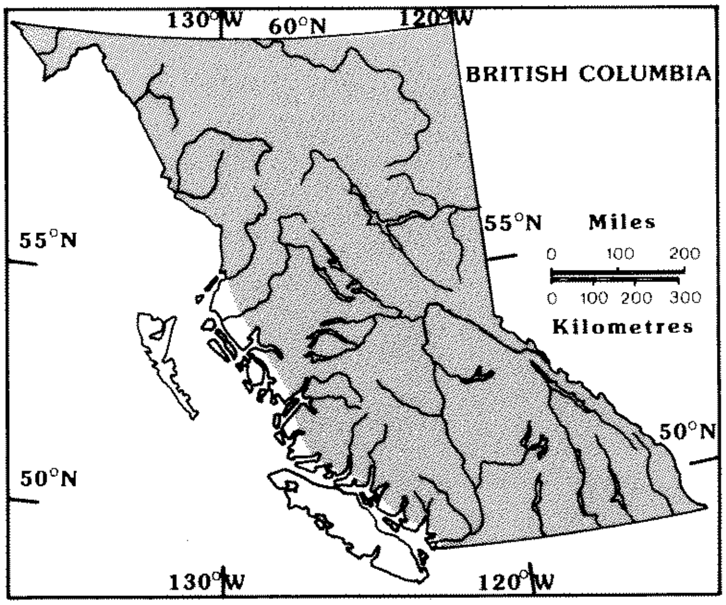
[256] Blower 1982.

[257] Ibid.

Rubus Idaeus
(red raspberry)





Distribution of *R. idaeus* in British Columbia.

***Rubus idaeus* L.** **Red raspberry**

(*R. idaeus* var. *strigosus*)

DESCRIPTION

Red raspberry is a deciduous shrub with erect, biennial stems arising from a perennial, subterranean, branching rhizome. The aerial stems, also known as canes, are 1–2 m tall with numerous bristles, prickles and hairs. In the first year the canes are vegetative only, in the second year they have flowering lateral branches. The leaves of raspberry are compound with 3 to 7 irregularly shaped, toothed lobes. The inflorescence contains 1 to 4 white flowers. The fruit is the familiar raspberry, an aggregate of many small, red drupelets (Viereck and Little 1972; Hultén 1974; Whitney 1982).

Variation: Red raspberry is a variable species with many geographical and cultivated varieties across the northern hemisphere (Viereck and Little 1972). The red raspberry of British Columbia is described as *R. idaeus* ssp. *melanolasius* (Hultén 1974; Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Red raspberry is found throughout British Columbia except west of the Coast Range (Taylor 1973b). It does not occur naturally on the Queen Charlotte Islands (Calder and Taylor 1968) nor on Vancouver Island where it may exist occasionally as a garden escapee (H. Roemer and A. Ceska, pers. comm., Nov. 1984). Red raspberry is found in all biogeoclimatic zones except the MH and AT but is rare in the PP and BG and only occurs in eastern portions of the CWH and CDF zones. It is most abundant in moist areas of the Interior and is uncommon in the dry areas of the southern Interior and west of the Fraser River in the central Interior (Angove and Bancroft 1983; R. Coupé, pers. comm., Nov. 1984).

Altitudinal Range: Red raspberry ranges from inland valley bottoms to subalpine elevations near timberline.

HABITAT

Climatic Relations: The broad distribution of this species across continental North America indicates that it is tolerant of a wide range of northern temperate climates and not limited by the short growing season and cold winter temperatures of the boreal forest. Its absence from the Pacific Coast suggests that it is poorly adapted to a perhumid environment with little annual temperature variation. Red raspberry is also absent from the hottest, most arid areas of British Columbia (Angove and Bancroft 1983). In the Pacific Northwest states, tall raspberry canes are easily damaged by wind and rain (Williamson *et al.* 1979).

Site and Soil Conditions: Throughout its range, red raspberry is found on disturbed sites, such as roadsides, burned areas, and openings and borders of forests (Viereck and Little 1972; Wright 1972; Taylor 1973b; Whitney 1982). It rarely occurs within undisturbed, mature forests.

Nutrient Relations: Red raspberry's preference for recently disturbed soils suggests that it may have a relatively high demand for soil nutrients. Swedish research indicates that raspberry requires and accumulates large quantities of nitrates in its tissues where it invades recently burned sites (Wright 1972). Whitney (1982) has speculated that raspberry's reproductive strategy is adapted to take advantage of high initial levels of soil nitrates during the first years of establishment following disturbance. As soil nitrate levels decrease, the plant may shift from vegetative growth to seed production in response to a change in the carbon:nitrogen ratio of plant tissue. In the SBS zone near Prince George, red raspberry was found on sites with moderately high rates of available calcium and magnesium but appeared to have a relatively broad ecological amplitude with respect to these nutrients. It was absent from sites with low nutrient availability (Wali 1969). Pojar *et al.* (1982) also indicate that in the SBS zone raspberry prefers sites with at least a moderate level of soil nutrients, but it can be found on nutrient-poor sites in the wettest subzones of southeastern British Columbia (Comeau *et al.* 1982).

Water Relations: In climatically dry areas, red raspberry is restricted to receiving sites. In moister regions it is abundant on mesic sites and occupies a broad range of soil moisture regimes (Comeau *et al.* 1982; Pojar *et al.* 1982; Angove and Bancroft 1983). Best growth typically occurs on subhygric sites. Late summer drought reduces stored carbohydrate levels in the plant (Crandall *et al.* 1974), and may thereby result in lower plant vigour.

Light Relations: Red raspberry is a species of open, early seral conditions and is rarely, if ever, found under a closed forest canopy. It is described as fairly shade intolerant by Whitney (1982). Whitney reports that with increased shading, raspberry dies out and puts more energy into fruit production.

Temperature Relations: The distribution of red raspberry indicates that it is a highly frost-tolerant species. Whitney (1982) reports that primocanes (canes in their first growing season) are more frost-hardy than floricanes (flowering canes in their second growing season). The overwintering flower buds require a certain period of cold to break dormancy, and after mild winters flower buds sometimes fail to develop (Hudson 1959).

GROWTH AND DEVELOPMENT

Red raspberry has a complex developmental cycle that has been studied in detail by Hudson (1959) and Williams (1959) in Britain and Whitney (1982) in the northeastern U.S. The natural habit of the species is to form dense colonies of short-lived aerial shoots that arise from a long-lived perennial root system. The following description of the morphological development of the raspberry plant is taken primarily from Hudson (1959).

When a young raspberry plant develops from seed, underground buds are formed in large numbers on the roots. These buds elongate, sending suckers to the soil surface, where they rest in a dormant state. The subterranean sucker can be as long as 50 cm. When conditions are favourable for growth, the shoot rapidly elongates, forming a new cane. At the same time, adventitious roots are produced at the base of the sucker.

During the first growing season in its 2-year life span the cane is known as a primocane. The primocane produces no flowers or fruit. It normally reaches a height of between 1.5 and 2 m, but total height growth is dependent on environmental conditions. In the laboratory or in favourable climates such as in New Zealand, canes can grow much taller. Towards the end of the growing season the primocane ceases to elongate and initiates the fruiting buds.

The second year cane (floricane) begins to grow in spring, following a suitable period of winter cold. The fruiting buds elongate to form lateral branches bearing both leaves and flowers. After fruiting is completed in late summer, the floricane dies back to ground level.

New primocanes emerge from the soil simultaneously with the maturation and death of the floricanes, repeating the 2-year cycle of growth. As successive shoots die back over a period of years they form a perennial woody rootstalk known as the stool. New shoots arising from the stool complete the same life cycle as shoots arising from root suckers.

Whitney (1982) studied the development of a raspberry stand or clone in the northeastern U.S. The first 2 years of life of the clone constitutes a building phase during which there is a rapid increase in the numbers of canes. Beginning in the third year, a process of self-thinning occurs. The average number of suckers produced drops and the survival of suckers declines. As stand density decreases, net biomass production increases, peaking during the fourth year of stand development. As the stand matures, food resources are channelled towards seed production rather than vegetative growth. In the northeastern U.S., few stands persist for more than 5–12 years before they are replaced by other longer-living species. The half-life of red raspberry on a site in north central New Hampshire was about 3 years (Whitney 1986). Mortality of red raspberry was related to plant density. Low densities of red raspberry were associated with a high rate of mortality with 58% of mortality occurring in 1-year-old root suckers. There was much less mortality where raspberry had a high density and a larger proportion (61%) of the mortality was in the older (>2 years) age classes (Whitney 1978, cited by Whitney 1986).

Phenology: In eastern Washington, flower buds were visible on May 19 and fruits were ripe by July 2 (Crandall *et al.* 1974). In Alaska, flowering occurs during June and July with fruit maturation occurring between July and September (Viereck and Little 1972). Leaf senescence in the floricanes coincides with fruit maturation. Primocanes retain their leaves much longer than floricanes (Whitney 1982).

REPRODUCTION

Seed Production and Dispersal: Rubus idaeus has perfect flowers with a floral structure adapted for pollination by bees (Faegri and van der Pijl 1971; USDA 1974). Wild plants are almost exclusively self-infertile (Keep 1968). Production of seed in a vigorous colony is prodigious. Approximately 70–90% of flowers eventually produce mature fruit. Good crops of fruit are produced nearly every year, but total production depends on environmental conditions (USDA 1974) and is also influenced by the stage of stand development. Towards the latter stages of development of the raspberry clone (approximately 4–12 years after establishment), progressively larger proportions of stored food reserves are devoted to seed production (Whitney 1982).

The fruit ripens unevenly over a period of several months, with each drupelet producing a single nutlet. Natural dispersal of the seed is by birds, small mammals, and bears (Ahlgren 1960; USDA 1974).

Seed Viability and Germination: The seeds of red raspberry remain viable for long time, probably over 50 years (Whitney 1982). This lengthy period of viability allows the species to bank seeds in the soil where they can remain dormant until conditions become suitable for germination and seedling survival. Raspberry seeds require a lengthy period of chilling (approx. 120 days) before they will germinate, and in some varieties acid treatment helps to improve germination. Light also helps to stimulate germination following chilling. Temperatures of between 10 and 25°C are favourable for germination (Jennings and Tulloch 1964; USDA 1974). High levels of soil nitrate may promote germination as well (Whitney 1986). Germination of stored or recently deposited seed is the primary means by which raspberry is able to become established on recently disturbed sites, but 1 year after stand initiation, further seedling establishment is almost nonexistent (Whitney 1982).

Vegetative Reproduction: Once red raspberry is established on a site, its ability to colonize the area rapidly depends primarily on its ability to reproduce vegetatively (Keep 1968; Whitney 1982). Formation of root suckers is the primary means of vegetative spread. Suckers develop into independent stools as intervening roots between the parent plant and the root sucker die off (Hudson 1959). Raspberry will regenerate readily from root cuttings taken during the dormant season, while cuttings taken between May and August usually fail to regenerate successfully (Williams 1959).

PESTS

Williamson *et al.* (1979) describe some of the important insect and disease problems of cultivated raspberries, but many of these pests may not occur in Canada.

EFFECTS ON CROP TREES

Competition: Red raspberry is an abundant species on clearcut and burned areas throughout most of the Interior of British Columbia. It is an aggressive invader that frequently forms an almost monospecific shrub layer during the first 3–5 years following large scale disturbance (Whitney 1982). Its abundance and aggressive behaviour enable red raspberry to preempt a site's resources and make it an important competitor with coniferous tree regeneration in many moist areas of the Interior. Because red raspberry is usually not present before canopy removal, it rarely becomes a significant factor in clearcut areas until 3–5 years following logging (Eis 1981; C. DeLong, pers. comm., Nov. 1984). In northern Maine, 6-year-old balsam fir seedlings overtopped by raspberry averaged 36.2 cm in height and 5.5 mm in diameter while open growing seedlings averaged 47.9 cm in height and 8.2 mm in diameter (Fox 1986).

Red raspberry's mode of competition with conifers is not discussed in the literature. It undoubtedly includes shading and mechanical damage to young seedlings on sites where raspberry is dense and vigorous. Raspberry may compete for moisture and nutrients on some sites, but this species is most abundant on moist, rich sites where these resources are plentiful. Competition is limited to the early stages of conifer stand establishment, since raspberry colonies are quickly eliminated once trees and shrubs begin to cast overhead shade (Core 1974; Whitney 1982).

Beneficial Effects: Possible beneficial effects of red raspberry on coniferous tree growth include its ability to reduce soil erosion on disturbed sites (Core 1974) and its ability to limit invasion of taller, longer-lived deciduous species during the early stages of succession.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Red raspberry is a pioneer species that depends on forest openings for establishment and survival. It is known to invade clearcut areas rapidly (Whitney 1982; J. Wright, pers. comm., July 1989). In the SBS zone north of Prince George, raspberry established itself on 3 of 4 site types within 6 years following logging (Eis 1981). Eis speculated that seeds were brought into a clearcut site by birds, but it is also probable that canopy removal provides suitable microsites for germination of long-buried seed.

Red raspberry does not compete well with established understory vegetation and will not invade moist productive alluvial site types where a diverse shrub layer is already well established prior to canopy removal.

Fire: Seedlings of *R. idaeus* often appear in high densities after a fire, and the species is consistently more abundant on burned than on unburned areas (Wright 1972). In British Columbia, red raspberry is frequently found in great abundance on sterile mineral soil that has been exposed by a very hot burn (R. Coupé, pers. comm., Nov. 1984). Burning promotes development of the species by stimulating germination of buried seeds (Sharp 1974; Stickney 1986) and resprouting underground rhizomes, which are quite resistant to burning (Ahlgren 1960; Wright 1972). In northeastern Minnesota, where red raspberry was present prior to a fire, reproduction was primarily vegetative with only minor seedling establishment (Ahlgren 1960).

Red raspberry is generally absent from mature SBSwk forests but is consistently present and has an average cover of 7–20% for the first 10 years after burning in this subzone (Hamilton and Yearsley 1988). In Alaska, plants were present the first year after fire on most areas studied by Foote (1983). Red raspberry has been observed to take 2–3 years to recover from burns in the ICH zone in the Salmon Arm Forest District (J. Wright, pers. comm., July 1989).

Some studies from the southwestern U.S report that cover and vigour begin to decline by the third and fourth years following fire (Wright 1972), while others find that it takes at least 5 years for raspberry to become dominant on a site (Ahlgren 1960). Hamilton and Yearsley (1988) reported that red raspberry tended to be scarce 4 years after burning on mesic and submesic SBSwk sites, presumably because it was shaded out by other species.

Cutting: Because raspberry canes are short-lived and perennial parts are situated underground, a single cutting of the canes will provide negligible control of the plant over the longer term. New shoots will rapidly be produced from root suckers and stools (Core 1974). Red raspberry has been observed to fully recover within 1 year of cutting (J. Wright, pers. comm., July 1989). Treatments that reduce the density of canes will improve the vigour of remaining canes (Lawson and Waister 1972a; Crandall *et al.* 1974).

Repeated heavy cutting will probably result in a depletion of stored food reserves and an eventual decline in the number and vigour of canes produced. Red raspberry plants showed severe signs of lost vigour 1 year after spring and early summer sheep grazing near Clearwater (G. Ellen, pers. comm., July 1989).

Herbicides: A number of studies indicate that glyphosate applications in August or September cause only light to moderate injury to red raspberry in British Columbia, even at maximum application rates (2.14 kg a.i./ha).[258,259,260] Raspberry completely recovers from glyphosate applications within 2 or 3 growing seasons (J. Wright, pers. comm., 1989).[261,262] Raspberry sometimes invades openings where other plant species have been removed by herbicides.

Red raspberry appears to be quite sensitive to mid-May broadcast applications of 2–5 kg a.i./ha hexazinone.[263]

Soil Disturbance: Raspberry will rapidly invade areas of bare disturbed soil where there is little competition from other plant species (Keep 1968; Whitney 1982). Red raspberry has been observed to recover from

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[258] Pollack and LePage 1986b.
[259] George 1989.
[260] Herring 1984c.
[261] Pollack and LePage 1986b.
[262] Dyke 1987.
[263] Teskey and Masterson 1984b.

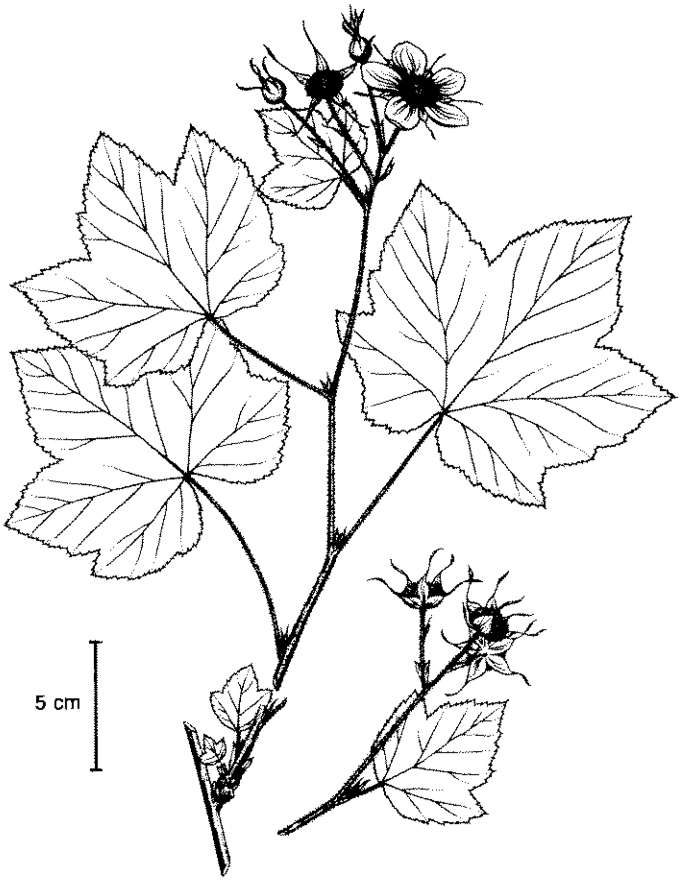
mechanical site preparation in 2–3 years in the ICH zone in the Salmon Arm Forest District. Recovery is mainly by seed (J. Wright, pers. comm., July 1989). Where mechanical site preparation is used within existing stands of raspberry, soil disturbance can fragment the root system, creating new independent stools (Hudson 1959) and stimulating root suckering (Core 1974). Repeated cultivation of the soil will control the spread of raspberry by root suckering, but this will be accompanied by an increase in the vigour of adjacent undisturbed plants (Lawson and Waister 1972a).

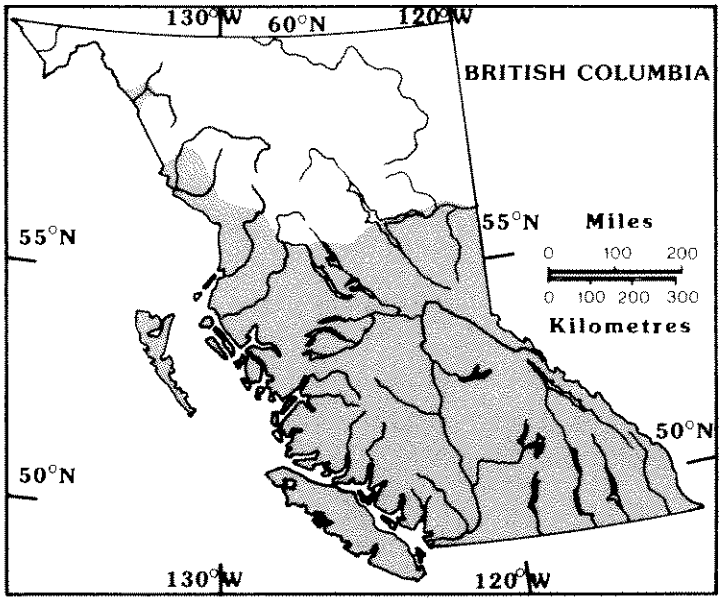
Fertilization: Application of nitrogen fertilizer to red raspberry can either increase suckering and have no effect on height growth, or increase height growth without affecting stand density (Lawson and Waister 1972b). Lawson and Waister (1972b) also observed increased levels of winter mortality following fertilization. This injury may be due to a delay in the onset of dormancy (Jennings and Cormack 1969) or to increased incidence of disease in fertilized plants (Goode 1970).

WILDLIFE

Food: Raspberries are a favourite summer food of wildlife (Banfield 1974; Chapman and Feldhamer (editors) 1983). They are important to many game and song birds; they are also eaten by small mammals such as skunks, racoons, chipmunks, squirrels, and mice. Deer and rabbits use leaves and stems extensively (Core 1974). Raspberry leaves have been consumed by snowshoe hares between June to September (Wolff 1978b). Bears also forage on the fruit and foliage (Ahlgren 1960; Lofroth 1988).

Rubus parviflorus
(thimbleberry)





Distribution of *R. parviflorus* in British Columbia.

Rubus parviflorus Nutt. — Thimbleberry

DESCRIPTION

Thimbleberry is a deciduous shrub which grows to a height of 2.5 m. This rhizomatous species has short-lived canes which are erect to semi-prostrate and without prickles. The leaves are large (up to 25 cm long), maple-shaped with 3–5 toothed lobes, and have a soft crinkly surface. The conspicuous, white flowers are borne in terminal infloresences. The soft, thimble-shaped red fruit is an aggregate of many small, hairy drupelets (Viereck and Little 1972; Taylor 1973b; Clark 1976; Marchant and Sherlock 1984).

Variation: Thimbleberry is a highly variable species (Hultén 1974) with several recognized subspecies. Only the typical ssp. *parviflorus* is found in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Thimbleberry is common throughout British Columbia to approximately 56°N latitude in the Interior and along the entire length of the coast including Vancouver Island and the Queen Charlotte Islands. It is absent from the SWB biogeoclimatic zone and from the BWBS outside of the Peace River Valley. Otherwise, thimbleberry is found in all forested biogeoclimatic zones. It is most abundant in the CWH zone and in wet subzones of the Interior and is very rare in the PP and BG zones and in other dry areas of the south and central Interior.

Altitudinal Range: Thimbleberry ranges from sea level to over 900 m on the coast of British Columbia and from valley bottoms to over 1200 m in the Interior (Lyons 1952; Taylor 1973b). Douglas (1972) reports that thimbleberry is common at elevations of 1800 m in the western Cascades of Washington.

HABITAT

Climatic Relations: Thimbleberry is tolerant of a wide range of climatic conditions in British Columbia but favours a moist to wet climate. It is poorly adapted to survive the extremely cold winters and short growing seasons of the boreal region and does not tolerate the extreme summer moisture stresses such as can be encountered in the driest areas of the southern Interior. Brand considers that in south coastal British Columbia thimbleberry favours sites with a drier, warmer and more continental microclimate than those favoured by salmonberry.[264]

Site and Soil Conditions: Thimbleberry grows on a wide variety of soils and landforms both under forest stands and on disturbed sites. It is common beneath open forests, on roadsides, in cutover areas, on avalanche tracks, and in riparian habitats (Viereck and Little 1972; Taylor 1973b; Gratkowski 1978; Gilbert 1980a). It is a common understory species on sites in the CWH, SBS, ICH, MS, and ESSF zones on morainal, fluvial, and lacustrine parent materials with Luvisol, Brunisol, or Podzol soils (see, e.g., Pojar *et al.* 1984).[265,266] In the CWH zone, thimbleberry is most abundant and vigorous on fluvial sites.

Nutrient Relations: Thimbleberry grows under a wide variety of nutrient conditions. In the SBS zone it is found on sites with a wide range of available calcium (Wali 1969) and on all but very poor soil nutrient regimes (Pojar *et al.* 1982). On the south coast, it grows well on medium to nutrient-rich sites.[267]

Water Relations: Thimbleberry occurs on sites with moisture regimes ranging from submesic to hygric (Pojar *et al.* 1982; Angove and Bancroft 1983). It is most abundant and vigorous on subhygric sites with well-aerated soils. Thimbleberry will reproduce and grow on drier sites, but it usually achieves low cover and small stature (Clark 1973; Marchant and Sherlock 1984). It does not grow well on wet, poorly drained soils.[268]

Light Relations: Thimbleberry grows under closed canopies of deciduous or coniferous forest stands and in open meadows and clearings. Cover and vigour of thimbleberry is usually greatest under partially open or open conditions (Gilbert 1980a).[269] As tree basal area and canopy cover increases and understory light

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[264] Brand 1984.
[265] Coupé and Yee (editors) 1982.
[266] DeLong *et al.* 1984.
[267] Brand 1984.
[268] Ibid.
[269] Brand 1984.

declines, thimbleberry cover and vigour also decline (Mueggler 1965; Irwin and Peek 1979). In southwestern Oregon, thimbleberry is found at all light levels down to below 3.5% of full light, but it has greatest cover at 60–100% of full light (Emmingham 1972). Studies of photosynthetic capacity carried out in Washington indicate that thimbleberry is less shade tolerant than salmonberry (Barber 1976). Barber used this evidence to explain why thimbleberry is never abundant in the understory of red alder stands in the Pacific Northwest states. However, on the north coast of British Columbia, thimbleberry is often one of the dominant understory species beneath red alder.[270] These conflicting data may indicate a difference in shade tolerance of thimbleberry under different environmental conditions, or they may indicate that presence or absence of thimbleberry is due not so much to light availability as to relative competition from other plant species.

GROWTH AND DEVELOPMENT

No published studies dealing specifically with the growth and development of thimbleberry were found. It is a strongly rhizomatous species that, like other *Rubus* species, produces relatively short-lived canes. Viereck and Little (1972) describe the canes as perennial. Our observations of a small number of plants in west central British Columbia indicate that the canes usually live 2 or 3 years, and produce flowers and fruit on short lateral branches during the second year.

When open-grown, thimbleberry produces a dense multi-layered canopy and has a very large leaf area.[271] Its photosynthetic capacity in full light is therefore higher than that of other associated species (Barber 1976) which enables it to achieve rapid initial height growth. Maximum growth occurs by the second or third growing season following establishment.[272] Dense cover can be achieved in as little as 5 or 6 years following disturbance (Eis 1981) following disturbance. Stickney (1986) reports that thimbleberry achieved maximum cover within 4 years on the Sundance burn in northern Idaho. Thimbleberry growing from rhizomes on moist soils in the British Columbia Interior and on the coast can reach 2 m in height in less than 10 years.

Phenology: In western Oregon and Washington, vegetative buds of thimbleberry can become active as early as late February (Stewart 1974b). In northern Idaho and western Montana, bud burst takes place between early April and early June depending on elevation and weather conditions. Leaves are fully grown approximately 1 month after bud burst. In the SBS zone near Prince George, thimbleberry reached half its maximum percent cover by the third week in June and leaves were fully developed by mid-July (DeLong 1988). Leaf senescence typically begins by late August in Idaho and Montana and leaf fall extends from late August to mid- to late October (Schmidt and Lotan 1980). Data from the central coast of British Columbia indicate similar timing of vegetative events.[273]

Flowering can extend from early May to early August but is centred on the months of June and July both in Alaska (Viereck and Little 1972) and in Idaho and Montana (Schmidt and Lotan 1980). In British Columbia, fruits ripen from early June to mid-September depending on elevation and other local factors (Marchant and Sherlock 1984).[274]

REPRODUCTION

Seed Production and Dispersal: The berry-like fruit of thimbleberry contains many small seeds. Seed production can be sparse at high elevations. Once ripe, the fruit fall readily to the ground (Marchant and Sherlock 1984). Wider dispersal of seed is primarily by birds (Core 1974; M. Newton, pers. comm., Dec. 1984) but also by mammals feeding on the fruit.

Seed Viability and Germination: Seeds of thimbleberry are believed to remain viable for a long period of time, like those of other members of the *Rubus* genus; consequently, the species is considered to be a seed banker. Thimbleberry seeds are common in seed banks in the SBS zone (E. Hamilton, pers. comm., July 1989). Kellman (1969) found buried viable seeds of thimbleberry (18 seeds per square metre) in a soil core taken from a mature conifer forest near Haney. Morgan (1984) found as many as 84 seeds per square

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[270] Pollack 1984.
[271] Brand 1984.
[272] Ibid.
[273] Hamilton 1984.
[274] Ibid.

metre in forest soils in Idaho. McGee (1988b) found 1–50 seeds per square metre in seed banks on the south coast of British Columbia, and most seeds were found where disturbance was lowest.

Viable thimbleberry seeds are present in soil seedbeds (Olmsted and Curtis 1947), but McGee (1988b) found a gradual decline in viable seed numbers with soil depth. Mild heat scarification appears to improve their germination in forest soils (Morgan 1984). Allelopathic effects of bracken and other species may inhibit germination of thimbleberry seeds (Stewart 1975). The seed has moderate viability in germination tests (maximum 62%) and requires approximately 90 days of chilling to germinate. Research in Oregon indicates that thimbleberry seed germination is initially very low but increases after 6 months of dry storage.[275] Acid treatment may also promote germination (Marchant and Sherlock 1984). Germination of buried and newly deposited seed is believed to be the principal means by which thimbleberry invades new areas. McGee (1988b) found that germination is significantly better in or on mineral soil than in or on the forest floor. Abundant seedlings are present on disturbed sites within the first year following disturbance (Kelpsas 1978; Stewart 1978). However, CRAFTS[276] considers that thimbleberry populations are unlikely to establish from seed on clearcuts in the central Oregon coast because of low germination rates and low seedling survival.

Vegetative Reproduction: Thimbleberry is a strongly rhizomatous species (Stickney 1981; Marchant and Sherlock 1984), and once it is established on a site, further expansion of the colony is achieved through the spread of rhizomes. The species can be readily propagated from cuttings and fragments of rhizomes (Hungerford 1984; Marchant and Sherlock 1984). At the end of one growing season in the Oregon Coast Range, thimbleberry plants grown from cuttings were 200–1000 times larger than plants grown from seed. After two seasons, however, sprouts from cuttings were only twice as large as seedlings. Absolute growth rates were significantly greater for sprouts than for seedlings.[277]

PESTS

Conspicuous galls caused by the cyanid wasp (*Diastrphus kincaidii*) occur widely on thimbleberry over much of western North America (Wangberg 1975). Some species of aphid (*Masonaphis* spp.) are common on thimbleberry (Frazer and Forbes 1968; Gilbert 1980a, 1980b), but their impact on plant growth is not known.

EFFECTS ON CROP TREES

Competition: Thimbleberry is a very important competitor with coniferous trees in British Columbia, particularly in the Prince Rupert and Prince George Forest Regions, where it may be the most widespread problem species. It very rapidly and aggressively takes over clearcut areas, particularly on moist, productive ecosystems. On coastal alluvial sites in northwestern British Columbia, it causes greater and more rapid mortality of young conifer seedlings than any other brush species (J. Pollack, pers. comm., Jan. 1985).

Thimbleberry produces a dense canopy of large leaves that allows very little light to penetrate.[278] On some cool, moist sites, thimbleberry can establish dense canopies with 100% cover, which allow less than 1% of full sunlight to reach overtopped seedlings (Comeau 1988). However, since thimbleberry leaves and canopies are often not fully developed until late July, the impact of thimbleberry cover on seedling growth may be substantially less than that of species which develop leaf area rapidly in the spring (e.g., fireweed). Exclusion of light seems to be the primary mode of competition with young seedlings. Thimbleberry annually produces large quantities of litter that can smother young seedlings (M. Newton, pers. comm., Dec. 1984). It will rarely invade a site already occupied by other species (M. Newton, pers. comm., Dec. 1984) because the presence of other vegetation interferes with its establishment (Eis 1981). Stickney (1981) reports that thimbleberry establishes and grows much slower when fireweed has colonized a site than when fireweed is absent.

Allelopathy: In a western Washington study, extracts of leaves and litter inhibited germination and growth of test plants in the laboratory (del Moral and Cates 1971). However, no evidence of allelopathic effects of thimbleberry have been reported under field conditions.

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[275] CRAFTS 1988.

[276] Ibid.

[277] Ibid.

[278] Brand 1984.

Beneficial Effects: On some sites, light to moderate thimbleberry cover may provide shade and reduce physiological stresses for establishing conifer seedlings.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Thimbleberry that is present prior to logging resprouts from rhizomes and rapidly increases in cover and vigour following canopy removal. It will also quickly invade unoccupied, cleared sites through germination of buried and recently deposited seed. In the SBS zone north of Prince George, thimbleberry increased to 40% cover on a Devil's Club site type and to 15% cover on an Alluvium site type 6 years after clearcutting but did not increase significantly on the drier site types (Eis 1981). On the Devil's Club site type it was apparently able to take advantage of vacant growing space caused by dieback of Devil's Club, while on the Alluvium site it faced stronger competition from other shrub species. In a study near Vancouver, thimbleberry increased in height from 1 to 2 m after canopy removal.[279] Above-ground biomass of thimbleberry approximately doubled 1 year after mortality of a girdled alder overstory in the CWHws subzone in the Kitimat Valley (K. Haworth, pers. comm., July 1989). Cover of thimbleberry declines as tree canopy cover and tree basal area increases (Mueggler 1965; Irwin and Peek 1979).

Fire: Thimbleberry cover is significantly increased by fire (Lafferty 1972; Wright 1972; Stickney 1981). If it is present prior to burning, plants usually survive fire and resprout vigorously from rhizomes and root crowns (Wright 1972; Crane *et al.* 1983). Thimbleberry also seeds in readily to unoccupied burned ground (Kelpsas 1978; Stewart 1978).

On moist, productive ecosystems in the CWH zone near Vancouver, thimbleberry was abundant from the first year following burning and remained abundant for at least 5 years after the fire.[280] In the ICH zone near Salmon Arm, thimbleberry has been observed to recover from burning in 1–2 years (J. Wright, pers. comm., July 1989). In the SBSwk subzone, thimbleberry established immediately after burning from seed and by resprouting from rhizomes. On drier SBSwk sites, Hamilton and Yearsley (1988) observed that thimbleberry was sometimes abundant immediately after burning but appeared to decrease over time. Thimbleberry may achieve maximum cover within 3–5 years of burning (Lafferty 1972; Dyrness 1973; Cholewa and Johnson 1983; Crane *et al.* 1983; Morgan 1984; Stickney 1985; Morgan and Neuenschwander 1988b). Schoonmaker and McKee (1988) found that thimbleberry was generally not present in undisturbed mature Douglas-fir forests in Oregon, but on sites receiving medium intensity burns, thimbleberry cover was 1, 2, 13, 6, 6, and 0% within 2, 5, 10, 15, 20, and 40 years of burning, respectively.

Low severity burns often lead to more rapid development of thimbleberry cover than moderate or high severity burns (Lafferty 1972; Morgan 1984; K. Haworth, pers. comm, July 1989). However, in northern Idaho, there was no significant difference in thimbleberry cover after low and high severity burns (Morgan and Neuenschwander 1988b).

Early dominance of burned sites by more aggressive species such as fireweed can delay development of thimbleberry cover (Stickney 1981).

Cutting and Grazing: Manual cutting generally gives ineffective control of thimbleberry because cutting stimulates rapid resprouting,[281] and it often returns to its original height and cover within 1 year of cutting (Gratkowski 1978; J. Wright, pers. comm., July 1989).[282] Manual cutting of thimbleberry with chainsaws on June 26, July 17, August 7, and August 28 in the ICH zone near Smithers was ineffective on all four dates. After two growing seasons, thimbleberry had resprouted to percent covers equal or greater than original levels.[283] D'Anjou found that thimbleberry recovered from cutting faster than salmonberry, red elderberry, black twinberry, and vine maple.[284]

Thimbleberry plants showed signs of lost vigour 1 year after spring and early summer sheep grazing near Clearwater (G. Ellen, pers. comm., July 1989).

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[279] Brand 1984.
[280] Ibid.
[281] Ibid.
[282] D'Anjou 1988d.
[283] LePage and Pollack 1988b.
[284] D'Anjou 1988d.

Herbicides: Foliar applications of 1.5–2.1 kg a.i./ha glyphosate in late summer (August and September) have consistently given good control of thimbleberry while June and July applications of the same rate have been ineffective.[285,286] Poor control in June and July was attributed to binding of the chemical in the above-ground actively growing canes, which prevents translocation to underground parts. Late May application of 2.0 kg a.i./ha glyphosate controlled thimbleberry on an alluvial floodplain site in the ICHmc subzone, but applications of 1.0 and 1.5 kg a.i./ha were ineffective.[287] Thimbleberry rapidly resprouts after glyphosate applications, even after extensive top-kill. Thimbleberry often recovers 50% of its pre-treatment cover after two seasons (J. Wright, pers. comm., July 1989)[288] and can fully recover within 3 years (J. Wright, pers. comm., July 1989).[289,290]

Hexazinone tends to be an ineffective herbicide for thimbleberry control because of high organic matter levels in soils where this plant grows. However, on some sites, mild to moderate injury has been attained. For example, in the CWH zone near Chilliwack, an April application of 4 kg a.i./ha liquid hexazinone caused moderate control of thimbleberry. Canopy cover and height were almost back to the pre-treatment level within three growing seasons.[291] Thimbleberry was mildly affected by late June spot applications of hexazinone at 4 mL per spot and 1 x 2 m spacing in the SBSmw subzone near Quesnel and was starting to recover the season after the herbicide was applied.

Available information indicates that 2,4-D causes light injury to thimbleberry in British Columbia (Boateng and Herring 1990). A summary of research trials in the U.S. Inland Northwest indicates that 2,4-D applied as a late summer aerial spray causes less than 20% cover reduction of thimbleberry (Miller 1985b). Spring foliar applications of 2,4-D are reported to be effective in northeastern Oregon and northern Idaho (Conard and Emmingham 1983; Hann 1986). In coastal areas of Washington and Oregon, 2,4-D has given variable results (Conard and Emmingham 1984a).

Application of triclopyr ester as a foliar spray in spring, late summer, or fall can give moderate control of thimbleberry (Warren 1982; Conard and Emmingham 1983, 1984a; William *et al.* 1987). Backpack spraying of triclopyr ester at 3 kg a.i./ha on June 4 in the CWH zone resulted in effective control of thimbleberry, but the same treatment on September 3 was ineffective.[292] Basal applications of triclopyr may also give control of thimbleberry (Warren 1982; Hamel 1983).

Conard and Emmingham (1984a) report that amitrol applied in the spring or summer causes moderate injury to thimbleberry in western Oregon and Washington.

Tests of other herbicides are described by Stewart (1974a, 1974b, 1974c), Gratkowski (1978), and Hamel (1983).

Soil Disturbance: Thimbleberry quickly invades disturbed soils either by resprouting from rhizomes or through germination of seeds (Dyrness 1973; Arno *et al.* 1985). In the CWH zone near Vancouver, thimbleberry rapidly increased in dominance and vigour following scarification of moist productive ecosystems.[293] Thimbleberry was the most vigorous invader of blade-scarified moist spruce–fir sites near Prince George (Arlidge 1967). Within 3 years of scarification it had totally occupied plots in the Devil's Club site type and had reached a height of over 1 m. Similar results occur in the ICH zone near Salmon Arm where thimbleberry typically regains pre-treatment levels within 2 or 3 years of mechanical site preparation (J. Wright, pers. comm., July 1989).

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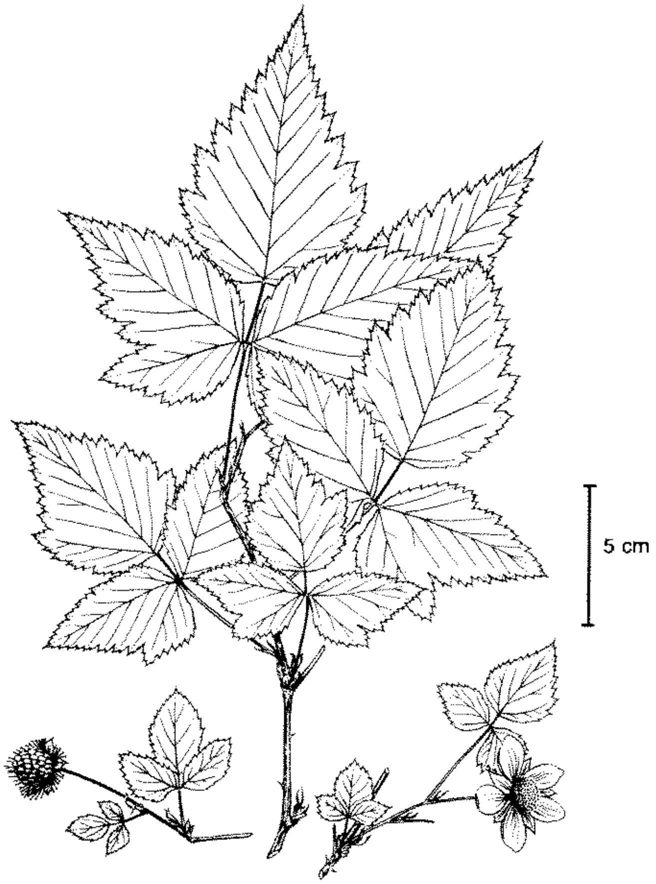
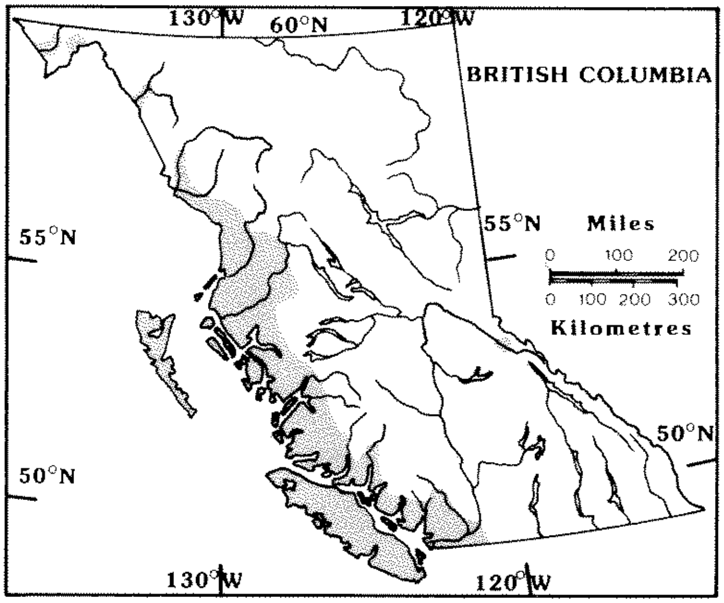
[285] D'Anjou 1988b.
[286] LePage and Pollack 1988b.
[287] Pollack and LePage 1986b.
[288] Dyke 1987.
[289] CRAFTS 1988.
[290] Reynolds *et al.* 1988.
[291] D'Anjou 1988d.
[292] D'Anjou 1988a.
[293] Brand 1984.

WILDLIFE

Food: Thimbleberry twigs and leaves are not very significant as ungulate browse (Morris *et al.* 1962; Halverson (compiler) 1986). It is moderately important for black-tailed deer in British Columbia (McTaggart-Cowan 1945; Singleton 1976; Rue 1978) and western Washington and Oregon (Lindzey 1943; Chatelin 1947; Brown 1961; Crouch 1964; Miller 1968). Black-tailed deer eat the berries, leaves, and stem (Brown 1961; Miller 1968). Thimbleberry has medium to low importance as winter and spring food for Roosevelt elk (Singleton 1976). It is preferred by squirrels, chipmunks (Banfield 1974), and juvenile blue grouse on Vancouver Island (Fowle 1960). Bears feed on the young shoots (Hamilton 1987). The fruit is favoured by many birds and mammals.

Rubus spectabilis
(salmonberry)





Distribution of *R. spectabilis* in British Columbia.

Rubus spectabilis Pursh. Salmonberry

DESCRIPTION

Salmonberry is a thicket-forming deciduous shrub arising from a branching rhizome. The stems are erect or curved, usually 0.6–3 m tall. Twigs are hairless, with scattered spines or prickles, and grow in a zigzag manner. Salmonberry has compound leaves with 3 sharply toothed leaflets. The flowers are showy and deep pink and the fruit is a glossy red to yellow "raspberry-like" aggregate consisting of many small drupelets (Viereck and Little 1972; Taylor 1973b; Hultén 1974).

Variation: No subspecies or varieties of salmonberry are described in British Columbia (Taylor and MacBryde 1977), but it is reported to hybridize with *R. idaeus* and *R. arcticus* in Alaska (Viereck and Little 1972; Hultén 1974).

DISTRIBUTION AND ABUNDANCE

Salmonberry occurs along the entire length of the coast of British Columbia including Vancouver Island and the Queen Charlotte Islands. It is found primarily on the west side of the Coast Mountains but penetrates inland along the Skeena and Fraser river drainages. It has been recorded from one location on the upper Fraser River (A. Ceska, pers. comm., Dec. 1984) but is otherwise absent from the Interior Wet Belt. Salmonberry is very abundant in the CWH and CDF biogeoclimatic zones and occurs frequently in the MH zone.

Altitudinal Range: Salmonberry extends from sea level to lower alpine elevations (Hultén 1974) but is most abundant below approximately 800 m (Lyons 1952). At low elevations it is common in a variety of habitats, but at high elevations it tends to be restricted to streambanks and rarely develops extensive stands (Barber 1976).

HABITAT

Climatic Relations: Salmonberry clearly favours a humid to perhumid coastal climate with relatively mild temperatures and a lengthy growing season. It reaches its best development in British Columbia at low elevations on the south coast. At the northeast extent of its range in the Nass and Bulkley valleys it occurs only in sheltered, humid locations and is noticeably reduced in size and vigour.

Site and Soil Conditions: Throughout its range, salmonberry is a species of lowland forests, moist slopes, and streambanks (Ruth 1970; Viereck and Little 1972; Barber 1976; Campbell and Franklin 1979). It occurs on a wide range of soil textures and parent materials from rich loams to loamy clays, on rapidly drained gravels and on peat (Barber 1976), but best growth occurs on floodplains. Soils on which salmonberry is abundant include Brunisols, Regosols, Gleysols, Podzols, and Organics (see e.g., Klinka and Carter 1980).[294,295]

Nutrient Relations: Salmonberry apparently favours sites with a medium to very rich nutrient status,[296] but Barber (1976) concluded that soil fertility is relatively unimportant for its growth and survival compared to other habitat factors. Salmonberry may have a fairly high demand for nitrogen (M. Newton, pers. comm., Dec. 1984). A soil nitrogen study by Barber (1976) indicates that salmonberry will survive and grow whether nitrogen is provided as ammonium or nitrates.

Water Relations: Salmonberry reaches its best development on mesic sites. Best growth occurs when soils are well aerated and near field capacity. In wet, poorly aerated soils, root growth is inhibited; the plant declines in size and vigour and occurs mainly on elevated hummocks (Barber 1976). Salmonberry is apparently poorly adapted to survive under droughty conditions as a young seedling (Ruth 1970). On dry sites, it has a compact growth form; an apparent delay in extensive shoot growth limits transpirational losses until roots are sufficiently developed to provide a continuous supply of soil moisture (Barber 1976).

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[294] Yole *et al.* 1982.
[295] Banner *et al.* 1984.
[296] Brand 1984.

Light Relations: Salmonberry is described as shade tolerant (Ruth 1970) or semi-tolerant.[297] Its ability to achieve net photosynthesis at low light levels permits it to inhabit sites too shady for other species of the *Rubus* genus (Barber 1976). Best growth occurs in forest openings and cleared areas where abundant moisture is available (Ruth 1970; Campbell and Franklin 1979). In some situations, salmonberry seedlings appear to prefer partial shading, but moisture stresses rather than excessive radiation limit the survival and growth of seedlings in full sunlight (Ruth 1970). Salmonberry is virtually eliminated under dense coniferous canopies (Barber 1976).

The shade tolerance of salmonberry may be greater in the Pacific Northwest states and in south coastal British Columbia than towards the northern limits of its range. Salmonberry is a dominant understory species under red alder and mixed alluvial forests in the southern half of its range, but it is uncommon as an understory species in southeastern Alaska (P. Alaback, pers. comm., Dec. 1984), and it frequently has low vigour under dense red alder on alluvial sites on the Skeena River (D. Coates, pers. comm., 1990).

Temperature Relations: Salmonberry is able to achieve net photosynthesis at relatively low temperatures. This may allow it to resume photosynthesis much earlier in the growing season than associated understory plants and overtopping deciduous species (Barber 1976).

GROWTH AND DEVELOPMENT

Like other *Rubus* species, salmonberry is a perennial rhizomatous shrub with relatively short-lived aboveground stems or canes. Viereck and Little (1972) report that the canes live only 2 years, like those of raspberry, but this seems to be untrue, at least in some portions of the species' range. Healthy canes of at least 10 years of age, and possibly as old as 15 years, have been found in southern British Columbia and Oregon (D. Bigley, pers. comm., Nov. 1984; J. Zasada, pers. comm., Sept. 1989).

Salmonberry forms dense thickets of erect to prostrate stems. It is normally 1–3 m tall but can be as tall as 5 m (Hitchcock *et al.* 1969). Under favourable conditions, height growth can be as much as 1.5–2 m in a single growing season (Barber 1976).

The rhizomes spread laterally beneath the soil, producing new shoots 1–2 m away from the parent plant. This lateral spread produces clonal colonies measuring several metres across. Pure stands of salmonberry which may have arisen from a single plant through vegetative reproduction can be more than 100 m across (Barber 1976).

Phenology: Both above- and below-ground growth commence very early in the spring, before associated plants such as red alder and thimbleberry have become active. This adaptation gives salmonberry a competitive advantage as an understory species (Barber 1976).

In western Washington and Oregon, leaf emergence can begin in March, even when snow is still present (Stewart 1974b; Barber 1976). Leaves flush during early April on the central British Columbia coast and are fully expanded by early May.[298] Flowering normally takes place between April and June on the south coast[299] and from April to July in southeastern Alaska (Viereck and Little 1972), but flowers have been recorded from southern Vancouver Island as early as late January during some mild winters (Clark 1976). Pojar (1975) notes that flowering in this species is correlated with the arrival of migrating Rufous Hummingbirds along the length of the Pacific coast. Fruiting begins early and can extend for a period of more than 2 months (Barber 1976). On the central British Columbia coast, ripe fruits were present from early June to July,[300] while in Alaska the first fruits are ripe in early July at low elevations and in August at higher elevations (Viereck and Little 1972). Salmonberry does not set terminal buds at the end of the growing season; stem elongation can potentially continue as long as soil moisture is available and temperatures are favourable (Barber 1976).

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[297] Brand 1984.

[298] Hamilton 1984.

[299] Brand 1984.

[300] Hamilton 1984.

REPRODUCTION

Seed Production and Dispersal: Salmonberry has a perfect, simple flower. Pollination is achieved primarily by insects and hummingbirds present during the early spring flowering period (Pojar 1975; Barber 1976). The fruit of salmonberry is an aggregate of small drupelets each containing a single hard-coated seed. Large quantities of seed are produced each year (Barber 1976). The fruit falls readily to the ground and most seed is probably deposited directly below the parent plant. Wider dispersal is primarily by birds and mammals.

Seed Viability and Germination: Seeds of many species of *Rubus* have extended viability that may last for as long as 100 years. Most researchers believe that storage of viable seed in the forest floor for long periods is an important aspect of the reproductive strategy of salmonberry (Ruth 1970; Barber 1976). Soil disturbance and increased sunlight apparently stimulate germination of the stored seed (Krygier and Ruth 1961).

Germination experiments in Oregon have indicated that untreated seed has a very low germination percentage, but that germination increases after 6 months of dry storage.[301] Germination of salmonberry seed normally requires several months of chilling followed by warm temperatures. Passage through the crop or gut of a bird apparently scarifies the seed and enhances germination. Treatment of seeds with concentrated sulfuric acid has been shown to stimulate germination[302] and seeds germinated under laboratory conditions are usually treated with acid (USDA 1974; Barber 1976). In a study in western Oregon, mechanical scarification had no effect on germination of salmonberry.[303] Seeds from both red and yellow fruit are equally viable (Barber 1976).

Seedlings of salmonberry are uncommon except where soil disturbance has occurred. Light is apparently not necessary for seed germination but is critical for subsequent seedling survival (Barber 1976). Seedlings will germinate on peat, decaying logs and stumps and in a variety of habitats (Barber 1976), but mineral soil is apparently required for successful establishment (Ruth 1970).

Seed is very important in allowing salmonberry to invade new areas and in enabling the species to re-establish itself in environments where natural disturbances are infrequent. Seedling production is not significant in perpetuating established colonies (Barber 1976).[304]

Vegetative Reproduction: Vegetative reproduction is the principal means by which expansion and perpetuation of established colonies of salmonberry takes place. Salmonberry is strongly rhizomatous and the lateral spread of rhizomes followed by production of new shoots is the primary mode of vegetative reproduction. Vigorous formation of adventitious shoots is usually stimulated by some form of disturbance (D. Bigley, pers. comm., Nov. 1984). Shoots also form from preformed buds (J. Zasada, pers. comm., Sept. 1989). Tip layering is another mode of asexual reproduction (Barber 1976). Where plants are fragmented by soil disturbance, rhizome and root fragments can be expected to reroot and produce new plants (Krygier and Ruth 1961). At the end of 1 growing season, salmonberry plants grown from cuttings were 200–1000 times larger than plants grown from seed. However, after 2 growing seasons, sprouts from cuttings were only twice as large as seedlings. Absolute growth rates were significantly greater than for seedlings.[305]

PESTS

Barber (1976) describes salmonberry as relatively free of insects and disease and lists some of the more important pest species.

EFFECTS ON CROP TREES

Competition: Salmonberry is a major competitor of young conifers on moist, productive sites in most of coastal British Columbia. Dense thickets of salmonberry inhibit establishment of natural and planted conifers

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[301] CRAFTS 1986.
[302] Ibid.
[303] Ibid.
[304] Ibid.
[305] Ibid.

(Gratkowski 1971; Viereck and Little 1972; Campbell and Franklin 1979). Light intensities beneath a dense stand of salmonberry are too low to permit seedling establishment (Barber 1976). Light competition is the primary cause of growth losses and mortality in conifer seedlings under salmonberry thickets in coastal British Columbia (T. Lewis, pers. comm., May 1989). Mats of leaf litter may prevent germination or smother young seedlings. Other competitive factors are presumably also at play (Barber 1976). In the Vancouver Forest Region, once salmonberry is established it can exclude conifers for decades, if not the whole rotation (T. Lewis, pers. comm., May 1989).

Barber (1976) suggests that Douglas-fir may be more susceptible to salmonberry competition than species such as western hemlock with greater shade tolerance. However, in an experiment by Newton and White (1983), small hemlock seedlings sustained more damage from salmonberry than did Douglas-fir or Sitka spruce. Once it is overtopped by conifers, salmonberry is quickly at a competitive disadvantage. It can be shaded out by a dense 15- to 20-year-old hemlock overstory (Barber 1976).

In the Oregon Coast Range, salmonberry was not affected by competition from seeded grass (Klinger 1986). However, in the CWH zone near Campbell River, B.C., seeded grass substantially decreased the establishment and vigour of salmonberry (J. McClarnon, pers. comm., May 1986).

Allelopathy: Although extracts of salmonberry leaves and litter inhibited growth of test plants in the laboratory, no allelopathic effects of salmonberry litter on conifer growth have been demonstrated under field conditions in western Washington (del Moral and Cates 1971).

Beneficial Effects: A dense colony of salmonberry can inhibit invasion of long-lived deciduous species such as red alder, bigleaf maple, and black cottonwood (Campbell and Franklin 1979). Salmonberry may also act to reduce soil erosion (Barber 1976).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Salmonberry often develops into dense thickets following timber harvest. On areas where salmonberry is present in the understory prior to logging, canopy removal results in a rapid increase in colony size, crown cover, and stand density (Ruth 1970). Ruth (1970) observed increases from 1.1 to 14.6% over a period of 7 years. Observations on northern Vancouver Island indicate that cover and height of salmonberry increases after overstory removal (D. Harrison, pers. comm., July 1989). However, D. Bigley (pers. comm., Nov. 1984) stated that height growth of salmonberry may not increase significantly following canopy removal.

Ruth (1970) reported prolific germination of salmonberry from seed stored in the duff following canopy removal and associated soil disturbance. The degree of canopy removal did not appear to affect the germination rate of seedlings, but some shade helped to prevent desiccation of young seedlings.

Ruth predicted that successive thinnings in intensively managed stands will allow salmonberry to persist in the understory longer than in undisturbed mature forests. This type of intensive management may lead to increased salmonberry competition in future rotations.

Fire: Salmonberry can rapidly increase in cover following natural or prescribed fire. Broadcast burning retards brush for about 1 season but subsequent sprouting of salmonberry is dense (Krygier and Ruth 1961). Invasion of unoccupied ground takes place through spread of rhizomes and natural seeding (Allen 1969). Eighteen months following prescribed burning near Haney, salmonberry seedlings were abundant (D. Bigley, pers. comm., Nov. 1984).

Morris (1970) found that salmonberry cover was higher on unburned clearcuts than on burned sites during the first 5 growing seasons in Washington and Oregon; however, by the eleventh to sixteenth growing seasons, there was no difference in relative abundance of salmonberry on burned and unburned sites. Eight years after a high severity burn in British Columbia, salmonberry cover was 20%, compared to 65% on an unburned control. In comparison, the cover of salmonberry after moderate severity burns was about 47% compared to 25% on an unburned area (Beese 1986). Effective control of salmonberry can be achieved with a severe burn that consumes the litter, destroying stored seed and underground organs; however, such a burn can cause significant site degradation (M. Newton, pers. comm., Dec. 1984).

Cutting: Manual cutting of salmonberry stimulates rapid resprouting from stem bases and rhizomes and can result in an increase in total leaf area (M. Newton, pers. comm., Dec. 1984; J. McClarnon, pers. comm. 1989).[306,307] Cover of salmonberry often regains pre-treatment levels within 1 season (Wagner 1984). In the Campbell River District, salmonberry has fully recovered from manual cutting in as little as 3–4 weeks (J. McLarnon, pers. comm, May 1989). In the CDF and CWH zones on southern Vancouver Island, salmonberry exhibited vigorous regrowth regardless of cutting season (R. Mueller, pers. comm., July 1989). Manual cutting is only successful in controlling salmonberry if it is repeated 2 or 3 times a year for several years.[308]

Herbicides: Before glyphosate became available for forestry use, salmonberry was very difficult to control with herbicides as subterranean parts were frequently unaffected, and the plant tended to resprout from rhizomes and stem bases (Stewart 1977). Broadcast application of 2.0 kg a.i./ha glyphosate in late summer and fall have resulted in moderate to severe injury to salmonberry (Conard and Emmingham 1984a).[309,310,311] Control tends to decline after 2 or 3 years.[312] D'Anjou[313] found that although mid-August and early September applications were effective in controlling salmonberry, mid-July applications were ineffective, and early June applications were only partially effective.

Broadcast applications of hexazinone have caused only light injury to salmonberry in British Columbia (Boateng and Herring 1990). Salmonberry was ineffectively controlled in 3 different trials near Chilliwack involving spot or broadcast application of liquid hexazinone at 2 or 4 kg a.i./ha in April. Lack of herbicide effectiveness was attributed to high organic levels in the soil.[314]

In western Washington and Oregon, 2,4-D causes light to moderate damage to salmonberry (Conard and Emmingham 1984a; S. Conard, pers. comm., Mar. 1985). Conard and Emmingham (1984a) report that in Washington and Oregon amitrol causes severe injury when applied in the spring and moderate injury when applied in the summer. D'Anjou found that in coastal British Columbia, triclopyr ester was more effective when applied in June than later in the summer.[315]

Soil Disturbance: Soil disturbance that exposes mineral soil provides a suitable seedbed for salmonberry germination and may stimulate germination of buried seed. Damage caused to existing salmonberry plants will stimulate resprouting, and fragments may re-root to produce new plants (Krygier and Ruth 1961; Ruth 1970; Barber 1976). Scarification of clearcut areas in the CWH zone near Vancouver resulted in a rapid increase in salmonberry cover over pre-logging conditions.[316] Deep scarification can reduce salmonberry cover if roots and rhizomes are completely removed from the soil (M. Newton, pers. comm., Dec. 1984). For example, heavy scarification with a caterpillar tractor in the CDF and CWH zones on southern Vancouver Island reduced salmonberry re-invasion (R. Mueller, pers. comm., July 1989).

WILDLIFE

Food: Salmonberry is relatively important for wildlife in coastal British Columbia. The fruit is the main plant part eaten.[317] The berries are a favourite late spring food of bears (Banfield 1974; Herrero 1985; National Wildlife Federation 1987; Lofroth 1988). Birds, small mammals, and coyotes also eat the berries (Viereck and Little 1972; Barber 1976; Halverson (compiler) 1986).

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[306] Brand 1984.
[307] D'Anjou 1988e.
[308] Simard and Mather 1989.
[309] D'Anjou 1988a.
[310] Reynolds *et al.* 1988.
[311] Pollack and LePage 1988.
[312] Reynolds *et al.* 1988.
[313] D'Anjou 1988a.
[314] D'Anjou 1986b.
[315] D'Anjou 1988a.
[316] Brand 1984.
[317] B.C. Min. Environ. (undated).

Although the berries are the main plant part eaten, the leaves and shoots are also browsed. Salmonberry is moderately important winter and spring browse for Roosevelt elk and black-tailed deer year-round (Singleton 1976; Leslie *et al.* 1984). The tender young shoots of salmonberry are important summer browse for Roosevelt elk on Vancouver Island (Devereux 1988).[318] Salmonberry (leaves, twigs, and fruit) can be among the 10 most important plant species in the diet of black-tailed deer (Brown 1961). On the Queen Charlotte Islands, high populations of introduced Sitka black-tailed deer have browsed salmonberry to the ground.[319]

Salmonberry shoots are a very important spring browse for black and grizzly bears in coastal British Columbia (Herrero 1985). Shoots made up 26% of the spring and early summer diet of black and grizzly bears near Knight Inlet (Lloyd 1979). The tender shoots and leaves are also a favourite summer food of mountain beaver. This mammal has limited range in the province but is common in the U.S. Pacific Northwest.

Other Resources: Salmonberry provides cover for birds and small mammals (Halverson (compiler) 1986).

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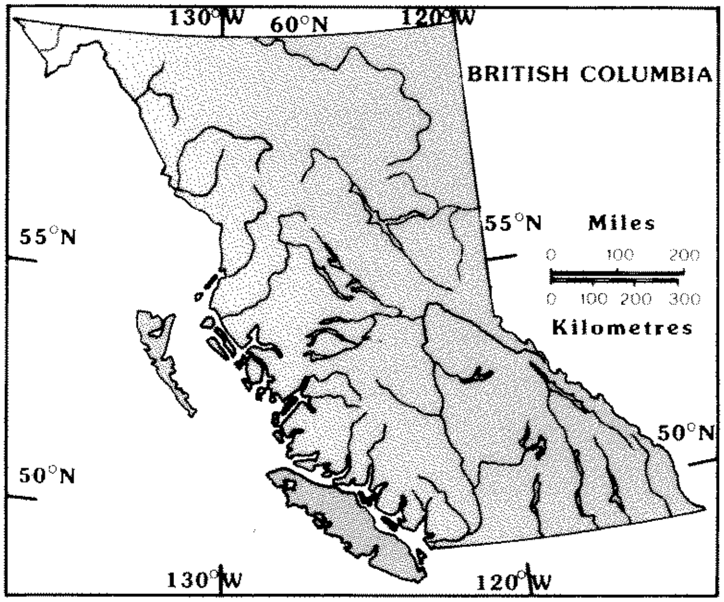
[318] Smith *et al.* (undated).

[319] Pojar and Banner 1984.

Salix bebbiana
(Bebb's willows)



Distribution of willows (*Salix* spp.) in British Columbia.

Salix spp. L. Willows

DESCRIPTION

Willows are a highly variable group of small trees, shrubs, and creeping woody plants. Form and leaf characteristics vary widely, but all willows have single-scaled buds and lack a terminal bud. Leaves are linear or lanceolate to orbicular but usually narrow and without large teeth. Male and female flowers are borne in catkins on separate plants. The fruit is a capsule that splits into 2 valves to release many, downy seeds (Argus 1973; Brayshaw 1978).

Variation: Salix is an extremely variable genus with extensive hybridization between species, although probably more hybrids have been described than exist in nature because of the high degree of intraspecific variation (Argus 1973; Brayshaw 1978). There are 48 species of willow in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Willows occur throughout British Columbia The following table lists some of the most important willows on forested sites and describes their distribution and habitat (after Brayshaw 1978; J. Pojar, pers. comm., Oct. 1984).[320]

Species	Distribution	Habitat
S. sitchensis	Common on the coast and scattered inland	River bars and uplands
S. scouleriana	Throughout B.C.; the most common coastal species	Uplands and moist draws
S. bebbiana	East of Coast Mtns; the most common Interior species	Uplands and disturbed sites
S. glauca	East of Coast Mtns.	Uplands and wetlands, low and high elevations
S. hookeriana	Along coast; very common in Fraser Valley	Swamp edges
S. lassiandra	Throughout B.C.	Alluvial habitats
S. pyrifolia	Northeastern B.C.; abundant in Peace River area	Wetland margins, riparian habitats
S. barclayi	Throughout B.C. at higher elevations and in northern areas	Variable
S. arbusculoides	Boreal forest and central Interior	Upland forest and wetlands
S. planifolia	Low to moderate elevations, mostly boreal forest	Wetland margins
S. maccalliana	Widely scattered; abundant in Chilcotin	Wetland margins
S. rigida	Throughout B.C., especially in southern Interior	Mostly in bottomland
S. drummondiana	East of Coast Mtns.	Alluvium and wetlands
S. alaxensis	Northern B.C.	Open, rocky soils and river bars

Altitudinal Range: Willows occur at all elevations in British Columbia, from sea level to alpine (Lyons 1952; Brayshaw 1978).

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[320] Roberts 1983.

HABITAT

Climatic Relations: Willows grow throughout the world but are best adapted to a cool, moist northern climate (Brayshaw 1978). The species in British Columbia are adapted to all extremes of climate found in this province. In temperate and warmer climates, willows are often most prevalent in locations with a cool microclimate.

Site and Soil Conditions: Best willow growth occurs in deep, moist, alluvial bottomlands (Rawson 1974), but there are willows on every type of site and soil. Most willow species are adapted to moist-to-wet riparian or swamp habitats with gleyed, regosolic, or organic soils, but some of the most abundant species favour well-drained sandy or gravelly parent materials (Rawson 1974; Brayshaw 1978).

Nutrient Relations: The general pH range for willows is 5.5 to 7.5. They will tolerate moderately alkaline soils but apparently do poorly on extremely alkaline or acidic soils (Rawson 1974). The genus contains species adapted to a wide variety of nutrient conditions, but the greatest diversity of forest species is found on nutrient-rich habitats. In the SBS zone, *S. bebbiana* (one of the most common upland willows) is found mainly on medium to nutrient-rich forest sites (Pojar *et al.* 1982).

Water Relations: Although willow species are adapted to the full range of soil moisture conditions in most forest zones in British Columbia, the majority are found on subhygric and wetter sites. Many species will tolerate standing water (Brayshaw 1978), but growth can be severely reduced when water levels are maintained at or above the root collar for extended periods (Knighton 1981). Porter states that ecological moisture regime is an important factor affecting willow species distribution and abundance.[321] He notes that in the SBS zone, *Salix bebbiana* and *S. discolor* perform best in the drier, warmer subzones, *S. scouleriana* prefers drier sites generally, and *S. sitchensis* thrives in the wetter, cooler subzones with some preference for wetter sites. Willows growing along waterways in arid areas transpire large quantities of water (Kozlowski 1972).

Light Relations: Willows are moderately to highly shade intolerant. Most species grow in the open or in partial shade, and vigour is much reduced under a forest canopy (Lyons 1952; Rawson 1974).

Temperature Relations: The ability of some willows to grow in the most extreme northern and alpine environments attests to their tolerance of extreme cold (Argus 1973; Brayshaw 1978).

GROWTH AND DEVELOPMENT

Willows range in size from medium-sized trees to dwarf shrubs, but most species of significance on forested sites are tall or medium-sized shrubs, or small trees no more than 10 m in height. They generally have a broad crown and are frequently multi-stemmed. Many species form dense thickets on wet sites (Rawson 1974; Brayshaw 1978), but upland willows often occur as scattered individuals. A remarkable characteristic of willows is their plasticity (Brayshaw 1978); the growth form adapts readily to habitat conditions, and there is extreme variability in branching habit, and foliage characteristics.

Willows exhibit rapid early growth from both seed or sprout (Rawson 1974). Sprout growth far exceeds that of seedlings and can exceed 2 m in 1 year (G. MacKinnon, pers. comm., Jan. 1985). Vegatatively reproduced willow was 6 times taller than willow growing from seed on a 6-year-old burn in Alaska (Zasada *et al.* 1987). Most willows are short-lived and become decadent at an early age (Spector 1956, cited by Rawson 1974; Fowells (compiler) 1965).

Phenology: A distinctive characteristic of some willows is the production of "pussy willows" early in spring before the snow has melted (Viereck and Little 1972). The genus typically has an early flowering phenology. Many species flower well before the leaves have emerged, others flower simultaneously with leaf emergence, while still others flower late in the year after the leaves have fully expanded. Seed ripening closely follows flower development, and most species disperse seed in early or mid-summer (Zasada and Viereck 1975; Brayshaw 1978; Marchant and Sherlock 1984).

See Porter[322] for phenology data on 4 major willow species in the SBS zone in British Columbia.

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[321] Porter 1989.
[322] Ibid.

REPRODUCTION

Seed Production and Dispersal: Willows are early producers and begin to flower between 2 and 10 years of age (USDA 1974). Male and female flowers occur on separate plants, so many plants never produce seed. Bees are apparently important in pollination. The optimum seed-bearing years of *S. bebbiana* are 10–30 years (Rawson 1974). In an Alaska study, a 2-year-old sprout produced seeds (Zasada *et al.* 1983). Most willows produce prolific quantities of seed (Brayshaw 1978). The capsular fruits split to release the minute, downy seeds that are then dispersed by either wind or water (USDA 1974).

Seed Viability and Germination: Willow seed has an extremely short period of viability. Under natural conditions, most seeds remain viable for only a few days. Seeds usually germinate within 12–24 hours of landing on a suitable seedbed (USDA 1974). In artificially sown seedbeds in Alaska, viable seeds were found after 4 weeks, but most germination occurred within 2 weeks of seeding (Zasada *et al.* 1983). In germination tests, willows normally have a high germinative capacity (70–100%) (USDA 1974; Zasada *et al.* 1983). Seed dormancy is absent in most species (USDA 1974; Marchant and Sherlock 1984), but has been observed in some late-flowering Alaskan species whose seed germinates in the spring of the following year (Zasada and Viereck 1975; Holloway and Zasada 1979). Germination is best under moist conditions with high relative humidity and full sunlight (USDA 1974). Exposed mineral soil is the best seedbed for many willow species, and germination of the small seed is inhibited on sites with a continuous cover of tree litter (Grime 1979).

Vegetative Reproduction: Willows are well known for their ability to root readily from stem cuttings (Edlin 1966; Marchant and Sherlock 1984). Cuttings taken during the growing season root particularly well (Holloway and Zasada 1979). Rooting is usually most successful on moist to wet sites (Rawson 1974; G. MacKinnon, pers. comm., Jan. 1985). Stem and root fragments root naturally if buried in moist soil. Damaged and cut stems produce prolific sprouts from the stem base or root collar (Fowells (compiler) 1965; Rawson 1974). Layering also occurs readily if branches are buried (Marchant and Sherlock 1984). The sandbar willow (*Salix interior*) reportedly expands by developing suckers from its extensive root system (Neiland and Viereck 1977).

PESTS

Furniss and Krebill (1972) recorded 52 species of insects and 39 species of fungi that attack willows in the western U.S. Insect infestations often lead to significant browsing or defoliation of leaves by late August. This may affect efficacy to foliar herbicides (J. Wright, pers. comm., July 1989).

EFFECTS ON CROP TREES

Competition: Willows compete with coniferous crop trees on a variety of sites throughout British Columbia. Willow competition is widespread throughout the Interior but is most intense in the northern SBS and in the BWBS where willows are extremely abundant and have become dominant over extensive areas as a result of repeated fire. On the coast, willow competition is significant primarily in wet or alluvial habitats.

Rapid early growth, especially in plants of sprout origin, allows willow to quickly outgrow its competitors (Rawson 1974). The plant can expand very rapidly following disturbance (Mueggler 1965), and its tendency to form dense thickets inhibits natural regeneration of conifers. The canopy of mature trees seldom creates deep shade, but juvenile growth may have larger leaves and dense sprouts can produce a solid canopy.

Beneficial Effects: No direct beneficial effects of willow on conifer growth are reported in the literature. Willows are useful in stabilizing streambanks and provide erosion control on severely disturbed sites (USDA 1974; Marchant and Sherlock 1984).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Willow generally increases in abundance on cutover areas (Mueggler 1965; Viereck and Little 1972; Eis 1981), but invasion is not always rapid. Trees damaged or cut during harvesting operations will sprout vigorously. Increased sunlight following overstory removal is very favourable to willow. Willow usually increases following canopy removal in the ICH zone near Salmon Arm (J. Wright, pers. comm., July 1989). It increases primarily by seeding-in. Mueggler (1965) found that crown cover of willow was 10 times greater on areas with low overstory cover than under a closed forest canopy. Removal of the overstory canopy on a site in Alaska resulted in very large increases in willow growth (Walker and Chapin 1986).

In a controlled experiment in Alaska, the response of feltleaf willow to winter browsing by snowshoe hares was investigated. Severe browsing of willow growing adjacent to alder thickets reduced willow height, thereby facilitating overtopping and shading by alder. Shading appeared to increase the palatability of willow stump sprouts, resulting in increased severity of browsing. A 50% reduction in light for 1 year caused a 2-fold increase in palatability. More severe shading over a longer period of time, as occurs under the canopy of an alder thicket, is expected to cause even greater increases in willow palatability (Bryant 1987).

Fire: Willow is greatly favoured by fire in most habitats (Wright 1972) and it can become the dominant cover in areas that have a history of frequent natural fire. It sprouts vigorously after fire and height growth can be dramatic (J. Wright, pers. comm., July 1989).[323] Cover of established plants increases substantially after burning. For example, in Montana, willow canopy increased more than 10-fold the first year following burning, and more than 30-fold the second year (Noste and Bushey 1987). Four years following a fire in Alaska, *S. scouleriana* density was 4 times greater than on adjacent unburned areas (Viereck and Dyrness 1979). In northern Idaho, cover of *S. scouleriana* was much higher on burned sites than unburned clearcuts, particularly where there had been repeated fires over a 30-year period (Mueggler 1965).

Willow that invades by seeding-in grows slower than willow that sprouts after burning. Stickney (1981) found numerous willow seedlings on burned sites in western Montana but noted that that the rate of cover development was quite slow. After 6–9 years its cover was less than 10% on most areas. Six years after a burn in Alaska, grayleaf willow seedlings were 5 times taller on severely burned microsites than on lightly burned areas (Zasada *et al.* 1987).

Prescribed fire is widely used as a wildlife management tool to rejuvenate decadent willow and stimulate sprouting. A quick, hot fire maximizes sprouting, while slower, longer burns cause more extensive damage and produce less browse (G. MacKinnon, pers. comm., Jan. 1985). However, in some situations, prescribed burning can reduce initial competition from willow in clearcut areas (C. Delong, W.R. Mitchell, and D. Lloyd, pers. comm., Nov. 1984).

Cutting: Willow will sprout vigorously following cutting, regardless of cutting season, but sprouting vigour is more pronounced if cutting takes place during the dormant season. Sprouting has been observed less than 2 weeks after cutting (B. Nash, pers. comm., June 1989). Sprouts often grow 1–2 m in the first season (Kellyhouse and Graanard 1984; B. Nash, pers. comm., June 1989; J. Wright, pers. comm., July 1989). It is possible for individual cut stems to produce 50 or 60 sprouts.

Willow is often cut to increase browse for wildlife. Production of overmature feltleaf willow that was mechanically crushed in March in Alaska increased 3 times by the end of the first season and 10 times by the end of the second growing season. Heavy clipping of willow in the northeastern U.S. produced a major increase in twig production (Aldous 1952). Annual production increased steadily to 855% of initial production over 5 years of cutting. Stem number was gradually reduced but individual stems were stouter and had greater vigour (Aldous 1952).

Herbicides: Response of willows to herbicides is poorly understood because of the difficulty of identifying willow species. Because of the great variability both between and within species, herbicide response can vary dramatically (M. Newton, pers. comm., Dec. 1984).

Late summer or fall applications of glyphosate have caused very severe injury to willow in Washington and Oregon (Conard and Emmingham 1984b). Effective control has also been reported after late summer and fall applications of glyphosate in British Columbia (Boateng and Herring 1990). For example, late

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[323] Porter 1989.

August and September broadcast applications of 2.1 kg a.i./ha in the Prince Rupert Forest Region provided excellent control of willow and no basal sprouting for at least 2 years after treatment.[324,325] However, control is often incomplete or very short-term (J. Wright, pers. comm., July 1989).[326,327] A summary of 36 trials in the U.S. Inland Northwest indicates that glyphosate usually causes less than 50% top-kill in the first year, declining to 30% by the third year after treatment. Waddington and Bittman (1987) found that willow trees less than 0.5 m high suffered less injury from glyphosate than did taller trees. Fall applications of glyphosate to cut surfaces has provided very effective control of willow in the IDFdk subzone in the Caribou and the ICH zone in the Salmon Arm District (J. Wright, pers. comm., July 1989).[328]

Broadcast applications of 3–4 kg a.i./ha hexazinone in late May and June result in effective first year control of willow, but application rates of 2 kg a.i./ha result in unacceptably poor control;[329,330] Pollack and LePage[331] found that willows receiving 2 kg a.i./ha sprouted vigorously and had twice as many sprouts as the willows treated with the higher application rates.

Spot applications of hexazinone have generally been successful in controlling willow in British Columbia and Alberta.[332,333,334,335] Effectiveness of spot applications of hexazinone does not seem to be related to date of application. Excellent first-year control of willow has been obtained in every month from May to October. Application rates of 8 mL per spot at 2 x 2 m or 1.5 x 1.5 m spacing, and 4 mL per spot at 1.5 x 1.5 m have usually controlled willow. An application rate of 4 mL per spot at 2 x 2 m spacing has tended to provide unsatisfactory first-year control of willow.

Information is lacking on the number of years of control provided by broadcast or spot applications of hexazinone, but in a trial involving spot applications of 9–11 mL per spot on a mesic SBSmc site, willow remained well controlled for at least 4 years (N. Endacott, pers. comm., July 1989).

In Washington and Oregon, spring or late summer applications of 2,4-D to cut surfaces cause very severe injury (Conard and Emmingham 1984b). A summary of 8 broadcast trials in the U.S. Inland Northwest indicates that 2,4-D causes less than 30% top-kill of willow the second year and 40–70% top-kill the third year after treatment (Boyd *et al.* 1985). 2,4-D amine is reported to moderately injure willow in British Columbia (Boateng and Herring 1990). On a backlog site in the Prince Rupert Forest Region, a 45% cover of 1.3-m tall *S. scouleriana* and *S. bebbiana* was not controlled by a late August broadcast spray of 3 kg a.i./ha 2,4-D ester in 10% oil. By the second year after treatment, willow had resprouted 98 cm.[336]

Soil Disturbance: Freshly disturbed sites may be colonized by willows that seed-in or sprout from damaged roots and stems.[337] Exposure of mineral soil favours the germination of willow seed (Grime 1979; Zasada *et al.* 1983; D. Greenley, pers. comm., May 1989; J. Wright, pers. comm., July 1989). In the SBSwk subzone near McGregor, B.C., exposed mineral soil was rapidly covered with willow (and birch) which densely overtopped planted spruce by 13 years after the site was treated (MacKinnon and McMinn 1988). Along streambanks, willows are among the first species to seed-in to newly exposed silt and gravel (Neiland and Viereck 1977). Windrowing can increase willow browse production since mechanical damage to stems stimulates prolific sprouting. Branch parts incorporated into the mineral soil during mechanical treatments can root and regenerate new plants (G. MacKinnon, pers. comm., Jan 1985).

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[324] Pollack and LePage 1987.
[325] LePage and Pollack 1988a.
[326] Noble-Hearle 1989.
[327] Herring 1984a.
[328] George 1989.
[329] Teskey and Masterson 1986a.
[330] Pollack and LePage 1986a.
[331] Ibid.
[332] Teskey and Masterson 1986f.
[333] Newhouse 1988a.
[334] George 1989.
[335] Drouin 1985.
[336] Pollack and LePage 1987.
[337] Porter 1989.

Fertilization: In Alaska, 3 consecutive years of fertilization of 5-year-old *Salix alaxensis* plants with nitrogen, phosphorus, and potassium increased twig production in unshaded plants but had little effect on shaded plants (Bryant 1987). Greenhouse studies in Washington (Adams and Dale 1980) and Alaska (Walker and Chapin 1986) showed that NPK fertilization of willow significantly increased height growth. Walker and Chapin (1986) found that NPK fertilization raised the shoot:root ratio from about 1 to 8. This author found that fertilization with nitrogen produced maximum willow growth at a concentration of 50 mg/L.

WILDLIFE

Food: Willows are very important for wildlife in British Columbia. They are a staple food year-round for moose (Murie 1954; Banfield 1974; Singleton 1976; Noste and Bushey 1987; Ritcey 1988).[338] Moose browse on twigs in winter (Ritcey 1988) and consume leaves and new shoots in summer (Harestad 1983). Species in the genus *Salix* are some of the most palatable foods to moose in central British Columbia (Hatter 1948, cited by Peterson 1978). Most upland willows, for example *S. scouleriana* and *S. bebbiana*, are highly palatable.[339] Porter found that in the SBS zone in north central British Columbia, selection of willow species for browsing appears to be mainly based on availability.[340]

Willows are a moderately important year-round browse for deer in British Columbia (Singleton 1976; Rue 1978).[341] In the East Kootenays, willows are most important to white-tailed deer in May and June[342] while in the IDF zone in south central British Columbia, willows are important in the winter.[343]

Willows are moderately important winter and spring browse for Rocky Mountain and Roosevelt elk and make up part of the summer and fall diet of Rocky Mountain elk (Singleton 1976; Devereux 1988). Willows were recorded as 70% of the December diet, 23% of the March diet, and 17% of the April diet of Roosevelt elk on Vancouver Island.[344] Willows are also a moderately important year-round food of Osborn Caribou (Singleton 1976).

Shoots and buds of willow are eaten by many small mammals (Rawson 1974) including pika, heather vole, and Columbia ground squirrel (Banfield 1974). Willows are highly preferred by beavers (Denney 1952, cited by Allen 1982; Banfield 1974; Sadoway 1986). Jenkins (1981, cited by Allen 1982) indicates, however, that beaver use of willow may be more a case of availability than of preference. Snowshoe hares browse willow heavily (Hansen and Flinders 1969; Walker *et al.* 1986), particularly in summer when leaves are tender (Banfield 1974). Wolff (1978) found that willow bark and twigs made up 10% of the diet of snowshoe hares between December and April and less than 2% the rest of the year. Leaves made up 5% of winter, 3% of April, 8% of May, 25% of summer, and 5% of the fall diet. In Oregon, the common mountain beaver consumes light to moderate amounts of willow (Crouch 1968).

Song birds and game birds feed on willow buds, twigs, leaves, and seeds (Rawson 1974). On Vancouver Island, willow leaves were found to be an important source of food for mature blue grouse in March and April and for chicks in the fall (King and Bendell 1982). King (1969) found that on Vancouver Island, leaves and twigs are important to adult ruffed grouse in the spring and leaves are important to juveniles in July and August. Buds and twigs of willow made up 29% of the winter diet of ruffed grouse at a site in Alberta (Doerr *et al.* 1974, cited by Cade and Sousa 1985) and 35% of the winter diet at a site in Alaska (McGowan 1973, cited by Cade and Sousa 1985).

Other Resources: Riparian willow stands provide winter range for moose from Wyoming to Alaska. Maximum use occurs from mid- to late winter and during months of the greatest snow depth (Chapman and Feldhamer (editors) 1983). Willow thickets are important habitat for birds and some small mammals. For example, they provide good winter cover for snowshoe hare (Wolff 1980 and Bailey 1946, cited by Carreker 1985) and habitat for heather vole (Banfield 1974). Willows are important cavity nesting trees for downy woodpeckers in British Columbia.[345] Many other species of birds including sparrow, blackbird, goldfinch, redstart, vireo, and flycatcher nest in willows (Cannings *et al.* 1987).

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[338] Blower 1982.

[339] Ibid.

[340] Porter 1989.

[341] Blower 1982.

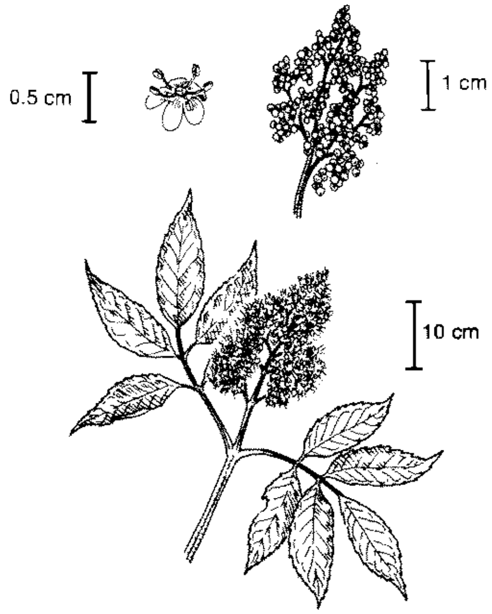
[342] Demarchi and Demarchi 1967.

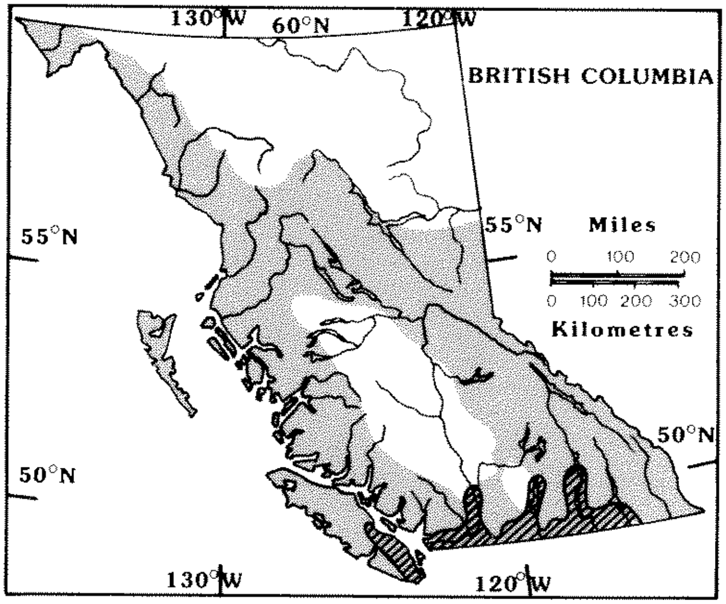
[343] Miles and Weikle (undated).

[344] Smith *et al.* (undated).

[345] Korol and Wallis 1983.

Sambucus racemosa
(red elderberry)





Distribution of elderberries (*Sambucus* spp.) British Columbia. The shaded area represents the distribution of *S. racemosa*, while the hatched area shows the distribution of *S. cerulea*.

Sambucus spp. L. — Elderberry (elder)

DESCRIPTION

Elderberry is a tall, coarse shrub or small tree with a broad, arching crown, 1–6 m tall. Stems are cane-like and branches are stout with a soft, pithy centre and large buds. Elderberry leaves are large and compound with 5–11 pointed, finely toothed leaflets. The flowers are small and white, borne in large, showy terminal clusters. The berry-like fruit can be bluish, purplish black, or brilliant red (Viereck and Little 1972; Hosie 1973; Clark 1976).

Variation: The taxonomy of the genus *Sambucus* in British Columbia is confusing because of the profusion of synonyms for each taxon. To most people there are three types of elderberry in British Columbia: a blue elderberry, a red elderberry, and a black elderberry; to the plant taxonomist it is not so simple.

There are two species of *Sambucus* in the province, one of which has several varieties. *Sambucus cerulea* is the large tree-like blue elderberry found only in southern British Columbia. *S. racemosa* occurs through most of the province (Taylor and MacBryde 1977).

Sambucus racemosa is found across the Northern Hemisphere. Its North American version is now known as ssp. *pubens*. It can have either red or black fruit. In British Columbia, the black-fruited variety (var. *melanocarpa*) is found only in the southern Interior. There are two varieties with red fruit in the province. Variety *leucocarpa* occurs virtually across Canada but is only found in southeastern British Columbia. Variety *arborescens* is found along the Pacific coast and through most of the province. To complicate the issue, there is a third red-fruited variety (var. *microbotrys)* found south of the border in the U.S. Rocky Mountains. Most of the literature used in this report refers to this southern variety.

DISTRIBUTION AND ABUNDANCE

The table below summarizes the taxonomy and distribution of *Sambucus* in British Columbia. In the remainder of this discussion, only the names of the two species, *S. cerulea* (blue fruit) and *S. racemosa* (either red or black fruit), will be used.

Scientific name (*synonym)*	**Common name**	**Distribution in British Columbia**
Sambucus cerulea *(S. glauca)*	Blue elderberry	Southern B.C. and Vancouver Island; ICH, IDF, PP, CDF, and southern CWH
Sambucus racemosa* ssp. *pubens *(S. racemosa, S. pubens)*		
(a) *S. racemosa* ssp. *pubens* var. *melanocarpa (S. melanocarpa)*	Black elderberry	Southeastern B.C. only; ICH, IDF, ESSF
(b) *S. racemosa* ssp. *pubens* var. *leucocarpa (S. pubens* var. *leucocarpa)*	Red elderberry (eastern)	Southeastern B.C. only; ICH, ESSF
(c) *S. racemosa* ssp. *pubens* var. *arborescens (S. callicarpa)*	Red elderberry (coastal)	Coastal and moist Interior areas, except southeastern B.C.: CWH, CDF, ICH, MH, ESSF, SBS

Altitudinal Range: Elderberry is found at low to moderate elevations within its range. *Sambucus racemosa* is most abundant below 600 m on the coast and 1200 m in the Interior (Lyons 1952).

HABITAT

Climatic Relations: S. cerulea is confined to the southern-most valley bottoms in British Columbia and apparently requires a warm, fairly dry climate with a long growing season. *S. racemosa* appears to tolerate a broader range and more severe conditions but is restricted to areas of coastal or humid continental climate. In the U.S. Rocky Mountains, *S. racemosa* is found in moist, subalpine climates where the majority of precipitation falls as snow and temperatures during the growing season range from 5 to 25°C (Conrad and McDonough 1972).

Site and Soil Conditions: Elderberry is common along streams and ravines, on disturbed sites, and in forest openings. It occurs on a wide variety of soils (UBC Bot. Garden 1971; Conrad and McDonough 1972; Viereck and Little 1972; Hosie 1973). *S. cerulea* is most common on gravelly or stony soils (Hosie 1973), while *S. racemosa* generally occurs on deep, well-drained soils with silt loam to sandy loam textures (Harcombe *et al.* 1983). Best growth is on deep, fluvial soils.

Nutrient Relations: Elderberry favours rich soils (Clark 1976) and is an indicator of high nitrate availability.[346] *S. racemosa* is most common on moderately rich to very rich sites (see, e.g., Haeussler *et al.* 1984)[347] but the species may be found under a broader range of nutrient conditions in seral ecosystems.

Water Relations: Elderberries favour moist soil conditions (UBC Bot. Garden 1971; Viereck and Little 1972; Clark 1976). In relatively dry climates such as the IDF zone, *S. racemosa* is restricted to subhygric and hygric sites. In wetter zones such as the ICH and CWH, it can tolerate a broader range of moisture conditions (Angove and Bancroft 1983). *S. racemosa* is common on some swampy skunk cabbage sites on the coast,[348] but on these poorly drained sites it tends to occur on elevated hummocks.

Light Relations: S. cerulea is described as slightly shade tolerant by Plummer *et al.* (1955). *S. racemosa* is tolerant of deep shade but grows best in forest openings and margins (Harcombe *et al.* 1983). In a growth chamber experiment, *S. racemosa* grew better under 18-hour photoperiods than under 12-hour photoperiods (Conrad and McDonough 1972).

Temperature Relations: Best growth of *S. racemosa* in the growth chamber was under a 25°C daytime and 15°C nighttime temperature regime (Conrad and McDonough 1972). Seedlings kept at 2°C for 4 months to simulate winter conditions grew better than those that did not receive a chilling treatment. Branches are highly susceptible to frost kill after growth has begun in spring.

GROWTH AND DEVELOPMENT

Seedlings of *S. cerulea* have a thick taproot and an expansive spreading lateral root systems (Landis and Simonich 1984; Shaw 1984). Once established, the shrub grows rapidly in height and produces a large, full crown. Shrubs can attain their full size of approximately 3 m in height and several metres in crown diameter within 3–4 years in the Intermountain U.S. (Plummer *et al.* 1955). Most individuals remain as large shrubs, but in favourable locations they can become small trees. Long-lived trees can reach 9 m in height and 36 cm in diameter (Hosie 1973; Clark 1976).

The growth and development of *S. racemosa* var. *microbotrys* has been studied in the U.S. Rocky Mountains where it forms pure dense stands in subalpine rangelands (McDonough and Tew 1967; Conrad and McDonough 1972). In this environment, red elderberry has a rhizomatous habit and spreads to form clones ranging from 1 to 16 m^2 in size. The variation in clone size is believed to reflect age differences. Once established, a single clone can occupy the same site for a long time. One rhizome was found to be 58 years old and the clone was probably much older. Roots extend to a depth of approximately 1 m in the soil, and there is a dense network of rhizomes and roots under the entire area of the clone.

In a greenhouse study it took 3 years before a red elderberry seedling was able to produce rhizomes. These rhizomes form buds that give rise to aerial stems. During the first growing season these stems are unbranched and strictly vegetative. Auxillary buds formed late in the growing season can develop into either vegetative or flowering branches the following year. Some axillary buds near the base of the stem remain dormant until branches higher on the stem are damaged. The erect stem produces secondary and then tertiary branches, but branches of tertiary or higher order are frequently killed by winter damage, so the branching habit of the plant remains quite simple. If stems are damaged or destroyed right to ground level, new stems will emerge from dormant buds on the rhizome. Aerial stems newly arising from rhizomes have a much higher growth rate than branches on older stems.

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[346] Brand 1984.
[347] Yole *et al.* 1982.
[348] Ibid.

There are no reports of rhizomatous suckering in *S. racemosa* growing on the coast (i.e., var. *arborescens).* On the Pacific Coast, seedlings can grow 30 cm in the first year (M. Newton, pers. comm., Dec. 1984), and young shrubs can grow 1.3–2 m in a single year once established (UBC Bot. Garden 1971). Following any form of disturbance, the species sprouts vigorously from the rootstock. Sprouts have considerably more rapid growth rates than seedlings and average 3–4 m in the first year (M. Newton, pers. comm., Dec. 1984).

Phenology: Growth of *S. racemosa* begins very early in the growing season. In the Rocky Mountains of the U.S., bud elongation begins while snow is still on the ground and stem growth is completed within 3–6 weeks following snowmelt (Conrad and McDonough 1972). On the central British Columbia coast, most shrubs are in full leaf by mid-June.[349]

Red elderberry blooms throughout May in southern British Columbia (Lyons 1952) and from May to July in Alaska (Viereck and Little 1972). In the U.S. Rocky Mountains, initiation of flower buds for the following year coincides with a sharp reduction in the rate of vegetative growth during late June and early July. Vegetative branches continue to elongate long after flowering branches have ceased to grow (Conrad and McDonough 1972). Berries become ripe in June in southern British Columbia (Lyons 1952) and on the central coast[350] and during July and August in Alaska and the Rocky Mountains (Conrad and McDonough 1972; Viereck and Little 1972).

Phenological observations of *S. cerulea* were made over a period of 9 years in the northern U.S. Rocky Mountains (Schmidt and Lotan 1980). Bud burst occurred from late April to mid-June, depending on location and weather conditions. Where it occurs together with *S. racemosa,* it usually leafs out about a month later than the red-fruited shrub (Clark 1976). Leaves were fully grown approximately 1 month after bud burst. Leaf senescence began in mid- to late August and leaf fall took place between mid-September and mid-October. Flowering of this species extends from late May through to August, and fruits ripen in August and September both in the U.S. and British Columbia (Lyons 1952; Schmidt and Lotan 1980).

REPRODUCTION

Seed Production and Dispersal: Approximately 60–90% of the flowers in an inflorescence develop a small, round fruit each with 2 to 5 seeds (Conrad and McDonough 1972; Hitchcock and Cronquist 1973). Good seed crops are produced virtually every year. Seed dispersal is primarily by birds and other animals that eat the fruit.

Seed Viability and Germination: Approximately 40% of seeds sampled by Conrad and McDonough (1972) were unfilled and only 50% of filled seed were viable. Seeds remain viable in storage for several years (at least 16 for *Sambucus cerulea). S. racemosa* is a seed-banking species in coastal British Columbia (McGee 1988b) and in the ESSF and SBS zones in northern British Columbia. It is particularly abundant in seed banks on subhygric SBSvk sites (E. Hamilton, pers. comm, July 1989). Seeds have both seed coat and embryo dormancy; they need several months of chilling before they will germinate. Additions of gibberellic acid can increase germination rates. Germination of *S. racemosa* did not take place at 2°C but some germination occurred at 13°C (McDonough 1969; UBC Bot. Garden 1971; USDA 1974; Landis and Simonich 1984; Shaw 1984).

Germination of *S. racemosa* in a field experiment was only 1–8% (Conrad and McDonough 1972). The low germination may have been caused by freezing of the seed before a protective snow cover developed. None of the seedlings survived the summer. Few established seedlings were observed on undisturbed sites where *S. racemosa* clones were well established, and the authors concluded that production of seedlings is not a significant means of perpetuating established colonies. In contrast, germinants are often abundant on disturbed sites (Stewart 1978; M. Newton, pers. comm., Dec. 1984). Kelpsas (1978) found great quantities of germinants the first growing season following disturbance in coastal Oregon. Seeds were able to germinate on broken decaying wood. Recent research in Oregon indicates that blue elderberry germinates on clearcuts but not under mature Douglas-fir canopies (Zasada *et al.* 1988).

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[349] Hamilton 1984.

[350] Ibid.

Vegetative Reproduction: Elderberries reproduce vegetatively from sprouts and rhizome suckers and by layering (Worley and Nixon 1974), although, as mentioned earlier, no suckering has been observed in coastal Oregon. Vegetative reproduction is responsible for persistence of established colonies (Conrad and McDonough 1972).

PESTS

The UBC Botanical Garden (1971) provides a list of insects and diseases found on *S. racemosa* ssp. *pubens* var. *arborescens* in British Columbia.

EFFECTS ON CROP TREES

Competition: Elderberry is a common shrub in moist, productive ecosystems in many areas of the province. It is an important component of the shrub complexes that can inhibit conifer establishment and growth on such sites, but it is rarely a primary competitor. The shrub usually occurs as isolated clumps that spread over lower brush species. It easily outgrows conifers, particularly when it is of sprout origin.

Allelopathy: Extracts of live plant material and litter of *S. racemosa* strongly inhibit germination and growth of Douglas-fir and grasses in the laboratory (McDonough and Tew 1967; del Moral and Cates 1971). However, these authors were unable to demonstrate that allelopathy is operative under field conditions.

Beneficial Effects: The presence of an overstory canopy of *S. cerulea* can aid in the establishment of other understory species in the relatively dry, hot climate of Idaho (Monsen 1984). Elderberry may also be helpful in erosion control on moist sites (Worley and Nixon 1974).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Harcombe *et al.* (1983) indicate that canopy removal will enhance cover of *S. racemosa.* A definite increase in cover of *S. racemosa* was recorded 6 years following canopy removal on 4 site types in the SBS zone north of Prince George (Eis 1981). D. Harrison (pers. comm., May 1989) observed an increase in cover of the plant following canopy removal on northern Vancouver Island. Cover and frequency of *S. racemosa* was not significantly greater following logging in northern Idaho, but the height of the shrub increased (Mueggler 1965). Increases in total height and bushiness of red elderberry have also been observed following logging in the Cariboo Forest Region (R. Coupé, pers. comm., Nov. 1984). Similarly, elderberry was observed to become vigorous after removal of an alder overstory in the CWH subzone in the Kitimat Valley (K. Haworth, pers. comm., July 1989).

Fire: There is conflicting evidence regarding the response of elderberry to fire. Several reports indicate that elderberry is favoured but not greatly enhanced by fire (Mueggler 1965; Lafferty 1972; Wright 1972). Existing plants respond to fire by sprouting from rootstocks (M. Newton, pers. comm., Dec. 1984). However, Isaac (1940) reported that *S. cerulea* is quickly eliminated by fire because it spreads slowly by seed rather than by vegetative means. Seed germination was observed to be prolific after burning on subhygric SBSvk sites in northern British Columbia (E. Hamilton, pers. comm., July 1989), and seedlings are reported to be common on coastal sites following fire (Stewart 1978).

Existing plants respond to fire by sprouting from rootstocks (M. Newton, pers. comm., Dec. 1984); however, Isaac (1940) reported that *S. cerulea* is quickly eliminated by fire because it spreads slowly by seed rather than rapidly by vegetative means.

Cutting: Red elderberry resprouts rapidly from stems and branches following cutting, but the plant cannot withstand repeated heavy clipping or browsing, especially when young (Aldous 1952; Harcombe *et al.* 1983). Conrad and McDonough (1972) conducted clipping experiments on *S. racemosa* var. *microbotrys* to simulate browsing by livestock. They found that cutting to ground level stimulated emergence of shoots from dormant rhizome buds within 2–4 weeks. Clipping in mid-June produced regrowth of 136% by the end of August. A second, late August clipping significantly reduced growth in the following year. Clipping once at the end of each growing season did not reduce the potential for regrowth. Clipping only lateral branches caused sprouting from buds at the base of the stem, whereas clipping back the entire stem caused new rhizome stems to emerge.

Herbicides: Studies in British Columbia indicate good initial control of elderberry after July, August, or September applications of 2.1 kg a.i./ha glyphosate.[351,352,353,354,355,356] Plants often resprout by the second growing season. Pollack and Thienen[357] found that 5 years after an August application of 2 kg a.i./ha glyphosate to a Skeena flood plain site, percent cover of red elderberry was not reduced but height was only 1.7 m on the treated plots compared to 2.8 m on the control.

Sixteen glyphosate trials involving application rates of 0.8–3.2 kg ai/ha in the U.S. Inland Northwest usually resulted in 80–100% plant kill the second and third years after treatment. In northeastern Oregon and northern Idaho, fall applications of glyphosate caused very severe injury to elderberry (Conard and Emmingham 1983). In western Washington and Oregon, late summer applications of glyphosate caused 60–90% injury (Conard and Emmingham 1984a).

Little information is available on the effectiveness of hexazinone in controlling elderberry. A broadcast application of 4 kg a.i./ha hexazinone in mid-April in the CWH zone near Chilliwack caused moderate control of elderberry after 1 year.[358]

Conard and Emmingham (1984a) report that 2,4-D causes moderate injury to elderberry when applied in the winter, spring, or summer in western Washington and Oregon. Application of 2,4-D ester in 7 trials in the U.S. Inland Northwest resulted in 70–80% top-kill after 3 years (Boyd *et al.* 1985).

Spring applications of triclopyr caused very severe damage to elderberry in Washington and Oregon (Conard and Emmingham 1984a). Nine trials in the U.S. Inland Northwest involving application of 1.1–2.2 kg a.i./ha triclopyr indicated that top-kill is usually at least 80% the second year and 60–95% the third year after treatment (Boyd *et al.* 1985).

Elderberry is reported to be extremely susceptible to amitrole (Boateng and Herring 1990).

Soil Disturbance: Soil disturbance can create favourable conditions for germination of elderberry seeds (Kelpsas 1978; Harcombe *et al.* 1983). Any soil disturbance that causes damage to stems and rhizomes will tend to stimulate vigorous resprouting from stem bases and possibly rhizome buds (Conrad and McDonough 1972; Worley and Nixon 1974; M. Newton, pers. comm., Dec. 1984).

WILDLIFE

Food: Elderberry is an important food for ungulates in British Columbia. The buds and bark of elderberry are eaten by moose, deer, elk, and porcupine. It is an important winter food of Roosevelt elk.[359] Smith *et al.*[360] indicated that 20–30% of the January diet of Roosevelt elk was comprised of *S. racemosa*. Elderberry is moderately important as winter and spring food for black-tailed deer, Rocky Mountain elk, and moose (Singleton 1976; Rue 1978). It is a common summer food of all species of deer in British Columbia including the high populations of introduced Sitka black-tailed deer on the Queen Charlotte Islands which have browsed *S. racemosa* to ground level.[361] The fruit is relished by many species of birds and mammals including grizzly bears (Plummer *et al.* 1955; Conrad and McDonough 1972; Worley and Nixon 1974; UBC Bot. Garden 1977; Harcombe *et al.* 1983; National Wildlife Federation 1987; Lofroth 1988).

Other Resources: Elderberry provides nest sites for birds.

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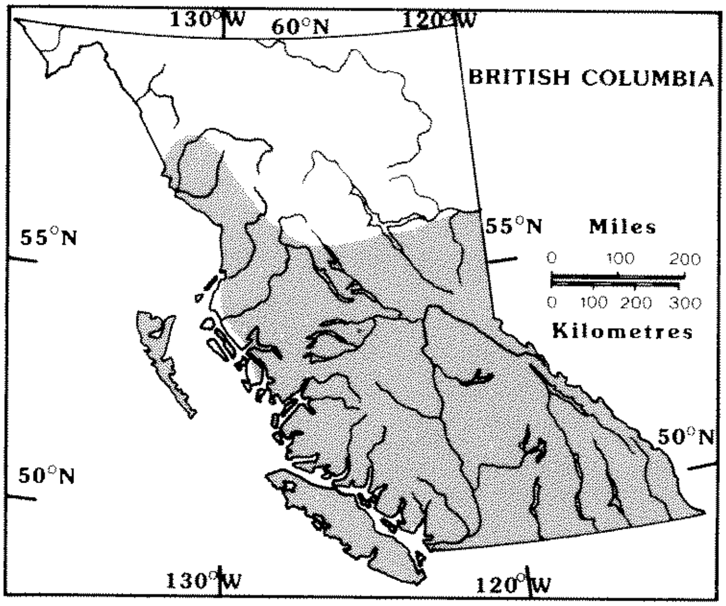
[351] Dyke 1987.
[352] Herring and Fahlman 1984.
[353] Pollack and LePage 1988.
[354] Pollack and van Thiesen 1986.
[355] Reynolds *et al.* 1988.
[356] Simard 1988.
[357] Pollack and van Thiesen 1986.
[358] D'Anjou 1988d.
[359] Blower 1982.
[360] Smith *et al.* (undated).
[361] Pojar and Banner 1984.

Symphoricarpos albus
(snowberry)



Distribution of *S. albus* in British Columbia.

Symphoricarpos albus (L.) Blake **Snowberry**

DESCRIPTION

Common snowberry is an erect, deciduous, small to medium-sized shrub (0.5–2 m tall) with a rhizomatous growth habit. It has slender twigs with distinctly opposite branching. The thin leaves are exceedingly variable in shape, but most are ovate to elliptic with an untoothed margin. The flowers are tiny pink bells borne in small clusters. The fruits are clustered white drupes, remaining on the twigs over winter (Jones 1940; Viereck and Little 1972).

Variation: *Symphoricarpos* is a complex genus found throughout North America. The western species, *S. albus,* has two recognized varieties in British Columbia. The typical form, var. *albus,* is found east of the Coast Mountains. The coastal form, var. *laevigatus,* is larger and is sometimes regarded as a distinct species (Jones 1940; Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Symphoricarpos albus is found throughout British Columbia to approximately 56°N latitude. It has been found at scattered locations further north in the Stikine–Iskut drainage and on the Liard River but is mostly absent from northern British Columbia. Common snowberry is found along the coast including Vancouver Island and the Queen Charlotte Islands but generally occurs slightly inland. It is most abundant in the IDF biogeoclimatic zone of southern British Columbia.

Altitudinal Range: Common snowberry is a species of low elevations and is rarely found at subalpine elevations. It is usually limited to elevations below approximately 600 m on the Coast and 900 m inland (Lyons 1952).

HABITAT

Climatic Relations: Within its broad range in British Columbia, snowberry seems to favour areas of warm meso- or microclimate, and it is most abundant in some of the warmest, driest climates in the province. The coastal variety is apparently tolerant of humid — but not excessively rainy — conditions, while the interior variety favours subhumid to semiarid conditions. Neither variety seems able to tolerate the heavy snows and short growing seasons of high altitudes. In contrast, in Colorado, towards the southern end of its range, common snowberry favours moist, high elevations and does not occur on dry south and west-facing slopes (Moore *et al.* 1975, cited by Watson *et al.* 1980)

Sites and Soil Conditions: Common snowberry has a broad ecological amplitude and can be found on a variety of sites and soils provided that climatic conditions are suitable. In the Interior it grows in rocky or dry soil, on riverbanks, in dry open rocky woods, and often at the base of cliffs (Jones 1940). It is often found on disturbed, coarse-textured and rocky soils in Alberta (Watson *et al.* 1980). On the coast, snowberry is found on a variety of soils and parent materials and is often abundant on floodplains (see, e.g., Harcombe *et al.* 1983; Haeussler *et al.* 1984).

Nutrient Relations: Common snowberry is tolerant of mildly acidic to moderately alkaline conditions. It is somewhat tolerant of salts and will survive under low nutrient conditions (Watson *et al.* 1980). In the SBS zone, snowberry is described as occurring on sites that are medium to rich in nutrients (Pojar *et al.* 1982), but in other areas of the province it is found on ecosystems with a broad range of ecological nutrient regimes (see, e.g., Mitchell and Green 1981).[362]

Water Relations: Common snowberry has a broad ecological amplitude with respect to soil moisture (see, e.g., Pojar *et al.* 1982). It can be found on very xeric sites and it is also abundant on subhygric and hygric sites. Although it tends to favour moist sites in dry subzones of the IDF zone, and drier sites in wetter subzones (Angove and Bancroft 1983), it is abundant on moist floodplains even in the wet CWH and ICH zones. It is most vigorous on sites that are well supplied with moisture. Watson *et al.* (1980) describe common snowberry as moderately drought-resistant.

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[362] Utzig *et al.* 1983.

Light Relations: Rowe (1983) describes snowberry as semi-tolerant to tolerant of shade, while Watson *et al.* (1980) indicate that it will grow in partial shade but prefers open sites. Quenet (1973) found that snowberry can survive under crown closures of over 80% in the IDF zone of southeastern British Columbia, but that very few shrubs were present at this level of canopy closure. Common snowberry is rarely found under a coniferous forest canopy in the CWH zone.

GROWTH AND DEVELOPMENT

Common snowberry is typically less than 1 m tall at maturity but can reach 2 m on productive coastal sites (Lyons 1952; Clark 1976). Once established, it spreads outwards to form a low thicket (Lyons 1952; Watson *et al.* 1980). Miller (1977) and Tisdale and Hironaka (1981) report that this spread is achieved by rhizomes. McLean (1969) notes that the roots and rhizomes of common snowberry are fibrous and grow mostly between 5 and 13 cm beneath the mineral soil surface. Bradley (1984) considers the rhizomes to be deep in the soil. Most rhizomes are horizontally oriented and their slender form makes them well adapted to snaking between rocks (Bradley 1984). The juvenile twigs are stouter and bear leaves that are larger and more variable in shape than those of older twigs (Jones 1940). A maximum shrub age of 20 years was found on a site in southeastern British Columbia (Quenet 1973). Maximum twig biomass was very low compared to other shrub species found on the same site.

Phenology: Bud burst normally occurs in early May in the northern U.S. Rocky Mountains, but can vary by more than a month in either direction depending on elevation and weather conditions. Leaves are full-grown approximately 1 month after emergence. The flowers appear any time from May to August and may be present as late as September in some locations. Peak flowering time is June and July. Fruit ripening times are equally variable but typically occur during late August and early September, coinciding closely with leaf fall (Schmidt and Lotan 1980). The characteristic white fruit persists on the stems through the winter (Lyons 1952; USDA 1974).

REPRODUCTION

Seed Production and Dispersal: Each berry-like fruit contains two flattened nutlets. A good seed crop is normally produced each year. Seeds are dispersed through the winter by birds and mammals (USDA 1974).

Seed Viability and Germination: Seeds of common snowberry remain viable for long periods of time and the species is considered to be a seed banker by Rowe (1983). *Symphoricarpos* seed has a tough outer coat and usually requires warm temperatures followed by chilling to break dormancy (USDA 1974). Zasada *et al.* (1988) found that most seeds germinated the second spring after sowing.

Vegetative Reproduction: Common snowberry reproduces by sprouts from roots and rhizomes, as well as by seed (Tisdale and Hironaka 1981; Cholewa and Johnson 1983). Rhizomes are connected to each other with large masses of woody tissue, which appear to be the central locations for bud and sprout production (Bradley 1984).

PESTS

No information.

EFFECTS ON CROP TREES

Competition: Common snowberry is one of the most widespread shrubs in British Columbia (Lyons 1952) and is common on a wide variety of forested sites following logging. The nature and magnitude of its competitive effect on conifers has not been documented. Common snowberry is most abundant in the drier forested zones of the southern Interior, and in these areas it may be an important competitor with crop trees, particularly for soil moisture. The canopy of common snowberry is generally open, except on some moist sites where it is extremely vigorous, so shading-out of conifers is not as severe as with many associated shrub species. It also does not grow rapidly to great heights, and may quickly be out-competed by other shrubs and even some trees (J. Pollack, pers. comm., Jan. 1985). In the northern forest regions it is not considered to be a major competitor with conifers although locally it can be very abundant (C. DeLong and R. Coupé, pers. comm., Nov. 1984; J. Pollack, pers. comm., Jan. 1985).

Allelopathy: del Moral and Cates (1971) showed that leaf and litter extracts of common snowberry can inhibit growth of other plants in laboratory tests, but they could find no evidence of allelopathic interference in the field.

Beneficial Effects: On dry, exposed sites in southern British Columbia, common snowberry may provide shade to seedlings during the early stages of establishment (W.R. Mitchell and D. Lloyd, pers. comm., Nov. 1984). As a rhizomatous species it affords some protection against soil erosion (Watson *et al.* 1980).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Quenet (1973) observed that common snowberry cover is inversely related to overstory cover in the IDF zone of southeastern British Columbia. It is moderately shade intolerant and can be expected to increase in cover and form low thickets following logging. It does not appear to grow significantly in height in response to canopy removal (J. Pollack, pers. comm., Jan. 1985).

Fire: Following a fire, common snowberry will resprout (Tisdale and Hironaka 1981) and spread through rhizomatous growth (Crane *et al.* 1983). However, the literature reports variable vegetative response to fire. First-year stem density may be slightly lower, the same, or greater than preburn density (Noste and Bushey 1987). The extent of damage to the rhizome system, and the vigour of sprouting, may depend on fire severity and soil moisture content at the time of burning (Miller 1977).

Common snowberry is moderately resistant to severe fires because its roots and rhizomes are located well below the soil surface (McLean 1969; Bradley 1984; Crane and Fischer 1986). However, very severe fires that successfully kill the deep root and rhizome system reduce suckering. Morgan and Neuenschwander (1988b) report that in northern Idaho there was significantly less common snowberry following high severity burns than low severity burns. In Montana, snowberry cover decreased from 6–11% to 2–3% 5 years after a severe burn (Bradley, 1984).

Common snowberry regenerates from roots and rhizomes following low and moderate severity fires. It also regenerates from buried seed following short-duration, low severity fires that remove little of the soil organic layer.

Studies in eastern Oregon, Montana, and Idaho (Anderson and Brooks 1975; Gordon 1976; Merrill 1982; Morgan and Neuschwander 1988b) indicate that common snowberry often regains its pre-fire cover and height within 2–5 years of fires which are not severe enough to kill its roots and rhizomes. In some cases, recovery may be slower. Crane *et al.* (1983) reported that initial sprouting in western Montana was slow and the plant only gained rapidly in volume during the third to fifth seasons following a fire. In the IDFdm subzone in the Kootenays, common snowberry sprouted much more prolifically 1 year after low severity burning in April, compared to the same treatment in October (Thompson 1989).

Cutting: Snowberry will resprout after cutting or grazing (Watson *et al.* 1980; Tisdale and Hironaka 1981) and is tolerant of heavy grazing (McLean 1979).

Herbicides: Conard and Emmingham (1983) indicate that common snowberry is very severly injured by spring or fall applications of glyphosate. For example, in the ICHxw subzone, mid-August foliar applications of 1.1 and 1.4 kg a.i./ha glyphosate successfully controlled common snowberry for at least 4 years. There was no difference in response between the two application rates (Thompson 1988). In the Prince Rupert Forest Region, common snowberry was heavily damaged following a late August foliar spray with 1.5–2 kg a.i./ha of glyphosate (J. Pollack, pers. comm., Feb. 1985). Foliar application of 1.0 kg a.i./ha glyphosate in late August to an alluvial floodplain site in the ICHmc subzone did not control snowberry; a rate of 1.5 kg a.i./ha produced incomplete top-kill, while 2.0 kg a.i./ha caused severe damage that lasted at least 3 years.[363]

Conard and Emmingham (1983) indicate that common snowberry receives very severe injury from spring applications of 2,4-D and moderate injury from late summer or fall applications of this herbicide. In the Vancouver Forest Region, early spring foliar treatments of 2,4-D ester at 3 kg a.i./ha provided excellent

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[363] Pollack and LePage 1986b.

control of common snowberry (M. Scott, pers. comm., Nov. 1984). In the U.S. Inland Northwest, snowberry cover was reduced by 21–40% following late summer aerial sprays of 2.2–3.2 kg a.i./ha of 2,4-D (Miller 1985b).

Soil Disturbance: Snowberry seedlings commonly establish on disturbed soils in the eastern Rocky Mountains (Russell 1979). Soil disturbance can stimulate germination of seed stored in the soil (Rowe 1983). Common snowberry was very dense and approximately 1 m tall on a productive, well-drained floodplain site on the Skeena River within 1 year following heavy soil disturbance. Common snowberry had been abundant on the site prior to logging, and most regeneration was probably of sprout origin (D. Coates, pers. observ.).

WILDLIFE AND RANGE

Food: Common snowberry provides browse for ungulates in the Interior (McLean 1979). It is moderately important in the Interior during winter, summer, and fall for deer and elk (Singleton 1976). Demarchi and Demarchi[364] noted that the leaves are important browse for deer during May and June in the East Kootenays. Use of common snowberry by deer is low during winter in the IDF subzone in south central British Columbia, possibly because it is buried by snow.[365] Snowberry is not an important winter food for moose, caribou, elk, bighorn sheep, or mountain goat (Singleton 1976).[366]

The berries are eaten by birds in winter but are apparently not a preferred species (Clark 1976). In the dry southern Interior, blue grouse eat the berries during the fall (Cannings *et al.* 1987). Fowle (1960) noted that on Vancouver Island, blue grouse commonly use the seeds as grit between July and September.

Common snowberry is not favoured by cattle but withstands grazing well.

Other Resources: Common snowberry provides cover and nesting sites for birds (Cannings *et al.* 1987).

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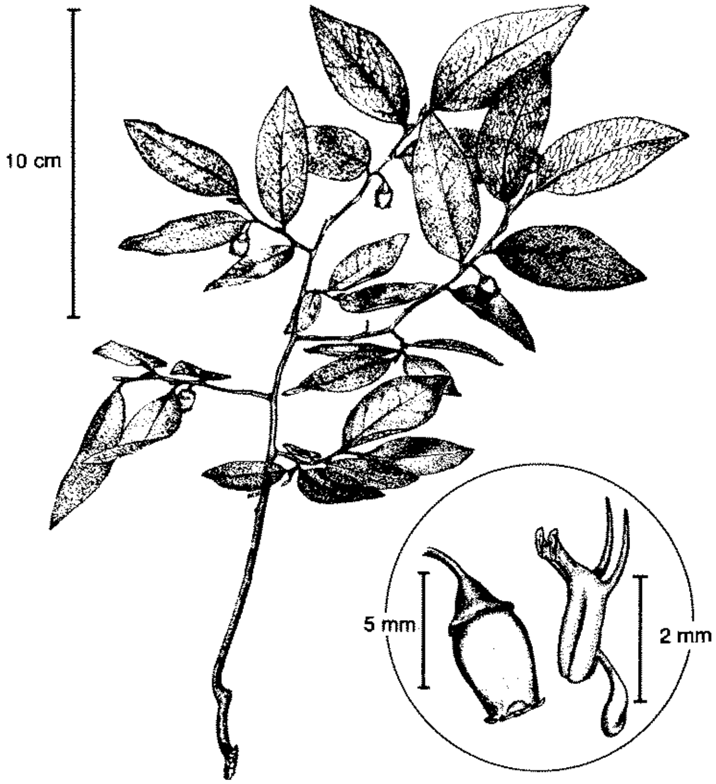
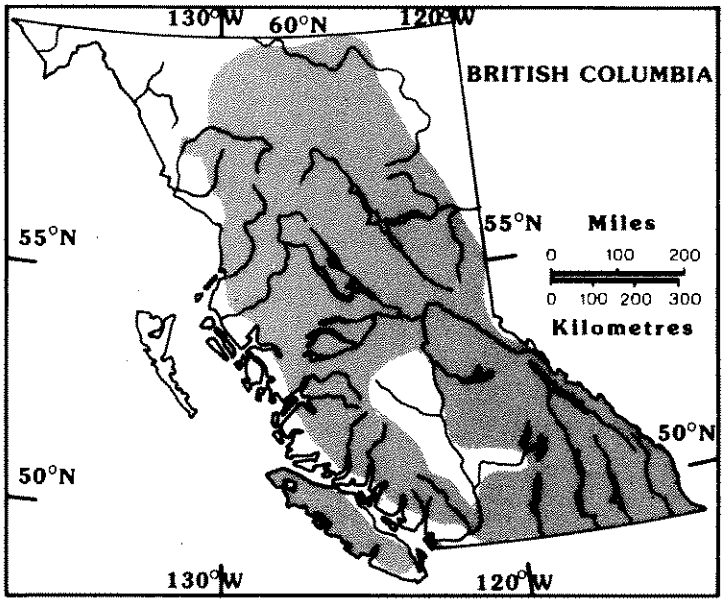
[364] Demarchi and Demarchi 1967.

[365] Miles and Weikle (undated).

[366] Blower 1982.

Vaccinium membranaceum
(black huckleberry)





Distribution of *V. membranaceum* in British Columbia.

Vaccinium membranaceum Dougl. **Black huckleberry**

(big huckleberry, thin-leaved huckleberry,
Mountain blueberry or bilberry)

DESCRIPTION

Black huckleberry is a low to medium-sized, erect, deciduous shrub 0.1–2 m tall. It is densely branched with an extensive network of underground rhizomes. Twigs are somewhat angled in cross-section, and the leaves are elliptic to oblong with a long, pointed tip and many tiny teeth. Flowers are pinkish bells borne singly on the underside of the twigs. The fruit is a round, purplish-black, shiny, edible berry (Szczawinski 1962; Hultén 1974).

Variation: No varieties or subspecies are described in British Columbia (Taylor and MacBryde 1977). This species is very closely related to the *V. globulare* found in southeastern British Columbia and east of the Rocky Mountains and is treated by some authorities as a synonym (Szczawinski 1962).

DISTRIBUTION AND ABUNDANCE

Black huckleberry is found through most of British Columbia but is very scattered in the far north, on the north coast, and in the dry Chilcotin Plateau and Kamloops areas. It is absent from the Queen Charlotte Islands (Calder and Taylor 1968). Black huckleberry is most abundant in mountainous areas of southeastern British Columbia in the ICH and ESSF zones. It is abundant in the MH zone and in the cool, moist subzones of the SBS.

Altitudinal Range: Black huckleberry grows at moderate to high elevations in the province. Along the coast it is found primarily in the subalpine forest above 800 m elevation (Lyons 1952). It is absent from many of the major valleys of the Interior, and appears mainly above 1200 m in the south (Lyons 1952). It occurs at lower elevations at northern latitudes and in climatically wetter areas.

HABITAT

Climatic Relations: The distribution of black huckleberry in British Columbia appears to coincide with areas receiving at least moderate amounts of snow in winter and not suffering from significant moisture stress during the summer. Its vigour is significantly reduced in dry areas (R. Coupé, pers. comm., Nov. 1984), and it is absent from southern valleys that have high summer temperatures and low precipitation. While it is able to tolerate the short growing season found at high elevations in the mountains of southern British Columbia, it apparently competes poorly in the rigorous climate of the far north. It is replaced by other species of *Vaccinium* in the mild, humid climate found at low elevations on the coast.

Site and Soil Conditions: Black huckleberry primarily occurs in coniferous forest understories and in forest openings on well-drained mountain slopes. Like many other members of its genus in British Columbia, it is characteristically found on acidic forest soils with a mor humus. Soils are typically Humo-Ferric Podzols, Dystric Brunisols, and Grey Luvisols on morainal, colluvial, or fluvial parent materials (see, e.g., Mitchell and Green 1981; Pojar *et al.* 1984).[367] Minore and Dubrasich (1978) could find no correlation between *V. membranaceum* cover and environmental variables such as slope percent, stoniness, and silt and clay content of soils in southwestern Washington.

Nutrient Relations: In British Columbia, black huckleberry grows on poor to rich sites (see, e.g., Mitchell and Green 1981; Pojar *et al.* 1984). In western Washington and Oregon, black huckleberry occurs on sites with relatively low productivity (Halverson (compiler) 1986).

Field and greenhouse experiments by Nelson (1974) indicate that additions of ammonium nitrogen improve growth of both roots and shoots of black huckleberry. In the greenhouse studies, nitrogen had a greater effect on growth than either potassium or phosphorus. When nitrogen levels were high, additions of potassium or phosphorus tended to increase growth; when nitrogen levels were low, increasing the levels of potassium and phosphorus either had no effect or reduced growth. For eastern species of *Vaccinium*, ammonium nitrogen (NH_4) is more favourable to growth than nitrate nitrogen (NO_3) (Cain 1952).

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[367] DeLong *et al.* 1984.

Vaccinium membranaceum is tolerant of high levels of manganese but is less tolerant of boron than seedlings of lodgepole pine (Minore 1975). In northern Idaho, Mueggler (1965) found that *Vaccinium* spp. were associated with soils low in potassium. Nelson (1974) also found that *V. membranaceum* tolerates a broad range of pH. Growth was slightly better at pH 5.0 than at 4.0 or 6.0. At a pH of 3.0, growth was reduced and there was some necrosis of foliage. Foliar concentrations of nitrogen were lowest and potassium concentrations were highest at pH 3.0. Under field conditions, a high abundance of huckleberry was related to an optimum pH of 5.5 (Minore and Dubrasich 1978).

Water Relations: In British Columbia, black huckleberry is found on sites with a wide range of available moisture (Pojar *et al.* 1982; Angove and Bancroft 1983), but it is most often dominant on mesic and drier ecosystems (see, e.g., Brooke *et al.* 1970; Mitchell and Green 1981; Pojar *et al.* 1984).[368] In western Washington and Oregon, black huckleberry usually grows on well-drained sites which develop deep snow packs but become droughty as the growing season progresses (Halverson (compiler) 1986).

Light Relations: Black huckleberry commonly grows as an understory plant in coniferous forests but it is most vigorous under partial canopies or in the open. Trees growing under moderately open forest stands seldom produce many berries (Minore 1972), and a dense overstory canopy can eliminate huckleberry production (Minore *et al.* 1979). Light shade may be more favourable than full sunlight (Minore *et al.* 1979). This is probably because shade aids in moisture conservation. Sunburning of foliage has been reported under high sunlight intensity in other species of *Vaccinium* (Smith 1962).

Temperature Relations: The range of black huckleberry suggests that it must be fairly tolerant of cold temperatures. It is less frost tolerant than *V. deliciosum*, a high altitude species (Minore and Smart 1978). Actively growing seedlings from Oregon suffered no visible damage when subjected to temperatures of 0° and -3°C, but wilted rapidly after exposure to -6° and -9°C. Early and late frosts can significantly damage the plant and destroy buds and flowers. Plants sheltered from cold beneath a protective blanket of snow or under a tree canopy are less susceptible to frost damage (Minore 1972; Nelson 1974; Minore and Smart 1978).

Excellent growth of *V. membranaceum* seedlings occurred in growth chambers set for 14-hour days at 20°C and 10-hour nights at 14°C (Minore *et al.* 1979).

GROWTH AND DEVELOPMENT

Black huckleberry grown from seed first produced blossoms and rhizomes during its third growing season (Minore *et al.* 1979). Minore (1975) excavated mature plants and found an extensive network of underground rhizomes. There was a complex system of lateral and fine roots, but no taproots. Occasional roots descended to depths of 70–100 cm. The rhizomes were from 1 to 3 cm in diameter and most occurred 8–30 cm below the soil surface. Most of the plant biomass was in the root/rhizome system. Numerous dormant vegetative buds were located along the length of the rhizomes. Shoots arise from these dormant buds, allowing a clone to develop as the rhizomes spread laterally. *Vaccinium membranaceum* plants that were buried under 5–20 cm of tephra from Mount St. Helens had no adventitious roots 3 months after tephra deposition, and only limited root development 1 year after deposition. (Antos and Zobel 1985).

The mature height of *V. membranaceum* differs considerably across the province. The species is typically a low shrub, 50 cm or less in height in the SBS and drier ESSF subzones of west central British Columbia (D. Coates, pers. observ.) and is reduced to a dwarf shrub in the Chilcotin Plateau (R. Coupé, pers. comm., Nov. 1984). In southern British Columbia, particularly in climatically moist areas such as the ICH zone, black huckleberry can reach 2.4 m in height (Clark 1976). Climatic factors, particularly moisture availability, appear to have a major effect on the height growth of the species. In addition, growth of black huckleberry is subject to extreme seasonal fluctuation (Garrison 1953, cited by Minore 1972).

Phenology: There is little published information about the phenology of black huckleberry. It apparently requires a longer period of warm temperatures in spring to stimulate bud burst than the high-elevation species *V. deliciosum* (Minore and Smart 1978). Flowering takes place in May and June in British Columbia (Lyons 1952) and fruits are ripe in August and September. The date when berries become ripe

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[368] DeLong *et al.* 1984.

varies from year to year depending on weather conditions (Minore and Dubrasich 1978). Cool spring weather delayed ripening of berries in Washington (Minore and Smart 1975).

REPRODUCTION

Seed Production and Dispersal: Black huckleberries contain numerous small seeds. Fruit production varies considerably from year to year depending on weather conditions, and production can be greatly affected by early fall or late spring frosts. Local environmental factors are less important than weather in determining the size of berry crops (Minore and Dubrasich 1978), but light conditions have a significant effect on berry production. Plants under closed forest produce few, if any berries, and production is heaviest in full sunlight or partial shade (Minore 1972; Minore *et al.* 1979; Minore 1984). Berry production can be as much as 720–935 L/ha from berry patches in Oregon and Washington (Minore *et al.* 1979). Dispersal of the seed is primarily by the many mammals and birds that feed on the fruit.

Seed Viability and Germination: The longevity of black huckleberry seed has not been determined, but the seed of most huckleberry species remains viable for many years (Rogers 1974). *Vaccinium membranaceum* seeds require no stratification or scarification and germinate within 16–21 days of sowing (McLean 1967; Minore *et al.* 1979). The seeds must be exposed to at least intermittent light during the entire pre-germination period (McLean 1967).

Vegetative Reproduction: The rhizomatous habit of black huckleberry allows it to form spreading clones, and to form new plants when rhizomes become separated from the parent plant through decay or disturbance. Minore *et al.* (1979) report that cuttings taken from rhizomes grow vigorously to produce new plants, but stem cuttings will not root. Miller (1977) indicates that in *V. globulare,* vegetative reproduction through rhizome sprouting is much more important than seedling regeneration following disturbance of an established colony.

PESTS

There are no reports of insect and disease pests.

EFFECTS ON CROP TREES

Competition: Throughout much of the Interior, black huckleberry is an abundant species on clearcut sites. However, in most subzones of the SBS zone in the central and northern Interior, black huckleberry is a small shrub that does not shade out or overtop conifers. For example, on sites disturbed up to ten years ago in the SBSwk subzone, plants are generally less than 50 cm tall (Hamilton 1988). In the ESSF zone, *Vaccinium membranaceum* usually occupies a co-dominant position under the taller rhododendron (Coates 1987).

Black huckleberry is generally not considered to be an important competitor with tree species on its own, but it is a component of the ericaceous shrub complex that dominates mesic and drier clearcuts in the ESSF zone and some adjacent mid-elevation subzones in the Interior Wet Belt (C. DeLong, R. Coupé, and D. Lloyd, pers. comm., Nov. 1984). In these areas it can reach a height of 2 m and potentially shade out young seedlings, but only a single study in British Columbia (Coates 1987) has described the plant's impact on seedling growth. Coates (1987) observed that in the ESSFwc subzone near Clearwater, regrowth of black huckleberry was slow after manual cutting or mechanical scarification. He concluded that as long as seedlings are planted promptly after shrub reduction treatments, trees are unlikely to be overtopped by the shrub. However, he noted that black huckleberry is not killed by manual treatments. This implies that if below-ground interference is important, then growth reductions of conifers can occur even when they are not overtopped by shrubs. Because the species produces a dense network of roots and rhizomes it may compete significantly for moisture and nutrients on dry and nutrient-poor sites.

In Oregon and Washington, where the autecology of *V. membranaceum* has received considerable attention, the species is not perceived as a significant competitor with crop trees. Naturally regenerated conifers quickly overtop the huckleberry bushes, causing a reduction in huckleberry cover and vigour (D. Minore, pers. comm., Dec. 1984). There is no information regarding possible allelopathic effects of black huckleberry on the growth of conifers and other plant species.

Beneficial Effects: No beneficial effects of *V. membranaceum* on coniferous tree growth are reported in the literature. The dense network of roots and rhizomes may help to reduce soil erosion. The species is highly prized as a berry producer and significant efforts have been made to manage this species as a recreational resource in Oregon and Washington (Minore *et al.* 1979).

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Removal of an overstory canopy of trees is reported to favour black huckleberry in the northwestern U.S., increasing growth, cover, frequency, and fruit production (Mueggler 1965; Minore *et al.* 1979; Minore 1984). In British Columbia, although most observers agree that black huckleberry becomes more vigorous and produces a heavier crop of berries following logging, there are no data to indicate that canopy removal causes increases in stem density or seeding-in. Black huckleberry was present but infrequent on four different site types in the SBS zone north of Prince George prior to logging (Eis 1981). Six years after clearcutting it had not become a significant competitor on any of the site types. Following timber harvesting, black huckleberry has not been observed to change much in cover or height unless there has been considerable soil exposure, in which case cover will decrease (D. Harrison, pers. comm., Mar. 1989; J. Wright, pers. comm, July 1989).

Fire: Light surface fires, carried out when soils and humus are moist, easily kill above-ground parts of huckleberry, but most rhizomes are buried deep enough to avoid damage. Such fires stimulate prolific sprouting from dormant vegetative buds on the rhizomes. Huckleberry cover is reduced for the first few years following burning but may return to pre-burn levels within 3–5 years. Production of flowers and fruit is delayed for several years and total berry production can be reduced for at least 7 years.

Severe burns, carried out when soils and humus are dry, greatly reduce resprouting and can significantly reduce stem density and cover of huckleberry if rhizomes are killed. The greater abundance of black huckleberry plants on mechanically treated compared to burned SBSmk clearcuts suggests that burning can kill the species (Hamilton 1988). Slow regrowth was reported for the first 10 years after burning in the SBSmk subzone (Hamilton and Yearsley 1988). Despite vigorous sprouting immediately after burning in the U.S. Pacific Northwest, black huckleberry shrubs had not regained their pre-fire height 7 years after the disturbance (Minore 1984). Black huckleberry gradually increased in cover after medium severity burns on Douglas-fir sites in the Western Cascade Mountains of Oregon. Maximum huckleberry cover was not attained until 15 years after burning (Schoonmaker and McKee 1988).

Seedlings of *Vaccinium spp.* are not considered to be important in recolonizing burned sites (Miller 1977; Stickney 1986; Hamilton 1988).

Cutting and Grazing: Black huckleberry does not sprout vigorously after cutting. For example, black huckleberry shrubs did not respond vigorously to pruning treatments that removed 50–80% of top growth (Minore *et al.* 1979). The time of clipping did not significantly affect the number of shoots produced. Cutting in early July in the ESSFwc subzone near Clearwater resulted in first-year height growth of 8 cm, or 16% of the pre-cut height, and first-year crown diameter regrowth of 30% of the pre-cut level. Almost all shoots arose from buds on old stems rather than as sprouts or suckers from the soil. Seventy-eight percent of original stems had new shoots after the first growing season. Stems with new shoots averaged 3.3 shoots per stem (Coates 1987).

Heavy grazing of huckleberry fields by sheep did not damage black huckleberry plants. The effects of sheep browsing were more than offset by the nitrogen added as sheep manure (Minore *et al.* 1979). In an earlier study, grazing by sheep reportedly produced thriftier, more vigorous huckleberry growth by lightly browsing the shrubs and reducing competition from other vegetation.[369]

Herbicides: In British Columbia, glyphosate has tended to provide ineffective control of black huckleberry at application rates below 2 kg a.i./ha (M. Newton, pers. comm., Dec. 1984).[370,371,372] Fall applications of glyphosate moderately injure black huckleberry in northeastern Oregon and northern Idaho (Conard and

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[369] Langford 1942.
[370] Dyke 1987.
[371] Herring 1984b.
[372] Simard 1988.

Emmingham 1983). Miller (1985b) reports that late summer aerial sprays of glyphosate result in cover reductions of 21–40% on sites in the U.S. Inland Northwest.

Limited information suggests that hexazinone has apparently caused moderate injury to black huckleberry in B.C. (Boateng and Herring 1990).

2,4-D amine is reported to severely injure black huckleberry in the province, making it the most effective herbicide for controlling this species (Boateng and Herring 1990). In Oregon, a mid-summer application of 2,4-D ester at 6.38 kg. a.i./ha significantly reduced huckleberry cover (Minore *et al.* 1979). However, herbicide-damaged plants recovered faster than plants damaged by burning in the same area. Moderate injury has resulted from spring and summer applications of 2,4-D in northeastern Oregon and northern Idaho (Conard and Emmingham 1983). Cover reductions of 21–40% have resulted from several late summer aerial sprays of 2,4-D in the U.S. Inland Northwest (Miller 1985b).

Soil Disturbance: Black huckleberry is effectively controlled with little recovery for at least 5 years following mechanical site preparation in the ICHwk and ESSFwc subzones in the Salmon Arm Forest District. In the ESSFwc subzone near Clearwater, scarification that uprooted entire black huckleberry plants provided excellent control for 2 growing seasons (the length of the study) (Coates 1987). Discing apparently stimulated rhizome sprouting of *V. membranaceum* in Washington (Minore *et al.* 1979).

Fertilization: Fertilization with ammonium sulphate significantly increases vegetative growth of black huckleberry (Nelson 1974).

WILDLIFE

Food: The berries are the most highly used part of black huckleberry plants.[373] They are prized by bears, small mammals, and many bird species. The berries are important for building up winter fat stores in black and grizzly bears and therefore are of high survival value (National Wildlife Federation 1987).

Bear, deer, rabbit, fox, and many other small mammals forage on the twigs and foliage of *Vaccinium* spp. (Rogers 1974). As winter and spring browse, black huckleberry has medium to high importance for black-tailed deer and medium importance for Roosevelt elk (Singleton 1976).

Species of *Vaccinium*, including *V. membranaceum*, have been described as the most important group of non-coniferous plants in the diet of grouse in the subalpine area at Forbidden Plateau on Vancouver Island. Buds, flowers, and leaves have been used in season (King 1973).

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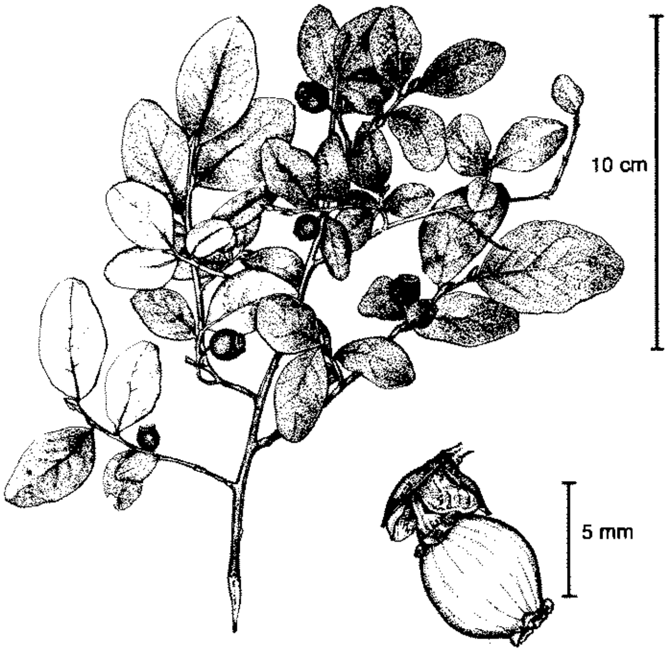
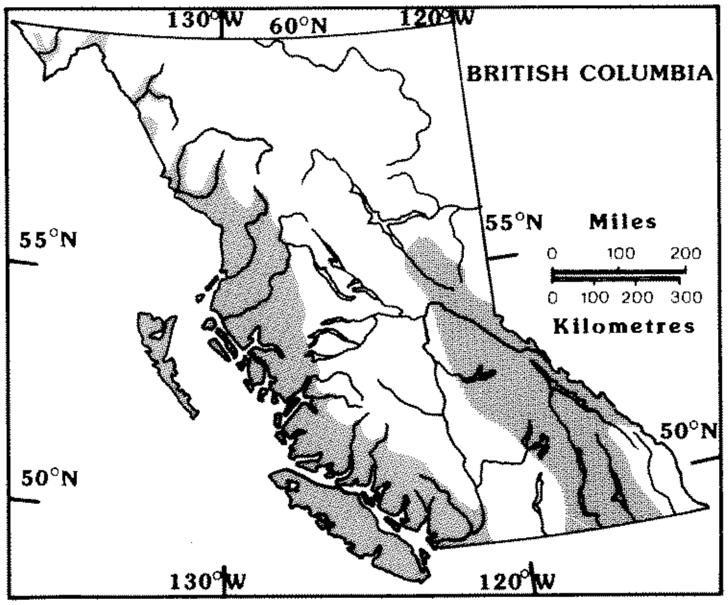
[373] Langford 1942.

Vaccinium ovalifolium
(oval-leaved blueberry)





Distribution of *V. ovalifolium* in British Columbia.

Vaccinium ovalifolium Sm. — **Oval-leaved blueberry**

DESCRIPTION

Oval-leaved blueberry is a spreading, diffusely branched, deciduous shrub, 1–2 m tall. Twigs are slender, reddish brown, and grooved. The leaves are thin, oval, and rounded at the base and tip. The pink urn-shaped flowers appear before the leaves on the underside of the twigs. The berry is round and blue to bluish-black, with a distinct frosty bloom (Szczawinski 1962; Viereck and Little 1972).

Variation: No varieties or subspecies of oval-leaved blueberry are described in British Columbia (Taylor and MacBryde 1977). It may hybridize with *V. alaskaense* on the coast where these two species occur together (Hultén 1974).

DISTRIBUTION AND ABUNDANCE

Oval-leaved blueberry is found along the entire length of the British Columbia coast and penetrates inland for some distance on the east side of the Coast Mountains. It is also found in moist mountainous areas of the Interior Wet Belt, as far north as Williston Lake, but is absent from the central and dry southern Interior and from the far north (Szczawinski 1962). Oval-leaved blueberry is most abundant in the CWH and MH biogeoclimatic zones on the coast and the ICH and moist southeastern subzones of the ESSF in the Interior. It is also present in some wetter subzones of the SBS.

Altitudinal Range: Oval-leaved blueberry is present from sea level to timberline along the coast, except in the Georgia Strait area where it becomes important at middle elevations. Throughout most of its range in the southern and central Interior, it is present from mid-elevations to timberline but is absent from major valley bottoms.

HABITAT

Climatic Relations: Oval-leaved blueberry apparently favours a humid to perhumid climate in which it is unlikely to suffer from moisture or high temperature stress during the summer. It is found in all areas of the province receiving either abundant rain or snow, except the far north, where the climate presumably is too severe.

Site and Soil Conditions: Species of the genus *Vaccinium* are described as being "exacting in their site requirements" (USDA 1974). In British Columbia, oval-leaved blueberry is typically associated with hemlock-dominated coniferous forests that have a thick acidic mor humus and a Podzolic soil. It is found on a wide variety of parent materials and is frequently rooted in organic or decaying wood substrates (see, e.g., Brooke *et al.* 1970; Annas and Coupé (editors) 1979; Klinka *et al.* 1979; Haeussler *et al.* 1984).

Nutrient Relations: Oval-leaved blueberry is found on sites ranging from very poor to very rich in nutrients (see, e.g., Klinka 1977b).[374] The pH of the rooting zone in ecosystems where it is abundant is usually low (i.e., pH < 5) (see, e.g., Haeussler *et al.* 1984; Meidinger *et al.* 1984).[375]

Water Relations: Oval-leaved blueberry can be abundant on sites ranging from xeric to hygric (Klinka 1977b; Angove and Bancroft 1983); however, it is most abundant and dominant on mesic and drier sites where the shrub layers are relatively species poor. On poorly drained sites it is usually found on elevated microsites (Haeussler *et al.* 1984).

Light Relations: Oval-leaved blueberry is a very shade-tolerant species. It will survive under the low light intensities found under a hemlock forest canopy, but growth rates and plant vigour under heavy shade are poor (P. Alaback, pers. comm., Dec. 1984). Cover and vigour of the species are greatest under an open tree canopy or on cutover forest land where it may form a nearly continuous shrub layer (Viereck and Little 1972). Camp (1942) describes it as less shade tolerant than *V. alaskaense,* a common associate in coastal forests.

Temperature Relations: No information.

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[374] Utzig *et al.* 1983.

[375] Coupé and Yee (editors) 1982.

GROWTH AND DEVELOPMENT

Oval-leaved blueberry is a rhizomatous species with an open, spreading crown that can reach heights of over 2 m under favourable conditions. The maximum annual growth rate of shoots in Alaska is approximately 30 cm. The growth rate of seedlings established under a dense forest canopy is extremely slow; seedlings can still be in the cotyledon stage after 2 growing seasons. Under low light conditions, the seedling can take on a juvenile form which has evergreen leaves and a semi-prostrate growth form. This juvenile form does not appear under favourable growing conditions in a greenhouse, and when the overstory shade is removed through windfall or logging, the plant soon takes on the erect, deciduous "adult" growth habit (P. Alaback, pers. comm., Dec. 1984).

Phenology: In coastal Alaska, flowering occurs during April and May before the leaves emerge (Viereck and Little 1972). Bud burst occurs in May and is followed by a period of rapid growth. Most vegetative elongation is complete by mid-June, but stems continue to increase in diameter until mid-July (P. Alaback, pers. comm., Dec. 1984). Hamilton[376] noted that leaf senescence did not begin until early September on the central British Columbia coast, and some leaves were still on the shrubs at the end of October. Ripe berries are present beginning in late June on the central British Columbia coast[377] and from mid-July to August in Alaska (Viereck and Little 1972).

REPRODUCTION

Seed Production and Dispersal: Light is critical for fruit production. Oval-leaved blueberry will only produce fruit in fairly open areas. In Alaska, heavy fruiting occurs only in large forest openings or along forest margins. A single fruit can contain 150 seeds and the total seed production in years of good berry crops is enormous (P. Alaback, pers. comm., Dec. 1984). Seeds are dispersed by birds and mammals that feed on the fruit.

Seed Viability and Germination: Seeds of oval-leaved blueberry are described as remaining viable for up to 12 years in storage (USDA 1974). Alaback (pers. comm., Feb. 1985), however, believes that, in Alaska at least, their viability is short-lived. The seeds have a short dormancy period and will germinate well after 15 days of warm temperatures followed by just 15 days of chilling (USDA 1974).

Germination rates of approximately 50–60% are obtained under favourable conditions. A minimum of 2% of full light is needed for germination to occur, so seeds are able to germinate under a forest canopy. The seed will germinate on a wide variety of substrates including mineral soil, moss, bare humus, and decaying wood, but conditions for subsequent seedling establishment are more critical. Survival is best on humus with no moss cover and poorest on mineral soil.[378] Survival is best in open old-growth stands and in clearcut areas, and poor in dense immature forests.

Alaback speculates that oval-leaved blueberry is a "seedling banker" (cf. Grime 1979) which produces shade-tolerant seedlings that persist for long periods of time in the understory until a disturbance creates favourable conditions for growth and seed production. Very few seeds germinate under the undisturbed forest canopy, but they often germinate in small windthrow openings. Stored, ungerminated seed is not considered to be important for regeneration of the species.

Vegetative Reproduction: Oval-leaved blueberry regenerates vegetatively by means of rhizomes and probably also by layering. Vegetative reproduction is the primary means by which this species survives for long periods in the absence of disturbance. Expansion of existing colonies also takes place by means of rhizomatous shoots (P. Alaback, pers. comm., Dec. 1984).

PESTS

No information.

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[376] Hamilton 1984.
[377] Ibid.
[378] Alaback (undated).

EFFECTS ON CROP TREES

Competition: Although oval-leaved blueberry is an abundant and often dominant shrub in both coastal and wet Interior forests, it is not thought of as an important competitor with coniferous trees. It is a component of the ericaceous shrub complex that dominates many southern Interior ESSF clearcuts after winter logging (Coates 1987).[379] A well-developed ericaceous shrub community can significantly reduce survival and growth of planted Engelmann spruce and lodgepole pine compared to where the community was controlled (Coates 1987); however, oval-leaved huckleberry was a minor component of the complex.

Beneficial Effects: No information.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: In the SBS zone north of Prince George, oval-leaved blueberry did not increase dramatically on any of 4 site types following logging (Eis 1981). Similarly, on northern Vancouver Island, oval-leaved huckleberry cover tends to remain constant following overstory removal (D. Harrison, pers. comm., May 1989). In a thinning study in southeast Alaska, *V. ovalifolium* seedlings were scattered on a site where trees had been spaced to 2.4 x 2.4 m. They were more abundant at wider spacings and produced flowers at the 4.9 x 4.9 m spacing.[380]

Fire: On a study site in southwestern British Columbia, oval-leaved blueberry was a common element of the post-logging preburn plant community (Lafferty 1972). In the first growing season after a burn of moderate severity, blueberry was absent, and three growing seasons after burning, it had not regained its vigour.

Cutting: Oval-leaved blueberry does not respond vigorously to cutting. After an early July cutting in the ESSFwc subzone near Clearwater, new shoots had grown to an average height of 6.2 cm, or 17% of the pre-treatment height by the end of the growing season. Crown diameter had recovered to 30% of the pre-treatment level. Fifty percent of the original stems produced sprouts. Sprouting stems averaged 2.9 shoots per stem. Almost all new shoots arose from buds on old stems rather than as suckers from the soil. By the end of the second growing season, the tallest shoot was 11.4 cm high, or 32% of its pre-treatment height, and crown area averaged 88% of pretreatment levels. A second cutting did not affect the regrowth vigour of oval-leaved blueberry (Coates 1987).

Herbicides: Vaccinium ovalifolium has been controlled with broadcast applications of 2.1 kg a.i./ha glyphosate applied in September to sites in the ESSFwc and ICHvk subzones.[381,382] Lower application rates (0.7 and 1.4 kg a.i./ha) did not control the species on the ESSFwc site.[383] On the ICHvk site, rates of 1.4 and 1.7 kg a.i./ha produced less mortality than the maximum rate of 2.1 kg a.i./ha.[384]

Soil Disturbance: In the ESSFwc subzone near Clearwater, scarification that removed tops, or uprooted entire oval-leaved blueberry plants provided excellent control for 2 growing seasons (Coates 1987).

WILDLIFE

Food: Oval-leaved blueberry is an important forage for elk and black-tailed deer during winter and spring (Singleton 1976; Harvey 1981; Nyberg *et al.* 1986)[385] and moderately important forage for caribou and black-tailed deer during summer and fall.

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[379] Mather 1987.
[380] Alaback (undated).
[381] Dyke 1987.
[382] Simard 1988.
[383] Ibid.
[384] Dyke 1987.
[385] Blower 1982.

The berries are the most highly used part of the shrub.[386] The fruit of *Vaccinium* spp., including *V. ovalifolium*, is popular summer food of black and grizzly bears and is an important source of energy and fat deposition (Herrero 1985; National Wildlife Federation 1987; Lofroth 1988). In addition to eating the berries, bears forage on the leaves in spring and summer (National Wildlife Federation 1987). *Vaccinium* spp. berries are favoured by many birds and small mammals which disperse the seed (Rogers 1974; Halverson (compiler)1986). Species of *Vaccinium*, including *V. ovalifolium*, have been described as the most important non-coniferous plant in the diet of blue grouse at Forbidden Plateau, a subalpine area near Courtenay on Vancouver Island. At this location, blue grouse have used buds, flowers, fruit, and leaves in season (King 1973). However, at another Vancouver Island location, oval-leaved blueberry had low value for blue grouse (Fowle 1960).

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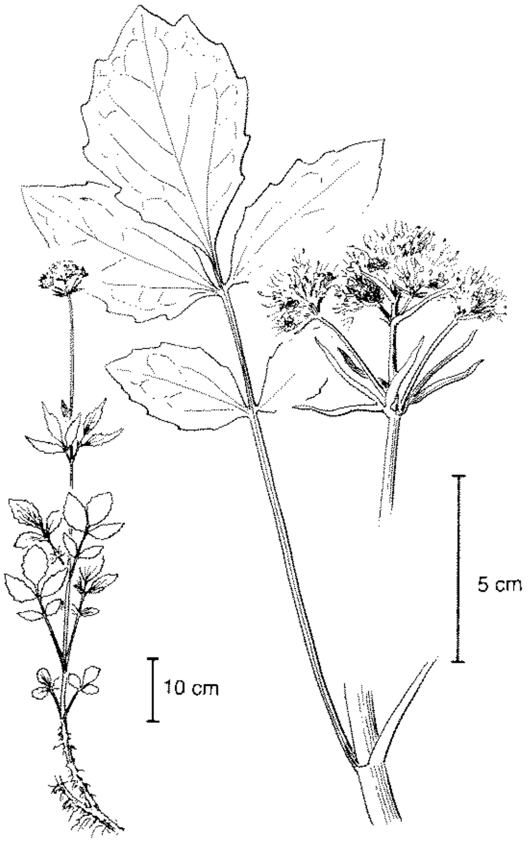
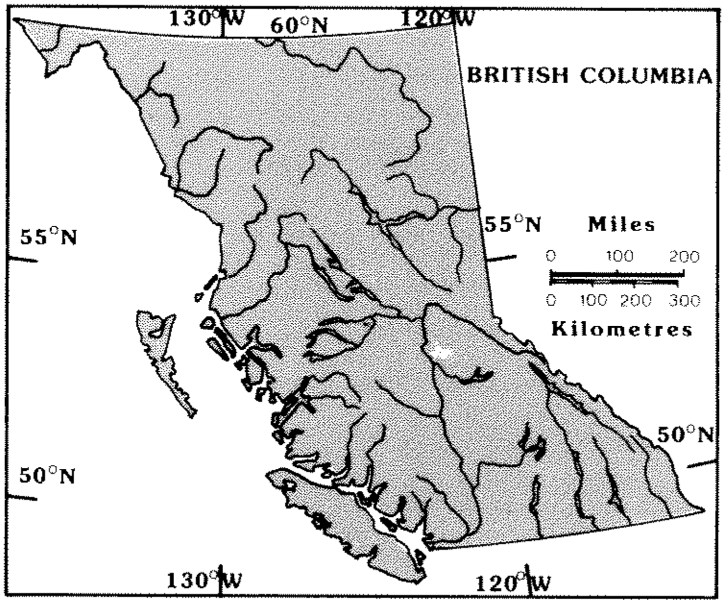
[386] B.C. Min. Environ. (undated).

Valeriana sitchensis
(Sitka valerian)





Distribution of *V. sitchensis* in British Columbia.

Valeriana sitchensis Bong. **Sitka valerian**

DESCRIPTION

Sitka valerian is an erect herbaceous perennial that forms extensive colonies through stout, branched rhizomes. Plants vary from 0.3 to 1.2 m in height. Stems grow either singly or as a small group from a somewhat fleshy root stalk. Each stem has 2 to 5 pairs of opposite compound leaves composed of 3 to 5 pinnately divided leaflets. The lowermost 1 or 2 pairs of leaves are ovate and the upper stem leaves are lanceolate. Each stem bears a showy, dense, rounded cluster of small, white to pinkish, sweetly scented flowers. Stamens are prominent. The fruit is small, hard and single-seeded with a feathery plume (Clark 1973; Looman and Best 1979; Porsild 1979; Comeau *et al.* 1982; Angove and Bancroft 1983).

Variation: There are 2 subspecies of *Valeriana sitchensis* in British Columbia (Meyer 1951; Taylor and MacBryde 1977). The subspecies *sitchensis* is widely distributed in upper elevation forests and subalpine and alpine meadows throughout British Columbia. It also occurs at upper elevations of the Queen Charlotte Islands (Calder and Taylor 1968). Basal leaves and stem leaves are similar in size. Flowers are white. The subspecies *scouleri* is found at low elevations on southern Vancouver Island and in the lower Fraser Valley. It differs from the subspecies *sitchensis* in that basal leaves are larger than stem leaves, leaflets are less deeply toothed, and flowers are red or white (Henry 1915; Meyer 1951; Taylor and MacBryde 1977). Hybridization between subspecies is possible (Pojar 1974).

DISTRIBUTION AND ABUNDANCE

Sitka valerian is common in cool, moist montane forests and lush alpine and subalpine meadows in the central and southern parts of British Columbia (south of 55°N latitude) (Hamet-Ahti 1978; Halverson (compiler) 1986). It grows in habitats ranging from lowland stream banks to wet alpine meadows (Soper and Szczawinski 1976). It is abundant in the ESSF and MH biogeoclimatic zones and also occurs in cold drainage areas at upper elevations of the ICH, SBS, and MS zones (Angove and Bancroft 1983).

Altitudinal Range: Valeriana sitchensis ssp. *sitchensis* grows at high elevations within B.C., from approximately 1200 to 2000 m (Lyons 1952). *V. sitchensis* ssp. *scouleri* occurs from sea level to about 1200 m in southwestern B.C. (Taylor and MacBryde 1977).

Climatic Relations: Valeriana sitchensis ssp. *sitchensis* is a species of subalpine and alpine climates that have a short growing season and high snowfall. It is most abundant in wet to moist climates where summer moisture deficits are uncommon.

Site and Soil Conditions: Sitka valerian is most common on moist, rich sites (Comeau *et al.* 1982). Soils are often Humo-Ferric or Ferro-Humic Podzols and occasionally Dystric Brunisols, Gleysols or Regosols. Humus forms are typically mors (Eady 1971; Mitchell and Green 1981) and moders in meadow-like communities (T. Lewis, pers. comm., July 1989). Parent material where Sitka valerian occurs in the ESSF zone is typically morainal or organic (Mitchell and Green 1981).

Nutrient Relations: Sites on which Sitka valerian dominates the herbaceous layer are typically nutrient-rich (Eady 1971; Yarie 1980). Although the plant is most vigorous on nutrient-rich sites, it also grows on oligotrophic sites (D. Lloyd, pers. comm., March 1989). Eady (1971) found low pH, high soil organic matter, and high amounts of potassium and sodium on Sitka valerian-dominated sites on Big White Mountain in the southern Interior of British Columbia. Sitka valerian-dominated sites in the ESSFwm subzone in the Coastal– Interior transition are rich and appear to be high in nitrogen and calcium (Klinka *et al.* 1982).

Water Relations: Sitka valerian tends to be most abundant on subhygric to subhydric moisture regimes. However, it occurs on all hygrotopes wetter than submesic in the ESSFxc and ESSFdc subzones, and all hygrotopes wetter than subxeric in the ESSFwc2, ESSFvc, and ESSFvv subzones (Angove and Bancroft 1983; D. Lloyd, pers. comm., March 1989). Soil moisture in Sitka valerian-dominated communities is typically not limiting to growth of conifer seedlings and remains above field capacity throughout the snow-free period (Eady 1971; Coates 1987).

Light Relations: Sitka valerian is moderately shade tolerant. It tends to be smaller and less robust in the shade than in the open (D. Lloyd, pers. comm., March 1989).

Temperature Relations: The range of Sitka valerian indicates that it is very tolerant of extreme cold.

GROWTH AND DEVELOPMENT

Little information is available about the growth of Sitka valerian. Plant ages cannot be determined because annual increments are not distinguishable on rhizomes (Antos and Zobel 1984).

Aerial shoots are produced vegetatively when a rhizome tip at the soil surface turns up. An average of two to three aerial shoots are produced per rhizome tip. When the rhizome turns up, new rhizomes form and branch out. Rhizomes range in diameter from 2–5 mm. Roots radiate from rhizomes in all directions. Most angle downwards and few remain in the litter layer. Roots are large and often reach 1 mm in diameter. They have few branches except near the end (Antos and Zobel 1984).

Phenology: Sitka valerian plants emerge from the ground in early spring, and growth begins under the snow cover just before it melts. Growth is complete by midsummer (C. Caza, pers. comm., Feb. 1989). Flowering of subspecies *scouleri* occurs from April to July (Taylor and MacBryde 1977) and subspecies *sitchensis* from June to September (Jones 1938; Taylor and MacBryde 1977). On cutovers in the ESSFwc2 variant near Clearwater, C. Caza (pers. comm., Feb. 1989) observed that flowering of *V. sitchensis* ssp. *sitchensis* occurred in late June to early July and seed was released in late July to early August. Plants in the forest flower several weeks later than those in the open.

Sitka valerian's flowers attract many insects by their strong fragrance and prominent position above the surrounding vegetation (Soper and Szczawinski 1976). Bumble bees, bee flies, butterflies, and skippers are common pollinators (Pojar 1974). Chances of pollination between flowers on the same plant are high for Sitka valerian because flowers are self-compatible, closely spaced, numerous, and bloom simultaneously within in an inflorescence.

REPRODUCTION

Seed Production and Dispersal: No information was found on seed production. The feathery plume on the seeds aids in seed dispersal.

Seed Viability and Germination: No information.

Vegetative Reproduction: Antos and Zobel (1984) found that the total dry weight of Sitka valerian plants was 35% roots, 33% rhizomes, and 32% above-ground parts. This suggests that vegetative reproduction plays an important role in propagation of the species. However, since rhizomes are short, vegetative spread may be limited. Antos and Zobel (1984) recorded an average rhizome length of 22 cm.

PESTS

Puccinia commutata (a foliar rust) is the most common pathogen of Sitka valerian. Other pathogens that occur on Sitka valerian are *Sphaerella vagans* (a stem canker) and *Synchytrium perforatum* (a wart causing fungus) (H. Merler, pers. comm., April 1989).

EFFECTS ON CROP TREES

Competition: Sitka valerian may be a serious competitor to small conifer seedlings. Sitka valerian is thought to compete with conifers primarily by reducing light levels (D. Coates, pers. comm., March 1989). C. Caza (pers. comm., Feb. 1989) observed that under dense patches of Sitka valerian, Engelmann spruce seedlings experienced less than 10% of full sunlight. In addition, soil temperature was lowered by the cover of Sitka valerian. Sitka valerian's extensive network of roots and rhizomes suggests that it may also compete with conifers for moisture and nutrients. Engelmann spruce seedlings can be damaged by the collapse of dead Sitka valerian stems and, to a lesser extent, leaves.

Beneficial Effects: Sitka valerian leaves have a moderate nutrient content (Yarie 1980) and may provide an important source of nutrients to a site. Sitka valerian and associated understory species have been shown to make significant annual contributions to the litterfall nutrients on poor sites in Garibaldi Provincial Park in southwestern British Columbia. These poor sites are characterized by very dry or very wet soil, low soil temperatures and slow overstory litter decomposition.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: Sitka valerian plants increase in vigour following canopy removal. Changes in cover following overstory removal have not been documented. However, percent cover of Sitka valerian appeared to increase after dominant plants (rhododendron and false azalea) were killed by glyphosate.[387]

Fire: No documented information was found. Sitka valerian appears to recover quickly from light to moderate fires. Severe fires that kill the rhizomes probably result in slower recovery.

Cutting and Grazing: The ability of Sitka valerian to recover from cutting is influenced by the amount of below-ground resources (i.e., roots and rhizomes). Plants growing in the open are generally larger and more robust than those in the shade, and this in turn seems to influence the regrowth capacity. Vigorous open growing plants can regain 1.5 times their original size within 6 weeks of cutting. They can completely recover vegetatively in the year they are cut. Shade-grown plants, with their low below-ground carbohydrate reserves, recover slowly. Coates (1987) found that multiple cuts decrease the vigour of Sitka valerian. This suggests that several consecutive years of grazing may provide good control of this species. Sheep favour Sitka valerian and will gain weight when they graze on this species (G. Ellen, pers. comm., August 1989).

Herbicides: Sitka valerian plants were healthy and vigorous 2 years after September broadcast applications of 2, 4, and 6 L/ha glyphosate to a clearcut in the ESSFwc2 variant near Blue River.[388] In comparison to Sitka valerian, rhododendron and false azalea plants on the same treatment unit suffered high rates of mortality after application of 6 L/ha glyphosate.

Soil Disturbance: Sitka valerian can recover its pre-treatment size within 1 or 2 seasons following mechanical site preparation in the ESSFwc2 variant near Clearwater (Coates 1987).

WILDLIFE AND RANGE

Sitka valerian is moderately used by wildlife as a summer food (T. Lea, pers. comm., Feb. 1989). The foliage is eaten by bears, mule deer, elk, caribou, bighorn sheep, mountain goat, marmots, foxes, rabbits, and pikas (D. Demarchi, pers. comm., June 1989). Sitka valerian is considered highly valuable summer and fall food for Rocky Mountain elk in the western United States and Canada (Kufeld 1973). Sheep and cattle also forage on this plant.

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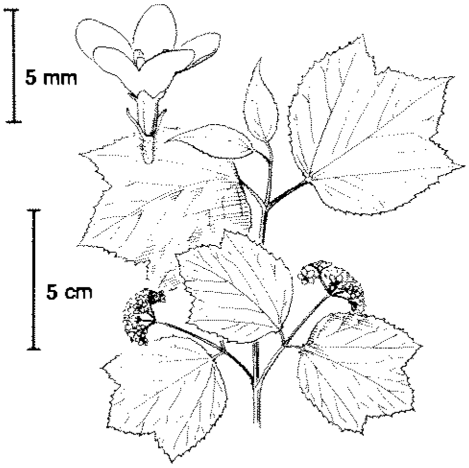
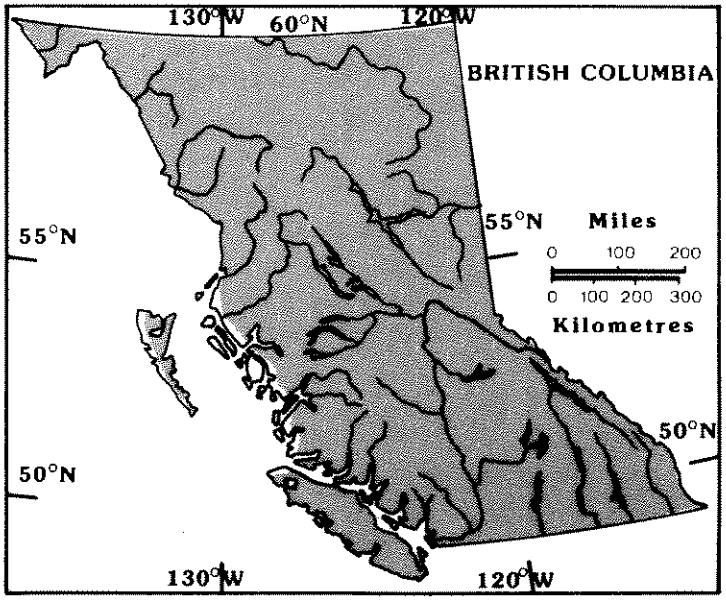
[387] Simard 1988.
[388] Ibid.

Viburnum edule
(highbush-cranberry)





Distribution of *V. edule* in British Columbia.

Viburnum edule (Michx.) Raf.

Highbush-cranberry
(squashberry)

DESCRIPTION

Highbush-cranberry is a straggling to erect, multi-stemmed deciduous shrub, 0.5–3 m tall. Stems have opposite branching and shiny red buds. The leaves are irregularly shaped with 3 shallow, toothed lobes and become bright red in fall. The small, dense, flat to rounded inflorescence has white flowers. The fruit, red drupes with a large flattened stone, remain on the twigs over winter (Hultén 1974; UBC Bot. Garden 1977).

Variation: No subspecies or varieties are described in British Columbia (Taylor and MacBryde 1977).

DISTRIBUTION AND ABUNDANCE

Highbush-cranberry is found throughout British Columbia to the Yukon border but is absent from the dry southern Interior and higher subalpine and alpine zones (Lyons 1952). It is found in all biogeoclimatic zones except the PP, BG, and AT, but it is uncommon to rare in the MH, SWB, and higher ESSF zones. It is particularly abundant in the central and northern Interior of the province in the SBS and BWBS zones.

Altitudinal Range: Highbush-cranberry ranges from sea level to approximately 1500 m in British Columbia (UBC Bot. Garden 1977).

HABITAT

Climatic Relations: Highbush-cranberry is found throughout northern North America but is primarily a species of the boreal climatic region. The southern extent of its range appears to be limited by high temperatures and low humidity. It appears to tolerate most of the climates present in British Columbia except the very hot, dry climate of the southern interior valleys, and the severe alpine climate. It is uncommon in extremely wet coastal areas.

Site and Soil Conditions: Most *Viburnum* species prefer moist well-drained soils, but soil texture is less critical than for many other genera (USDA 1974). In British Columbia, *V. edule* is a species of moist, forested slopes, stream or lake margins, and gravelly or rocky banks (Clark 1976; UBC Bot. Garden 1977). It is found on a wide range of parent materials and soil types including Luvisols, Brunisols, Humo-Ferric Podzols, Regosols, and Gleysols. Its best development occurs on floodplain sites where it can be a dominant shrub under a black cottonwood or balsam poplar overstory (see e.g., Zasada *et al.* 1981; Pojar *et al.* 1984).[389,390]

Nutrient Relations: Highbush-cranberry grows best in rich soil with a pH of about 6.5 (UBC Bot. Garden 1977), but in nature it is usually found on soils with greater acidity (see, e.g., Pojar *et al.* 1984).[391] It is typically found on sites that are medium to very rich in nutrients (Comeau *et al.* 1982; Pojar *et al.* 1982).

Water Relations: Throughout the province, highbush-cranberry is associated with moist soils (Lyons 1952; UBC Bot. Garden 1977). It grows on sites with a submesic to subhydric moisture status in areas of moist climate and at northern latitudes, but is restricted to subhygric and wetter moisture regimes in drier climates in central and southern British Columbia (Comeau *et al.* 1982; Pojar *et al.* 1982; Angove and Bancroft 1983).

Light Relations: Highbush-cranberry is described as semi-tolerant to shade tolerant by Rowe (1983), and several authors report that it prefers shady locales (Lyons 1952; Clark 1976; UBC Bot. Garden 1977). It is more commonly found growing in the open at high elevations (Lyons 1952) and probably also at northerly latitudes. Highbush-cranberry is a common understory species in deciduous and coniferous forests (see, e.g. Pojar *et al.* 1984)[392] but like many shrub species it probably attains its best development under full sunlight provided that it is not exposed to excessive evapotranspirative stresses.

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[389] Trowbridge *et al.* 1983.
[390] DeLong 1983.
[391] Ibid.
[392] Ibid.

Temperature Relations: The presence of highbush-cranberry at northern latitudes indicates that it must have high frost tolerance and an ability to grow at low soil and air temperatures. Its preference for shady locations in the southern half of its range may indicate that it is not tolerant of high temperatures.

GROWTH AND DEVELOPMENT

There is little published information regarding the growth and development of highbush-cranberry. It is a multi-stemmed shrub with a rather scraggly habit because of frequent natural layering. It has a fairly extensive underground system and underground rhizomes are present to a depth of 20–30 cm beneath the soil surface.[393] Its mature height can range from 0.15 m to 3.5 m (UBC Bot. Garden 1977), but average heights are in the range of 0.75–2 m (Clark 1976). Highbush-cranberry grows at a moderate rate throughout its life (UBC Bot. Garden 1977). It can reach a height of 1 m in 4 years in Alaska (Zasada *et al.* 1981).

Phenology: Observations in the Kimsquit Valley on the central British Columbia coast indicate that leaf flush occurs in April or early May, but leaves are not fully expanded until late May. Flowering usually occurs from May to July. Leaf senescence and abscission appear to take place earlier on highbush-cranberry than on most associated shrubs.[394] Fruits are ripe from late August to October, but remain on the twigs throughout the winter (UBC Bot. Garden 1977).

REPRODUCTION

Seed Production and Dispersal: Fruits of highbush-cranberry are first produced when the plant is approximately 5 years of age and are then produced in quantity nearly every year. Each fruit contains exactly 1 seed (UBC Bot. Garden 1977). Dispersal is by birds and mammals that feed on the fruit through the winter, and by gravity (USDA 1974).

Seed Viability and Germination: Seeds of highbush-cranberry remain viable in storage for up to 10 years (UBC Bot. Garden 1977). Rowe (1983) considers highbush-cranberry a seed-banking species. The seeds of *Viburnum* spp. are difficult to germinate because they have both seed coat and embryo dormancy. Treatment of the seed coat has not been shown to improve germination. Best germination normally occurs if a period of warm temperatures is followed by several months of near freezing temperatures. Germination is slow even after this treatment, and in nature most northern species of *Viburnum* do not germinate until the second year after fruit ripening (Giersbach 1937; USDA 1974; UBC Bot. Gardens 1977).

Vegetative Reproduction: Highbush-cranberry regenerates vegetatively by natural layering, and by sprouting from damaged root stocks and stem bases (UBC Bot. Garden 1977; Foote 1983). The plant is rhizomatous (Holloway and Zasada 1979),[395] but there is no evidence that it spreads laterally from the parent plant by means of root or rhizome suckers. Dormant cuttings taken in fall root poorly, but actively growing cuttings produce prolific roots; rhizome cuttings can be readily propagated (Holloway and Zasada 1979).

PESTS

A leaf spot (*Ascochyta viburni*) has been found on highbush-cranberry on the coast, while a rust (*Puccinia linkii*) is present in northern British Columbia (Toms 1964). Neither of these diseases is considered serious. Aphids, thrips, spider mites, and scale are likely to occur on *Viburnum* (UBC Bot. Garden 1977).

EFFECTS ON CROP TREES

Competition: Highbush-cranberry is not considered to be a primary competitor with coniferous trees in British Columbia. However, throughout much of its range it is a common member of the complex of brush species that appears on very moist, productive sites, particularly on floodplains or under deciduous canopies. It is most abundant and dominant in northern subzones of the SBS and in the BWBS zone throughout the northern province, where it can compete significantly with natural or planted white spruce.

Beneficial Effects: No information.

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[393] Parminter 1983.

[394] Hamilton 1984.

[395] Parminter 1983.

RESPONSE TO DISTURBANCE OR MANAGEMENT

Forest Canopy Removal: There are varying reports in the literature of the response of highbush-cranberry to canopy removal. In the SBS zone north of Prince George, Eis (1981) found that although highbush-cranberry was present on four site types prior to logging, it had not become a significant component of the vegetation on any of these site types 6 years after clearcutting. In the sub-boreal forest of Alberta, *V. edule* had a substantially lower cover in 6- to 12-year-old clearcut areas than in the mature lodgepole pine forest (Corns and LaRoi 1976). In contrast, logging of a balsam poplar stand in Alaska (Zasada *et al.* 1981) dramatically increased the density of highbush-cranberry.

Fire: Burning has promoted both vegetative reproduction and regeneration from seed. The underground rhizomes of *V. edule* survive shallow burns, and sprouting occurs at the base of fire-killed above-ground stems.[396] In the boreal forest of interior Alaska, highbush-cranberry resprouts within weeks of fire on white spruce sites and is one of the dominant post-fire shrubs. Light, short duration fires that remove very little of the humus layer favour regeneration of highbush-cranberry from seed stored in the soil (Rowe 1983).

Herbicides: Information on the effects of herbicides on highbush-cranberry is limited. A summary of available information indicates that in British Columbia, glyphosate and hexazinone generally provide only moderate control of the species (Boateng and Herring 1990). In a study conducted near Dawson Creek a young aspen–balsam poplar stand was aerially sprayed in June with 3 kg a.i./ha glyphosate.[397] Highbush-cranberry was 95% defoliated and suffered heavy mortality. A late May application of hexazinone gridballs at 4 kg a.i./ha in the BWBSmw subzone near Dawson Creek had no effect on highbush-cranberry. Several other species on the site were controlled extremely well.[398] In Alberta, spot application of 4 mL of hexazinone at 2-m grid spacing in the spring resulted in 30–40% defoliation of highbush-cranberry 3 years after treatment. On the same site, a spring spot application of 8 mL of hexazinone at 1.5-m grid spacing resulted in 90% defoliation.[399]

Soil Disturbance: Soil disturbance is expected to favour germination of stored seed, and it should provide a favourable seedbed for germination of freshly deposited seed. In addition, plants damaged or fragmented during site preparation can be expected to sprout back. Highbush-cranberry increased more on a summer-logged balsam poplar stand than on one that had been winter logged (Zasada *et al.* 1981). Soil disturbance was probably higher on the summer-logged site and may have stimulated resprouting of the shrub.

Soil disturbance has not always favoured *V. edule*. For example, cover of *V. edule* remained unchanged 2 years after moderate intensity windrowing in the SBSwk subzone north of Prince George (D. Greeley, pers. comm., May 1989) and scarification did not appear to enhance the cover of highbush-cranberry on clearcut areas near Edson, Alberta (Corns and LaRoi 1976).

WILDLIFE

Food: V. edule has moderate importance as a wildlife food in British Columbia. The fruit is more commonly consumed than the leaves and twigs.[400] Highbush-cranberry is a preferred winter food for moose. The plant is moderately important food for Rocky mountain elk in summer and fall but has low importance to this animal in winter and spring (Singleton 1976). Highbush-cranberry is common winter food for white-tailed deer in North America (Rue 1978).

When available, highbush-cranberry is a favourite summer food of grizzly bear (Meehan 1961; Banfield 1974; Herrero 1985; National Wildlife Federation 1987). Rabbits and beavers also browse on highbush-cranberry and small animals eat the fruit (UBC Bot. Garden 1977). The plant is considered unpalatable to snowshoe hares in Alberta (Keith *et al.* 1984, cited by Carreker 1985), but the bark and twigs made up 1% of their October to May diet in Alaska.

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[396] Parminter 1983.

[397] Herring 1984c.

[398] Herring 1988b.

[399] Drouin 1985.

[400] B.C. Min. Environ. (undated).

4 LITERATURE CITED

Adams, A.B. and V.H. Dale. 1980. Vegetative succession following glacial and volcanic disturbances in the Cascade Mountain Range of Washington, U.S.A. *In* Mount St. Helens 1980: Botanical consequences of the explosive eruptions. D.E. Bilderback (editor). Univ. Cal. Press, Berkley, Cal.

Ahlgren, C.E. 1960. Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota. Ecology 41:431-445.

Alaback, P.B. 1982. Forest community structural changes during secondary succession in southeast Alaska. *In* Forest succession and stand development research in the Northwest. J.E. Means (editor). Proc. Symp. March 26, 1981.

Alaback, P.B. and F.R. Herman. 1988. Long term response of understory vegetation to stand density in *Picea-Tsuga* forests. Can. J. For. Res. 18:1522-1530.

Alaska Rural Development Council. 1977. A revegetative guide for Alaska. Rural Development Council Publ. No. 2, P-238. Univ. of Alaska, Coop. Exten. Serv., Fairbanks, Alaska.

Aldous, S.E. 1952. Deer browse clipping study in the Lake States Region. J. Wildl. Manage. 16:401.

Allen, A.W. 1982. Habitat suitability index models: beaver. U.S. Dep. Int., Fish Wildl. Serv., Washington, D.C.

Allen, H.H. 1969. The inter-relationship of salmonberry and Douglas-fir in cut-over areas. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Anderson, E.W. and L.E. Brooks. 1975. Reducing erosion hazard on a burned forest in Oregon by seeding. J. Range Manage. 28(5):394-398.

Anderson, H.G. 1967. The phytosociology of some vine maple communities in the Marys Peak Watershed. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

_______. 1969. Growth form and distribution of vine maple (*Acer circinatum*) on Marys Peak, western Oregon. Ecology 50:127-130.

Angove, K. and B. Bancroft. 1983. A guide to some common plants of the southern interior of British Columbia. B.C. Min. For., Victoria, B.C. Land Manage. Handb. No. 7.

Annas, R.M. and R. Coupé, (editors). 1979. Biogeoclimatic zones and subzones of the Cariboo Forest Region. B.C. Min. For., Victoria, B.C.

Antos, J.A. and D.B. Zobel. 1984. Ecological implications of below ground morphology of nine coniferous forest herbs. Bot. Gaz. 145:508-517.

_______. 1985. Upward movement of underground plant parts into deposits of tephra from Mount St. Helens. Can. J. Bot. 63:2091-2096.

Archibold, W.O. 1980. Seed input into a postfire forest site in northern Saskatchewan. Can. J. For. Res. 10: 129-134.

Argus, G.W. 1973. The genus *Salix* in Alaska and the Yukon. National Museums of Canada. Publ. in Botany No. 2. Ottawa, Ont.

Arlidge, J.W.C. 1967. The durability of scarified seedbeds for spruce regeneration. B.C. For. Serv. Res. Note 42.

Arno, S.F., D.G. Simmerman, and R.F. Keene. 1985. Forest succession on four habitat types in western Montana. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-177.

Asherin, D.A. 1974. Prescribed burning effects on nutrition, production and big game use of key northern Idaho browse species. Diss. Abst. 35B(2):620.

Atkinson, W.A. and W.I. Hamilton. 1978. The value of red alder as a source of nitrogen in Douglas-fir/alder mixed stands. *In* Utilization and management of red alder. D.G. Briggs, D.S. DeBell, and W.A. Atkinson (editors). U.S. Dep. Agric. Gen. Tech. Rep. PNW-70. Portland, Oreg. pp. 337-351.

Bailey, A.W. 1966. Forest associations and secondary plant succession in the southern Oregon Coast Range. Ph.D. thesis. Oreg. State Univ., Corvallis, Oreg.

Bailey, A.W. and H.G. Anderson. 1979. Brush control on sandy rangelands in central Alberta. J. Range Manage. 32:29-32.

Bailey, J.A. and D. Hoogland. 1984. The response of *Epilobium* species to a range of soil and foliar-acting herbicides. Aspects Appl. Biol. 8:43-52.

Bailey, A.W. and C.E. Poulton. 1968. Plant communities and environmental interrelationships in a portion of the Tillamook burn, northwestern Oregon. Ecology 49:1-13.

Banfield, A.W.F. 1974. The Mammals of Canada. Univ. Toronto Press, Toronto, Ont.

Barber, W.J. 1976. An autecological study of salmonberry in western Washington. Ph.D. thesis. Univ. Wash., Seattle, Wash.

Barbour, M.G., J.H. Burk, and W.D. Pitts. 1980. Terrestrial Ecology. The Benjamin/Cummings Publ. Co. Inc., Menlo Park, Cal.

Barnes, B.V. 1966. The clonal growth habit of American aspens. Ecology 47:439-447.

Barr, W. and H. Pellett. 1972. Effect of soil temperature on growth and development of some woody plants. J. Am. Hort. Sci. 97(5):632-635.

Barring, U. 1988. On the reproduction of aspen (*Populus tremula* L.) with emphasis on its suckering ability. Scand. J. For. Res. 3:229-240.

Bartos, D.L. and W.F. Mueggler. 1981. Early succession in aspen communities following fire in western Wyoming. J. Range Manage. 34:315-318.

Basham, J.T. 1982. Scarification of 3-year old aspen suckers: 4- and 6-year effects on, and a preliminary forecast of the internal pathological quality of the survivors. Can. For. Serv., Inf. Rep. 0-X-341.

______. 1988. Decay and stain 10 years later in aspen suckers subjected to scarification at age 3. Can. J. For. Res. 18:1507-1521.

Beals, E.W. 1966. Vegetation of cottonwood forests on Kodiak Island. Can. Field Naturalist 80:167-171.

Bedard, J., M. Crete, and E. Audy. 1978. Short-term influence of moose upon woody plants of an early seral wintering site in Gaspe Peninsula, Quebec. Can. J. For. Res. 8:407-415.

Beese, W.J. 1986. The impact of prescribed burning on brush regrowth. Assoc. B.C. Prof. Foresters and South. Interior Silv. Co., Vegetation Manage. Symp. Proc., Jan. 21-22, Kamloops, B.C.

Behrend, D.F. and E.F. Patrick. 1969. Influence of site disturbance and removal of shade on regeneration of deer browse. J. Wildl. Manage. 33:394-398.

Bella, I.E. 1986. Logging practices and subsequent development of aspen stands in east-central Saskatchewan. For. Chron. 2:81-83.

Benecke, J. 1970. Nitrogen fixation by *Alnus viridis* (Chaix) DC. Plant and Soil 33: 30-48.

Bidwell, R.G.S. 1974. Plant Physiology. MacMillan Publ. Co. Inc., New York, N.Y.

Binkley, D. 1981. Nodule biomass and acetylene reduction rates of red alder and Sitka alder on Vancouver Island, B.C. Can. J. For. Res. 11:281-286.

______. 1982a. Case studies of red alder and Sitka alder in Douglas-fir plantations: nitrogen fixation and ecosystem production. Ph.D. thesis. Oreg. State Univ., Corvallis, Oreg.

_______. 1982b. Nitrogen fixation and net primary production in a young Sitka alder stand. Can. J. Bot. 60:281-284.

_______. 1984. Douglas-fir stem growth per unit of leaf area increased by interplanted Sitka alder and red alder. For. Sci. 30:259-263.

Bjorkbom, J.C. 1967. Seedbed preparation methods for paper birch. U.S. Dep. Agric., For. Serv. Res. Pap. NE-79.

_______. 1972. Ten-year growth of planted birch in old fields in Maine. U.S. Dep. Agric. For. Serv., Res. Pap. NE-79.

_______. 1973a. Response of paper birch seedlings to nitrogen, phosphorus, and potassium. U.S. Dep. Agric. For. Serv., Res. Note NE-157.

_______. 1973b. The effects of various combinations of nitrogen, phosphorus, and potassium on paper birch seedling growth. U.S. Dep. Agric. For. Serv., Res. Note NE-158.

Bjorkbom, J.C., D.A. Marquis, and F.E. Cunningham. 1965. The variability of paper birch seed production, dispersal, and germination. U.S. Dep. Agric. For. Serv., Res. Pap. NE-41.

Black, T.A., C.S. Tan, and J.U. Nnyamah. 1980. Transpiration rate of Douglas-fir trees in thinned and unthinned stands. Can. J. Soil Sci. 60:625-631.

Blackmore, D.G. and W.G. Corns. 1979. Lodgepole pine and white spruce establishment after glyphosate and fertilizer treatments of grassy cutover forest land. For. Chron. 55:102-105.

Blauer, A.C., A.P. Plummer, E.D. McCarthur, R. Stevens, and B.C. Giuntia. 1975. Characteristics and hybridization of important Intermountain shrubs. I. Rose family. U.S. Dep. Agric. For. Serv., Res. Pap. INT-169.

Boateng, J.O. and L. Herring. 1990. Site Preparation: Chemical. *In* Regenerating British Columbia's Forests. D.P. Lavender, R. Parish, C.A. Johnson, G. Montgomery, A. Vyse, and R. Willis (editors). UBC Press, Vancouver, B.C. pp. 164-178.

Bollen, W.B., K.C. Lu, J.M. Trappe, and R.F. Tarrant. 1969. Influence of Sitka alder on soil formation and microbiological succession on a land slide of alpine origin on Mount Rainier. U.S. Dep. Agric, For. Serv., Pac. NW For. Range Exp. Sta., Res. Note 103:1-5.

Bormann, B.T. and D.S. DeBell. 1981. Nitrogen content and other soil properties related to age of red alder stands. Soil Sci. Soc. Am. J. 45:428-432.

Bormann, B.T. and J.C. Gordon. 1984. Stand density effects in young red alder plantations; productivity, photosynthate partitioning, and nitrogen fixation. Ecology 65:394-402.

Bowers, C.G. 1960. Rhododendrons and Azaleas; their origins, cultivation, and development. 2nd ed. Macmillan Publ., New York, N.Y.

Bowes, G.G. 1976. Control of aspen poplar, balsam poplar, and prickly rose by picloram alone and in mixtures with 2,4-D. J. Range Manage. 29:148-150.

_______. 1981. Control of aspen regrowth in western Canada when there is an understory of established alfalfa. J. Range Manage. 34(5):412-415

Boyd, R.J., D.L. Miller, F.A. Kidd, and C.P. Ritter. 1985. Herbicides for forest weed control in the Inland Northwest: a summary of effects on weeds and conifers. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-195.

Bradley, A.F. 1984. Rhizome morphology, soil distribution, and the potential fire survival of eight woody understory species in western Montana. M.A. thesis. Univ. Montana, Missoula, Mont.

Brand, D.G. 1978. Early growth and development of Douglas-fir in relation to interspecific competition. Ph.D. thesis. Univ. B.C., Vancouver, B.C.

Bray, E. and M.L. Brenner. 1980. Temperature, photoperiod, and plant growth regulator interactions during cold acclimation of red osier dogwood. Plant Physiol. 65(6) Suppl.: 46 [Annual Meeting Abstracts].

Brayshaw, T.C. 1978. Catkin bearing plants of British Columbia. Prov. Museum. Occas. Pap. Series 18.

Briggs, D.G., D.S. Debell, and W.A. Atkinson. 1978. Utilization and management of alder. Proc. Symp. Ocean Shores, Wash. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-70.

Brissette, J.C. and B.V. Barnes. 1984. Comparisons of phenology and growth of Michigan and western North American sources of *Populus tremuloides*. Can. J. For. Res. 14: 789-793.

Brooke, R.C., E.B. Peterson, and V.J. Krajina. 1970. The subalpine mountain hemlock zone. *In* Ecology of Western North America. V.J. Krajina and R.C. Brooke (editors). 2:148-349.

Brown, E.R. 1961. The black-tailed deer of western Washington. Wash. State Game Dep., Biol. Bull. 13.

_______. 1985a. Management of wildlife and fish habitats in forests of western Oregon and Washington. U.S. Dep. Agric. For. Serv. Pac. Northwest Div. Portland, Oreg.

Brown, J.K. 1985b. Fire effects and application of prescribed fire in aspen. *In* Rangeland fire effects: a symposium. K. Sanders and J. Durham (editors). U.S. Dep. Int., Bur. Land Manage. and Univ. Idaho, Boise, Idaho. pp. 38-47.

Bryant, J.P. 1987. Feltleaf willow-snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. Ecology 68:1319-1327.

Bryant, J.P., F.S. Chapin III, P.B. Reichardt, and T.P. Clausen. 1987. Response of winter chemical defense in Alaska paper birch and green alder to manipulation of plant carbon/nutrient balance. Oecologia 72:510-514.

Buckman, R.E. 1964. Effects of prescribed burning on hazel in Minnesota. Ecology 45:626-629.

Buckman, R.E. and L.H. Blankenship. 1965. Abundance and vigor of aspen root suckering. J. For. 63: 23-25.

Burns, R.M. (compiler). 1983. Silvicultural systems for the major forest types of the United States. U.S. Dep. Agric. For. Serv., Handb. No. 445.

Cade, B.S. and P.J. Sousa. 1985. Habitat suitability index models: ruffed grouse. Fish Wildl. Serv., U.S. Dep. Int., Washington, D.C.

Cain, J.C. 1952. Comparison of ammonium and nitrate nitrogen for blueberries. Am. Soc. Hort. Sci. Proc. 59:161-166.

Calder, J.A. and R.L. Taylor. 1968. Flora of the Queen Charlotte Islands (I). Can. Dep. Agric., Ottawa, Ont. Monogr. No. 4(1).

Camp, W.H. 1942. A survey of the American species of *Vaccinium* subgenus Euvaccinium. Brittonia 4: 205-247.

Campbell, A.G. and J.F. Franklin. 1979. Riparian vegetation in Oregon's western Cascade Mountains: composition, biomass, and autumn phenology. U.S. Intern. Biol. Prog. Coniferous For. Biome Ecosystem Anal. Studies Bull. No. 14.

Cannings, R.A., R.J. Cannings, and S.G. Cannings. 1987. Birds of the Okanagan Valley, British Columbia. Royal B.C. Museum, Victoria, B.C.

Carlisle, A., A.H.F. Brown, and E.J. White. 1967. The nutrient content of tree stem flow and ground flora litter and leachates in a sessile oak (*Quercus petraea*) woodland. J. Ecology 55:615-627.

Carlton, G.C. 1988. The structure and dynamics of red alder communities in the central Coast Range of western Oregon. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Carpenter, C.V., L.E. Baribo, L.R. Robertson, F. Van DeBogart, and G.M. Onufer. 1979. Acetylene reduction by excised root nodules from *Alnus rubra* and *Alnus sinuata*. *In* Symbiotic nitrogen fixation in the management of temperate forests. J.C. Gordon, C.T. Wheeler, and D. Perry (editors). Oreg. State Univ., Corvallis, Oreg. p. 475.

Carreker, R.G. 1985. Habitat suitability index models: snowshoe hare. U.S. Dep. Int., Fish Wildl. Serv., Washington, D.C.

Chambers, M. 1988. Deer in British Columbia. B.C. Min. Environ., Fish Wildl. Br., Inf. and Education Section, Victoria, B.C.

Chan, S.S., S.R. Radosevich, and J.D. Walstad. 1988. Physiological, morphological and carbon allocation strategies of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) and red alder (*Alnus rubra* Bong.) under varied light and soil moisture levels: third year results. WSSA Abstr. 28:60.

Chan, S.S. and J.D. Walstad. 1987. Correlations between overtopping vegetation and development of Douglas-fir saplings in the Oregon Coast Range. West. J. Appl. For. 2:117-119.

Chapman, J.A. and G.A. Feldhamer (eds.). 1983. Wild Animals of North America. Johns Hopkins Univ. Press, London.

Chatelain, E.F. 1947. Food preferences of the Columbia black-tailed deer on the Tillamook burn, Oregon. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Chavasse, C.G.R. and N.A. Davenhill. 1973. A review of chemical control of bracken and gorse for forest establishment. *In* Proc. 26th New Zealand Weed and Pest Control Conf. N.Z. For. Serv. Reprint No. 679:2-6.

Chen, H. and P.H. Li. 1978. Interactions of low temperature, water stress, and short days in the induction of stem frost hardiness in red-osier dogwood. Plant Physiol. 62:833-835.

Chester, R.A. 1988. Management and use of red alder in the Vancouver Forest Region. M.Sc. thesis. Simon Fraser Univ., Burnaby, B.C.

Cholewa, A.F. and F.D. Johnson. 1983. Secondary succession in the *Pseudotsuga menziesii/Physocarpus malvaceus* association. Northwest Sci. 57(4):273-282.

Clark, L.J. 1973. Wildflowers of the Pacific Northwest. Gray's Publishing Ltd., Sidney, B.C.

______. 1976. Wildflowers of the Pacific Northwest from Alaska to northern California. Gray's Publishing Ltd., Sidney, B.C.

Clark, M.B. and A. McLean. 1975. Growth of lodgepole pine seedlings in competition with different densities of grass. B.C. For. Serv. Res. Note. No. 70.

Cline, R.G. and G.S. Campbell. 1976. Seasonal and diurnal water relations of selected forest species. Ecology 57:367-373.

Coates, K.D. 1987. Effects of shrubs and herbs on conifer regeneration and microclimate in the *Rhododendron-Vaccinium-Menziesia* community in south-central British Columbia. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Cody, W.J. and C.W. Crompton. 1975. The biology of Canadian weeds 15: *Pteridium aquilinum* (L) Kuhn. Can. J. Plant Sci. 55:1059-1072.

Cole, E.C. 1984. Fifth-year growth responses of Douglas-fir to crowding and other competition. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Cole, E.C. and M. Newton. 1986. Nutrient, moisture, and light relations in 5-year-old Douglas-fir plantations under variable competition. Can. J. For. Res. 16:727-732.

______. 1987. Fifth-year response of Douglas-fir to crowding and nonconiferous competition. Can. J. For. Res. 17:181-186.

Comeau, P. 1988. Light attenuation by thimbleberry-fireweed communities in the ICH zone and its potential effects on conifer growth. *In* Vegetation competition and responses: proceedings of the 3rd annual vegetation management workshop, Feb. 15-17. E. Hamilton and S. Watts (editors). Can. For. Serv. and B.C. Min. For., Victoria, B.C. FRDA Rep. 026. pp. 5-6.

Comeau, P.G., M.A. Comeau, and G.F. Utzig. 1982. A guide to plant indicators of moisture for southeastern British Columbia with engineering interpretations. B.C. Min. For., Victoria, B.C. Land Manage. Handb. No. 5.

Conard, S.G. 1983. Phenology of shrub species: its importance to forest vegetation management. *In* Proc. 5th Annual Forest Vegetation Management Conf. Sacramento, Cal., pp. 90-99.

Conard, S.G. and W.H. Emmingham. 1983. Herbicides for shrub control on forest sites in northeastern Oregon and northern Idaho. Oreg. State Univ., For. Res. Lab. Corvallis, Oreg. Special Publ. 5.

_______. 1984a. Herbicides for brush and fern control on forest sites in western Oregon and Washington. Oreg. State Univ., For. Res. Lab. Corvallis, Oreg. Special Publ. 8.

_______. 1984b. Herbicides for clump and stem treatments of trees and shrubs in Oregon and Washington. Oreg. State Univ., For. Res. Lab. Corvallis, Oreg. Special Publ. 9.

Conklin, J.G. 1969. Insect enemies of birch. *In* Birch Symp. Proc. E. vH. Larson (editor). U.S. Dep. Agric. For. Serv., NE For. Exp. Sta. pp. 151-154.

Conrad, P.W. and W.T. McDonough. 1972. Growth and reproduction of red elderberry on subalpine rangeland in Utah. Northwest Sci. 46:140-148.

Conway, E. 1952. Bracken – the problem plant. Scott. Agric. 31:181-184.

_______. 1957. Spore production in bracken. J. Ecology 45: 273-284.

Core, E.L. 1974. Brambles. *In* Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (compilers). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NE-9, pp. 16-19.

Corns, I.G.W. and H. LaRoi. 1976. A comparison of mature with recently clearcut and scarified lodgepole pine forests in the lower foothills of Alberta. Can. J. For. Res. 6:20-32.

Corns, W.G. and R.J. Schraa. 1962. Seasonal productivity and chemical composition of marsh reed grass (*Calamagrostis canadensis* (Michx.) (Beauv.) harvested periodically from fertilized and unfertilized native soil. Can. J. Plant Sci. 42:651-659.

Coupé, R., C.A. Ray, A. Comeau, M.V. Ketcheson, and R.M. Annas (compilers). 1982. A guide to some common plants of the Skeena area, British Columbia. B.C. Min. For., Victoria, B.C. Land Mgmt. Handb. No. 4.

Coyne, P.I. and K. van Cleve. 1977. Fertilizer induced morphological and chemical responses of a quaking aspen stand in interior Alaska. For. Sci. 23:92-102.

Crabtree, G. and L.H. Fuchigami. 1979. Vegetative maturity of red-osier dogwood and response to herbicides. Hort. Sci. 14(6):753-755.

Crandall, P.C., D.F. Allmendinger, J.D. Chamberlain, and K.A. Biderbost. 1974. Influence of cane number and diameter, irrigation and carbohydrate reserves on the fruit number of red raspberries. J. Am. Soc. Hort. Sci. 99:524-526.

Crane, M.F. and W.C. Fischer. 1986. Fire ecology of the forest habitat types of central Idaho. U.S. Dep. Agric. For. Serv., Intermountain Gen. Tech. Rep. INT-218.

Crane, M.F., J.R. Habeck, and W.S. Fischer. 1983. Early postfire revegetation in western Montana Douglas-fir forests. U.S. Dep. Agric. For. Serv., Res. Paper INT-319.

Crocker, R.L. and J. Major. 1955. Soil development in relation to vegetation and surface age of Glacier Bay, Alaska. J. Ecol. 43:427-448.

Cross, J.R. 1981. The establishment of *Rhododendron ponticum* in the Killarney Oakwoods, S.W. Ireland. J. Ecol. 69:807-824.

Crouch, G.L. 1964. Forage production and utilization in relation to deer browsing of Douglas-fir seedlings in the Tillamook burn, Oregon. Ph.D. thesis. Oreg. State. Univ. Corvallis, Oreg.

______. 1968. Clipping of woody plants by mountain beaver. J. Mammalogy 49:151-152.

______. 1986. Effects of thinning pole-sized lodgepole pine on understory vegetation and large herbivore activity in central Colorado. U.S. Dep. Agric. For. Serv., Rocky Mountain For. Range Exp. Sta., Res. Pap. RM-268.

Dalton, D.A. and A.W. Naylor. 1975. Studies on nitrogen fixation by *Alnus crispa*. Am. J. Bot. 62:76-80.

Daubenmire, R.F. 1974. Plants and Environment: A Textbook of Plant Autecology. 3rd ed. John Wiley & Sons, New York, N.Y.

Davis, T.D. and J.R. Potter. 1987. Physiological response of Rhododendron cuttings to different light levels during rooting. L. Am. Soc. Hortic. Sci. 112(2):256-259

DeBell, D.S. and L.T. Alford. 1972. Sprouting characteristics and cutting practices evaluated for cottonwood. Tree Planter's Notes 23:1-3.

DeBell, D.S., M.A. Radwan, C.A. Harrington, and D.L. Reukema. 1984. Culture of red alder (*Alnus rubra)* in biomass plantations. *In* Energy from biomass: building on a generic technology base. Proc. 2nd Tech. Review Meet., Chicago, Ill.

DeBell, D.S., M.A. Radwan, and J.M. Kraft. 1983. Influence of red alder on chemical properties of a clay loam soil in western Washington. U.S. Dep. Agric. For. Serv., Res. Pap. PNW-313.

DeBell, D.S. and T.C. Turpin. 1989. Control of red alder by cutting. U.S. Dep. Agric. For. Serv., Res. Pap. PNW-414.

del Moral, R. and R.G. Cates. 1971. Allelopathic potential of the dominant vegetation of western Washington. Ecology 52:1030-1037.

DeLong, C. 1988. Changes in structure of three vegetation complexes over the growing season and their effect on competition for light with hybrid spruce. *In* Vegetation competition and responses: Proc. 3rd annual vegetation management workshop, Feb. 15-17, 1988. E. Hamilton and S. Watts (editors). Can. For. Serv. and B.C. Min. For., Victoria, B.C. FRDA Rep. 026. pp. 8-9.

Demarchi, D.A. and S. Lofts. 1985. The effects of spring burning on the productivity and nutrient concentration of several shrub species in the southern Rocky Mountain Trench. B.C. Min. Environ., Victoria, B.C. Tech. Rep. 19.

Densmore, R. and J.C. Zasada 1977. Germination requirements of Alaska *Rosa acicularis*. Can. Field-Nat. 9:58-59.

Devereux, S. 1988. Elk in British Columbia. B.C. Min. Environ., Fish and Wildlife Branch, Inf. and Education Section, Victoria, B.C.

de Vos, A. 1964. Food utilization of snowshoe hares on Manitoulin Island, Ontario. J. For. 62:238-244.

de Vos, A. and R.H. Bailey. 1970. The effect of logging and intensive camping on vegetation in Riding Mountain National Park. For. Chron. 49-55.

Dimock, E.J. II. 1964. Supplemental treatments to aid planted Douglas-fir in dense bracken fern. U.S. Dep. Agric. For. Serv., Res. Note PNW-11.

Dimock, E.J. II., T.F. Beebe, and E.B. Collard. 1983. Planting-site preparation with herbicides to aid conifer reforestation. Weed Sci. 31:215-221.

Douglas, G.W. 1972. Subalpine plant communities of the western North Cascades, Washington. Arct. Alp. Res. 4:147-166.

Drew, S.E. 1968. Soil moisture depletion trends under five plant species present on the Douglas-fir clearcuts of Marys Peak, Oregon. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Dugle, J.R. 1966. A taxonomic study of western Canadian species in the genus *Betula*. Can. J. Bot. 4:929-1007.

Dukes, J.H., S.R. Radosevich, J.R. Potter, and L.J. Shainsky. 1988. Response of the gas exchange characteristics of Douglas-fir and red alder in an addition series experiment. WSSA Abstr. 28:59.

Dyrness, C.T. 1965. The effect of logging and slash burning on understory vegetation in the H.J. Anderson Experimental Forest. U.S. Dep. Agric. For. Serv., Res. Note PNW-31.

______. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology 54:57-69

Eady, K. 1971. Ecology of the alpine and timberline vegetation of Big White Mountain, British Columbia. Ph.D. thesis. Univ. of B.C., Vancouver, B.C.

Edlin, H.L. 1966. A modern sylva or a discourse of forest trees: 16 willows: *Salix* spp. Quarterly J. Forestry 60:23-34.

Edwards, R.Y. and R.W. Ritcey. 1960. Foods of caribou in Wells Gray Park, British Columbia. Can. Field-Nat. 74:3-7.

Eis, S. 1981. Effect of vegetative competition on regeneration of white spruce. Can. J. For. Res. 11:1-8.

Elliot, D.M. and I.E.P. Taylor. 1981. The importance of fertility and physical characteristics of soil in early development of red alder seedlings grown under controlled environmental conditions. Can. J. For. Res. 11:522-529.

Emmingham, W.H. 1972. Conifer growth and plant distribution under different light environments in the Siskiyou Mountains of southwestern Oregon. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Etherington, J.R. 1983. Control of germination and seedling morphology by ethene: differential responses, related to habitat of *Epilobium hirsutum* L. and *Chamerion angustifolium* (L.). J. Holub. Ann. Bot. 52:633-658.

______. 1984. Comparative studies of plant growth and distribution in relation to water logging. Differential formation of adventitious roots and their experimental excision in *Epilobium hirsutum* and *Chamerion angustifolium*. J. Ecol. 72:389-404.

Faegri, K. and L. van der Pijl. 1971. The Principles of Pollination Ecology. 2nd ed. Pergamon Press, Toronto, Ont.

Fergerson, W. 1978. A comparison of red alder, Douglas-fir, and western hemlock productivities as related to site: a panel discussion. *In* Utilization and management of alder. D.G. Briggs, D.S. Debell, and W.A. Atkinson (editors). U.S. Dep. Agric. Gen. Tech. Rep. PNW-70. pp. 175-182.

Ferguson, D.E. and R.J. Boyd. 1988. Bracken fern inhibition of conifer regeneration in northern Idaho. U.S. Dep. Agric. For. Serv., Intermountain Res. Sta., Res. Pap. INT-388.

Filauro, A. 1982. TSI on northern hardwoods using triclopyr or hexazinone. Proc. NE Weed Sci. Soc. 36: 229-233.

Fischer, W.C. and B.D. Clayton. 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-141.

Fitter, A.H. and R.K. Hay. 1981. Environmental Physiology of Plants. Academic Press, London.

Fitzgerald, R.D. and A.W. Bailey. 1984. Control of aspen regrowth by grazing with cattle. J. Range Manage. 37:156-158.

Flescher, M.D., C.C. Delwiche, and C.R. Golman. 1976. Measuring rates of symbiotic nitrogen fixation by *Alnus tenuifolia*. Am. J. Bot. 63:945-950.

Fletcher, W.W. and R.C. Kirkwood. 1979. The bracken fern (*Pteridium aquilinum* L. Kuhn): its biology and control. *In* The experimental biology of ferns. A.F. Dyer (editor). Academic Press, London, pp. 591-636.

Foote, M.J. 1983. Classification, description, and dynamics of plant communities after fire in the taiga of interior Alaska. U.S. Dep. Agric., For. Serv., Res. Pap. PNW-307.

Fosberg, F.R. 1942. *Cornus sericea* L. *(C. stolonifera* Michx). Bull. Torrey Bot. Club 69:583-589.

Foster, D.R. 1984. Phytosociological description of the forest vegetation of southeastern Labrador. Can. J. Bot. 62:899-906.

______. 1986. Vegetation development following fire in *Picea mariana* (black spruce) - *Pleurozium* forests of southeastern Labrador, Canada. J. Ecol. 73: 517-534.

Foster, D.R. and G.A. King. 1986. Vegetation pattern and diversity in S.E. Labrador, Canada: *Betula papyrifera* (birch) forest development in relation to fire history and physiography. J. Ecol. 74:465-483.

Foster, R.E. and G.W. Wallis. 1974. Common tree diseases of British Columbia. Can. Dep. Environ., Can. For. Serv. Publ. No. 1285.

Fowells, H.A. (compiler). 1965. Silvics of forest trees of the United States. U.S. Dep. Agric., For. Serv., Agric. Handb. No. 271.

Fowle, C.D. 1960. A study of the blue grouse (*Dendragapus obscurus* (Say)) on Vancouver Island, British Columbia. Can. J. Zool. 38:701-713.

Fox, T.R. 1986. Raspberry (*Rubus idaeus* L.) competition effects on balsam fir (*Abies balsamea* (L.) Mill.) seedlings in northern Maine. Tree Planter's Notes 37:20-23.

Fralish, J.S. 1972. Youth, maturity and old age. *In* Aspen: Symp. Proc., Univ. Minn. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NC-1, pp. 52-58.

Frazer, B.D. and A.R. Forbes. 1968. *Masonaphis maxima* (Mason) (Homoptera: Aphididae), an aphid on thimbleberry with an unusual life history. J. Entomol. Soc. B.C. 65:36-39.

Fredskild, B. 1984. Distribution and occurrence of Onagraceae in Greenland. Nord. J. Bot. 4:475-480.

Freyman, S. and A.L. van Ryswyk. 1969. Effect of fertilizer on pinegrass in southern British Columbia. J. Range Manage. 22:390-395.

Fried, J.S. 1985. Two studies of *Acer macrophyllum*: I. The effects of bigleaf maple on soils in Douglas-fir forests. II. The ecology of bigleaf maple seedling establishment and early growth in Douglas-fir forests. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Fried, J.S., Tappeiner J.C., II, and D.E. Hibbs. 1988. Bigleaf maple seedling establishment and early growth in Douglas-fir forests. Can. J. For. Res. 18:1226-1233.

Frye, T.C. 1934. Ferns of the northwest. Binfords and Mort Publ., Portland, Oreg.

Furlow, J.J. 1979. The systematics of the American species of *Alnus* (Betulaceae). Rhodera 81:1-121; 151-248.

Furniss, R.L. and V.M. Carolin. 1977. Western forest insects. U.S. Dep. Agric. For. Serv., Misc. Publ. No. 1339.

Furniss, M.M. and R.G. Krebill. 1972. Insects and diseases of shrubs on western big game ranges. *In* Wildland shrubs - their biology and utilization. C.M. McKell, J.P. Blaisdell, and J.R. Goodin (editors). Proc. Symp. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-1, pp. 218-226.

Galloway, G. and J. Worrall. 1979. Cladoptosis: a reproductive strategy in black cottonwood? Can. J. For. Res. 9:122-125.

Gara, R.I. and L.L. Jaeck. 1978. Insect pests of red alder: potential problems. *In* Utilization and management of alder. D.G. Briggs, D.S. Debell, and W.A. Atkinson (editors). U.S. Dep. Agric. Gen. Tech. Rep. PNW-70. Portland, Oreg. pp. 265-270.

Gashwiler, J.S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology 51:1018-1026.

Gerber, H.S., N.V. Tonks, and D.A. Ross. 1980. The recognition and life history of the major insect and mite pests of ornamental shrubs and shade trees of British Columbia. B.C. Min. Agric., Publ. 80-5.

Germain, A. 1985. Fertilization of stagnated Sitka spruce plantations on northern Vancouver Island. M.Sc. thesis. Univ. B.C., Vancouver, B.C.

Gholz, H.L., G.M. Hawk, A. Campbell, K. Cromack, Jr., and A.T. Brown. 1985. Early vegetative recovery and element cycles on a clear-cut watershed in western Oregon. Can. J. For. Res. 15:400-409.

Giersbach, J. 1937. Germination and seedling production of seedlings of *Viburnum*. Contrib. Boyce Thompson Ins. 9:79-90.

Gilbert, N. 1980a. Comparative dynamics of a single-host aphid: I. The evidence. J. Anim. Ecol. 49:351-369.

_______. 1980b. Comparative dynamics of a single-host aphid. II. Theoretical consequenses. J. Anim. Ecol. 49:371-380.

Gill, J.D. and W.M. Healy (compilers). 1974. Shrubs and vines for northeastern wildlife. U.S. Dep. Agric. For. Serv., Gen Tech. Rep. NE-9.

Gill, J.D. and F.L. Pogge. 1974. *Rosa* L. *In* Seeds of woody plants in the United States. C.S. Schopmeyer (editor). U.S. Dep. Agric. For. Serv., Agric. Handb. 450.

Gliessman, S.R. 1976. Allelopathy in a broad spectrum of environments as illustrated by bracken. Bot. J. Linn. Soc. 73:95-104.

Goode, J.E. 1970. Nitrogen nutrition and susceptibility of Malling Jewel raspberries to infection by spur blight (*Didymella applanata*). Plant Path. 19:108-110.

Gordon, F.A. 1976. Spring burning on an aspen-conifer stand for maintenance of moose habitat, West Boulder River, Montana. *In* Proc. Tall Timbers Fire Ecology Conf. No. 14 and Intermountain Fire Research Council Fire and Land Management Symp. October 8-10, 1974, Missoula, Mont. Tall Timbers Res. Sta. pp. 501-538.

Granstrom, A. 1987. Seed viability of fourteen species during five years of storage in a forest soil. J. Ecol. 75:321-331.

Grant, W.F. and B.K. Thompson. 1975. Observations on Canadian birches, *Betula cordifolia, B. neoalaskana, B. populifolia, B. papyrifera* and *B. x. caerulea*. Can. J. Bot. 53:1478-1490.

Gratkowski, H. 1971. Midsummer foliage sprays on salmonberry and thimbleberry. U.S. Dep. Agric. For. Serv., Res. Note PNW-171.

_______. 1978. Herbicides for shrub and weed tree control in western Oregon. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-77.

Gregory, R.A. 1966. The effect of leaf litter upon establishment of white spruce beneath paper birch. For. Chron. 42:251-255.

Grime, J.P. 1979. Plant Strategies and Vegetation Processes. John Wiley and Sons, Chichester, England.

Hadfield, M. 1968. The grey alder. Quarterly J. Forestry 62:170-172.

Haeussler, S. 1987. Germination and first-year survival of red alder seedlings in the central Coast Range of Oregon. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Haeussler, S. and J.C. Tappeiner. 1988. Germination, survival and early growth of red alder seedlings in the central coast range of Oregon. *In* Vegetation competition and responses: Proc. 3rd. annual vegetation management workshop, Feb. 15-17. E. Hamilton and S. Watts (editors). Can. For. Serv. and B.C. Min. For., Victoria, B.C. FRDA Rep. 26. pp. 43-44.

Haeussler, S., J. Pojar, B.M. Geisler, D. Yole, and R.M. Annas. 1984. A guide to the Coastal Western Hemlock zone: northern drier maritone subzone (CWHf) in the Prince Rupert Forest Region, British Columbia. B.C. Min. For., Land Manage. Rep. No. 21.

______. 1985. A guide to the Interior Cedar-Hemlock zone: northern transitional subzone (ICHg) in the Prince Rupert Forest Region, British Columbia. B.C. Min. For., Land Management Rep. No. 26.

Hall, I.V., L.E. Aalders, N.L. Nickerson, and S.P. Vander Kloet. 1979. The biological flora of Canada. 1. *Vaccinium angustifolium* Ait. Can. Field-Nat. 93:415-430.

Hall, J.W., D.G. Stout, and B. Brooke. 1987. Recovery of pinegrass after clipping (simulated grazing). Can. J. Plant Sci. 67:259-262.

Halverson, N.M. (compiler). 1986. Major indicator shrubs and herbs on national forests of western Oregon and southwestern Washington. U.S. Dep. Agric. For. Serv., Pac. NW Region, R6-TM-229-1986.

Hamel, D.R. 1983. Forest management chemicals: a guide to use when considering pesticides for forest management. U.S. Dep. Agric. For. Serv., Agric. Handb. 585.

Hamilton, A.N. 1987. Classification of coastal grizzly bear habitat for forestry interpretations and the role of food in habitat use by coastal grizzly bears. M.Sc. thesis. Univ. B.C., Vancouver, B.C. 86 p.

Hamilton, E.H. 1988. Impacts of prescribed burning on soil-vegetation relationships in the Sub-Boreal Spruce zone. *In* Wildlife and Range Prescribed Burning Workshop Proc. Oct. 27-28,1988. M.C. Feller and S.M. Thompson (editors). Univ. B.C., Fac. For., Vancouver, B.C. pp. 171-184.

Hamilton, E.H. and K.H. Yearsley. 1988. Vegetation development after clearcutting and site preparation in the SBS zone. Can. For. Serv. and B.C. Min. For., Victoria, B.C. FRDA Rep. 018.

Hanley, T.A. 1987. Physical and chemical response of understory vegetation to deer use in southeastern Alaska. Can. J. For. Res. 17:195-199.

Hann, W.J. 1986. Evaluation of site preparation and conifer release treatments in north Idaho shrubfields. *In* Weed control for forest productivity in their interior west. Symp. Proc., Feb. 5-7. D.M. Baumgartner, R.J. Boyd, D.W. Breuer, and D.L. Miller (editors). U.S. Dep. Agric. Spokane, Wash., pp. 115-119.

Hansen, R.M. and J.T. Flinders. 1969. Food habits of North American hares. Range Sci. Dep., Colo. State Univ., Fort Collins, Colo. Science Series No. 1.

Harcombe, A., B. Pendergast, B. Petch, and D. Janz. 1983. Elk habitat management: Salmon River Valley. B.C. Min. Environ., Working Rep. No. 1.

Harestad, A. 1983. Natural history of vertebrate pests in forests of British Columbia. B.C. Min. For., Res. Branch, Victoria, B.C. WHR-4.

Harniss, R.O. and D.L. Bartos. 1985. Survey of aspen stands treated with herbicides in the western United States. U.S. Dep. Agric. For. Serv., Res. Pap. INT-340.

Harrington, C.A. 1984. Factors influencing initial sprouting of red alder. Can. J. For. Res. 14:357-361.

______. 1987. Responses of red alder and black cottonwood seedlings to flooding. Phys. Plant. 69:35-48.

Harrington, C.A. and R.L. Deal. 1982. Sitka alder, a candidate for mixed stands. Can. J. For. Res. 12:108-111.

Harvey, D.A. 1981. A literature review of deer damage and controls in the Pacific Northwest with special reference to British Columbia. M.Sc. thesis. Simon Fraser Univ., Burnaby, B.C.

Hawk, G.M. and D.B. Zobel. 1974. Forest succession on alluvial landforms of the McKenzie River Valley, Oregon. Northwest Sci. 48:245-265.

Healy, W.M. and J.D. Gill. 1974. Alders *In* Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (compilers). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NE-9, pp. 6-9.

Heilman, P. 1983. Effects of surface treatment and interplanting of shrub alder on growth of Douglas-fir coal spoils. J. Environ. Qual. 12:109-113.

Heilman, P. and G. Ekuan. 1982. Nodulation and nitrogen fixation by red alder on coal mine spoils. Can. J. For. Res. 12:992-997.

Heilman, P.E. and R.F. Stettler. 1985. Mixed, short-rotation culture of red alder and black cottonwood: growth, coppicing, nitrogen fixation, and allelopathy. For. Sci. 31:607-616.

Heinrich, B. 1976. Flowering phenologies: bog, woodland, and disturbed habitats. Ecology 57:890-899.

Helgerson, O.T., J.C Gordon, and D.A. Perry. 1984. Nitrogen fixation by red alder and scotch broom planted under commercially thinned Douglas-fir. Plant and Soil 86:221-233.

Hellum, A.K. and R. Zahner. 1966. The frond size of bracken fern on forested outwash sand in northern lower Michigan. Soil Sci. Soc. Am. Proc. 30:520-524.

Heninger, R.L. and D.P. White. 1974. Tree seedling growth at different soil temperatures. For. Sci. 20:363-367.

Henry, J.K. 1915. Flora of Southern British Columbia. W.J. Gage & Co., Ltd., Toronto, Ont.

Hernandez, H. 1973. Revegetation studies – Norman Wells, Inuvik, and Tuktoyaktuk, N.W.T. and Prudhoe Bay, Alasta. *In* Botanical studies of natural and man-modified habitats in the Mackenzie Valley, eastern Mackenzie delta region and the Arctic islands. L.C. Bliss (editor). Environ. Soc. Committee North. Pipelines Task Force on North. Oil Devel. Rep. No. 73-44, pp. 77-149.

Herrero, S. 1985. Bear attacks. Winchester Press, Piscataway, N.J.

Hetherington, J.C. 1964. Brush control in coastal British Columbia. B.C. For. Serv. Res. Note 38.

Hibbs, D.E. 1982. Gap dynamics in a hemlock-hardwood forest. Can. J. For. Res. 12:522-527.

______. 1987. The self-thinning rule and alder management. For. Ecol. Manage. 18:273-281.

Hibbs, D.E. and C.G. Landgren. 1987. Thin-line treatment of red alder. West. J. Appl. For. 2:130-131.

Hickman, J.C. and M.P. Johnson. 1969. An analysis of geographical variation in western North American *Menziesia* (Ericaceae). Madrona 20:1-32.

Hill, R.H. 1976. Cold requirements of several ferns in southeastern Michigan. Am. Fern J. 66:83-88

Hitchcock, A.S. 1971. Manual of the Grasses of the United States. 2nd. ed. Vol. 1. Dover Publ. Inc., New York, N.Y.

Hitchcock, C.L. and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. Wash. Press, Seattle, Wash.

Hitchcock, C.L., A. Cronquist, M. Ownbey, and J.W. Thompson. 1969. Vascular Plants of the Pacific Northwest. Univ. Wash. Press, Seattle, Wash.

Hobbs, N.T., D.L. Baker, J.E. Ellis, and D.M. Swift. 1981. Composition and quality of elk winter diets in Colorado. J. Wildl. Manage. 45:156-171.

Holloway, P. and J. Zasada. 1979. Vegetative propagation of 11 common Alaska woody plants. U.S. Dep. Agric. For. Serv., Res. Note PNW-334.

Hook, D.D., M.D. Murray, D.S. DeBell, and B.C. Wilson. 1987. Variation in growth of red alder families in relation to shallow water table levels. For. Sci. 33:224-229.

Horsley, S.B. and H.G. Abbott. 1970. Direct seeding of paper birch in strip clearcutting. J. For. 68:635-638.

Horton, K.W. and E.J. Hopkins. 1965. Influence of fire on aspen suckering. Can. Dep. Forestry Publ. No. 1095.

Hosie, R.C. 1973. Native Trees of Canada. 7th ed. Can. For. Serv. and the Can. Publ. Cent. Fitzhenry and Whiteside Ltd., Don Mills, Ont.

Hosier, P.E. 1974. Mountain maple. *In* Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (compilers). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NE-9, pp. 93-95.

Howard, K.M. and M. Newton. 1984. Overtopping by successional Coast Range vegetation slows Douglas-fir seedlings. J. For. 82:178-180.

Hoyer, G.E. and D. Belz. 1984. Stump sprouting related to time of cutting red alder. State Wash., Dep. Natural Resources Rep. 45.

Hoyles, S.E. 1979. Range improvements. Chap. 5. *In* Range management handbook for British Columbia. A. McLean (editor). Agric. Can. Res. Sta., Kamloops, B.C.

Hubbard, W.A. 1969. The grasses of British Columbia. B.C. Prov. Museum, Victoria, B.C. Handb. No. 9.

Hudson, J.P. 1959. Effects of environment on *Rubus idaeus* L. I. Morphology and development of the raspberry plant. J. Hort. Sci. 34:163-169.

Hultén, E. 1974. Flora of Alaska and neighbouring territories: a manual of the vascular plants. Stanford Univ. Press, Stanford, Cal.

Hungerford, R.D. 1984. Native shrubs: suitability for revegetating road cuts in northwestern Montana. U.S. Dep. Agric. For. Serv., Res. Pap. INT-331. 13 p.

______. 1985. Vegetation response to stand cultural operations on small stem lodgepole pine stands in Montana. *In* Weed control for forest productivity in the interior west, Symp. Proc., Feb. 5-7, 1985. D. M. Baumgartner, R.J. Boyd, D.W. Breuer, and D.L. Miller (editors). Spokane, Wash., pp. 63-71.

______. 1988. Soil temperatures and suckering in burned and unburned aspen stands in Idaho. U.S. Dep. Agric. For. Serv., Res. Note INT-378.

Hunt, R.S. 1978. *Melampsora* foliage rusts in British Columbia. Can. For. Serv., Pac. For. Res. Cent., Pest Leaflet 49.

Hutchinson, T.C. and J.A. Hellebust. 1978. Vegetation recovery in the Canadian artic after crude and diesel oil spills. Can. Dep. Ind. and Northn. Affairs. ALUR75-76-83.

Hyvarinen, M.J. 1968. Paper birch – its characteristics, properties, and uses: a review of recent literature. U.S. Dep. Agric. For. Serv., Res. Pap. NC-22.

Irwin, L.L. and J.M. Peek. 1979. Shrub production and biomass trends following five logging treatments within the cedar-hemlock zone of northern Idaho. For. Sci. 25:415-429.

Isaac, L.A. 1940. Vegetative succession following logging in the Douglas fir region with special reference to fire. J. For. 38:716-721.

Jennings, D.L. and M.R. Cormack. 1969. Factors affecting the water content of overwintering raspberry canes. Hort. Res. 9:18-25.

Jennings, D.L. and B.M.M. Tulloch. 1964. Studies on factors which promote germination of raspberry seeds. J. Exp. Bot. 16:329-340.

Jobidan, R. 1986. Allelopathic potential of coniferous species to old-field weeds in eastern Quebec. For. Sci. 32:112-118.

Jobidan, R. and J.R. Thibault. 1981. Allelopathic effects of balsam poplar on green alder germination. Bull. Torrey Bot. Club 108:413-418.

Johansson, T. 1985a. Treatment of broad-leaved trees in stands. Swedish Univ., Agric. Sci., Dep. For. Yield Res., Garpenburg, Sweden.

______. 1985b. Reducing the number of deciduous trees by preventative methods. J. Swedish For. Assoc. No. 3-4.

Johansson, T. and J.E. Lundh. 1988. Sucker production from root cuttings of *Populus tremula* in relation to growing conditions. Scand. J. For. Res. 3:75-82.

Johnson, F.D. 1968. Taxonomy and distribution of northwestern alders. *In* Biology of alders. J.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen (editors). Proc. Symp. U.S. Dep. Agric. For. Serv., Portland, Oreg., pp. 9-22.

Johnston, M. and P. Woodward. 1985. The effect of fire severity level on postfire recovery of hazel and raspberry in east-central Alberta. Can. J. Bot. 63: 672-677.

Jones, G.N. 1940. A monograph of the genus *Symphoricarpos*. J. Arnold Arboretum 21: 201-252.

Jones, G.W. 1975. Aspects of the winter ecology of black-tailed deer (*Odoccoileus hemionus columbianus* Richardson) on northern Vancouver Island. M.Sc. thesis. Univ. B.C., Vancouver, B.C.

Jones, J.R. 1974. Silviculture of southwestern mixed conifers and aspen: the status of our knowledge. U.S. Dep. Agric. For. Serv., Res. Rep. RM-122.

Jones, J.R. and N.V. DeByle. 1985. Fire. *In* Aspen: ecology and management in the western United States. N.V. DeByle and R.P. Winokur (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. RM-119. pp. 77-81.

Kato, Y. 1963. Consequences of ultraviolet irradiation on the differentiation of fern gametophytes. New Phytol.53: 21-27.

Keeley, J.E. 1981. Reproductive cycles and fire regimes. *In* Proc. Conf. on Fire Regimes and Ecosystem Properties. Honolulu, Hawaii. U.S. Dep. Agric. Gen. Tech. Rep. WO-26.

Keep, E. 1968. Incompatibility in *Rubus* with special reference to *Rubus idaeus* L. Can. J. Genet. Cytol. 10: 253-262.

Keeton, W.T. 1972. Biological Science. 2nd ed. W.W. Norton and Co. Inc., New York, N.Y.

Keisker, D.G. 1986. Nest tree selection by primary cavity-nesting birds in south-central British Columbia. M.Sc. thesis. Simon Fraser Univ., Burnaby, B.C.

Kelleyhouse, D. and D. Grangaard. 1984. Food for moose. Alaska Dep. Fish and Game, Juneau, Alaska.

Kelliher, F.M. 1985. Salal understory removal effects on the soil water regime and tree transpiration rates in a Douglas-fir forest. Ph.D. thesis. Univ. B.C., Vancouver, B.C.

Kellman, M.C. 1969. Plant species interrelationships in a secondary succession in coastal British Columbia. Syesis 2:201-212.

Kelpsas, B.R. 1978. Comparative effects of chemical, fire, and machine site preparation in an Oregon coastal brushfield. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Kemperman, J.A. 1978. Sucker-root relationships in aspen. Ont. Min. Nat. Resources, For. Res. Note No. 12.

Kemperman, J.A. and B.V. Barnes. 1976. Clone size in American aspens. Can. J. Bot. 54:2603-2607.

Kenady, R.M. 1978. Regeneration of red alder. *In* Utilization and management of alder. D.G. Briggs, D.S. DeBell, and W.A. Atkinson (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-70, pp. 183-192.

King, D.G. 1973. Feeding habits of blue grouse in the subalpine. Syesis 6:121-125.

King, P.H. 1980. Review of seed pretreatments required for germination of candidate native tree and shrub species in the eastern slopes of the Rocky Mountains and foothills of Alberta. Alta. For. Serv. ENR, Rep. No. 154.

King, R.D. 1969. Spring and summer foods of ruffed grouse on Vancouver Island. J. Wildl. Manage. 33:440-442.

King, R.D. and J.F. Bendell. 1982. Foods selected by blue grouse (*Dendragapus obscurus fuliginosis*). Can. J. Zool. 60:3268-3281.

Kirkwood, J.E. 1902. The vegetation of northwestern Oregon. Torreya 9:129-134.

Kittredge, J. Jr. and S.R. Gevorkiantz. 1929. Forest possibilities of aspen lands in the Lake states. Univ. Minn., Agric. Exp. Sta., Tech. Bull. 60.

Klein, D.R. 1965. Ecology of deer range in Alaska. Ecol. Monogr. 35:259-284.

Klinger, G.E. 1986. Effects of grass legume competition on shrub and hardwood invasion in newly harvested clearcuts. M.Sc. thesis. Univ. Wash., Seattle, Wash.

Klinka, K. 1977a. Guide for the tree species selection and prescribed burning in the Vancouver Forest District. 2nd. approx. B.C. Min. For., Vancouver, B.C.

______. 1977b. Guide for the tree species selection and prescribed burning in the Vancouver Forest Distrtict – an abbreviated version. B.C. Min. For., Vancouver, B.C.

Klinka, K. and R.E. Carter. 1980. Ecology and silviculture of the most productive ecosystems for growth of Douglas-fir in southwestern British Columbia. B.C. Min. For., Victoria, B.C. Land Manage. Rep. No. 6.

Klinka, K. and A.M. Scagel. 1984. Selected ecological characteristics of some tree and shrub species in British Columbia: genera *Juniperus, Taxus, Populus, Alnus, Betula, Quercus, Prunus, Rhamnus, Acer, Cornus,* and *Arbutus*. Can. Cartographics Ltd., Coquitlam, B.C.

Klinka, K., M.C. Feller, and R.K. Scagel. 1982. Characterization of the most productive ecosystems for the growth of Engelmann spruce in southwestern British Columbia. B.C. Min. For., Victoria, B.C. Land Manage. Rep. No. 9.

Klinka, K., F.C. Nuszdorfer, and L. Skoda. 1979. Biogeoclimatic units of central and southern Vancouver Island. B.C. Min. For., Victoria, B.C.

Knighton, M.D. 1981. Growth response of speckled alder and willow to depth of flooding. U.S. Dep. Agric. For. Serv., Res. Pap. NC-198.

Knowlton, S. and J.O. Dawson. 1983. Effects of *Pseudomonas cepacia* and cultural factors on the nodulation of *Alnus rubra* roots by *Frankia*. Can. J. Bot. 61:2877-2882.

Kobayashi, K., L. Fuchigami, and K. Brainerd. 1981. Dormancy stages and cold hardiness of red-osier dogwood. Hort. Sci. Abstracts from 77th annual meeting of Am. Soc. Hort. Sci. July 27 - August 1, 1981.

Koch, J.M. 1983. Salal plant structure, growth and allometric relationships under several forest stand densities in south coastal British Columbia. B.S.F. thesis. Univ. B.C., Vancouver, B.C.

Kozlowski, T.T. 1972. Physiology of water stress. *In* Wildland shrubs: their biology and utilization. C.M. McKell, J.P. Blaisdell, and J.R. Goodin (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-1, pp. 229-244.

Krajina, V.J., K. Klinka, and J. Worrall. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Univ. B.C., Fac. Forestry, Vancouver, B.C.

Kramer, N.B. and F.D. Johnson. 1987. Mature forest seed banks of three habitat types in central Idaho. Can. J. Bot. 65:1961-1966.

Kramer, P.J. and T.T. Kozlowski. 1979. Physiology of woody plants. Acad. Press, New York, N.Y.

Krueger, W.C. 1983. Cattle grazing in managed forests. *In* Forestland Grazing. Proc. Symp. Feb. 23-25, Spokane, Wash. B.F. Roche and D.M. Baumgartner (editors). Wash. State Univ., Pullman, Wash. pp. 29-41.

Krygier, J.T. and R.H. Ruth. 1961. Effects of herbicides on salmonberry and on Sitka spruce and western hemlock seedlings. Weeds 9(3):416-422.

Kufeld, R. 1973. Foods eaten by Rocky Mountain elk. J. Range Manage. 26:106-112.

Kunzli, N. 1985. Effects of a red alder overstory on growth of Sitka spruce and incidence of Sitka spruce weevil damage. B.S.F. thesis. Univ. B.C., Vancouver, B.C.

Lafferty, R.R. 1972. Regeneration and plant succession as related to fire intensity on clear-cut logged areas in the coastal cedar-hemlock type: an interim report. Can. For. Serv., Pac. For. Res. Cent. Internal Rep. BC-33.

_______. 1980 Post-burn evaluation of plant succession and forest regeneration in coastal Douglas-fir, western Hemlock, redcedar types. Supply and Services Canada, Havco Res. Serv. Ltd. Contract No. 75.

Landis, T.D. and E.J. Simonich. 1984. Producing native plants as container seedlings. *In* The challenge of producing native plants for the Intermountain area. Proc. Intermountain Nurseryman's Assoc. P.M. Murphy (editor). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-168., pp. 16-25.

Laughlin, W.M., G.R. Smith, and M.A. Peters. 1982. Influence of N, P, and K fertilization on yield and mineral composition of native bluejoint grass on the Lower Kenai Peninsula, Alaska. Agron. J. 76:389-397.

Lauterbach, P. and L.E. Warren. 1982. Control of resprouting hardwood clumps with applications of triclopyr ester by hovering helicopter. Proc. West. Soc. Weed Sci. 35:36-38.

Lavender, D.P. 1981. Environment and shoot growth of woody plants. Oreg. State Univ., School of Forestry, For. Res. Lab., Corvallis, Oreg. Res. Pap. 45.

Lawson, H.M. and P.D. Waister. 1972a. The effects of soil cultivation techniques on the growth and yield of the raspberry crop. Weed Res. 12:96-106.

_______. 1972b. The response to nitrogen of a raspberry plantation under contrasting systems of management. Hort. Res. 12:43-55.

Lees, J.C. 1966. Release of white spruce fron aspen competition in Alberta's spruce-aspen forest. Can. Dep. For., Publ. No. 1163.

Leslie, D.M., Jr., E.E. Starkney, and M. Vavra. 1984. Elk and deer diets in old-growth forests in western Washington. J. Wildl. Manage. 48:762-775.

Lewis, W.H. 1959. A monograph of the genus *Rosa* in North America. I. *Rosa acicularis.* Brittonia 11:1-24.

Lindzey, J.S. 1943. A study of the Columbia black-tailed deer and its habits in Oregon. M. Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Lloyd, K.A. 1979. Aspects of the ecology of black and grizzly bears in coastal British Columbia. M.Sc. thesis. Univ. B.C., Vancouver, B.C.

Lofroth, E.C. 1988. Grizzly bears in British Columbia. B.C. Min. Environ., Fish Wildl. Branch, Inf. and Education Section, Victoria, B.C.

Long, J.N. 1977. Trends in plant species diversity associated with development in a series of *Pseudotsuga menziesii/Gaultheria shallon* stands. Northwest Sci. 51:119-130.

Long, J.N. and J. Turner. 1975. Aboveground biomass of understory and overstory in an age sequence of four Douglas-fir stands. J. Appl. Ecol. 12:179-188.

Looman, J. and K.F. Best. 1979. Budd's flora of the Canadian prairie provinces. Agric. Can., Res. Branch. Publ. 1662.

Lutz, H.J. 1955. Ecological effects of forest fires in the interior of Alaska. U.S. Dep. Agric., Tech. Bull. No. 1133.

Lyon, L.J. 1966. Initial vegetal development following prescribed burning of Douglas-fir in south-central Idaho. U.S. Dep. Agric. For. Serv., Res. Pap. INT-29.

______. 1971. Vegetal development following prescribed burning of Douglas-fir in south-central Idaho. U.S. Dep. Agric. For. Serv., Res. Pap. INT-105.

Lyons, C.P. 1952. Trees, Shrubs and Flowers to Know in British Columbia. J.M. Dent and Sons Ltd., Vancouver, B.C.

McDonald, P.M. 1986. Grasses in young conifer plantations: hindrance and help. Northwest Sci. 60:271-278.

McDonough, W.T. 1969. Effective treatments for the induction of germination in mountain rangeland species. Northwest Sci. 43:18-22.

______. 1979. Quaking aspen-seed germination and early seedling growth. U.S. Dep. Agric. For. Serv., Res. Pap. INT-234.

McDonough, W.T. and R.K. Tew. 1967. Inhibitors of germination and growth from red elderberry: a laboratory evaluation. U.S. Dep. Agric. For. Serv., Res. Note INT-72.

McGee, A.B. 1988a. Effects of prescribed burning on vegetation and natural tree regeneration in mature cedar-hemlock forests in the Pacific Rim National Park. B.S.F. thesis. Univ. B.C., Vancouver, B.C.

______. 1988b. Vegetation response to right-of way clearing procedures in coastal British Columbia. Ph.D. thesis. Univ. of B.C., Vancouver, B.C.

McGeough, D.M. 1985. Effects of prescribed burning on vegetation and natural tree regeneration in mature cedar-hemlock forests in the Pacific Rim National Park. B.S.F. thesis. Univ. B.C., Vancouver, B.C.

MacKinnon, A. and B. McMinn. 1988. Response of vegetation to mechanical site preparation treatments in north central B.C. *In* Vegetation competition and responses: Proc. 3rd Annual Vegetation Management Workshop, Feb. 15-17, 1988. E. Hamilton and S. Watts (editors). Can. For. Serv. and B.C. Min. For., Victoria, B.C. FRDA Rep. 026. pp.19-23.

McLean, A. 1967. Germination of forest range species from southern British Columbia. J. Range Manage. 20:321-322.

______. 1969. Fire resistance of forest species as influenced by root systems. J. Range Manage. 22:120-122.

______. 1970. Plant communities of the Similkameen Valley, British Columbia, and their relationships to soils. Ecol. Monogr. 40:403-424.

______. 1979. Range plants. *In* Range management handbook for British Columbia. A. McLean (editor). Agric. Can. Res. Sta., Kamloops, B.C., pp.12-28

McLean, A. and E.W. Tisdale. 1960. Chemical compositions of native forage plants in British Columbia in relation to grazing practices. Can. J. Plant Sci. 40:405-423.

McLean, A., T.M. Lord, and A.J. Green. 1971. Utilization of the major plant communities in the Similkameen Valley, British Columbia. J. Range Manage. 24:346-351.

McMinn, R.G., S. Eis, H.E. Hirvonen, E.T. Oswald, and J.P. Senyk. 1976. Native vegetation in British Columbia's Capital Region. Can. For. Serv. Rep. BC-X-140.

McTaggart-Cowan, I. 1945. The ecological relationships of the food of the Columbia black-tailed deer, *Odocoileus hemionus columbianus* (Richardson), in the Coast Forest Region of southern Vancouver Island, British Columbia. Ecol. Monogr. 15:110-139.

Maini, J.S. 1972. Silvics and ecology in Canada. *In* Aspen: Symp. Proc. Univ. Minn. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NC-1, pp. 67-73.

Marchant, C. and J. Sherlock. 1984. A guide to selection and propagation of some native woody species for land rehabilitation in British Columbia. B.C. Min. For., Victoria, B.C. Res. Rep. RR84007-HQ.

Marquis, D.A. 1966. Germination and growth of paper birch and yellow birch in simulated strip cuttings. U.S. Dep. Agric. For. Serv., Res. Pap. NE-54

Marquis, D.A., J.C. Bjorkbom, and G. Yelenoxky. 1964. Effect of seedbed condition and light exposure on paper birch regeneration. J. For. 62:876-881.

Martin, D.J. 1976. Control of bracken. Bot. J. Linn. Soc. 73:241-246.

Mather, J. 1988. An overview of vegetation problems in the ICHm2 and ICHb subzones of the southern interior. *In* Vegetation competition and responses: Proc. 3rd annual vegetation management workshop, Feb. 15-17, 1988. E. Hamilton and S. Watts (editors). Can. For. Serv. and B.C. Min. For., Victoria, B.C. FRDA Rep. 026. p.50.

Meehan, W.R. 1961. Observations on feeding habits and behaviour of grizzly bears. Am. Midl. Nat. 65:405-412.

Meidinger, D.V., G.D. Hope, and A.J. McLeod. 1984. Classification and interpretation of some ecosystems of the Rocky Mountain Trench, Prince George Forest Region, British Columbia. 1st approx. B.C. Min. For., Land Manage. Rep. No. 22.

Mellen, T.K. 1987. Home range and habitat use of pileated woodpeckers, western Oregon. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Merrill, E.H. 1982. Shrub responses after fire in an Idaho ponderosa pine community. J. Wildl. Manage. 46:496-502.

Meyer, F.D. 1951. *Valeriana* in North America and the West Indies (*Valerianaceae*). Ann. Miss. Bot. Gard. 38:377-401.

Miller, D.L. 1985a. Conifer release in the inland Northwest – effects. *In* Weed control for forest productivity in the interior west, Symp. Proc., Feb. 5-7, 1985. D.M. Baumgartner, R.J. Boyd, D.W. Breuer, and D.L. Miller (editors). Wash. State Univ. Coop. Ext. Service, Spokane, Wash. pp. 17-24.

______. 1985b. Conifer release in the inland Northwest – chemical methods. *In* Weed control for forest productivity in the interior west, Symp. Proc., Feb. 5-7, 1985. D.M. Baumgartner, R.J. Boyd, D.W. Breuer, and D.L. Miller (editors). Wash. State Univ. Coop. Ext. Service, Spokane, Wash. pp. 109-113.

Miller, D.L., F.A. Kidd, and W.W. Pope. 1983. Effects of Garlon 4, 2,4-D, and Velpar herbicides on north Idaho shrubs. Potlatch Corp., Res. Note 83-7. Lewiston, Idaho.

Miller, F.L. 1968. Observed use of forage and plant communities by black-tailed deer. J. Wildl. Manage. 32:142-148.

Miller, M. 1977. Response of blue huckleberry to prescribed fires in a western Montana larch-fir forest. U.S. Dep. Agric. For. Serv., Res. Pap. INT-188.

Miller, M.M. and J.W. Miller. 1974. Succession after wildfire in the North Cascades national park complex. Ann. Tall Timbers Fire Ecol. Conf. 15:71-83.

Miller, R.E. and M.D. Murray. 1978. The effects of red alder on growth of Douglas-fir. *In* Utilization and management of alder. D.G. Briggs, D.S. Debell, and W.A. Atkinson (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-70, pp. 283-306.

______. 1979. Fertilizer versus red alder for adding nitrogen to Douglas-fir forests of the Pacific Northwest. *In* Symbiotic nitrogen fixation in the management of temperate forests: Proc. Workshop, Apr. 2-5, 1979. J.C. Gordon, C.T. Wheeler, and D.A. Perry (editors). Oreg. State Univ., Corvallis, Oreg. pp. 356-373.

Minore, D. 1972. The wild huckleberries of Oregon and Washington – a dwindling resource. U.S. Dep. Agric. For. Serv., Res. Pap. PNW-143.

______. 1975. Observations on the rhizomes and roots of *Vaccinium membranaceum*. U.S. Dep. Agric. For. Serv., Res. Note PNW-261.

______. 1979. Comparative autecological characteristics of northwestern tree species – a literature review. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-87.

______. 1984. *Vaccinium membranaceum* berry production seven years after treatment to reduce overstory tree canopies. Northwest Sci. 58:208-212.

Minore, D. and M.E. Dubrasich. 1978. Big huckleberry abundance as related to environment and associated vegetation near Mount Adams, Washington. U.S. Dep. Agric. For. Serv., Res. Note PNW-322.

Minore, D. and A.W. Smart. 1978. Frost tolerance in seedlings of *Vaccinium membranaceum, Vaccinium globulare,* and *Vaccinium deliciosum*. Northwest Sci. 52:179-185.

Minore, D., A.W. Smart, and M.E. Dubrasich. 1979. Huckleberry ecology and management research in the Pacific Northwest. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-93.

Miquelle, D.G. 1983. Browse regrowth and composition following summer defoliation by moose. J. Wildl. Manage. 47:17-24.

Mitchell, W.R. and R.E. Green. 1981. Identification and interpretation of ecosystems of the Western Kamloops Forest Region. B.C. Min. For., Victoria, B.C. Land Manage. Handb. No. 2.

Mitchell, W.W. 1968. On the ecology of Sitka alder in the subalpine zone of south-central Alaska. *In* Biology of alder. T.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen (editors). Proc. Symp. U.S. Dep. Agric. For. Serv., Portland, Oreg., pp. 45-56.

______. 1974. Native bluejoint: a valuable forage and germplasm resource. Agroborealis 6(1):21-22.

______. 1978. Development of plant materials for revegetation in Alaska. *In* Proc. High Altitude Revegetation Workshop No. 3. S.T. Kerny (editor). Colorado State Univ., Inform Series No. 21.

Mitchell, W.W. and J. Evans. 1966. Composition of two disclimax bluejoint stands in southcentral Alaska. J. Range Manage. 19:65-68.

Monaco, P.A., T.M. Ching, and K.K. Ching. 1980. Rooting of *Alnus rubra* cuttings. Tree Planters' notes. 31:22-24.

Monaco, P.A., K.K. Ching, and T.M. Ching. 1982. Host-endophyte effects on biomass production and nitrogen fixation in *Alnus rubra* actinorhizal symbiosis. Bot. Gazette. 143: 298-303.

Monsen, S.B. 1984. Use of shrubs on mine spoils. *In* The challenge of producing native plants for the Intermountain area. Proc. Intermountain Nurseryman's Assoc. P.M. Murphy (compiler). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-168, pp. 26-31.

Morgan, P. 1984. Modelling shrub succession following clearcutting and burning. Ph.D. thesis. Univ. Idaho, Moscow, Idaho. 146 p.

Morgan, P. and L.F. Neuenschwander. 1988a. Seed-bank contributions to regeneration of shrub species after clearcutting and burning. Can. J. Bot. 66:169-172.

______. 1988b. Shrub response to high and low severity burns following clearcutting in northern Idaho. West. J. Appl. For. 3:5-9.

Morris, M.S., J.E. Schmautz, and P.F. Stickney. 1962. Winter field key to the native shrubs of Montana. For. and Conserv. Exp. Sta., U.S. Dep. Agric., For. Serv. Intermountain For. and Range Sta., Montana State Univ., Bozeman, Mont. Bull. 23.

Morris, W.G. 1970. Effects of slash burning in overmature stands of the Douglas-fir region. Forest Sci. 16: 258-270.

Mosquin, T. 1966. A new taxonomy for *Epilobium angustifolium* L. (Onagraceae). Brittonia 18:167-188.

Moss, E.H. 1936. The ecology of *Epilobium angustifolium* with particular reference to rings of periderm in the wood. Am. J. Bot. 23:114-120.

Mueggler, W.F. 1965. Ecology of seral shrub communities in the cedar-hemlock zone of northern Idaho. Ecol. Monogr. 35:165-185.

______. 1984. Aspen ecology. U.S. Dep. Agric. For. Serv., Proc. Aspen Symp., May 22-24, Colorado Springs, Colo. RM-16. pp. 6-14.

Mueller-Dombois, D. 1965. Initial stages of secondary succession in the Coastal Douglas-fir and Western Hemlock zones. Ecol. West. N. Am. 2:38-41.

Mueller-Dombois, D. and H.P. Sims. 1966. Response of three grasses to two soils and a water table depth gradient. Ecology 47: 644-648.

Munro, J.A. 1919. Notes on some birds of the Okanagan Valley, British Columbia. Auk 36:64-74.

Murie, O. 1954. A Field Guide to Animal Tracks. Houghton Mifflin Co., Boston, Mass.

Murray, M.D. and R.E. Miller. 1986. Early survival and growth of planted Douglas-fir with red alder in four mixed regimes. U.S. Dep. Agric. For. Serv., Res. Pap. PNW-366.

Myerscough, P.J. 1980. Biological flora of the British Isles: *Epilobium angustifolium* L. J. Ecol. 68: 1047-1074.

Myerscough, P.J. and F.H. Whitehead. 1966. Comparative biology of *Tussilago farfara* L., *Chamaenerion angustifolium* (L.) Scop., *Epilobium montanum* L. and *Epilobium adenocaulon* Hausskn. I. General biology and germination. New Phytol. 65:192-210.

______. 1967. Comparative biology of *Tussilago farfara* L., *Chamaenerion angustifolium* (L.) Scop., *Epilobium montanum* L. and *Epilobium adenocaulon* Hausskn. II. Growth and ecology. New Phytol. 66: 785-823.

National Wildlife Federation. 1987. Grizzly bear compendium. U.S. Fish Wildl. Serv. and U.S. Dep. Int., Washington, D.C.

Neiland, B.L. and L.A. Viereck. 1977. Forest types and ecosystems. *In* North American forest types at latitudes north of 60 degrees. Proc. Symp. Univ. Alaska, Fairbanks, Alaska. pp. 109-136.

Nelson, E.A. 1974. Greenhouse and field fertilization of thin-leaved huckleberry. U.S. Dep. Agric. For. Serv., Res. Note PNW-236.

Nelson, E.E., E.M. Hanson, C.Y. Li, and J.M. Trappe. 1978. The role of alder in reducing losses from laminated root rot. *In* Utilization and management of alder. D.G. Briggs, D.S. Debell, and W.A. Atkinson (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-70, pp. 273-282.

Newton, M. 1978. A comparison of red alder, Douglas-fir, and western hemlock productivities as related to site: a panel discussion. *In* Utilization and management of alder. D.G. Briggs, D.S. DeBell, and W.A. Atkinson (editors). U.S. Dep. Agric. Gen. Tech. Rep. PNW-70. pp. 175-182.

Newton, M., B.A. El Hassan, and J. Zavitkovski. 1968. Role of red alder in western Oregon forest succession. *In* Biology of Alder. T.M. Trappe, J.F. Franklin, R.F. Tarrant, and G.M. Hansen (editors). Proc. Symp. U.S. Dep. Agric. For. Serv., pp. 73-84.

Newton, M. and F.B. Knight. 1981. Handbook of weed and insect control chemicals for forest resource managers. Timber Press, Beaverton, Oreg.

Newton, M. and D.E. White. 1983. Effect of salmonberry on growth of planted conifers. *In* Proc. West. Soc. Weed Sci. Vol. 36-1983. Las Vegas, Nev., pp. 59-64.

Nichols, G.E. 1934. The influence of exposure to winter temperatures upon seed germination in various native American plants. Ecology 15:364-373.

Nicholson, A.C. 1989. Water relations, survival and growth of Douglas-fir seedlings at a pinegrass dominated site in the Interior Douglas-fir zone of south-central British Columbia. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Nicholson, A. and I.S. Paterson. 1976. The ecological implications of bracken control to plant/animal systems. Bot. J. Linn. Soc. 73:269-283.

Nilsen, E.T. 1986a. Causes and significance of winter leaf movements in rhododendrons. Am. Rhododendron Soc. 40:14-15.

______. 1986b. Quantitative phenology and leaf survivorship of *Rhododendron maximum* in contrasting irradiances environments of the Southern Appalachian Mountains. Am. J. Bot. 73:822-831.

Norby, R.J. and T.T. Kozlowski. 1983. Flooding and SO_2 stress interaction in *Betula papyrifera* and *B. nigra* seedlings. For. Sci. 29:739-750.

Noste, N.V. and C.L. Bushey. 1987. Fire response of shrubs of dry forest habitat types in Montana and Idaho. U.S. Dep. Agric. For. Serv., Intermountain Res. Sta., Gen. Tech. Rep. INT-239.

Nuszdorfer, K.L. and F.C. Nuszdorfer. 1988. Increasing seedling growth on salal sites using controlled-release fertilizer. *In* Vegetation competition and responses: Proc. 3rd annual vegetation management workshop, Feb. 15-17, 1988. E. Hamilton and S. Watts (editors). Can. For. Serv. and B.C. Min. For., Victoria, B.C. FRDA Rep. 026. pp. 54-55.

Nyberg, J.B., F.L. Bunnell, D.W. Janz, and R.M. Ellis. 1986. Managing young forests as black-tailed deer winter ranges. B.C. Min. For., Victoria, B.C.

Oberbauer, S. and P.C. Miller. 1982. Effect of water potential on seed germination. Holarct. Ecol. 5:218-220.

O'Brien, T.P. 1964. Problems in the control of the bracken fern in Victoria. J. Australian Inst. Agric. Sci. 29:119-127.

Ohmann, L.F. 1982. Tall shrub layer biomass in conifer plantations of northeastern Minnesota. U.S. Dep. Agric. For. Serv., Res. Pap. NC-219.

Ohmann, L.F., H.O. Batzer, R.R. Buech, D.C. Lothner, D.A. Perala, A.L. Schipper, Jr., and E.S. Verry. 1978. White paper birch: type description; and evaluation discussion. Some harvesting options and their consequences for the aspen, birch, and associated conifer forest types of the Lake states. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NC-48, pp. 12-14

Olmsted, N.W. and J.D. Curtis. 1947. Seeds of the forest floor. Ecology 28:49-52.

Packee, E.C. 1976. An ecological approach toward yield optimization through species allocation. Ph.D. thesis. Univ. Minn., St. Paul, Minn.

Page, C.N. 1976. The taxonomy and phytogeography of bracken – a review. Bot. J. Linn. Soc. 73:1-34.

______. 1979. Experimental aspects of fern ecology. Chap. 15. *In* The experimental biology of ferns. A.F. Dyer (editor). Academic Press, London.

______. 1982. The Ferns of Britain and Ireland. Cambridge Univ. Press, Cambridge, England.

Parke, J.L., R.G. Linderman, and J.N. Trappe. 1983. Effects of forest litter on mycorrhizal development and growth of Douglas-fir and western redcedar seedlings. Can. J. For. Res. 13:660-671.

Peeler, K.C. and D.S. DeBell. 1987. Variation in damage from growing season frosts among open-pollinated families of red alder. U.S. Dep. Agric. For. Serv., Res. Note PNW-RN-464.

Perala, D.A. 1971. Controlling hazel, aspen suckers, and mountain maple with picloram. U.S. Dep. Agric., For. Serv. Res. Note NC-129.

______. 1984. How endemic injuries affect early growth of aspen suckers. Can. J. For. Res. 14:755-762.

Petersen, T.D. 1988. Effects of interference from *Calamagrostis rubescens* on size distributions in stands of *Pinus ponderosa*. J. Appl. Ecol. 25:265-272.

Petersen, T.D. and B.D. Maxwell. 1987. Water stress of *Pinus ponderosa* in relation to foliage density of neighbouring plants. Can. J. For. Res. 17:1620-1622.

Peterson, E.B. 1965. The subalpine mountain hemlock zone. Part 1: Phytocoenoses. Ecol. West. North Am. 1:76-78.

Peterson, E.B., R.D. Kabzems, and N.M. Peterson. 1989. Hardwood Management Problems in Northeastern British Columbia: an information review. For. Can. and B.C. Min. For., Victoria, B.C. FRDA Rep. 066.

Peterson, R.L. 1978. North American Moose. Univ. Toronto Press, Toronto, Ont.

Pezeshki, S.R. and T.M. Hinkley. 1988. Water relations characteristics of *Alnus rubra* and *Populus trichocarpa*: responses to field drought. Can. J. For. Res. 18:1159-1166.

Pezeshki, S.R. and C.D. Oliver. 1985. Early growth patterns of red alder and black cottonwood in mixed species plantations. For. Sci. 31:190-200.

Plocher, A.E. and K.L. Carvell. 1987. Population dynamics of rosebay rhododendron thickets in the southern Appalachians. Bull. Torrey Bot. Club 114:121-126.

Plummer, A.P., A.C. Hull, Jr., G. Stewart, and J.H. Robertson. 1955. Seedling rangelands in Utah, Nevada, southern Idaho and western Wyoming. U.S. Dep. Agric., Handb. No. 71.

Pojar, J. 1974. The relation of the reproductive biology of plants to the stucture and function of four plant communities. Ph.D. thesis. Univ. B.C., Vancouver, B.C.

_______. 1975. Hummingbird flowers of British Columbia. Syesis 8: 25-28.

_______ (editor). 1983. Forest ecology. *In* Forestry handbook for British Columbia. 4th ed. S.B. Watts (editor). D.W. Friesen & Sons Ltd., Cloverdale, B.C., pp. 221-318.

Pojar, J., R. Love, D. Meidinger, and R. Scagel. 1982. Some common plants of the Sub-boreal spruce zone. B.C. Min. For., Victoria, B.C. Land Manage. Handb. No. 6.

Pojar, J., R. Trowbridge, and D. Coates. 1984. Ecosystem classification and interpretation of the Sub-Boreal Spruce zone, Prince Rupert Forest Region, British Columbia. B.C. Min. For., Victoria, B.C. Land Manage. Rep. No. 17.

Pomerleau, R. and M. Lortie. 1962. Relationships of dieback to the rooting depth of white birch. For. Sci. 8:19-224.

Porsild, A.E. 1979. Rocky Mountain Wildflowers. National Museums of Natural Sciences and National Museums of Canada, Ottawa, Ont.

Post, B.W., W.H. Carmean, and R.O. Curtis. 1969. Birch soil-site requirements. *In* Birch Symp. Proc. U.S. Dep. Agric. For. Serv., NE For. Exp. Sta., pp. 95-101.

Pratt, D.W., R.A. Black, and B.A. Zamora. 1984. Buried viable seed in a ponderosa pine community. Can. J. Bot. 62:44-52.

Price, D.T., T.A. Black, and F.M. Kelliher. 1986. Effects of salal understory removal on photosynthetic rate and stomatal conductance of young Douglas-fir trees. Can. J. For. Res. 16:90-97.

Quenet, R.V. 1973. Growth simulation of trees, shrubs, grasses and forbs on a big-game winter range. Ph.D. thesis. Univ. B.C., Vancouver, B.C.

Radwan, M.A. 1987. Effects of fertilization on growth and foliar nutrients of red alder seedlings. U.S. Dep. Agric. For. Serv., Res. Pap. PNW-375.

Rawson, J.W. 1974. Willows. *In* Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (compilers). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NE-9, pp. 147-149.

Reid, E.H., L.A. Isaac, and G.D. Pickford. 1938. Plant succession on a cut-over, burned, and grazed Douglas-fir area. U.S. Dep. Agric. For. Serv., Portland, Oreg. For. Res. Note 26.

Rice, E.L. 1974. Allelopathy. Academic Press, New York, N.Y.

Richardson, J. 1979. Relationships between natural reproduction of hardwoods and softwoods in western Newfoundland. Can. Fish. Environ., For. Serv. Nfld. For. Res. Cent., St. John's, Nfld., Info. Rep. N-X-166.

Rickett, H.W. 1944. *Cornus stolonifera* and *Cornus occidentalis.* Brittonia 5:149-159.

Risenhoover, K.L. and S.A. Maass. 1987. The influence of moose on the composition and structure of Isle Royale forests. Can. J. For. Res. 17:357-364.

Ritcey, R. 1988. Moose in British Columbia. B.C. Min. Environ. Fish Wildl. Branch., Inf. and Education Section, Victoria, B.C.

Roberts, C. 1977. Vegetative response to manual brush control. Proc. 1977 West. For. Conf., Portland, Oreg.

Roe, A.L. 1958. Silvics of black cottonwood. U.S. Dep. Agric., For. Serv. Misc. Publ. 17.

Rogers, R. 1974. Blueberries. *In* Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (compilers). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NE-9, pp. 12-15.

Rouse, C. 1986. Fire effects in northeastern forests: aspen. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NC-102.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. *In* The role of fire in northern circumpolar ecosystems. R.W. Wein and D.A. Micheal (editors). John Wiley & Sons Ltd., New York, N.Y., pp. 135-154.

Rue, L.L.,III. 1978. The Deer of North America. Book Division, Times Mirror Magazines, Inc., Crown, New York, N.Y.

Ruppel, D.H. 1968. Tent caterpillars in British Columbia. Can. For. Serv., Pac. Res. Cent., Victoria, B.C. Pest Leaflet 17.

Russell, D.W. 1973. The life history of vine maple on the H.J. Andrews Experimental Forest. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Russell, W.B. 1979. Native grass reclamation research: container plantings in the eastern slopes of Alberta. Alta For. Serv., Alta Energy and Nat. Res. Rep. 140.

Ruth, R.H. 1970. Effect of shade on germination and growth of salmonberry. U.S. Dep. Agric. For. Serv., Res. Pap. PNW-96.

Sabhasri, S. 1961. An ecological study of salal (*Gaultheria shallon*). Ph.D. thesis. Univ. Wash., Seattle, Wash.

Sabhasri, S. and W.K. Ferrell. 1960. Invasion of brush species into small stand openings in the Douglas-fir forests of the Willamette Foothills. Northwest Sci. 34:77-80.

Sadoway, K.L. 1986. Effects of intensive forest management on non-ungulate mammals of Vancouver Island: problem analysis. B.C. Min. Environ. and B.C. Min. of For., IWIFR-24, Victoria, B.C.

Safford, L.O. 1982. Correlation of greenhouse bioassay with field response to fertilizer by paper birch. Plant Soil 64:167-176.

Safford, L.O. and M.M. Czapowskyj. 1986. Fertilizer stimulates growth and mortality in young *Populus-Betula* stand: 10-year results. Can. J. For. Res. 16:807-813.

Salisbury, E. 1961. Weeds and Aliens. Collins, London.

Sampson, A.W. 1989. Effect of grazing upon aspen reproduction. U.S. Dep. Agric., Bull. No. 741.

Schier, G.A. 1978. Effect of girdling, decapitation, and defoliation on root suckering by young aspen. *In* Proc. 5th North Am. For. Biol. Workshop. A. Hollis and A.E. Squillace (editors). Univ. Fla., School For. Resources Conserv., Gainesville, Fla., pp. 259-267.

_______. 1981. Physiological research on adventitious shoot development in aspen roots. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-107.

Schier, G.A. and R.B. Campbell. 1978. Aspen sucker regeneration following burning and clearcutting on two sites in the Rocky Mountains. For. Sci. 24(2):303-308.

Schier, G.A., J.R. Jones, and R.P. Winokur. 1985. Vegetative reproduction. *In* Aspen: ecology and management in the western United States. N.V. Debyle and R.P. Winokur (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. RM-119.

Schmidt, W.C. and J.E. Lotan. 1980. Phenology of common forest flora of the northern Rockies – 1928 to 1937. U.S. Dep. Agric. For. Serv., Res. Pap. INT-259.

Schmitt, M.D.C., M.M. Czapowskyj, L.O. Safford, and A.L. Leaf. 1981. Biomass and elemental uptake in fertilized and unfertilized *Betula paperifera* Marsh. and *Populus grandidentata* Michx. Plant Soil 60:111-121.

Schneller, J.J. 1979. Biosystematic investigations on the lady fern *(Athyrium filix-femina)*. Plant Systematics and Evolution 132:255-277.

Schoonmaker, P. and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. For. Sci. 34:960-979.

Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. U.S. Dep. Agric. For. Serv., Wash., D.C., Agric. Handb. No. 450.

Schroeder, R.L. 1982. Habitat suitability index models: yellow warbler. U.S. Dep. Int., Fish Wildl. Serv., Washington, D.C.

Scott, D.R. 1978. A comparison of red alder, Douglas-fir, and western Hemlock productivities as related to site: a panel discussion. *In* Utilization and management of alder. D.G. Briggs, D.S. Debell, and W.A. Atkinson (editors). U.S. Dep. Agric. Gen. Tech. Rep. PNW-70.

Shainsky, L.J. 1988. Competitive interactions between Douglas-fir and red alder seedlings: growth analysis, resource use, and physiology. Ph.D. thesis. Oreg. State Univ., Corvallis, Oreg.

Sharp, W.M. 1974. Ecology of shrubs and vines. *In* Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (compilers). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NE-9., pp. 2-5.

Shaw, N. 1984. Producing bareroot seedlings of native shrubs. *In* The challenge of producing native plants for the Intermountain area. P.M. Murphy (editor). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-168., pp. 6-15.

Sheppard, R., III, and H. Pellet. 1976. Light intensity effects on red-osier dogwood. Hort. Sci. 11(3):200-202.

Shigo, A.L. 1969. Diseases of birch. *In* Birch Symp. Proc. E. vH. Larson (editor). U.S. Dep. Agric. For. Serv., NE For. Range Exp. Sta. pp. 147-150.

Shulte, P.G., T.M. Hinkley, and R.F. Stettler. 1987. Stomatal responses of *Populus* to leaf water potential. Can. J. Bot. 65:255-260.

Simard, S. 1989. Competition among lodgepole pine seedlings and plant species in a Sitka alder-dominated-shrub community in the southern Interior of British Columbia. M.Sc. thesis. Oreg. State Univ., Corvallis, Oreg.

Simpson, K. and G.P. Woods. 1984. Movements and habitats of caribou in the mountains of southern British Columbia. B.C. Min. Environ. and Parks, Nelson, B.C. Wildl. Bull. 13-57. ISSN0829-9560.

Sims, H.P. and D. Mueller-Dombois. 1968. Effect of grass competition and depth to water table on height growth of coniferous tree seedlings. Ecology 49:597-603.

Singleton, J. 1976. Food habits of wild ungulates in British Columbia: Bibliography and plant synopsis. B.C. Min. Environ., Terrestrial Studies Branch, Victoria, B.C.

Smith, B.A. 1988. Selection of flood-resistant and susceptible seedlings of *Populus trichocarpa* Torr. & Gray. Can. J. For. Res. 18:271-275.

Smith, D.W. 1962. Ecological studies of *Vaccinium* species in Alberta. Can. J. Plant Sci. 42:82-90.

Smithberg, M. 1974. Red-osier dogwood. *In* Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (compilers). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NE-9., pp. 44-47.

Smithberg, M. and J.D. Gill. 1974. Roses. *In* Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (compilers). U.S. Dep. Agric., Gen. Tech. Rep., NE-9. pp.116-121.

Smithberg, M. and C.J. Weiser. 1968. Patterns of variation among climatic races of red-osier dogwood. Ecology 49:495-504.

Solbreck, C. and D. Andersson. 1987. Vertical distribution of fireweed, *Epilobium angustifoilium*, seeds in the air. Can. J. Bot. 65:2177-2178.

Solomon, D.S. and W.B. Leak. 1969. Stocking, growth, and yield of birch stands. *In* Birch Symp. Proc. E. vH. Larson (editor). U.S. Dep. Agric. For. Serv., NE For. Exp. Sta. pp. 106-118.

Soper, J.H. and A.F. Szczawinski. 1976. Mount Revelstoke National Park wildflowers. Natural History Series, No. 3.

Stalmaster, M.V. and J.R. Newman. 1979. Perch-site preferences of wintering bald eagles in northwest Washington. J. Wildl. Manage. 43:221-224.

Stanek, W., D. Beddows, and D. State. 1979. Fertilization and thinning effects on a Douglas-fir ecosystem at Shawnigan Lake on Vancouver Island: some observations on salal and bracken fern undergrowth. Can. For. Serv., Victoria, B.C. Inf. Rep. BC-R-1.

Stark, N. and R. Steele. 1977. Nutrient content of forest shrubs following burning. Am. J. Bot. 64:1218-1224.

Stearns, F.W. 1974. Hazels. *In* Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (compilers). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NE-9, pp. 65-70.

Steen, H.K. 1966. Vegetation following slash fires in one western Oregon locality. Northwest Sci. 40:113-120.

Steneker, G.A. 1976. Guide to the silvicultural management of trembling aspen in the Prairie Provinces. Can. For. Serv., Inf. Rep. NOR-X-164.

Steneker, G.A. and R.E. Wall. 1970. Aspen clones: their significance and recognition. Can. For. Serv., For. Res. Lab. Liaison and Serv. Note MS-L-8.

Stewart, G.H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. Can. J. For. Res. 16:558-568.

Stewart, R.E. 1972. Foliage applied herbicides for control of Oregon Coast Range brush species. Proc. West. Soc. of Weed Sci., Vol. 25, March 14-16, Salt Lake City, Utah.

_______. 1974a. Foliage sprays for site preparation and release from six coastal brush species. U.S. Dep. Agric. For. Serv., Res. Paper PNW-172.

_______. 1974b. Budbreak sprays for site preparation and release from six coastal brush species. U.S. Dep. Agric. For. Serv. Res., Paper PNW-176.

_______. 1974c. Repeated spraying to control four coastal brush species. U.S. Dep. Agric. For. Serv., Res. Note PNW-238.

_______. 1975. Allelopathic potential of western Bracken. J. Chem. Ecol. 1:161-169.

_______. 1976. Herbicides for control of western swordfern and western bracken. U.S. Dep. Agric. For. Serv., Res. Note PNW-284.

_______. 1977. Ammonium thiocyanate does not increase herbicidal control of salmonberry. U.S. Dep. Agric. For. Serv., Res. Note PNW-308

_______. 1978. Origin and development of vegetation after spraying and burning in a coastal Oregon clearcut. U.S. Dep. Agric. For. Serv., Res. Note PNW-317.

_______. 1986. First decade plant succession following the Sundance forest fire, Northern Idaho. U.S. Dep. Agric. For. Serv., Rep. INT-197.

Stewart, R.E. and T. Beebe. 1974. Survival of ponderosa pine seedlings following control of competing grasses. Proc. West. Soc. Weed Sci. 21:55-58.

Stickney, P.F. 1980. Data base for post-fire succession, first 6 to 9 years, in Montana larch-fir forests. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-62.

_______. 1981. Vegetative recovery and development. *In* Clearcutting and fire in the larch-Douglas-fir forests of western Montana. U.S. Dep. Agric. For. Serv., Gen Tech. Rep. INT-99, pp.33-40.

_______. 1985. Database for early postfire succession on the Sundance Burn, northern Idaho. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-189.

_______. 1986. First decade plant succession following the Sundance forest fire, Northern Idaho. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-197.

Stiell, W.M. and A.B. Berry. 1986. Productivity of short rotation aspen stands. For. Chron. 62:10-15.

Stine, R., J.C. Gordon, and K.K. Ching. 1981. Variation in early growth of black cottonwood (*Populus trichocarpa*) clones in the Willamette Valley. Oreg. State Univ., School For. Res. Pap. 43.

Stout, D.G. and B. Brooke. 1985. Growth and development of pinegrass in Interior British Columbia. J. Range Manage. 38:4. pp. 312-317.

_______. 1987. Tiller production of grazed and clipped pinegrass. Can. J. Plant Sci. 67: 503-508.

Stout, D.G., J. Hall, B. Brooke, and A. McLean. 1981. Influence of successive years of simulated grazing (clipping) on pinegrass growth. Can. J. Plant Sci. 61: 939-943.

Strain, B.R. 1966. The effect of late spring frost on the radial growth of variant quaking aspen biotypes. For. Sci. 12:334-337.

Strothman, R.O. and Z.A. Zasada. 1957. Silvical characteristics of quaking aspen (*Populus tremuloides*). U.S. Dep. Agric. For. Serv., Res. Pap. 49.

Sund, J.D. and J.M. Finnis. 1978. Year round control of bigleaf maple. Weyerhaeuser Co. West. For. Res. Cent., Centralia, Wash.

Sutton, R.F. 1958. Chemical herbicides and their uses in the silviculture of forests of eastern Canada. Can. Dep. North. Affairs and Nat. Res. For. Branch., For. Res. Div. Tech. Note 68.

_______. 1984. Plantation establishment in the boreal forest: glyphosate, hexazinone and manual weed control. For. Chron. 60:283-287.

Svejcar, T. 1986. Comparative water relations of *Carex geyeri* and *Calamagrostis rubescens*. Bot. Gaz. 147:71-77.

Sylvester, T.W. and R.W. Wein. 1981. Fuel characteristics of arctic plant species and simulated plant community flammability by Rothermel's model. Can. J. Bot. 59:898-907.

Szczawinski, A.C. 1962. The Heather family (Ericaceae) of British Columbia. B.C. Prov. Museum, Handb. No. 19.

Tamm, C.O. 1956. The response of *Chamaenerion angustifolium* (L.) Scop. to different nitrogen sources in water culture. Physiol. Planta. 9: 331-337.

Tang, Z.C. and T.T. Kozlowski. 1982. Some physiological and growth responses of *Betula papyrifera* seedlings to flooding. Physiol. Plant. 55: 415-420.

Tappeiner, J.C. 1971. Invasion and development of beaked hazel in red pine stands in northern Minnesota. Ecology 52:514-519.

Tappeiner, J.C. 1979. Effect of fire and 2,4-D on the early stages of beaked hazel (*Corylus cornuta)* understories. Weed Sci. 27:162-166.

Tappeiner, J.C. and A.A. Alm. 1972. Effect of hazel on the nutrient composition of litter and forest floor in jack and red pine stands. Minn. For. Res. Note No. 235.

Tappeiner, J.C. and H.H. John. 1973. Biomass and nutrient content of hazel undergrowth. Ecology 54: 1352-1348.

Tarrant, R.F. 1983. Nitrogen fixation in North American forestry: research and application. *In* Biological nitrogen fixation in forest ecosystems: foundations and applications. J.C. Gordon and C.T. Wheeler (editors). Martinus Nijhoff/Dr. W. Junk Publ. pp. 261-277.

Tarrant, R.F. and R.E. Miller. 1963. Accumulation of organic matter and soil nitrogen beneath a plantation of red alder and Douglas-fir. Soil Sci. Soc. Am. Proc. 27: 231-234.

Taylor, R.F. 1932. The successional trend and its relation to second-growth forests in southeastern Alaska. Ecology 13:382-391.

Taylor, R.L. and B. MacBryde. 1977. Vascular plants of British Columbia: a descriptive resource inventory. Bot. Garden, Univ. B.C., Vancouver, B.C. Tech. Bull. No. 4.

Taylor, T.M.C. 1973a. The ferns and fern-allies of British Columbia. B.C. Prov. Museum, Handb. No. 12.

____________. 1973b. The Rose family of British Columbia. B.C. Prov. Museum, Handb. No. 30.

Thompson, C. 1988. The effect of glyphosate treatments on a mixed brush community in the ICHd subzone (SX 83407). *In* Vegetation competition and responses: Proc. 3rd annual vegetation management workshop, Feb. 15-17, 1988. E. Hamilton and S. Watts (editors). Can. For. Serv. and B.C. Min. For., Victoria, B.C. FRDA Rep. 026. pp. 57-60.

Thompson, S. 1989. The effects of vegetation on prescribed burning for wildlife habitat and range improvement in southeastern British Columbia. *In* Wildlife and Range Prescribed Burning Workshop Proc. Oct. 27-28, 1988. M.C. Feller and S.M. Thompson (editors). Univ. B.C., Fac. For., Vancouver, B.C. pp. 120-133.

Tiedemann, A.R. and G.O. Klock. 1976. Development of vegetation after fire, seeding, and fertilization on the Entiat Experimental Forest. *In* Proc. Annual Tall Timbers Fire Ecol. Conf. (Pac. Northwest), Oct. 16-17, 1974. 15:171-192.

Tinnin, R.O. and L. A. Kirkpatrick. 1985. The allelopathic influence of broadleaved trees and shrubs on seedlings of Douglas-fir. For. Sci. 31:945-952.

Tisdale, E.W. and M. Hironaka. 1981. The sagebrush-grass region: a review of the ecological literature. Univ. Idaho, Coll. For., Wildl. and Range Sci. Bull. No. 13.

Toms, H.N.W. 1964. Plant diseases in southern British Columbia: a host index. Can. Dep. Agric. Reprinted from Canadian Plant Disease Survey 44:143-225.

Tripp, L.N., D.F. Bezdicek, and P.E. Heilman. 1979. Seasonal and diurnal patterns and rates of nitrogen fixation by young red alder. For. Sci. 25:371-380.

Triska, F.J. and J.R. Sedell. 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. Ecology 57:783-792.

Turner, D.J. and W.G. Richardson. 1979. Herbicide evaluation for forestry uses. Report on Forest Research 1979. London, U.K. HMSO 55-57.

Turner, J. 1979. Effects of fertilization on understory vegetation. *In* Proc. Forest Fertilization Conf. S.P. Gessel, R.M. Kenady, and W.A. Atkinson (editors). Univ. Wash., Coll. For. Resources, Seattle, Wash. Contrib. No. 40, pp. 168-173.

University of British Columbia Botanical Garden. 1970. *Gaultheria shallon* Pursh. Davidsonia 1(3):29-31.

______. 1971. *Sambucus racemosa* L. ssp. *pubens* (Michx.) House var. *arborescens* (T. & G.) Gray. Davidsonia 2(3):33-36.

______. 1976. *Acer circinatum.* Davidsonia 7(3):32-37.

______. 1977. The genus *Viburnum* in British Columbia. Davidsonia 8(3):41-47.

______. 1978. The genus *Rosa* in British Columbia. Davidsonia 9(2):30-43.

______. 1979. The genus *Lonicera* in British Columbia. Davidsonia 10(3):54-63.

U.S. Department of Agriculture. 1974. Seeds of woody plants of the United States. For. Serv., Agric. Handb. 450.

______. 1981. Fire effects on Pacific Northwest forest and range vegetation. For. Serv., Pac. N.W. Rep. 41.

Valentine, K.W.G., R.N. Sprout, T.E. Baker, and L.M. Lavkulich (editors). 1978. The soil landscapes of British Columbia. B.C. Min. Environ., Resource Analysis Branch, Victoria, B.C.

Vales, D.J. 1986. Functional relationships between salal understory and forest overstory. B.C. Min. Environ. and B.C. Min. For., IWIFR-32, Victoria, B.C.

van Andel, J. 1975. A study on the population dynamics of the perennial plant species *Chamaenerion angustifolium* (L.) Scop. Oecologia 19:329-337.

______. 1976. Growth and mineral nutrition of *Chamaenerion angustifolium* (L.) Scop. (=*Epilobium angustifolium* L.). Ecol. Plant. 1:25-40.

van Andel, J., J.W. Bos, and W. Ernst. 1978. An experimental study on two populations of *Chamaenerion angustifolium* (L.) Scop. (=*Epilobium angustifolium* L.) occurring on contrasting soils, with particular reference to the response to bicarbonate. New Phytol. 81:763-772.

van Andel, J. and H.J.M. Nelissen. 1979. Nutritional status of soil and plant species in several clearings in coniferous woods compared to that in two related habitats. Vegetatio 39:115-121.

van Andel, J. and J. Rozema. 1974. An experiment in reproduction from seed within existing populations of *Chamaenerion angustifolium* (L.) Scop. Plant Soil 41:415-419.

van Andel, J. and F. Vera. 1977. Reproductive allocation in *Senecio sylvaticus* and *Chamaenerion angustifolium* in relation to mineral nutrition. J. Ecol. 65:747-758.

van Cleve, K. and L.A. Viereck. 1972. Distribution of selected chemical elements in even-aged alder (*Alnus*) ecosystems near Fairbanks, Alaska. Arct. Alp. Res. 4(3):239-255.

van der Kamp, B.J. 1986. Nitrogen fixation in cottonwood wetwood. Can. J. For. Res. 16:1118-1120.

Vander Born, W.H. and N. Malik. 1984. Herbicide use in North American forestry: a literature survey and an assessment of its environmental impact and its future potential for forest management in the prairie provinces of Canada. Univ. Alta., Dep. Plant Sci., Edmonton, Alta.

Viereck, L.A. 1983. The effects of fire in black spruce ecosystems of Alaska and northen Canada. *In* The role of fire in northern circumpolar ecosystems. R.W. Wein and D.A. McLean (editors). John Wiley & Sons Ltd. New York, N.Y. pp. 201-220.

Viereck, L.A., and C.T. Dyrness. 1979. Ecological effects of the Wickersham dome fire near Fairbanks, Alaska. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-90.

Viereck, L.A. and E.L. Little. 1972. Alaska trees and shrubs. U.S. Dep. Agric. For. Serv., Handb. No. 410.

Vihanek, R.E. 1985. The effects of slashburning on the growth and nutrition of young Douglas-fir plantations in some dry, salal dominated ecosystems. M.Sc. thesis. Univ. B.C., Vancouver, B.C. 98 p.

Vogel, S.A. 1985. Influence of canopy cover and simulated grazing on water relations, stomatal conductance and photosynthesis of pinegrass and elk sedge. M.Sc. thesis. Univ. Mont., Missoula, Mont.

Waddington, J. and S. Bittman. 1987. Control of brush regrowth in northeastern Saskatchewan by several concentrations of herbicides applied with a roller. Can. J. Plant Sci. 67:467-475.

Wagner, D. 1979. Systematics of *Polystichum* in western North America north of Mexico. Pterid. 1: 1-64.

Wagner, R.G. 1984. Two year response of eight Coast Range brush species to six release treatments. Oreg. State Univ., For. Res. Lab., Corvallis, Oreg.

Waldron, R.M. 1959. Hazel foliage treatments to reduce suppression of white spruce reproduction. Can. Dep. Northern Affairs and Nat. Resources, For. Branch, Res. Div., Tech. Note No. 75.

Wali, M.K. 1969. Vegetation-environment relationships of Sub-Boreal Spruce zone ecosystems in British Columbia. Ph.D. thesis. Univ. B.C., Vancouver, B.C.

Walker, L.R. and F.S. Chapin, III. 1986. Physiological controls over seedling growth in primary succession on an Alaska floodplain. Ecology 67:1508-1523.

Walker, L.R., J.C. Zasada, and F.S. Chapin, III. 1986. The role of life history processes in primary succession on an Alaskan floodplain. Ecology 67:1243-1253.

Wangberg, J.K. 1975. Biology of the thimbleberry gallmaker *Diastrophus kincaidii*. Pan-Pacific Entomologist. 51:39-48.

Warren, L.F. 1982. Garlon herbicides control hardwoods, release conifers in western forests. Industrial Veg. Manage. 14:18-21.

Watson, L.E., R.W. Parker, and D.F. Polster. 1980. Manual of species suitability for reclamation in Alberta. Alta. Land Conserv. Reclamation Council Rep No. RRTAC 80-5. 2 Vols.

Watt, A.S. 1940. Contributions to the ecology of bracken (*Pteridium aquilinum*). (I). New Phytol. 39:401-422.

______. 1976. The ecological status of bracken. Bot. J. Linn. Soc. 73:217-239.

Watts, S. (editor). 1983. Forestry handbook for British Columbia. 4th ed. Univ. B.C., Fac. Forestry, Forest Undergraduate Society, Vancouver, B.C.

Weetman, G.F., H.H. Krause, E. Koller, and J.M. Veilleux. 1987. Interprovincial forest fertilization trials: 5- and 10-year results. For. Chron. 63:184-192.

Wein, R.W. and L.C. Bliss. 1973. Changes in arctic Eriophorum tussock communities following fire. Ecology 54: 845-852.

Wein, R.W. and D.A. MacLean. 1973. Cottongrass (*Eriophorum vaginatum*) germination requirements and colonizing potential in the arctic. Can. J. Bot. 51:2509-2513.

Weinberg, E.S. and B.R. Voeller. 1969. External factors inducing germination of fern spores. Am. Fern J. 59:153-167.

Wendel, G.W. and J.N. Kochendorfer. 1982. Glyphosate controls hardwoods in West Virginia. U.S. Dep. Agric. For. Serv., Res. Pap. NE-497.

West, N.E. and P.T. Tueller. 1972. Special approaches to studies of competition and succession in shrub communities. *In* Wildland shrubs – their biology and utilization. C.M. McKeel, J.P. Blaisdell, and J.R. Goodin (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-1., pp. 165-171.

Westcott, C. 1971. Plant Disease Handbook. 3rd ed. Van Nostrand Reinhold Co., New York, N.Y.

Wheeler, C.T., M.E. McLaughlin, and P. Steele. 1981. A comparison of symbiotic nitrogen fixation in Scotland in *Alnus glutinosa* and *Alnus rubra*. Plant and Soil. 61:169-188.

Whitney, G.G. 1982. The productivity and carbohydrate economy of a developing stand of *Rubus idaeus*. Can. J. Bot. 60: 2697-2703.

______. 1986. A demographic analysis of *Rubus idaeus* and *Rubus pubescens*. Can. J. Bot. 64:2916-2921.

Wile, B.C. 1981. A test of five herbicides and three methods of ground application for cleaning young stands and clearcut areas. Can. For. Serv., Inf. Rep. M-X-126.

William, R.D., L.C. Burrill, R. Parker, D.G. Swan, S.W. Howard, and D. Kidder. 1987. Pacific Northwest weed control handbook. Exten. Serv., Oreg. State Univ., Wash. State Univ., and Univ. Idaho. 239 p.

Williams, I.H. 1959. Effects of environment on *Rubus idaeus* L. (II). Field observations on the variety Malling Promise. J. Hort. Sci. 34: 170-175.

Williamson, B., H.M. Lawson, J.A.T. Woodfern, A.J. Hargreaves, J.S. Wiseman, and S.C. Gordon. 1979. Vigour control, and integrated approach to cane, pest and disease management in red raspberry (*Rubus idaeus*). Ann. Appl. Biol. 92:359-368.

Willms, W., A. McLean, R. Tucker, and R. Ritcey. 1980. Deer and cattle diets on summer range in British Columbia. J. Range Manage. 33:55-59.

Winship, L.J. and J.D. Tjepkema. 1984. Nitrogen fixation and respiration by root nodules of *Alnus rubra* Bong.: effects of temperature and oxygen concentration. Plant and Soil 64:91-106.

Wittinger, W.T., W.L. Pengelly, L.L. Irwin, and J.M. Peek. 1977. A 20-year record of shrub succession in logged areas in the cedar-hemlock of northern Idaho. Northwest Sci. 51:161-171.

Wolff, J.O. 1978. Food habits of snowshoe hares in Interior Alaska. J. Wildl. Manage. 42:148-153.

Worley, D.M. and C.M. Nixon. 1974. Elders. *In* Shrubs and vines for northeastern wildlife. J.D. Gill and W.M. Healy (compilers). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NE-9, pp. 48-51.

Wright, H.A. 1972. Shrub response to fire. *In* Wildland shrubs: their biology and utilization. C.M. McKell, J.P. Blaisdell, and J.R. Goodin (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. INT-1, pp. 204-217.

Yarie, J. 1978. The role of understory vegetation in the nutrient cycle of forested ecosystems in the Mountain Hemlock biogeoclimatic zone. Ph.D. thesis. Univ. B.C., Vancouver, B.C.

______. 1980. The role of understoy vegetation in the nutrient cycle of forested ecosystems in the Mountain Hemlock biogeoclimatic zone. Ecology 61:1498-1514.

Yerkes, V.P. 1960. Occurrence of shrubs and herbaceous vegetation after clearcutting old-growth Douglas-fir in the Oregon Cascades. U.S. Dep. Agric. For. Serv., Res. Pap. PNW-34.

Zasada, J.C. 1971. Natural regeneration of interior Alaska forest-seed, seedbed and vegetative reproduction considerations. *In* Proc. Symp. on Fire in the Northern Environment. C.W. Slaughter, R.J. Barney, and G.M. Hansen (editors). Fairbanks, Alaska. pp.231-246.

Zasada, J.C., R.A. Norum, C.E. Teusch, and R. Densmore. 1987. Survival and growth of planted black spruce, alder, aspen, and willow after fire on black spruce/feather moss sites in Interior Alaska. For. Chron. 63: 84-88.

Zasada, J.C., R.A. Norum, R.M. van Veldhuizen, and C.E. Teutsch. 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. Can. J. For. Res. 13:903-913.

Zasada, J.C., J.C. Tappeiner, II, P. Ryan, and B. Maxwell. 1988. Ecology and management of broadleaved species in the Oregon Coast Range. *In* Vegetation competition and responses: Proc. 3rd annual vegetation management workshop, Feb. 15-17, 1988. E. Hamilton and S. Watts (editors). Can. For. Serv. and B.C. Min. For., Victoria, B.C. FRDA Rep. 026. p. 61-62.

Zasada, J.C. and L.A. Viereck. 1975. The effect of temperature and stratification on germination in selected members of the *Salicaceae* in interior Alaska. Can. J. For. Res. 5:333-337.

Zasada, J.C., L.A. Viereck, M.J. Foote, R.H. Parkenson, J.O. Wolff, and L.A. Lankford, Jr. 1981. Natural regeneration of balsam poplar following harvesting in the Susitna Valley, Alaska. For. Chron. 57:57-65.

Zavitkovski, J. and R.D. Stevens. 1972. Primary productivity of red alder ecosystems. Ecology 53:235-242.

Zieroth, E. 1984. Burning to improve aspen suckering. Proc. Aspen Symp., May 22-24, 1984. Colorado Springs, Colo.

Zimmer, K. 1976. Untersuchungen zum Wachstum von Freilandfarnen. Gartenbauwissenschaft 41(3):137-140.

Zwickel, F.C. and J.F. Bendell. 1972. Observations on food habits of incubating female blue grouse. The Condor 74:493-494.

5 UNPUBLISHED REFERENCES

Alaback, P. [Undated]. Oregon State Univ., Corvallis, Oreg. Unpublished data.

Balfour, P. 1989. Summary of herbicide effects on major forage species. B.C. Min. Environ., Victoria, B.C. Unpublished report.

Bancroft, B. 1989. Can aspen regeneration in the southern Interior of British Columbia be reduced by preharvest treatments? A literature review. Can. For. Serv. and B.C. Min. For., FRDA Proj. 2.57. Unpublished report.

Bancroft, B., G. Butt, and D. Lousier. 1988. Alder seed tree control – a review. FRDA Proj. 2.57. Unpublished report.

Banner, A., J. Pojar, and R. Trowbridge. 1983. Ecosystem classification of the Coastal Western Hemlock Zone, Queen Charlotte Island Subzone (CWHg), Prince Rupert Forest Region, British Columbia, B.C. Min. For., Smithers, B.C. Unpublished report.

________. 1984. Representative wetland types of the Pacific Oceanic Wetland Region. B.C. Min. For., Smithers, B.C. Unpublished report.

Barker, J.E. 1988. Control of salal with Garlon (1988 update). Expert Committee on Weeds (ECW). Research report. p. 194. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1989, Winnipeg, Man. Unpublished.

Barker, J.E. and G.F. Weetman. 1986. Salal eradication study: growth and nutrition results. Western Forest Products and Univ. B.C., Faculty of Forestry, Vancouver, B.C. Unpublished report.

Barker, J.E., G.F. Weetman, and R.M. Fournier. 1987. Growth and nutrition of sitka spruce, western hemlock and western red cedar following fertilization of coastal cedar/hemlock sites. Final report. Prepared for: Western Forest Products Ltd. Section 88 Contract No. NV99034. 14 p. Unpublished.

Belz, D. 1989. Red alder cutting window. Wash. State Dep. Nat. Res. First year report 400 series. Olympia, Wash. Unpublished.

Blower, D. 1982. Key winter forage plants for B.C. ungulates. Terr. Studies Br., B.C. Min. Env., Victoria, B.C. Unpublished mimeo.

Boateng, J.O. and G. Ackerman. 1988. Manual and chemical control treatments of bigleaf maple coppices. Expert Committee on Weeds (ECW). Research report. p. 192. Western Canada Section meeting. Nov. 29-Dec. 1, 1988. Winnipeg, Man. Unpublished.

Brand, D.G. 1984. Assessment of the growth of Douglas-fir plantations. IV. Characteristics and dynamics of competing vegetation. Univ. B.C., Vancouver, B.C. Unpublished report.

B.C. Ministry of Environment. [Undated]. Plant Forage Species List. Unpublished mimeo.

Carr, W.W. [Undated]. The use of a grass-legume cover as a silvicultural tool (EP 834). B.C. Min. For., Research Branch, Victoria, B.C. Unpublished report.

Caza, C.L. and J.P. Kimmins. 1987. Composition and structure of plant communities on NSR cutovers in the ESSF, Clearwater Forest District. FRDA 3.32 contract report. B.C. Min. For., Kamloops, 96p. Unpublished.

Clark, M.B. 1975. Grass - conifer compatability: a problem analysis. B.C. Min. For., Kamloops, B.C. Unpublished report.

Conard, S.G. 1982. A preliminary study of the influences of environment, phenology, and application variables on the responses of major conifer and brush species to glyphosate. Weyerhaueser Co., Tacoma, Wash. Unpublished report.

Coordinated Research on Alternative Forestry Treatments and Systems (CRAFTS). 1986. Annual report. For. Res. Lab., Oregon State Univ., Corvallis, Oreg. Unpublished.

______. 1987. Annual report. For. Res. Lab., Oreg. State Univ., Corvallis, Oreg. Unpublished.

______. 1988. Annual report. For. Res. Lab., Oreg. State Univ., Corvallis, Oreg. Unpublished.

Coupé, R. and A.R. Yee (editors). 1982. Identification and interpretation of ecosystems of the Cariboo Forest Region (EP 822.04). B.C. Min. For., Williams Lake, B.C. Unpublished report.

D'Anjou, B.N. 1986a. Conifer release with triclopyr ester: 2nd year results. Expert Committee on Weeds (ECW). Research report, p. 196. Western Canada Section Meeting. Nov. 25-27, 1986, Saskatoon, Sask. Unpublished.

______. 1986b. Efficacy trial of granular and liquid hexazinone and sulfometuron methyl. 2nd year results. Expert Committee on Weeds (ECW). Research report, p. 197. Western Canada Section Meeting. Nov. 25-27, 1986, Saskatoon, Sask. Unpublished.

______. 1988a. Effect of application timing on the impact of glyphosate and triclopyr ester on non-crop vegetation species. FRDA 2.14. Unpublished report.

______. 1988b. Effect of treatment timing on the impact of glyphosate and triclopyr ester on several non-crop vegetation species. Expert Committee on Weeds (ECW). Research report, p. 201. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1988, Winnipeg, Man. Unpublished.

______. 1988c. Growth response of several vegetation species and Douglas-fir saplings to application of granular and liquid hexazinone, sulfometuron and manual vegetation removal. B.C. Min. For. FRDA 2.8. 3rd Progress report. Unpublished.

______. 1988d. Growth response of several vegetation species to applications of granular and liquid hexazinone, sulfometuron methyl, and manual vegetation removal. Expert Committee on Weeds (ECW). Research report, p. 199. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1988, Winnipeg, Man. Unpublished.

______. 1988e. Response of several vegetation species and grand fir saplings to the herbicides sulfometuron methyl, hexazinone and methsulfuron methyl and the manual cutting of non-crop vegetation. Expert Committee on Weeds (ECW). Research report, p. 198. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1988, Winnipeg, Man. Unpublished.

D'Anjou, B. and F. Pendl. 1989. Effect of manual treatment timing on red alder regrowth and conifer response. FRDA 2.12. Fifth year report. Unpublished.

DeLong, C. 1983. B.C. Min. For., Prince George, B.C. Unpublished data.

DeLong, S.C. 1988. Control of trembling aspen using pre-harvesting treatment with glyphosate. Expert Committee on Weeds (ECW). Research report, p. 202. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1988, Winnineg, Man. Unpublished.

DeLong, S.C., S. Jenvey, and A. McLeod. 1984. A field guide for the interpretation of ecosystems of the SBSf in the Prince George Forest Region. First approx. B.C. Min. For., Prince George, B.C. Unpublished Field Manual.

Demarchi, R.A. and D.A. Demarchi. 1967. Winter and spring food habits of whitetailed deer in the East Kootenays. Presented to: 4th Annual Meeting. B.C. Fish and Wildl. Branch, April, 1967, Kamloops, B.C. Unpublished report.

Drouin, J.A. 1985. Conifer release with hexazinone and spot gun on spring application. Expert Committee on Weeds (ECW). Research report, p. 216. Western Canada Section Meeting. Dec. 3-5, 1985, Edmonton, Alta. Unpublished.

Dunsworth, B.G. 1986. Salal removal and its impact on crop tree performance. Expert Committee on Weeds (ECW). Research report, p. 197. Western Canada Section Meeting. Nov. 25-27, 1986, Saskatoon, Sask. Unpublished.

______. 1987. Northwest Bay alder control trial. Expert Committee on Weeds (ECW). Research report, p. 196. Western Canada Section Meeting. Dec. 1-3, 1987, Victoria, B.C. Unpublished.

Dyke, B. 1987. A comparison of effectiveness one and two years following treatments of 1985 Roundup application in the Revelstoke Forest District. Prepared for: B.C. Min. For., Revelstoke Forest District. Unpublished report.

Expert Committee on Weeds (ECW). 1984. Research report. Western Canada Section Meeting. Dec. 3-6, 1984. Winnipeg, Man. Unpublished.

______. 1985. Research report. Western Canada Section Meeting. Dec. 3-5, 1985, Edmonton, Alberta. Unpublished.

______. 1986. Research report. Western Canada Section Meeting. Nov. 25-27, 1986, Saskatoon, Sask. Unpublished.

______. 1987. Research report. Western Canada Section Meeting. Dec. 1-3, 1987, Victoria, B.C. Unpublished.

______. 1988. Research report. Western Canada Section Meeting. Nov. 29-Dec. 1, 1988, Winnipeg, Man. Unpublished.

Fahlman, R. and L.J. Herring. 1984. Grassy site preparation using four herbicides. Expert Committee on Weeds (ECW). Research report, p. 267. Western Canada Section Meeting. Dec. 3-6, 1984, Winnipeg, Man. Unpublished.

______. 1985. Grassy site preparation using four herbicides: 2nd year results. Expert Committee on Weeds (ECW). Research report, p. 211. Western Canada Section Meeting. Dec. 3-5, 1985, Edmonton, Alta. Unpublished.

George, G. 1984. Second year investigations of the impacts of two forest herbicides in the Cariboo Subregion. B.C. Min. Environ. Habitat Protection Section, Williams Lake, B.C. Unpublished report.

Hamilton, E. 1988. Impacts of prescribed burning on soil-vegetation relationships in the Sub-boreal Spruce zone. *In* Wildlife and Range Prescribed Burning Workshop Proceedings. M.C. Feller and S.M. Thomson (editors). Fac. For., Univ. B.C., Vancouver, B.C. pp. 171-189.

Hamilton, T. 1984. B.C. Min. Environ., Victoria, B.C. Unpublished data.

Harrington, C.A. 1981. U.S. Dep. Agric. For. Serv., Olympia, Wash. Unpublished data.

Herring, L.J. 1984a. Grassy site preparation with glyphosate. Expert Committee on Weeds (ECW). Research report, p. 264. Western Canada Section Meeting. Dec. 3-6, 1984, Winnipeg, Man. Unpublished.

______. 1984b. Site preparation with glyphosate and fosamine ammonium. Expert Committee on Weeds (ECW). Research report, p. 268. Western Canada Section Meeting. Dec. 3-6, 1984, Winnipeg, Man. Unpublished.

______. 1984c. Site preparation with glyphosate and hexazinone gridballs. Expert Committee on Weeds (ECW). Research report, p. 266. Western Canada Section Meeting. Dec. 3-6, 1984, Winnipeg, Man. Unpublished.

______. 1988a. Performance of white spruce following an early glyphosate brushing and weeding treatment. Expert Committee on Weeds (ECW). Research report, p. 205. Western Canada Section Meeting. Nov. 29-Dec. 1, 1988, Winnipeg, Man. Unpublished.

______. 1988b. White spruce seedling performance following site preparation with hexazinone. Expert Committee on Weeds (ECW). Research Report, p. 206. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1988, Winnipeg, Man. Unpublished.

Herring, L.J. and R. Fahlman. 1984. Site preparation with glyphosate. Expert Committee on Weeds (ECW). Research report, p. 220. Western Canada Section Meeting. Dec. 3-6, 1984, Winnipeg, Man. Unpublished.

Hibbs, D.E. and K. Cromack. 1989. Actinorhizal plants in Pacific Northwest forests. Oreg. State Univ., For. Res. Lab., Corvallis, Oreg. Unpublished report.

Ketcheson, M.V., A.R. Warner, and S. Thompson. 1985. An evaluation of published climax ecosystem associations as a framework for predicting vegetation hazard rating system for the ICHa1, ICHa2, and ESSFc biogeoclimatic units in the Nelson Forest Region. B. C. Min. For., Nelson, B.C. (draft report).

Korol, J. and P. Wallis. 1983. Snag management for dependent wildlife. Univ. B.C., Vancouver, B.C. Unpublished Forestry 495 term paper.

Ladd, M. 1989. Forest herbicides and effects on wildlife browse in the Okanagan sub-region. Prepared for B.C. Min. Environ., Habitat Protection Section, Penticton, B.C. Unpublished report.

Langford, K.C. 1942. Effect of grazing on huckleberry production. U.S. Dep. Agric., For. Serv. report, cited by Minore 1972. On file at Mount Adams Ranger District, Trout Lake, Wash. Unpublished.

LePage, P. and J.C. Pollack. 1988a. Conifer release with glyphosate and western hemlock tolerance: 2nd year results. Expert Committee on Weeds (ECW). Research report. p. 266. Western Canada Section Meeting. Nov. 29-Dec. 1, 1988, Winnipeg, Man.

______. 1988. Site preparation rate x timing trial. Expert Committee on Weeds (ECW). Research report, p. 208. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1988, Winnipeg, Man. Unpublished.

Lloyd, D. (compiler). 1984. Identification and interpretation of ecosystem units in the North Thompson - Shuswap drainage basins. First Approx. B.C. Min. For. Res. Sect., Kamloops, B.C. Unpublished draft.

Lloyd, D., K. Angove, G. Hope, C. Thompson, and B. Ivanco. 1989. A field guide for the interpretation of ecosystems in the Kamoloops Forest Region. B.C. Min. For., Res. Sect., Kamloops Forest Region. Unpublished draft.

Macadam, A., J. Pollack, and R. Trowbridge. 1984. Trials of prescribed fire for vegetation management. The rehabilitation of coastal alluvial sites in the Prince Rupert Region (EP 885.03). B.C. Min. For., Smithers, B.C. Unpublished draft.

Mather, J. 1986. An assessment of silvicultural practices used in the IDFa and IDFb subzones of the Western Kamloops Forest Region. B.C. Min. For. Silv. Sect., Kamloops, B.C. Unpublished report.

______. 1987. Assessment of silvicultural practices used in the ESSFe and ESSFm subzones in the Kamloops Forest Region. B.C. Min. For., Kamloops, B.C. Unpublished report.

______. 1988. Assessment of silvicultural practices used in the Interior Cedar Hemlock zone of the southern Interior: ICHm2, b. and v subzones: Salmon Arm, Vernon and Revelstoke Districts. B.C. Min. For., Kamloops, B.C. FRDA Project 3.47. Unpublished report.

Messier, C. and J.P. Kimmins. 1988. Below-ground interactions between salal and coniferous crop seedlings in the CWHb on northern Vancouver Island - first year report. B.C. Min. For., Vancouver, B.C. FRDA 2.31. Unpublished report.

Messier, C., T. Honer, and J.P. Kimmins. 1989. Photosynthetic photon flux density, red: far-red ratio, and minimum light reqirement for survival of *Gaultheria shallon* in western redcedar hemlock stands in coastal British Columbia. Dep. of For. Sci., Fac. of Forestry, Univ. of B.C., Vancouver, B.C. Unpublished report.

Mihajlovich, M. and A. Switzer. 1984. Conifer release with triclopyr ester. Expert Committee on Weeds (ECW). Research report, p. 270. Western Canada Section Meeting. Dec. 3-6, 1984, Winnipeg, Man. Unpublished.

Miles, J. and K. Weikle. [Undated]. Browse utilization by wintering deer in the Interior Douglas-fir zone of south central British Columbia. Agric. Can. Program UP-B-290, Report No. 1. Unpublished.

Newhouse, F.C. 1988a. Effects of hexazinone applied on a 1 year old pine plantation. Expert Committee on Weeds. Research report, p. 210. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1988, Winnipeg, Man. Unpublished.

______. 1988b. Effects of hexazinone applied operationally in Prince Rupert. Expert Committee on Weeds (ECW). Research Report, p. 211. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1988, Winnipeg, Man. Unpublished.

Newton, M. and T. O'Dell. 1973. High site rehabilitation in western Oregon: A survey. Unpublished manuscript.

Noble-Hearle, G. 1989. Treatment effectiveness checks: brushing and weeding program. B.C. Min. For., Penticton Forest District, Kamloops Forest Region. Unpublished report.

Parminter, J. 1983. Fire ecological relationships for the biogeoclimatic zones and subzones of the Fort Nelson Timber Supply Area. Summary Report. B.C. Min. For. Protection Branch, Victoria, B.C. Unpublished report.

Pendl, F. and B. D'Anjou. 1984. Operational trial of the herbicide "Roundup" at Pender Harbour. Establishment Report. B.C. Min. For., Vancouver, B.C. Unpublished report.

Perry, J. 1983. Hardwood invasion on cutblocks in the Cariboo Forest Region. B.C. Min. For., Williams Lake, B.C. Unpublished report.

Pojar, J. and A. Banner. 1984. Old-growth forests and introduced black-tailed deer on the Queen Charlotte Islands, British Columbia. Unpublished report.

Pollack, J. 1984. B.C. Min. For., Smithers, B.C. Unpublished data.

Pollack, J.C. 1988. Conifer release with glyphosate. Expert Committee on Weeds (ECW). Research report, p. 223. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1988, Winnipeg, Man. Unpublished.

Pollack, J.C. and P. LePage. 1986a. Pronone 10G (Granular Hexazinone) herbicide trial at the Paul Fire, Lakes District. 2nd year report: SX85503R. B.C. Min. For. Res. Sect., Prince Rupert Forest Region. Unpublished report.

______. 1986b. Roundup (glyphosate) herbicide trial at Hells Bells, Kispiox Forest District. 3rd year progress report: SX82704R. B.C. Min. For. Res. Sect. Prince Rupert Forest Region. Unpublished report.

______. 1987. Site preparation using three herbicides for willow control. Expert Committee on Weeds (ECW). Research report, p. 202. Western Canada Section Meeting. Dec. 1-3, 1987, Victoria, B.C. Unpublished.

______. 1988. Site preparation with glyphosate by broadcast ground spray and hack-and-squirt methods on a coastal alluvial site. First year results. Expert Committee on Weeds (ECW). Research report, p. 212. Western Canada Section Meeting. Nov. 29 - Dec. 1, 1988, Winnipeg, Man. Unpublished.

Pollack, J.C. and F. van Thienen. Conifer release with glyphosate. Expert Committee on Weeds (ECW). 1986. Research report, p. 224. Western Canada Section Meeting. Nov. 25-27, 1986, Saskatoon, Sask. Unpublished.

Porter, G.L. 1989. Willow species of disturbed sites in the sub-boreal spruce zone in north-central British Columbia. B.C. Min. of For., Res. Branch, Victoria, B.C. Unpublished report.

Revel, J. 1983. The impact of some hardwoods on silviculture in the Prince Rupert Forest Region. B.C. Min. For., Prince George, B.C. Unpublished discussion paper.

Reynolds, P.E., D.G. Pitt, R. Whitehead, and K. King. 1988. Three-year weed efficacy results of a glyphosate conifer release trial. Expert Committee on Weeds (ECW). Research report, p. 218. Western Canada Section Meeting. Nov. 29-Dec. 1, 1988, Winnipeg, Man. Unpublished.

Roberts, A. 1983. A guide to the willows of the Cariboo Forest region. B.C. Min. For., Williams Lake, B.C. Unpublished report.

Roberts, C. 1980. Cooperative brush control study: 2nd year report. Project co-ordinated with Oreg. State Univ. For. Res. Lab., Corvallis, Oreg. Unpublished report.

Simard, S. 1988. Interim results of 1986 Roundup trial. Prepared for: B.C. Min. For., Clearwater Forest District. Unpublished report.

Simard, S. and J. Mather. 1989. Operational summaries of coastal complexes. B.C. Min. For. Victoria, B.C. FRDA Project 2.56. Unpublished report.

Smith, I.D., M.A.M. Bell, B.L. Zirul, D.A. Blood, and G.W. Smith. [Undated]. Food habits of Vancouver Island Roosevelt elk. B.C. Fish Wildl. Branch, Victoria, B.C. Unplublished report.

Teskey, K.K. and S.O.S. Masterson. 1984a. Hexazinone fall application with spot gun for conifer release. Expert Committee on Weeds. Research report, p. 280. Western Canada Section Meeting. Dec. 3-6, 1984, Winnipeg, Man. Unpublished.

_______. 1984b. Hexazinone liquid, aerially applied for conifer release. Expert Committee on Weeds (ECW). Research report. p. 272. Western Canada Section Meeting. Dec. 3-6, 1984, Winnipeg, Man. Unpublished.

_______. 1984c. Hexazinone liquid for aerial site prepration and conifer release. Expert Committee on Weeds (ECW). Research report, p. 274. Western Canada Section Meeting. Dec. 3-6, 1984, Winnipeg, Man. Unpublished.

_______. 1985a. Hexazinone in granular form for conifer release. Expert Committee on Weeds (ECW). Research report, p. 275. Western Canada Section Meeting. Dec. 3-5, 1985, Edmonton, Alta. Unpublished.

_______. 1985b. Hexazinone liquid, aerially applied, for conifer release. Expert Committee on Weeds (ECW). Research report, p. 272. Western Canada Section Meeting. Dec. 3-5, 1985, Edmonton, Alta. Unpublished.

_______. 1985c. Hexazinone liquid for aerial site preparation and conifer release. Expert Committee on Weeds (ECW). Research report, p. 273. Western Canada Section Meeting. Dec. 3-5, 1985, Edmonton, Alta. Unpublished.

_______. 1985d. Hexazinone liquid, spot gun applied, for conifer release. Expert Committee on Weeds (ECW). Research report, p. 241. Western Canada Section Meeting. Dec. 3-5, 1985, Edmonton, Alta. Unpublished.

_______. 1986a. Hexazinone liquid, aerially applied, for conifer release. Expert Committee on Weeds (ECW). Research report, p. 237. Western Canada Section Meeting. Nov. 23-27, 1986, Saskatoon, Sask. Unpublished.

_______. 1986b. Hexazinone liquid for aerial site preparation and conifer release. Expert Committee on Weeds (ECW). Research report, p. 239. Western Canada Section Meeting. Nov. 23-27, 1986, Saskatoon, Sask. Unpublished.

_______. 1986c. Hexazinone liquid for conifer release with spot and broadcast methods. Expert Committee on Weeds (ECW). Research report, p. 228. Western Canada Section Meeting. Nov. 25-27, 1986, Saskatoon, Sask. Unpublished.

_______. 1986d. Hexazinone liquid for conifer release with spot and broadcast methods. Expert Committee on Weeds (ECW). Research report, p. 229. Western Canada Section Meeting. Nov. 25-27, 1986, Saskatoon, Sask. Unpublished.

______. 1986e. Hexazinone liquid, spot gun applied, for conifer release. Expert Committee on Weeds (ECW). Research report, p. 201. Western Canada Section Meeting. Nov. 23-27, 1986, Saskatchewan, Sask. Unpublished.

______. 1986f. Hexazinone summer application with spot gun for conifer release. Expert Committee on Weeds (ECW). Research report, p. 232. Western Canada Section Meeting. Nov. 25-27, 1986, Saskatoon, Sask. Unpublished.

Trowbridge, R., J. Pojar, and T. Lewis. 1983. Interim classification of the Boreal White and Black Spruce biogeoclimatic zone in the Prince Rupert Forest Region. B.C. Min. For., Smithers, B.C. Unpublished report.

Utzig, G., D. MacDonald, and P. Comeau. 1978. Ecological classification for the Nelson Forest District. Second approx. B.C. Min. For., Nelson, B.C. Unpublished report.

Utzig, G., D. MacDonald, G. Still, M. Ketcheson, T. Braumandl, and A. Warner. 1983. Ecological classification for the Nelson Forest District. Third approx. B.C. Min. For., Nelson, B.C. Unpublished report.

Wellman, R. and C. Harrison. 1987. Granular hexazinone site prep. Expert Committee on Weeds (ECW). Research report, p. 207. Western Canada Section Meeting, Victoria, B.C. Unpublished.

Yole, D., J. Pojar, and B. Robinson. 1982. Ecosystem classification of the Coastal Western Hemlock Zone within the Mid Coast Timber Supply Area, Prince Rupert Forest Region, British Columbia. B.C. Min. For., Smithers, B.C. Unpublished report.

6 LIST OF PERSONAL CONTACTS

Alaback, P. Research Associate. Department of Forest Science, Oregon State University, Corvallis, Oreg.

Armleder, H. Wildlife Habitat Ecologist. B.C. Ministry of Forests, Research Section, Williams Lake, B.C.

Bancroft, B. Ecologist. Madrone Forestry Consultants, Victoria, B.C.

Barron, B. District Silviculturist. B.C. Ministry of Forests, District Office, Grand Forks, B.C.

Bigley, D. Graduate Student. Faculty of Forestry, University of British Columbia, Vancouver, B.C.

Burke, M. Department of Agricultural Sciences, Oregon State University, Corvallis, Oreg.

Caza, C. Ph.D. Candidate. Forest Science Department, Faculty of Forestry, University of British Columbia, Vancouver, B.C.

Ceska, A. Botanist. Royal B.C. Museum, Victoria, B.C.

Coates, D. Research Silviculturist. B.C. Ministry of Forests, Research Section, Smithers, B.C.

Conard, S. Ecologist. U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Riverside, Cal.

Coupé, R. Ecologist. B.C. Ministry of Forests, Research Section, Williams Lake, B.C.

Craven, S. Resource Forester. Fletcher Challenge, Vancouver, B.C.

D'Anjou, B. Research Silviculturist. B.C. Ministry of Forests, Forest Sciences Section, Vancouver, B.C.

DeBell, D. Project Leader. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Olympia, Wash.

DeLong, C. Ecologist. B.C. Ministry of Forests, Research Section, Prince George, B.C.

de Montigne, L. Ph.D. Candidate. Forest Science Department, Faculty of Forestry, University of British Columbia, Vancouver, B.C.

Dunsworth, B. Silviculturist-Reforestation. MacMillan Bloedel Ltd., Woodland Services, Nanaimo, B.C.

Ellen, G. Range Resource Officer. B.C. Ministry of Forests, District Office, Clearwater, B.C.

Endacott, N. Acting Stand Tending Coordinator. B.C. Ministry of Forests, Smithers, B.C.

Geisler, B.M. Stand Tending Coordinator. B.C. Ministry of Forests, Silviculture Section, Smithers, B.C.

Gray, R. Stand Tending Forester. B.C. Ministry of Forests, Silviculture Section, Kamloops, B.C.

Greenley, D. District Silviculturist. B.C. Ministry of Forests, District Office, MacKenzie, B.C.

Hamilton, E. Research Ecologist. B.C. Ministry of Forests, Research Branch, Victoria, B.C.

Hamilton, T. Wildlife Biologist. B.C. Ministry of Environment, Wildlife Branch, Victoria, B.C.

Harcombe, A. Habitat Research Specialist. B.C. Ministry of Environment, Research and Development Section, Wildlife Branch, Victoria, B.C.

Harrison, D. Silviculture Forester. Canadian Forest Products Ltd., Woss, B.C.

Haworth, K. District Silviculturist. B.C. Ministry of Forests, District Office, Kitimat, B.C.

Herring, L. Forest Research Officer. B.C. Ministry of Forests, Research Section, Prince George, B.C.

Ivanco, B. (former) Silviculture Planning Forester. B.C. Ministry of Forests, Silviculture Section, Kamloops, B.C.

Kennah, G. Silviculture Officer. B.C. Ministry of Forests, Silviculture Section, Vancouver, B.C.

Lea, T. Vegetation Ecologist. B.C. Ministry of Environment, Habitat Inventory Section, Victoria, B.C.

Lewis, T. Consultant. Burnaby, B.C.

Lindeburgh, S. Forestry Consultant. Clearwater, B.C.

Lloyd, D. Regional Research Ecologist. B.C. Ministry of Forests, Research Section, Kamloops, B.C.

Lloyd, G. Silviculture Officer. B.C. Ministry of Forests, Silviculture Section, Smithers, B.C.

McGee, A. Graduate of Ph.D. Program. Faculty of Forestry, University of British Columbia, Vancouver, B.C.

MacKinnon, G. Habitat Technician. B.C. Ministry of Environment, Smithers, B.C.

MacLauchlin, L. Forest Entomologist. B.C. Ministry of Forests, Protection Section, Kamloops, B.C.

McLarnon, J. District Silviculturist. B.C. Ministry of Forests, District Office, Campbell River, B.C.

McLennan, D. Ph.D. Candidate. Faculty of Forestry, University of British Columbia, Vancouver, B.C.

McRuer, S. District Silviculturist. B.C. Ministry of Forests, District Office, Port Alberni, B.C.

Mather, J. Forester. Skyline Forestry Consultants Ltd., Kamloops, B.C.

Merler, H. Forest Pathologist. B.C. Ministry of Forests, Protection Section, Kamloops, B.C.

Messier, C. Ph.D. Candidate. Faculty of Forestry, University of British Columbia, Vancouver, B.C.

Miles, J. Silviculture Resource Assistant. B.C. Ministry of Forests, District Office, Revelstoke, B.C.

Minore, D. Principal Plant Ecologist. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Corvallis, Oreg.

Mitchell, W. Regional Research Pedologist. B.C. Ministry of Forests, Research Section, Kamloops, B.C.

Muller, R. Silviculture Resource Officer. B.C. Ministry of Forests, District Office, Duncan, B.C.

Mullett, D. District Silviculturist. B.C. Ministry of Forests, District Office, Invermere, B.C.

Nash, B. Resource Assistant. B.C. Ministry of Forests, District Office, Merritt, B.C.

Newton, M. Professor. Department of Forest Science, Oregon State University, Corvallis, Oreg.

Pojar, J. Ecologist. B.C. Ministry of Forests, Research Section, Smithers, B.C.

Pollack, J. Forest Science Officer. B.C. Ministry of Forests, Research Section, Nelson, B.C.

Raymer, B. Resource Assistant. B.C. Ministry of Forests, District Office, Lillooet, B.C.

Roemer, H. Assistant Director. Ecological Reserves Unit, Victoria, B.C.

Russell, F. Research Biologist. B.C. Ministry of Forests, Research Section, Kamloops, B.C.

Salayka, D. District Silviculturist. B.C. Ministry of Forests, District Office, McBride, B.C.

Scott, M. Stand Tending Coordinator. B.C. Ministry of Forests, Silviculture Section, Vancouver, B.C.

Simard, S. Forestry Consultant. Kamloops, B.C.

Steen, O. Ecologist. B.C. Ministry of Forests, Research Section, Williams Lake, B.C.

Sullivan, T. Applied Animal Research Institute, Langley, B.C.

Tanner, M. Operations Superintendent. B.C. Ministry of Forests, District Office, Clearwater, B.C.

Tappeiner, J. Professor. Department of Forest Science, Oregon State University, Corvallis, Oreg.

Tucker, R. Range Planning Agrologist. B.C. Ministry of Forests, Range Section, Kamloops, B.C.

Wadey, P. District Silviculturist. B.C. Ministry of Forest, District Office, Fort St. John, B.C.

Weetman, G. Professor. Faculty of Forestry, University of British Columbia, Vancouver, B.C.

Whitehead, R. Silviculturist. Pacific Forestry Centre, Victoria, B.C.

Whynot, T. M.Sc. Candidate. Faculty of Forestry, University of British Columbia, Vancouver, B.C.

Wright, J. District Silviculturist. B.C. Ministry of Forests, District Office, Salmon Arm, B.C.

Zasada, J. Scientist. Forest Sciences Lab, Oregon State University, Corvallis, Oreg.