

The biology of Canadian weeds. 105. *Rubus strigosus* Michx., *Rubus parviflorus* Nutt., and *Rubus spectabilis* Pursh.

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Oleskevich, C., Shamoun, S. F. and Punja, Z. K. 1996. **The biology of Canadian weeds. 105. *Rubus strigosus* Michx., *Rubus parviflorus* Nutt., and *Rubus spectabilis* Pursh.** Can. J. Plant Sci. **76**: 187–201. Wild raspberry (*Rubus strigosus* Michx.), thimbleberry (*Rubus parviflorus* Nutt.), and salmonberry (*Rubus spectabilis* Pursh) are native perennial deciduous shrubs that rapidly invade disturbed areas. Through prolific vegetative growth, these shrubs form dense, multilayered, and monospecific stands and form extensive clonal colonies. They create habitat and supply food sources for a variety of forest fauna and are important in nutrient cycling and reducing soil erosion. These *Rubus* shrubs may effectively outcompete economically valuable regenerating conifers. A review of chemical, manual, and biological control methods is presented. Reproductive biology, growth and development, and population dynamics are discussed in detail.

Key words: *Rubus strigosus*, *Rubus idaeus*, *Rubus parviflorus*, *Rubus spectabilis*, wild red raspberry, thimbleberry, salmonberry, forest weed biology, competition, distribution

Oleskevich, C., Shamoun, S. F. et Punja, Z. K. 1996. **Biologie des mauvaises herbes du Canada. 105. *Rubus strigosus* Michx., *R. parviflorus* Nutt., et *R. spectabilis* Pursh.** Can. J. Plant Sci. **76**: 187–201. Le framboisier sauvage (*Rubus strigosus* Michx.), la ronce parviflore (*R. parviflorus* Nutt.) et la ronce remarquable (*R. spectabilis* Pursh) sont des arbrisseaux vivaces caducifoliés indigènes qui colonisent rapidement les terrains perturbés. Grâce à leur abondante croissance végétative, ces espèces forment des peuplements uni spécifiques denses, à étages multiples, ainsi que de vastes colonies clônales. Elles offrent refuge et nourriture à toutes sortes d'animaux forestiers et jouent un rôle important dans le renouvellement des nutriments et dans la protection des sols contre l'érosion. Par ailleurs, la compétition causée par ces espèces peut étouffer la régénération des conifères. Les auteurs font une mise au point des méthodes de lutte chimique, manuelle et biologique. L'article passe également en revue les divers aspects de la biologie de ces espèces: reproduction, croissance et développement, ainsi que la dynamique de leurs populations.

Mots clés: *Rubus strigosus*, *R. idaeus*, *R. parviflorus*, *R. spectabilis*, framboisier sauvage, ronce parviflore, ronce remarquable, biologie des adventices forestières, compétition, aire de répartition

1. Names

I. *Rubus strigosus* Michx. In North America, also referred to as *Rubus idaeus* L. or *R. idaeus* var. *strigosus* (Michx.) Focke (Kartesz 1994); **wild red raspberry**, **framboisier sauvage** (Mulligan 1992).

II. *Rubus parviflorus* Nutt. (*Rubus nutkanus* Moc.); **thimbleberry** (Taylor and MacBryde 1977); **ronce parviflore** (Anonymous 1974a).

III. *Rubus spectabilis* Pursh; **salmonberry** (Taylor and MacBryde 1977); **ronce remarquable** (Anonymous 1974a).

Rosaceae, rose family, brambles, Rosacées.

2. Description and Account of Variation

(a) *Rubus strigosus*, *R. parviflorus*, and *R. spectabilis* are perennial deciduous shrubs, spreading principally by the production of root suckers or rhizomes.

Rubus strigosus (Fig. 1). Erect biennial stems (canes) arising from perennial subterranean branching root suckers and stolons, up to 2 m tall, often arched. First-year stems (primocanes) with broadly based prickles, slender bristles

and glandular hairs; leaves alternate, pinnately compound, 3–5 or 3–7 foliate, leaflets from broadly ovate to narrowly lanceolate, irregularly serrate pointed, petioles bristly–hispid, stipules slender. Second-year stems (floricanes) armed with weak spines and bristles, often glandular–hairy, bark brownish, exfoliating, older stems smooth striate; leaves approximately ternate, 7–10 cm long, margins evenly double-serrate, green above, white–tomentose beneath. Inflorescence of 2–5 flowers in terminal or axillary racemes or solitary in upper leaf axils, flower stalks and hypanthium bristly and glandular hispid, flowers drooping or in small thyrsoid clusters; flowers white, 1 cm broad, elliptical petals 5–6 mm long, shorter than sepals, carpels numerous. Fruit an aggregate of many small drupelets, mature fruit red, ovoid, sweet, falling intact from dry receptacle, receptacle persistent on plant (Hitchcock et al. 1961; Rouleau 1964; Scoggan 1978; Roland 1983).

Abbreviations: a.e., acid equivalent; a.i., active ingredient, TNC, total nonstructural carbohydrate

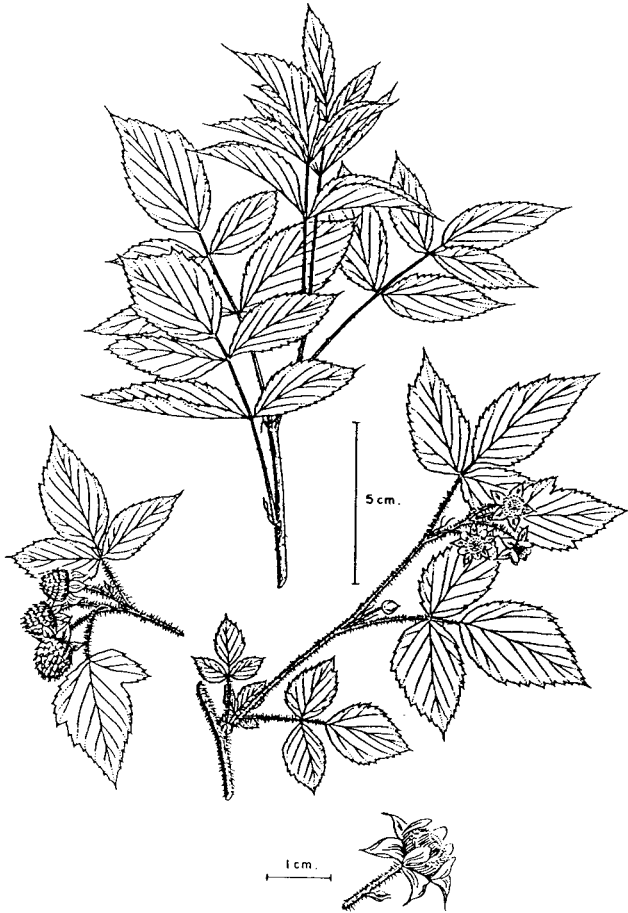


Fig. 1. *Rubus strigosus* Michx. [*Rubus idaeus* var. *strigosus* (Michx.) Foche] (Taylor 1973).

Chromosome number differs because of the highly variable nature of this species. Worldwide, most raspberries are reported as diploid, with $2n = 14$ (Ellis et al. 1991), although a range of ploidies exists in Canadian populations, including $2n = 14, 21, 28, 35,$ and 42 (Moss 1983). Karyotype variation was investigated by Pool et al. (1981), and Nybom and Schaal (1990) reported DNA fingerprinting identified genotypic distribution in natural populations.

Rubus parviflorus (Fig. 2). Rhizomatous shrub with erect to semi-prostrate stems, reaching 0.5–2.5 m tall, unarmed, glandular hairy, bark shredding. Leaves simple, large, 12–20 cm long, palmately 3–5 or 3–7 lobed, with deep basal sinus, lobes triangular, cordate, twice dentate–serrate, soft, slightly pilose on both surfaces to densely pilose beneath; petioles glandular–pubescent, up to twice as long as blade; stipules narrow, 6–13 mm long. Flowers in terminal inflorescences, long peduncled corymbs (Hulten 1974) or cymes (Taylor and MacBryde 1977; Scoggan 1978) of 3–11 white flowers, each 4–5 cm across; sepals broadly ovate and 15 mm long, petals ovate, usually 5, and 15–30 mm long; stamens and carpels numerous, ovaries pubescent, style glabrous and club shaped. Fruit an aggregate of many small, red, pubescent drupelets, 1.5–2 cm wide, hemispheric, very

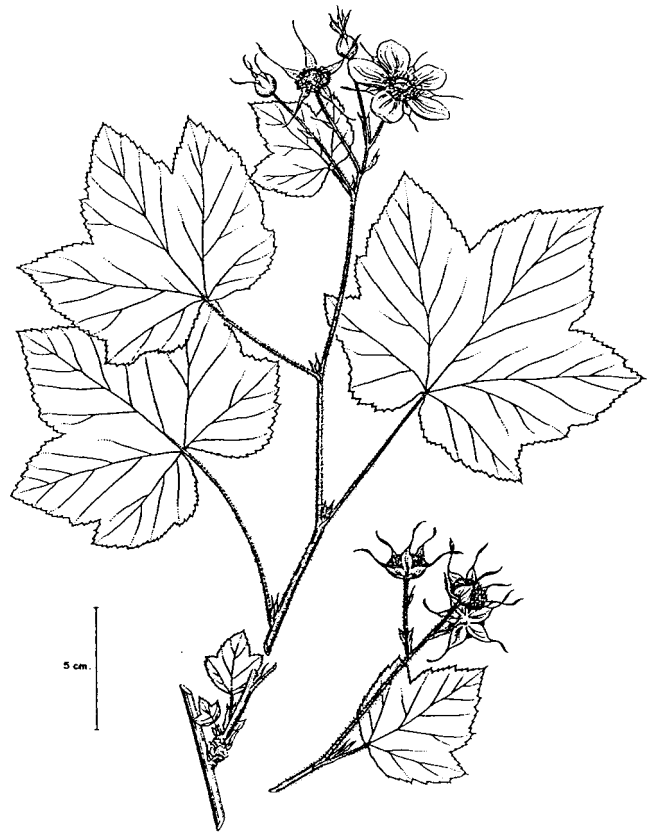


Fig. 2. *Rubus parviflorus* Nutt. (Taylor 1973).

soft, juicy and palatable. Chromosome number reported as $2n = 14$ (Taylor and MacBryde 1977).

Rubus spectabilis (Fig. 3). Erect or curved stems arising from extensive branching rhizomes, reaching 0.5–5 m tall, young stems strongly bristly, especially below, with acicular prickles; mature stems woody, weakly armed with scattered spines or prickles, hairless, yellow–brown bark shredding. Leaves compound, 12–20 cm long, mostly trifoliate; leaflets thin, glabrous or sparingly pubescent above, biserrate or lobulate–serrate; terminal leaflet largest, acuminate at apex, truncate or cuneate at base; lateral leaflets obliquely ovate, stipules linear or setaceous. Flowers usually solitary, 2–4 on short leafy shoots, 2–4 cm across; sepals pubescent and ovate, petals showy, deep pink (reddish purple), elliptical, and 1.5 times longer than sepals; stamens very numerous. Mature fruit an aggregate of small drupelets, yellow to glossy red, ovoid, up to 2 cm long, glabrous or with fine hairs, readily separated from dry receptacle, receptacle persistent on pedicel, palatable (Hitchcock et al. 1961; Taylor 1973). Chromosome number reported as $2n = 14$ (Taylor and MacBryde 1977).

(b) *Distinguishing features* — *Rubus strigosus* is distinguished from other raspberry-like *Rubus* species by being an erect shrub without rooting at shoot tips and having white flowers, canes with numerous bristles and prickles, and a

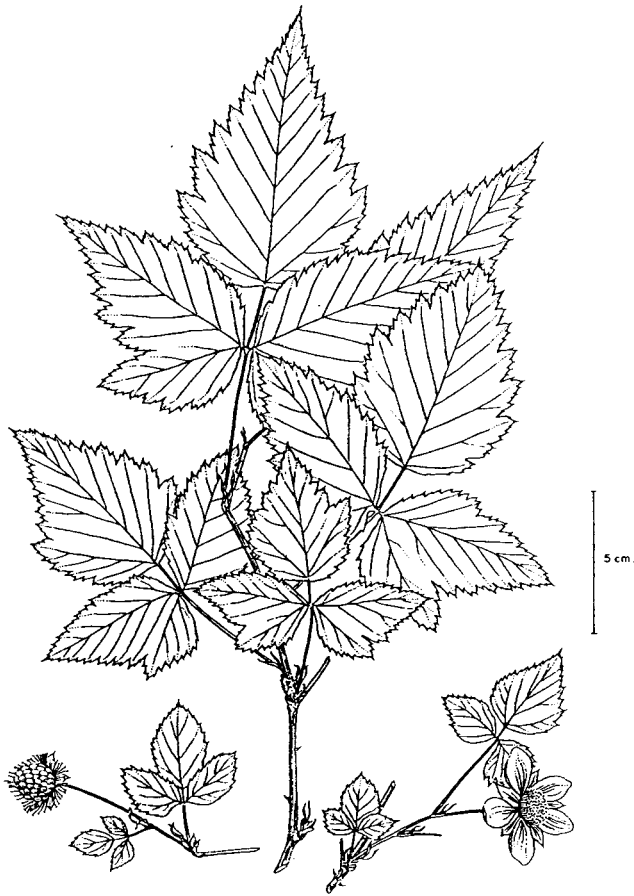


Fig. 3. *Rubus spectabilis* Pursh (Taylor 1973).

red mature fruit falling intact from the receptacle. *Rubus strigosus* can be distinguished from many blackberries (*Rubus* species) mainly by the fruit, which separates easily from a receptacle (torus) that remains attached to the raspberry plant (Ellis et al. 1991). *Rubus strigosus* is distinguished from cultivated raspberry varieties by having more numerous but thinner, shorter canes, thin laterals bearing small flowers, and fruit 2–3 times smaller (Jennings 1988).

Rubus parviflorus is easily distinguished from most *Rubus* species by tall, erect, unarmed stems and large, palmately lobed, simple leaves. *Rubus odoratus* L. has a similar growth habit and foliage but characteristically has rose-purple flowers and a dry, unpalatable fruit (Soper and Heimburger 1985).

Rubus spectabilis is distinguished from other *Rubus* species by having compound leaves and showy, deep-pink, solitary flowers and by often reaching heights of more than 2 m.

(c) *Intraspecific variation* — Across Europe, Asia, and North America, red raspberries are highly variable with many geographical and cultivated varieties. Two main ecotypes are described, *R. idaeus vulgatus* Arrhen. and *R. idaeus strigosus* Michx., and the two forms readily inter-

cross (Jennings 1988). *Rubus strigosus* (or *R. idaeus strigosus*) is the diploid form of east Asia and North America, characterized by glandular inflorescences and round fruit. Many synonyms have been suggested, notably *R. idaeus* ssp. *melanolasius* (Dieck) Focke and *R. idaeus* ssp. *sachalinensis* (Lev) Focke (Hulten 1974), although *R. strigosus* remains the prevailing term for wild red raspberry in Canada (H. A. Daubeney, pers. commun., 1994).

Wide variations are found among populations of *R. strigosus* collected from different sites. Collections across British Columbia and Alberta showed significant differences in cane length, number of buds per cane, percentage buds growing, number of inflorescences and flowers per bud, number of autumn-flowering canes, and fruit weight, size, and number of seeds (van Adrichem 1972). As in studies on wild raspberry in Europe by Jennings (1964) and Rousi (1965), van Adrichem (1972) found little or no ecotype differentiation and was unable to correlate plant characteristics with climate, location, or elevation.

Rubus parviflorus was previously described as having at least seven varieties and subspecies distributed between its western and Great Lakes ranges (Fassett 1941; Scoggan 1978). For example, *R. parviflorus* ssp. *parviflorus* was reported in British Columbia (Taylor and MacBryde 1977); *R. parviflorus* var. *grandiflorus* Farw., throughout the northwest (Hulten 1974). Kartesz (1994) considered *R. parviflorus* as having only two varieties, namely var. *parviflorus* and var. *velutinus* (Hook & Arn.) Greene.

Rubus spectabilis has no reported varieties or subspecies in Canada, although var. *franciscanus* (Rybd). [synonym, var. *menziesii* (Hook.) S. Wats. (Kartesz 1994) is reported in California, and ssp. *vernus* Focke is reported in Asia (Hulten 1974).

Rubus parviflorus is described as being highly variable, particularly for traits such as degree of pubescence and glandularity (Fernald 1970). Both *R. parviflorus* and *R. spectabilis* have shown variations in leaf size, reaching >20 cm long when found growing in a moderately shady understory in British Columbia. *Rubus spectabilis* has shown terminal leaflets reaching 15 cm in length and 13 cm in width (C. Oleskevich, pers. obs., 1994).

3. Economic Importance

(a) *Detrimental* — *Rubus strigosus*, *R. parviflorus*, and *R. spectabilis* are important competitors of conifer seedlings and can significantly reduce the successful establishment and growth of young conifers in planted or naturally regenerated forest renewal sites. These *Rubus* species are aggressive invaders of areas disturbed by logging, burning and site-preparation activities and can impede reforestation efforts by effectively monopolizing site resources, such as nutrients, moisture, space, and, in particular, light.

Rubus strigosus quickly invades disturbed forest lands and often becomes a competitive factor in reforestation sites within 1–5 yr after logging (Whitney 1982; Reynolds and Roden 1995a). The species can become detrimental because of rapid invasion of the site, particularly if tree planting is delayed after harvesting practices (Eis 1981). In eastern Canada, *R. strigosus* dominates certain clearcut areas and is

referred to as the most unwanted woody weed in northeastern Quebec (Jobidon et al. 1989). *Rubus strigosus* cover increased from 49 to 75% within 1 yr in cleared *Picea mariana* (P. Mill.) B.S.P. sites in New Brunswick (Reynolds and Roden 1995a). *Rubus strigosus* can effectively reduce height, diameter growth, and survival of conifer seedlings, including *Abies balsamea* (L.) P. Mill. (Wall 1983; Fox 1986; Ruel 1992), *Picea glauca* (Moench) Voss (Eis 1981; Adam 1989), and *P. mariana* (Adam 1989). In Maine, the height and diameter of *A. balsamea* seedlings are estimated to be reduced by approximately 22 and 33%, respectively, by *R. strigosus* competition (Fox 1986). Most coniferous and deciduous trees are able to overcome the shade-intolerant *R. strigosus* shrubs within 5–12 yr (Whitney 1982; Cromwell and Freedman 1994), although some sites can remain dominated by this weedy species for up to 25 yr (Ruel 1992).

Throughout the coastal ranges and the interior wet belt of the Pacific Northwest, *R. parviflorus* is a common forest weed and may cause greater conifer mortality than any other brush species (Haeussler et al. 1990). *Rubus parviflorus* can often dominate clearcut and burned sites immediately after a site disturbance in coastal and interior British Columbia (Hamilton and Yearsley 1988). Conifer seedlings are severely inhibited by continuous dense canopies of *R. parviflorus*, which may create a survival threshold for light competition (Comeau 1988) and can reduce photosynthetically active radiation that reaches seedlings by 50–100% between early and late June (Spittlehouse and Stathers 1990). LePage and Coates (1994) suggested that a threshold of <5% *R. parviflorus* cover is required for substantial growth to occur in hybrid spruce [*P. glauca* (Moench) Voss × *Picea sitchensis* (Bong.) Carr.] and lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.) seedlings. Abundant leaf litter of *R. parviflorus* may also smother seedlings. *Rubus parviflorus* and *R. spectabilis* leaf and litter extracts initially inhibited seed germination and growth of certain test plants, although no further allelopathic effects were observed under field conditions (del Moral and Cates 1971).

Rubus spectabilis is considered one of the most severe competitors in many Pacific coastal forest areas and can establish dense, continuous thickets, producing pure stands of >30 000 stems ha⁻¹, >2 m tall, within 2–3 yr (Allen 1969). Tappeiner et al. (1991) found that *R. spectabilis* communities maintained 80–100% crown closure over areas of 0.5 ha in a variety of study sites. *Rubus spectabilis* is a major competitor of conifers, including *Pseudotsuga menziesii* (Mirb.) Franco, *Tsuga heterophylla* (Raf.) Sarg., and *Picea sitchensis* (Bong.) Carr. (Barber 1976; Newton and White 1983) and may exclude even shade-tolerant conifers (Ruth 1970; Tappeiner et al. 1991; Zasada et al. 1994). Newton and White (1983) found that 11 species of conifers overtopped by *R. spectabilis* required an additional 4.1 yr to reach survival height, and further studies showed that conifers less than 60 cm tall were often killed by 4-yr-old *R. spectabilis* (Newton et al. 1993). Dense cover of *R. spectabilis* can substantially inhibit regeneration of trees through shading and smothering with mats of leaf litter.

(b) *Beneficial* — *Rubus strigosus*, *R. parviflorus*, and *R. spectabilis* are important plants in forest ecosystems and

play a role in nutrient cycling and conservation, reducing soil erosion on disturbed sites, and reducing the invasion of longer-lived competitive deciduous species in reforestation areas (Haeussler et al. 1990). They are valued for land rehabilitation in avalanche areas, for bank stabilization along steep road cuts and streams, and for dune stabilization (Hungerford 1984; Marchant and Sherlock 1984; Minore and Weatherly 1994). *Rubus parviflorus* cover may protect young conifer seedlings from frost damage, as hybrid spruce showed increased damage as cover was reduced from 35 to 17% (LePage and Coates 1994). These *Rubus* species provide important habitat and food sources for wildlife, as the fruit and foliage form a significant part of the spring and summer diets of many animals and birds. Leaves and stems provide browse for large (e.g., deer and elk) and small mammals (e.g., bears, coyotes, rabbits, squirrels, beaver and raccoons), and fruit are consumed extensively by birds (e.g., songbirds, grouse, pheasant and quail) and by other animals. For example, *R. spectabilis* shoots may constitute up to 26% of spring and summer diets of coastal black and grizzly bears (Lloyd 1979) and form a significant portion of summer diets of Roosevelt elk (Jenkins and Starkey 1991).

These *Rubus* species are valued for their genetic contributions to domestic raspberry breeding programs by providing new sources of resistance to root rot and cane diseases, viruses, weevils and nematodes (Bristow et al. 1988; Knight 1991; Daubeney and Anderson 1993; Davidson 1995). *Rubus strigosus* is also used in breeding programs for other desirable characteristics, such as winter hardiness, self-supporting habit, early and late fruiting, and an easily removed, non-darkening red fruit. Flowers and foliage of *R. parviflorus* and *R. spectabilis* are considered to have economic ornamental value (Taylor and McBryde 1977), and fruit of all three species are valued by berry pickers.

(c) *Legislation* — *Rubus strigosus*, *R. parviflorus*, and *R. spectabilis* are not listed in the Canada Seeds Act and Regulations (Agriculture Canada 1985) or any provincial weed and seeds acts.

4. Geographical Distribution

Rubus strigosus, *R. parviflorus*, and *R. spectabilis* are native to North America, and their Canadian distribution is outlined in Figs. 4, 5, and 6.

Rubus strigosus. Distributed from Yukon to Newfoundland, *R. strigosus* occurs in low subarctic–high temperate regions as far north as southwest Mackenzie District to Hudson Bay, northern Ontario (55° N 88° W), northern Quebec (to Ungava Bay and Côte Nord), and Labrador (approximately 56°30'N) (Scoggan 1978). In British Columbia, it is common except west of the Coast Mountains, not naturally occurring on Vancouver Island and Queen Charlotte Islands (Taylor 1973; Taylor and MacBryde 1977). In North America, it is distributed from Alaska, south to California, Arizona, northern Mexico, New Mexico, and North Carolina. Elevation ranges from inland valley bottoms to subalpine elevations near timberline.

Rubus parviflorus. Distributed through British Columbia (to 55°N) and southwestern Alberta, *R. parviflorus* becomes

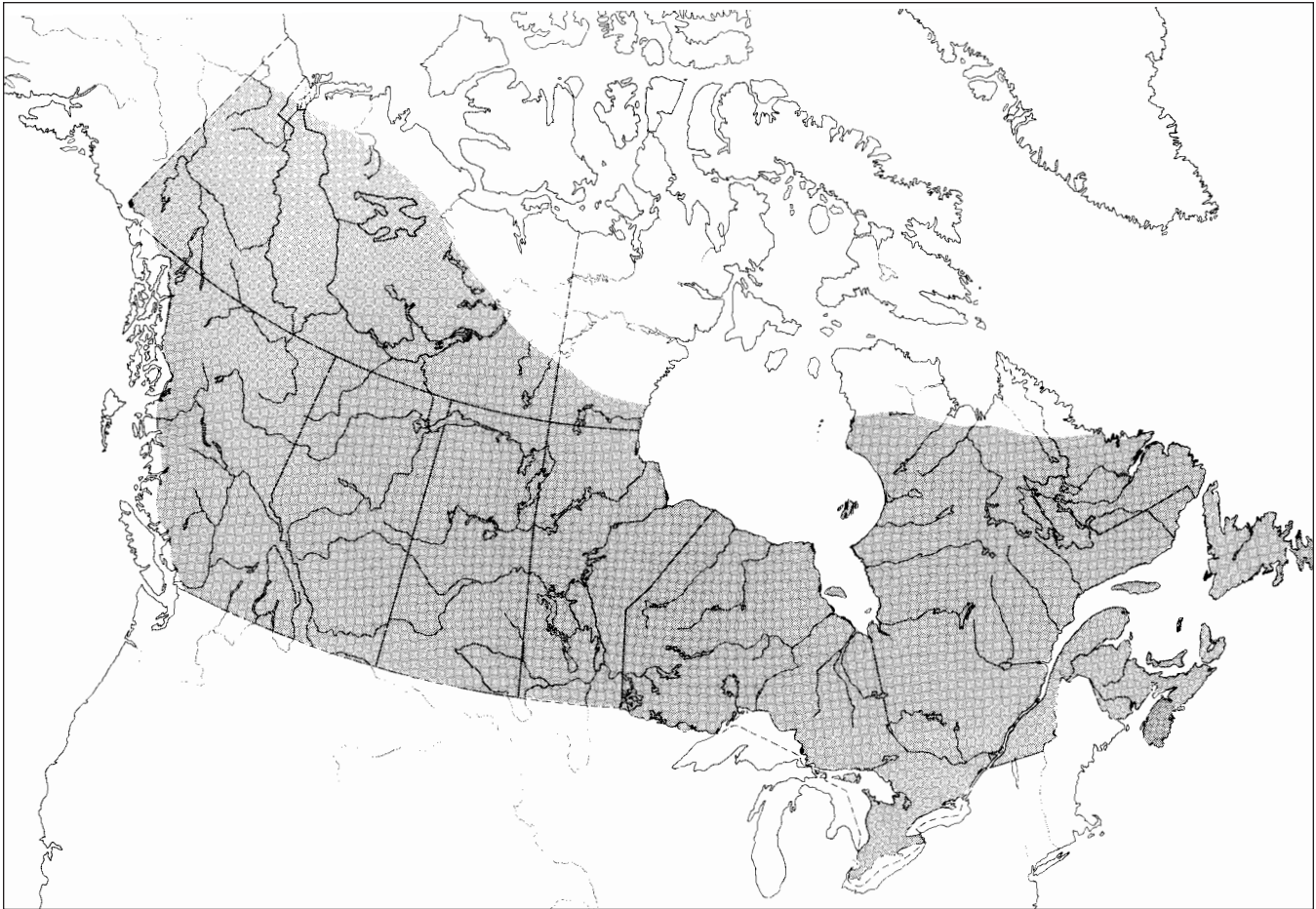


Fig. 4. Distribution of *Rubus strigosus* Michx. in Canada (adapted from Hulten 1974; Scoggan 1978; Porsild and Cody 1980).

rarer in the Cypress Hills, Alberta (Moss 1983) and is also restricted to isolated patches along shores and on islands of Lake Superior, to Bruce Peninsula, Ontario. In North America, from southeastern Alaska, restricted to coast, to 55°N, south to California, northern Mexico, New Mexico, South Dakota, and in isolated areas in the Great Lakes region (Scoggan 1978). Elevation ranges from sea level to >900 m on the coast of British Columbia and from valley bottoms to >1200 m in interior British Columbia (Haeussler et al. 1990), and is common at 1800 m in the western Cascades, Washington (Douglas 1972).

Rubus spectabilis. Primarily found west of Coast Mountains British Columbia, from low subarctic–high temperate regions in the Aleutian Islands and southern Alaska, south to northwestern California. *R. spectabilis* is common along the west coast of British Columbia and penetrates inland, along Skeena River and Fraser River drainages (Haeussler et al. 1990). Its elevation ranges from sea level to lower alpine elevations (Hulten 1974), and it is most abundant below approximately 800 m (Barber 1976).

5. Habitat

(a) *Climatic conditions* — The main climatic factors limiting the distribution of *R. strigosus*, *R. parviflorus*, and *R.*

spectabilis within their habitat are light and moisture. These species are restricted by their intolerance of moderate or high shade and their preference for moist, water-receiving sites. *Rubus spectabilis* is also limited by cold temperatures.

Rubus strigosus is the most widely adapted to environmental conditions among the three *Rubus* species and survives cold temperatures and short growing seasons (Haeussler et al. 1990). Restrictions to *R. strigosus* distribution include humid, maritime climates with low annual temperature variation (e.g., west of the Pacific Coast Mountains), xeric, subxeric, and subhydric moisture regimes (Angove and Bancroft 1983), and extreme wind and rains, which may damage canes (Williamson et al. 1979). *Rubus parviflorus* tolerates a wide range of conditions but is limited by cold winters, short growing seasons, and summer moisture stress. It has been found to tolerate low light levels under closed forest canopies, although it achieves greater cover under 60–100% full light (Haeussler et al. 1990). *Rubus spectabilis* is the most susceptible of these *Rubus* species to cold temperatures and a short growing season and is restricted entirely to mild maritime climates, preferring humid water-receiving or -collecting sites, including subhydric regimes (Klinka et al. 1989). Ruth (1970) reported that young seedlings are significantly limited by drought condi-

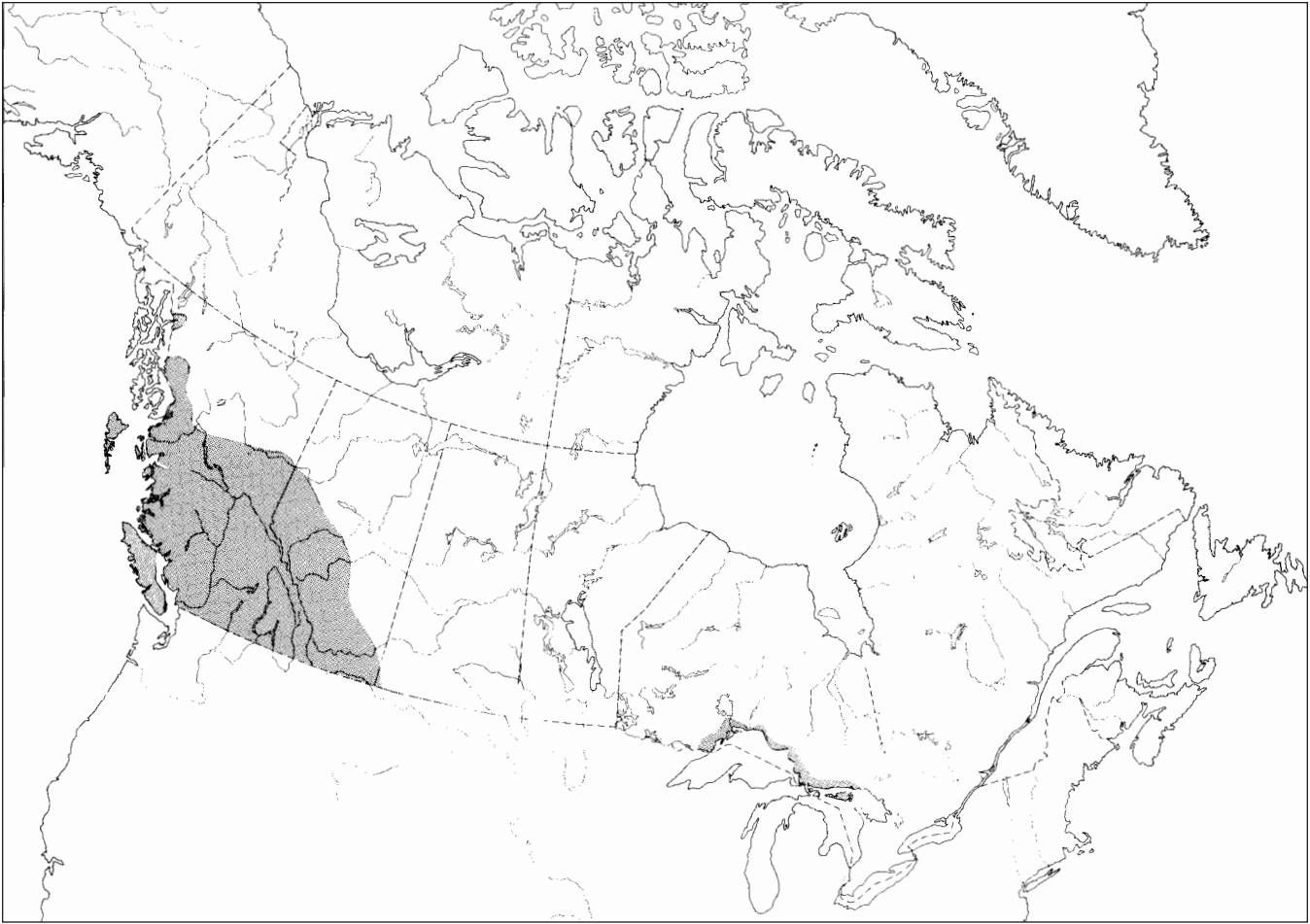


Fig. 5. Distribution of *Rubus parviflorus* Nutt. in Canada (adapted from Moss 1983; Soper and Heimburger 1985; Haeussler et al. 1990).

tions. *Rubus spectabilis* has a relatively high shade tolerance and can achieve net photosynthesis at low light levels, reaching maximum photosynthesis at lower light radiation levels ($150 \mu\text{E m}^{-2} \text{s}^{-1}$) than *R. parviflorus* (Barber 1976).

(b) *Substratum* — These *Rubus* species are found on a wide range of soil types, including Luvisolic, Brunisolic, and Podzolic soils with fluvial, morainal, and lacustrine parent material; optimum growth occurs on soils with high nutrient levels. All these shrubs are nitrophytic species and are indicator plants for nitrogen-rich forest soils (Klinka et al. 1989). Optimum growth may be reached by *R. strigosus* on sandy loams from glacial tills (Whitney 1986); by *R. parviflorus*, on fluvial and alluvial soils; and by *R. spectabilis*, on floodplains with well-aerated soils, near field capacity (Haeussler et al. 1990).

(c) *Communities in which the species occur* — *Rubus strigosus*, *R. parviflorus*, and *R. spectabilis* prefer open forest sites disturbed by logging, fire, or silvicultural activities and are pioneer invaders that often form monospecific shrub communities. In British Columbia, Eis (1981) found that *R. strigosus* was common on Cornus-moss sites with *Ribes*

species and on Aralia–Dryopteris sites with *Acer glabrum* Torr., *Alnus sinuata* (Regel) Rybd., *Salix* species, *Equisetum* species, grasses and forbs. In the Prairie provinces, *R. strigosus* is found in open sites, including bluffs and riverbanks, with *Populus tremuloides* Michx. and *Populus balsamifera* L., *Betula papyrifera* Marsh., *Lonicera involucrata* (Richards.) Banks ex Spreng., *Rosa acicularis* Lindl., and *Thalictrum venulosum* Trel. (Dix and Swan 1971; Looman and Best 1979; Corns 1983). In eastern Canada, *R. strigosus* is found in both hardwood and softwood regions, including the Tsuga–Pinus–Acer–Betula–Fagus region and the Picea–Abies regions, where it is often associated with *Prunus pensylvanica* L., *P. tremuloides*, *Epilobium angustifolium* L., *Sambucus pubens* Michx. and *Sambucus canadensis* L. (Whitney 1982, 1986).

Rubus parviflorus is found in moist, open woods along streams and forest margins and may be associated with *Abies grandis* (Dougl.) Lindl., *Thuja plicata* Donn., *P. menziesii*, *P. glauca* × *englemannii* (Parry) Boivin, *P. tremuloides*, *P. contorta* Dougl., *Alnus rubra* Bong., *Viburnum edule* (Michx.) Raf., *L. involucrata*, *Ribes* species, *R. spectabilis*, *Sambucus racemosa* L., *Oplopanax horridus* (Sm.) Miq., *Streptopus roseus* Michx., *E. angustifolium*,

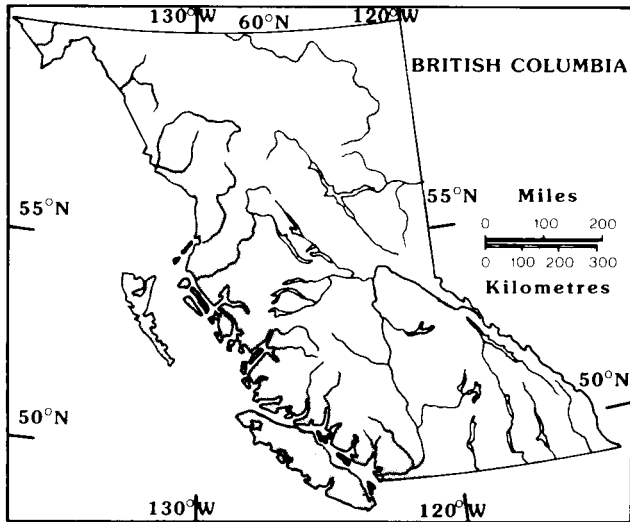


Fig. 6. Distribution of *Rubus spectabilis* Pursh in British Columbia (Haeussler et al. 1990).

Thalicum occidentale Gray, *Tiarella unifoliata* Hook., and *Athyrium filix-femina* (L.) Roth (Pojar et al. 1984; Klinka et al. 1989).

Rubus spectabilis is often found growing in moist, disturbed coastal areas, swampy places, along banks of streams at low elevations, and under old- and second-growth forests with plants similar to those associated with *R. parviflorus* and with wetland plants, such as *Lysichiton americanum* Hult. & St. John (Klinka et al. 1989).

6. History

The genus *Rubus* (Latin *ruber* = red) subgenus *Idaeobatus* is considered as having its centre of origin in eastern Asia. Preserved leaf impressions (approximately 10 000 yr old) in northern California have indicated that *R. parviflorus* and *R. spectabilis* were part of the closed-cone pine forest during the Pleistocene period (Mason 1934 (in Barber 1976); Langenheim and Durham 1962). Fassett (1941) suggested that the present distribution of *R. parviflorus* is due to a migration of western colonies across Canada to the Great Lakes region during a postglacial period, with the range later bisected by the aridity of the Great Plains.

Native peoples of North America have long used these *Rubus* species primarily as food plants since fruits and shoots were gathered in abundance (Pojar and MacKinnon 1994). In British Columbia, the Nuxalk, Tsimshian, and perhaps the Heiltsuk consumed *R. strigosus* fruit fresh, boiled, mashed with other berries, and dried into cakes (Turner 1975), and the Coast Salish also used the berries as a purple stain (Pojar and MacKinnon 1994). Coastal native peoples, including the Nuu-chah-nulth, the Kwakwaka'wakw, and Nuxalk, extensively used young sprouts of *R. parviflorus* and *R. spectabilis* as a green vegetable eaten peeled and raw, and canoes were observed laden with shoots (Turner 1975). *Rubus parviflorus* berries were often dried into cakes, while *R. spectabilis* berries were mostly eaten fresh, sometimes with salmon. *Rubus spectabilis* patches, like those of other

food plants, were owned by families or individuals, and certain groups, such as the Nuu-chah-nulth, gave permission for communal harvest after the owner had collected enough to hold a feast (Pojar and MacKinnon 1994).

Domestication of raspberries occurred within the last 400–500 yr, with cultivated varieties of *R. idaeus* available by the 16th century in Europe and by the 17th century in North America. It was not until the 1850s that *R. strigosus* was selected for cultivation and crossed with European varieties, resulting in great advancements in raspberry breeding (Jennings 1988).

The first botanical records of these plants in North America include *R. strigosus* in *Flora Boreali-Americana* in 1803, *R. parviflorus* in *Generum Plantarum* in 1818, and *R. spectabilis* in *Flora Americae Septentrionalis* in 1814 (Hitchcock et al. 1961).

In North America, extensive logging and land-clearing practices of the last century contributed to an increased distribution and abundance of these invasive *Rubus* species.

7. Growth and Development

(a) *Morphology* — The rapid development of extensive foliage and root systems allows these *Rubus* species to colonize new habitats and survive for many years. The bristly and spiny nature of young *R. strigosus* and *R. spectabilis* shoots may enhance survival by discouraging grazing.

(b) *Perennation* — Perennation of these *Rubus* species occurs primarily by vegetative reproduction. The biennial canes of *R. strigosus* normally fruit and senesce in a 2-yr period, with replacement canes arising from buds at the base of the floricanes. The perennial *R. strigosus* stools may produce new shoots for up to 1–2 decades (Whitney 1986). *Rubus parviflorus* and *R. spectabilis* generally produce annual shoots and maintain extensive bud banks and rhizome systems, with clones surviving for up to 45 yr (Tappeiner et al. 1991; Zasada et al. 1992; Maxwell et al. 1993). *Rubus strigosus* and *R. parviflorus* show bud set and dormancy in the winter months, while *R. spectabilis* may become dormant or continue minimum shoot elongation throughout a mild coastal winter (i.e., mean temperature of 6°C) (Barber 1976).

(c) *Physiological data* — Few physiological studies have been completed on these *Rubus* species. *Rubus strigosus* physiology may be similar to that of cultivated raspberry, for which extensive studies have been completed on leaf pigment content, gas exchange, percentage water content, macroelement concentration and distribution among plant parts, acclimation, onset of dormancy, artificial cultivation of plantlets, germplasm storage, and others (Donnelly and Vidaver 1984; Jennings 1988; Reed 1993; Kowalenko 1994). In studies on nitrate assimilation by brush species in recent clearcut areas, *R. strigosus* was found to show high nitrate reductase activity (Truax et al. 1994).

These *Rubus* species store reserves of carbohydrate energy for the dormant season, and several studies have been completed on the TNC content. In studies on the dichotomy

of energy demands in *R. strigosus*, carbohydrate content was shown to be proportionally highest in developing primocanes in spring and fall; in floricanes, by midsummer; and in roots, by late summer (Whitney 1982). The TNC of *R. spectabilis* rhizome segments was found to reach a high of 13% of dry weight during the winter season and to fall to 7% with spring shoot production and summer growth until early fall (Zasada et al. 1994).

(d) *Phenology* — *Rubus strigosus* canes have differing leaf phenology, with peak leaf biomass occurring on floricanes in late June and on primocanes at the end of the summer season. Floricane shoots are active earlier and are shorter lived than primocanes. Floricane leaves flush by early spring, reach full development in May–June, and begin senescing by the end of June, coinciding with fruit maturation. Primocane leaves are developed by May and persist through the summer to as late as October (Whitney 1982). In the southern range of *R. strigosus*, flower buds appear in May, and fruit ripens in early June (Haeussler et al. 1990). In the northern range, flowering occurs in June–July, with fruit set in July–October (Viereck and Little 1972). Seed dispersal generally occurs from July to October.

Rubus parviflorus and *R. spectabilis* buds may be active very early in the spring (i.e., February), with bud burst and leaf flush occurring in April–May and March–April, respectively. Leaves are generally fully expanded from May to late August, with senescence and leaf drop occurring until late October (Maxwell et al. 1993). *Rubus parviflorus* flowering occurs mainly in June–July but can extend from early May to early August, with fruit maturation from early June to mid-September (Haeussler et al. 1990). *Rubus spectabilis* flowering occurs between April and June in its southern range, continuing for 1 mo longer in its northern range. Fruiting may vary from June–July in the south to July–August in the north and at higher elevations. *Rubus spectabilis* seeds may germinate by early April, with new seedlings appearing in early June (Ruth 1970).

Maximal root growth for *R. strigosus* and *R. spectabilis* occurs from August through October (Whitney 1982; Zasada et al. 1994).

(e) *Mycorrhiza* — Malloch and Malloch (1982) found no mycorrhiza on *R. strigosus* roots examined from the boreal forest region of Ontario. Fine vesicular–arbuscular mycorrhiza, caused by *Glomus tenuis* (Greenhall) Hall, were found to form on cultivated *R. idaeus* in Europe (Gianinazzi-Pearson et al. 1981). Bioassays (in vitro) by Côté and Thibault (1988) showed leachates from *R. strigosus* inhibited the growth of ectomycorrhizal fungi found on *P. mariana* roots in Quebec. No mycorrhizal associations have been reported on *R. parviflorus*, although small, nodule-shaped expansions have been observed on roots (R. E. Wall, pers. commun. 1994). The occurrence of *Glomus microcarpus* Tul. & Tul. and *Glomus fasciculatus* Gerdemann & Trappe vesicular–arbuscular mycorrhiza was reported on *R. spectabilis* in pot culture (Gerdemann and Trappe 1974).

8. Reproduction

(a) *Floral biology* — Flowers are self-infertile in *R. strigosus*, *R. parviflorus*, and *R. spectabilis* (Keep 1968), and seed is produced through cross-pollination followed by fertilization. Embryo development was found to be normal in *R. strigosus* (Jennings 1988) and *R. spectabilis* (Virdi and Eaton 1969a). Apomixis is rare in the *Rubus* subgenus *Idaeobatus*, only occurring in a few triploid specimens, and is more commonly found in the subgenus *Rubus* (i.e., blackberries) (Jensen and Hall 1979; Nybom 1988).

Flowers are pollinated primarily by insects, with *R. spectabilis* also being visited by hummingbirds. *Rubus strigosus* has an advanced floral structure, attracting mainly bees (Whitney 1984), while *R. spectabilis* has a more primitive flower suited to unspecialized vectors, such as beetles (Barber 1976). Whitney (1984) recorded *R. strigosus* flowers producing an abundant supply of nectar towards the end of the flowering season, reaching 18 kg ha⁻¹ d⁻¹ in a 4-yr-old site dominated by wild raspberry in northeastern United States. High pollen viability is typical of sexually reproducing *Rubus* species (Nybom and Schaal 1990), and high pollination rates were observed in *R. strigosus*, with 85% of the flowering individuals producing seed (Whitney 1986). The fruits are aggregates of small drupelets, with each drupelet producing one hard-coated pyrene normally containing one seed. *Rubus strigosus* fruit may be similar to that of *R. idaeus*, which consists mainly of water, with 14% solids, of which <1% are pectins. *Rubus idaeus* fruit has a total sugar content (mainly glucose and fructose) of 1.5–5.3% wt wt⁻¹ and contains relatively high amounts of vitamin C (Jennings 1988). Yellow coloration of fruit produced by *R. spectabilis* may be due to the predominance of pelargonin glycosides, rather than the anthocyanidin pigments found in red-coloured fruit.

(b) *Seed production and dispersal* — *Rubus strigosus*, *R. parviflorus*, and *R. spectabilis* are major seedbank species that annually produce a prolific number of small seeds (average length, 2 mm), depending on environmental conditions, stand development, and elevation. *Rubus spectabilis* produces more than 300 000 seeds kg⁻¹ (Tapeiner and Zasada 1993). Dense populations of *R. strigosus* growing on southeast facing slopes in previously cleared areas produced >26 000 seeds m⁻² over a 4-yr period (Whitney 1986). At later stages of stand development, *R. strigosus* was found to devote a greater proportion of reserves to seed production (Whitney 1982). Haeussler et al. (1990) reported that *R. parviflorus* seed production decreased at high elevations.

Seeds are dispersed either directly below the parent plant (as ripe fruit falls readily) or throughout the soil by burrowing animals; or the fruit is consumed and the seeds are dispersed by birds and mammals. In seedbank analysis of deciduous- and coniferous-dominated sites in the Acadian forests, Moore and Wein (1977) found *R. strigosus* constituted 90% of the seedlings arising from soil core samples. In early- and mid-seral forest communities, *R. parviflorus* produced >75 seeds m⁻² with 60% constancy (McGee and Feller 1993) and up to 84 seeds m⁻² with 75% constancy (Morgan and Neuenschwander 1988). *Rubus spectabilis*

sites under timber accumulated 2–125 seeds m⁻² (Ruth 1970; Barber 1976), with seed predation appearing to be a minimal factor (Tappeiner and Zasada 1993). Greatest seed numbers for *R. parviflorus* and *R. spectabilis* were found on forest floors in undisturbed and low-disturbance areas, while the lowest seed numbers were found in rights-of-way and in burned sites (Morgan and Neuenschwander 1988; McGee and Feller 1993; Zasada et al. 1994). Seed dispersal is the primary means by which these *Rubus* species colonize new sites.

(c) *Viability of seeds and germination* — Seeds can remain viable buried in the soil for many years; an estimated >50 yr for *R. strigosus* and at least 100 yr for *R. spectabilis*. Under artificial conditions, viability may be reduced, as domestic raspberry seeds showed only 0–22% germination after 26 yr of dry storage (Clarke and Moore 1993). Both the red and yellow fruit of *R. spectabilis* produce viable seeds (Barber 1976). A gradual decline in seed viability, constancy, and number with soil depth was found for *R. strigosus* (Moore and Wein 1977) and *R. parviflorus* (McGee and Feller 1993).

Seeds must pass through a dormant phase before being stimulated to germinate by increased light and temperature, conditions normally associated with soil disturbances. Germination of buried *R. strigosus* seed is also stimulated by soil nitrates and nitrate-N fertilization (Whitney 1982; Jobidon 1993). The dense, impermeable seedcoat of these *Rubus* species inhibits germination, and passage through the crop or gut of a bird may enhance germination (Haeussler et al. 1990). Jennings (1988) determined that *R. strigosus* seeds remained dormant because of the presence of an acidic, ether-soluble, growth-inhibiting substance. To induce germination, dried seeds generally require a lengthy procedure of chemical scarification, warm stratification, and pre-chilling to break dormancy, followed by an alternating temperature regime (Anonymous 1974b, 1994). Other studies show that raspberry seeds may require only cold stratification at 2°C for 120 d to break dormancy (Hills and Morris 1992) and that germination time can be greatly reduced by halving fresh seeds (Ke et al. 1985) or by nicking or removing the seed coat (Nesme 1985).

For *R. parviflorus* seeds, variable germination results were obtained with a sulfuric acid soak followed by cold stratification for 90 d (Marchant and Sherlock 1984), although cold stratification at 3°C for 90 d followed by warm stratification and alternating 5 and 15°C temperatures resulted in increased germination (Costanzo 1980). *Rubus spectabilis* seeds germinated following scarification in sulfuric acid, cold stratification, and alternating temperatures of 2 and 3°C for 5 mo (Barber 1976; Tappeiner and Zasada 1993).

Seed germination decreases with increasing soil depth for these small-seeded *Rubus* species. Reduced *R. parviflorus* germination occurred at depths of >1 cm on the forest floor and at 3 cm in mineral soil (McGee and Feller 1993). Soil disturbance may be critical for seed germination, as *R. spectabilis* consistently emerged on disturbed mineral soils

but showed low emergence rates on undisturbed forest floor (Tappeiner and Zasada 1993).

(d) *Vegetative reproduction* — Once these *Rubus* species seedlings are established on a site, the principal means of spread and perpetuation is vegetative reproduction through extensive clonal colonies. *Rubus strigosus* primarily spreads by short-lived root suckers, establishing up to 16 suckers m⁻² and 20–50 independent stools m⁻² in a 3-yr-old plot (Whitney 1982, 1986). *Rubus parviflorus* and *R. spectabilis* spread via an extensive rhizome system, with annual ramets arising from a large rhizomal bud bank or, if the plant has been cut back, from buds associated with the basal stem and root collar (Zasada et al. 1992, 1994). Tappeiner et al. (1991) found *R. spectabilis* clones produced 1–2 new rhizomes yr⁻¹ with annual rhizomal extensions of 0.1–0.8 m yr⁻¹, reaching an average rhizomal length of <1.7 to 18.3 m, depending on the stand type. All three *Rubus* species are readily propagated from dormant root cuttings for research purposes.

9. Hybrids

Rubus strigosus, *R. parviflorus*, and *R. spectabilis* can be crossed with cultivated red and black raspberries and blackberry plants (Virdi and Eaton 1969b; Jennings and Ingram 1983; Daubeney and Anderson 1993). Pool et al. (1981) recognized *R. idaeus* chromosomes in F₁ hybrid crosses with cultivated raspberry plants in Europe. *Rubus spectabilis* has been known to naturally hybridize with *R. strigosus* and *Rubus arcticus* L. in Alaska (Viereck and Little 1972).

10. Population Dynamics

Rubus strigosus, *R. parviflorus*, and *R. spectabilis* populations follow two general stages of growth in a new site: (1) an initial building phase lasting 1–2 yr, which involves seed germination and a rapid increase in stem number; and (2) a growth phase, involving vegetative growth and reproduction, increased stand density, and the establishment of extensive clonal colonies. Seed production continues throughout the growth phase, resulting in abundant seedbanks. Whitney (1986) suggested seedbank build-up and the lengthy seed dormancy of *R. strigosus* may be considered as a third phase in population growth.

Within *R. strigosus* stands, seedling establishment from buried seed is soon replaced by the extensive production of root suckers and development of independent stools. With an increase in stand density and in net biomass production under an open canopy, a self-thinning phase may follow that results in a decrease in stool number. As interspecific competition and shading become influential factors, *R. strigosus* may shift energy sources from clonal, vegetative production to prolific seed production (Whitney 1982).

Rubus parviflorus and *R. spectabilis* become established from seed in new sites, with seedling survival rates reaching up to 44 and 32%, respectively (Maxwell 1990). Sprouts arising from buds on stems and rhizomes show greater initial growth rates and greater mean survival rates (100 and 70%, respectively) than seedlings, and thus populations become dominated by ramets and stems. Within 2–3 yr after

R. parviflorus and *R. spectabilis* establishment, extensive rhizomal growth can spread up to 50 m² from the parent plant, and canopy closure may be complete (Maxwell 1990; Tappeiner et al. 1991). Mature populations consist mainly of above-ground ramets interconnected by extensive rhizome systems (Maxwell et al. 1993). Rhizome-generated ramets show a high annual turnover, and populations are made up of stems decreasing in number from small to large size classes (Tappeiner et al. 1991; Zasada et al. 1992). In work on population simulation models for *R. parviflorus* and *R. spectabilis*, Maxwell et al. (1993) found basal stem buds to be the main factor in initiating shoot production in natural populations.

Rubus parviflorus and *R. spectabilis* population growth is generally regulated by density and interspecific competition, mainly from the growth of overstory trees (Maxwell 1990). *Rubus spectabilis* can maintain a persistent cover once established, unless a severe disturbance allows for succession of trees and other shrubs (Tappeiner et al. 1991). *Rubus spectabilis* clone size may be influenced by stand type, since larger clones, with a greater production of ramets and aerial stems, were found in alder stands than in conifer stands. Tappeiner et al. (1991) also determined that *R. spectabilis* clonal biomass was negatively related to basal area of overstory trees and suggested that rhizome length and biomass could be predicted from the measurement of basal area of clonal stems and of overstory trees.

11. Response to Herbicides and Other Chemicals

Herbicide applications offer varying levels of control, as even extensive foliar damage may be followed by rapid resprouting as root systems remain unaffected. Late-season applications of glyphosate are most effective in reducing *Rubus* species cover. For *R. strigosus*, foliar applications of 2.14 kg a.e. glyphosate ha⁻¹ in August–September caused only light to moderate injury in several trials in British Columbia (Haeussler et al. 1990). Greater control is often obtained in eastern Canada, and Pitt et al. (1992) demonstrated >60% *R. strigosus* cover reduction with refined aerial applications of 0.5 kg a.e. glyphosate ha⁻¹ in a New Brunswick trial. In *R. parviflorus* stands, glyphosate applications of 1.4 kg a.e. ha⁻¹ were shown to be as effective as the higher rate of 2.4 kg a.e. ha⁻¹ in reducing cover when applied in early to late August, after full leaf expansion was complete (LePage et al. 1991). Glyphosate generally causes moderate to severe injury in *R. spectabilis* (D'Anjou 1990), and July–September applications of 1.4–2 kg a.e. ha⁻¹ gave good control (Newton et al. 1986; William 1994).

Hexazinone was shown to be effective in reducing *R. strigosus* cover with aerial applications of 2 kg a.i. ha⁻¹ applied in early summer site-preparation treatments over cleared sites in northwestern New Brunswick (Reynolds and Roden 1995a). Hexazinone is generally ineffective or causes only light injury in *R. parviflorus* and *R. spectabilis*, although a liquid formulation of 4 kg a.i. ha⁻¹ caused 25–60% injury in approximately 4-yr-old *R. parviflorus* stands in southwestern British Columbia (D'Anjou 1990).

Sulfometuron reduced *R. strigosus* cover by 35 and 30% in spring site-preparation when applied at 0.3 and 0.45 kg

a.i. ha⁻¹, respectively (Reynolds and Roden 1995b). Sulfometuron also gave good control of *R. parviflorus* and *R. spectabilis* with a broadcast spray of 0.6 kg a.i. ha⁻¹ in March–April (D'Anjou 1990). Metsulfuron applied as a spot spray at 0.6 kg a.i. ha⁻¹ or as an aerial spray at 0.03 kg a.i. 100 L⁻¹ ha⁻¹ may give excellent control of *R. spectabilis* in site-preparation practices (Cole et al. 1988; William 1994). A site-preparation application combining picloram and 2,4-D (0.25 g a.i. + 0.9 kg a.i. ha⁻¹) gave good control of *R. parviflorus* and *R. spectabilis* in the Pacific Northwest region (William 1994). Triclopyr esters applied in early summer at 2.9 kg a.e. ha⁻¹ caused up to 60–90% injury of *R. parviflorus* and *R. spectabilis* (D'Anjou 1990).

In studies on herbicide residues in *R. strigosus* fruit in Ontario, Roy et al. (1989) reported <10% of glyphosate sprayed at 2 kg a.e. ha⁻¹ penetrated the fruit within 9 h and that glyphosate levels dissipated to 50% with 5.55 ± 0.880 ppm residues in fruit after 13 d. Preliminary residue testing by Hoyles and Wilson (1994) showed much lower glyphosate residue levels in *R. strigosus* fruit, with 0.27 ppm reported at 10 d postapplication in central British Columbia. Frank et al. (1983) found that 2,4-D sprayed at 1.1–3.9 a.e. ha⁻¹ initially left residues of 2.6–31 mg kg⁻¹ fruit, with residues decreasing to 0.1–3.3 mg kg⁻¹ within 2–5 wk. No glyphosate or 2,4-D residues were found in fruit produced in the following year in the above-mentioned studies. In Newfoundland, *R. strigosus* foliage accumulated up to 400 ppm fluoride from phosphorus plant emissions (healthy foliage had 8 ppm), causing up to 70% flower mortality and resulting in reduced fruit dry weight and seed size, foliar injury, delayed leaf fall, and increased vegetative spread (Staniforth and Sidhu 1984).

12. Response to Human Manipulations

A variety of manipulations aimed to reduce *R. strigosus*, *R. parviflorus*, and *R. spectabilis* cover, including site preparation (scarification and prescribed burning) and manual cutting, often stimulate germination and prolific resprouting, allowing stands to recover to pretreatment levels or greater within 1–3 yr.

Mechanical site preparation can fragment roots, increasing individual stool number for *R. strigosus* (Hudson 1959) and stem density for *R. parviflorus* and *R. spectabilis*. Scarification treatments, which expose mineral soil, stimulate germination of buried *Rubus* seed. On disturbed sites with the soil organic layer and vegetation removed, *R. strigosus* showed 1.2–1.5 times greater germination and greater seedling survival than on undisturbed sites (Roberts et al. 1993). In unsatisfactorily restocked sites of *Picea* species and *P. contorta*, site-preparation treatments such as windrowing and disc trenching stimulated *R. strigosus* and *R. parviflorus* to exceed pretreatment cover levels by the second growing season (Taylor et al. 1991). In comparison, Oswald and Brown (1992) found that scarification treatments (with brush blade, flex-track forwarder with blade, or dip and dive) successfully reduced *R. strigosus* in *Picea englemannii* Parry ex Engl. plantations.

Prescribed burning, especially low-severity burns, may create seedbeds for *Rubus* species and stimulate germination of buried seed and resprouting of the remaining stems, resulting in greater cover on burned sites than found on unburned sites (Allen 1969; Wright 1972; Lafferty 1972; Delaney and Cahill 1978; Johnson and Woodard 1985; Hamilton and Yearsley 1988). These *Rubus* species are moderately to highly resistant to fire, with adaptive traits (i.e., buried seed, buried rhizomes, and rapid regrowth), and show decreased vigour only after severe burns, particularly on dry sites (Haeussler 1991). Broadcast burning and spray-and-burn-treatments achieving soil temperatures of >60°C at a 3-cm depth for 3–5 min did not successfully control *R. strigosus* and *R. parviflorus* regrowth (Taylor et al. 1991).

Cutting these *Rubus* shrubs stimulates resprouting, as *R. parviflorus* and *R. spectabilis* can regrow to 60–90% of pre-treatment height within 1 yr of manual cutting (Hart and Comeau 1992). LePage et al. (1991) found that a single cutting of *R. parviflorus* stands with brush saws at time of full leaf development was ineffective and resulted in only limited control for 1–2 growing seasons. With a disturbance of overstory and understory plants, mature *R. spectabilis* stands rapidly initiated new rhizomes and aerial stems, annually producing 1–2.5 m of rhizomes m⁻² and 25–50 stems m⁻² for at least two growing seasons (Tappeiner et al. 1991). *Rubus spectabilis* stands can be temporarily diminished by cutting in June–July, although plants can recover even after 9 mo of intensive, monthly cutting treatments (Zasada et al. 1990).

Fertilization with N-fertilizers in conifer renewal sites stimulates *R. strigosus* and *R. spectabilis* sprouting and height growth (Lawson and Waister 1972; Jobidon 1993).

Grazing trials have demonstrated that sheep will graze on *R. strigosus*, *R. parviflorus* and *R. spectabilis* in reforestation areas, although *R. strigosus* and *R. parviflorus* have only moderate palatability for sheep (Irving and Bailey 1985; Sutherland et al. 1991; Pickering and Richards 1993; Dereshkevich et al. 1994). Net *R. parviflorus* growth in grazed stands in *P. menziesii* plantations was 32% of that on ungrazed sites, although the net annual growth in scattered *R. spectabilis* stands showed no decrease due to grazing (Sharrow et al. 1989).

Seeding of recently scarified sites with legumes, bunchgrasses, and sod-forming grasses diminished the reestablishment of *R. parviflorus* and *R. spectabilis*, allowing *P. sitchensis* to outgrow these *Rubus* species in northwestern British Columbia (Coates et al. 1993). Applying grass–legume seed mixtures and fertilizer to burned sites substantially reduced the frequency of cover and height of *R. parviflorus* and *R. spectabilis*, especially during the first 3 yr in *P. menziesii* plantations (Kastner and Monthey 1992). Seeding with a grass–*Medicago sativa* L. mixture controlled *R. strigosus* sucker growth better than spraying and burning among *Populus* species in Alberta parkland (Irving and Bailey 1985).

Cover mulches of barley, oat, or wheat straws or mixtures of all three significantly reduced *R. strigosus* establishment through allelopathy of decomposing straw, and resulted in reduced spring seed germination and height growth of seedlings (Jobidon et al. 1989).

13. Response to Parasites

These *Rubus* species may act as reservoirs of plant pathogenic microorganisms. *Rubus parviflorus* is known to harbour apple mosaic, thimbleberry ringspot, and raspberry bushy dwarf viruses, which may be transferred through aphids (*Masonaphis* species) and by pollen to cultivated raspberry (Credi et al. 1986; Stace-Smith 1987; Stace-Smith and Martin 1989; Stace-Smith and Shier 1989; Bulger et al. 1990). A single-host aphid, *Masonaphis maxima* Mason, is reported to emerge with bud break on *R. parviflorus*, although damage to the host was not reported (Frazer and Forbes 1968; Gilbert 1980). A cyanid wasp, *Diastrophus kincaidii* Gillette, causes dieback of *R. parviflorus* because of the formation of numerous stem galls (each containing about 10 parasites) consisting of parenchyma tissue, which interferes with translocation of plant materials (Wangberg 1975; Kraft and Erbsich 1990).

Rubus strigosus, *R. parviflorus*, and *R. spectabilis* are hosts to several fungal parasites (Ginns 1986; Farr et al. 1989), although these shrubs are often found with few disease symptoms. Wall and Shamoun (1990a) reported *Septoria rubi* West. was the most common leaf-spot pathogen found on *R. parviflorus* and *R. spectabilis*, with symptoms appearing in early June and continuing throughout the summer. *Phragmidium occidentale* Arth. is also reported to be common on *R. parviflorus*, although it is not associated with the foliar necrosis and dieback frequently observed in mid-summer stems (Wall and Shamoun 1990a). Widespread distribution of leaf-spot symptoms on *R. spectabilis* observed by the authors in coastal British Columbia may be attributed to *Phomopsis* species, which are frequently present as endophytes in *R. spectabilis* foliage.

Biological control of *Rubus* species has been attempted in trials in Australia, New Zealand, and Chile, using a rust fungus, *Phragmidium violaceum* (Schultz) Winter, to control naturalized blackberry (Bruzzese and Hasan 1986), and in Hawaii, using necrotic and rust fungi on native and non-native *Rubus* species (Gardner 1983). In Canada, biocontrol trials of *Rubus* species have involved mainly bacterial and native fungal pathogens and have generated successful preliminary results. Foliar sprays of bialaphos, a phytotoxin produced from an actinomycete, *Streptomyces viridochromagenes*, applied at 2–2.5 kg a.i. ha⁻¹ in late July–late August, was highly successful in controlling shoot height growth and resurgence in *R. strigosus* shrubs (Jobidon 1991). Wall (1989) evaluated and demonstrated mild disease symptoms with several pathogens on *R. strigosus*, including bacteria associated with fire blight [*Erwinia amylovora* f. sp. *rubi* (Burr.) Winslow et al.] and fungi associated with leaf and shoot blights. Investigations by Thibault (1989) to control *R. strigosus* in Quebec have included pathogen surveys and identification of potential biocontrol agents, such as *Didymella applanata* (Niessl) Sacc. Potential mycoherbicides incorporating *Septoria rubi*, *Cylindrocarpon destructans* (Zinf.) Schöhlen or *Hainesia lythri* (Desm.) Höhnelt have shown initial suppression of *R. parviflorus* by rendering leaves non-functional through successful inoculations (Wall and Shamoun 1990b; Shamoun

and Callan 1992). In shadehouse trials, *Fusarium avenaceum* (Fr.) Sacc. and a *Colletotrichum* species, both isolated from *R. strigosus*, were found to cause extensive foliar lesions on *R. strigosus*, *R. parviflorus*, and *R. spectabilis* plants when combined with surfactants and applied in inundative doses (Oleskevich et al. 1995).

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