Reproduction of Conifers

A handbook for cone crop assessment

Forestry Technical Report 31

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ABSTRACT

Reproductive process of conifers is briefly described. Morphological characteristics of different stages of the process are identified and presented on photographs to provide an aid for estimating next year's cone crops. Advance knowledge of prospective cone crops should allow for better planning of reforestation programs. The handbook will be published in a loose-leaf format so that other species can be added as material becomes available.

RESUME

L'auteur décrit brièvement le processus de reproduction des conifères. Il identifie les caractéristiques morphologiques des différentes phases du processus et en présente des photographies pour aider à l'évaluation de la récolte de cônes de la prochaine année. Il est plus facile de planifier les programmes de reboisement si les perspectives de récolte des cônes sont connues à l'avance. Le manuel sera publié sous forme de feuilles mobiles et par étapes, au fur et à mesure que les espèces seront disponibles.

Cette publication est aussi disponible en francais sous le titre "La reproduction des coniferes."

ACKNOWLEDGEMENTS

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Table of Contents

INTRODUCTION

Throughout Canada, more than 22 000 kg of seed are processed annually for reforestation programs. It is anticipated that these requirements will rapidly expand as Canada continues to emphasize the need for reforestation.

The propagation and collection of these tree seeds, particularly those of superior genetic quality, requires the ability to forecast and identify developing cone crops even several months in advance of cone maturation. The ability to estimate seed crops in advance will come with understanding of the reproductive cycle of individual tree species and with the knowledge of the morphology of the reproductive structures.

This handbook was written with that in mind. Its text is simplified for the layman and only a few technical terms are used. The photographs concentrate on the main stages of development, generally only those that may be recognized by an unaided eye; a hand lens may be useful in the early stages of development.

The handbook will be published in a loose-leaf format, so that other species may be added as they become available.

Summary of the Reproductive Cycle of Conifers

The majority of conifers are tall evergreen forest trees. Since they are a large group, represented by 40 living genera widely scattered throughout the temperate zone, they exhibit a wide variation in their features. They differ in size and form, the structure and size of the leaf, anatomy and technical properties of the wood, and other characteristics. Resin ducts are abundant in some genera and entirely missing in others. Wood parenchyma may be conspicuous in the xylem of certain genera and absent in others.

Even greater diversity exists in the reproductive structures. The gametophytes—or haploid generations, both male and female—and the embryo—or young sporophyte, the beginning of the diploid generation—vary greatly in the methods of their development and in structure. The number of cotyledons of the embryo varies from 2 to 15. Some conifers do not have buds, others do not even produce cones; but most genera native to Canada do. Because of this great diversity, only the most typical features of the reproduction of coniferous species are discussed.

BUDS

In most conifers, the growth ends at the end of summer with the formation of buds. Generally, buds contain undeveloped next-year's shoots protected by several layers of bud scales. In the earliest or primordial stage, the growing tips are merely masses of undifferentiated or **meristematic** cells but, in most conifers, they soon become elaborate structures. They are **dormant** during the unfavorable growing period of late autumn and winter. During this period, they are protected by a series of overlapping **scales**. Bud scales are often covered by wax or hair, which increases their efficiency as protective organs.

According to their position on the stem, buds may be classified as **terminal, subterminal** or **lateral**. Terminal and subterminal buds are usually largest and best developed. Lateral buds are often small and inconspicuous. Most of them remain dormant but damage to terminal buds often reactivates their development.

According to their function, buds may be **vegetative**, which will give rise to vegetative shoots, or **reproductive**, which will develop reproductive structures. By the time buds enter dormancy, they are usually well developed.

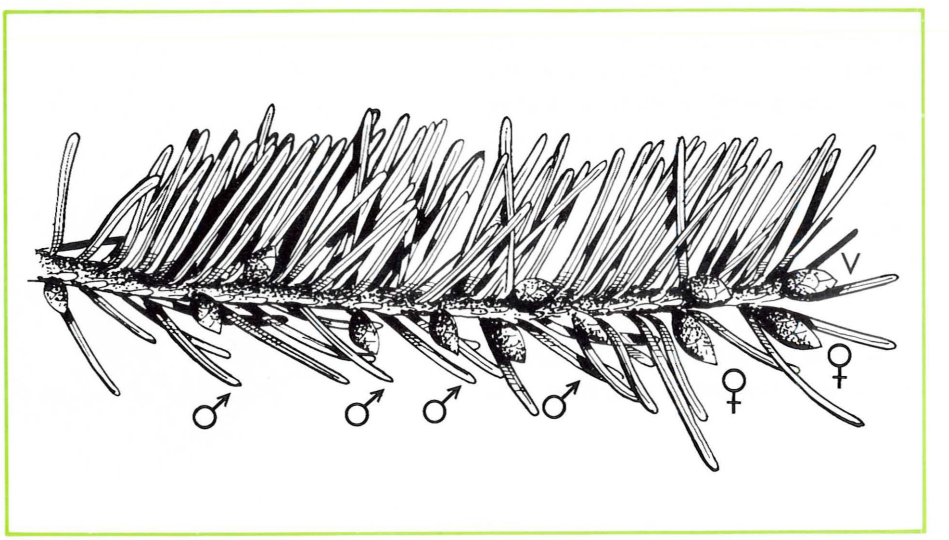


Fig. 1. Some species may have vegetative and reproductive buds of both sexes on the same shoot. Position, shape and size are usually typical, though the size may decrease with the distance from the tip.

STROBILI

The reproductive buds develop into **strobili** or **cones***. The cones are of two kinds, the **microsporangiate** or male** which produce **pollen** and the **ovulate, megasporangiate** or female** which produce the seed. When mature, the latter are the structures commonly recognized as cones.

In most genera of conifers, the microsporangiate or male bud during dormancy contains a well-developed miniature pollen cone, consisting of a simple **axis** or stem, bearing a series of spirally arranged, compressed, scalelike **microsporophylls**, each of which bears, attached to its lower surface, two sacklike **microsporangia** filled with pollen. The **megasporangiate** or female bud contains a cone that consists of an axis and usually spirally arranged **bracts**. At the base of the bracts, attached to the axis and the bract, is an **ovuliferous scale** which bears, freely attached to its upper surface, two **ovules**.

Most conifers are monoecious, i.e., bear both kind of cones on the same tree. Each cone is usually separate from the other kind and generally they occur on separate branches.

In spring, usually before much activity takes place in the vegetative buds, the axes of male strobili elongate, separating the rapidly enlarging microsporangia. Then, during dry weather, microsporangia dry out and separate along distinct lines and pollen is released. Female strobili resume development at the same time as male strobili. In some genera, more bracts and ovuliferous scales are initiated at the apex. Before pollination, internodes elongate, separating the

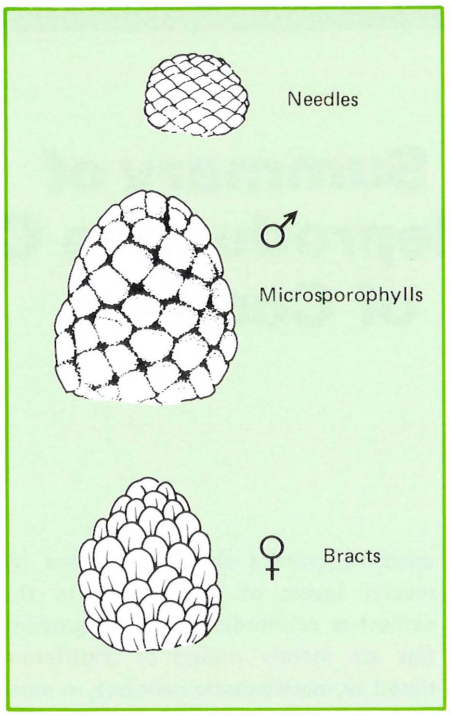


Fig. 2. When bud scales are removed, vegetative tip and reproductive strobili can be easily recognized.

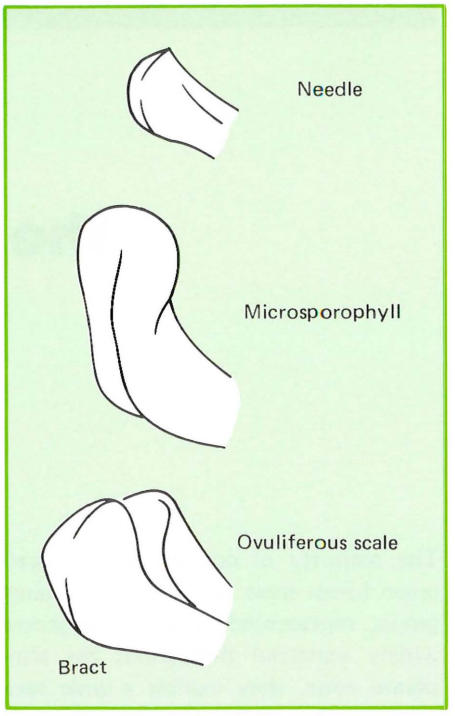


Fig. 3. Though color may be similar, the primordia of needles, microsporophylls and bracts with ovuliferous scales above are distinctly different.

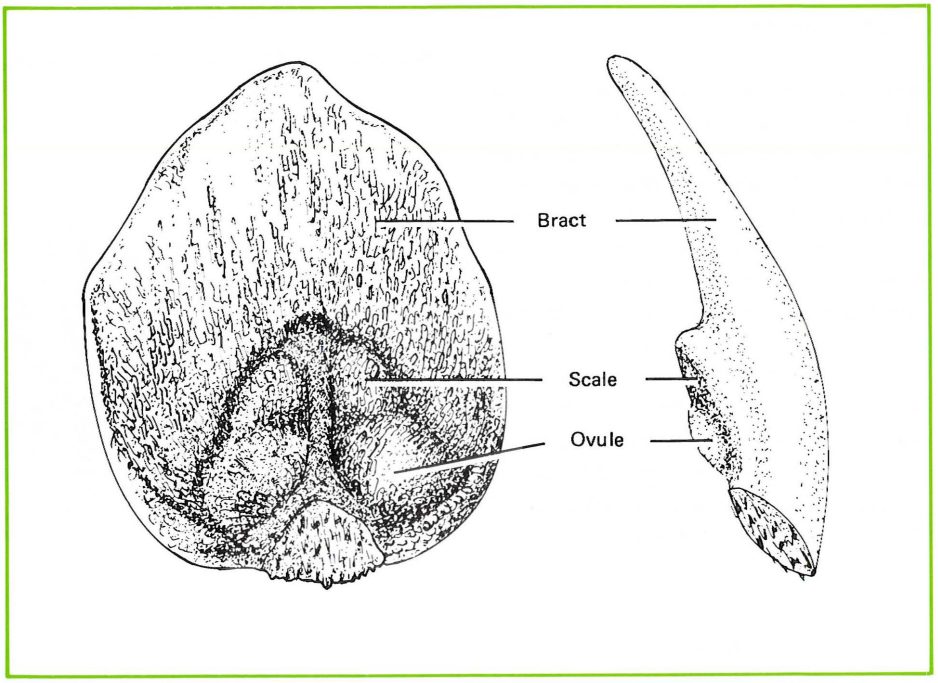


Fig. 4. During winter dormancy, the ovuliferous scale is only an appendix on the adaxial side of the bract. Each scale bears on its surface two ovules.

* Conifers do not produce true flowers.

** Botanically, the terms male and female, in reference to conifer buds and cones, are incorrect terms. They are, however, commonly used and understood.

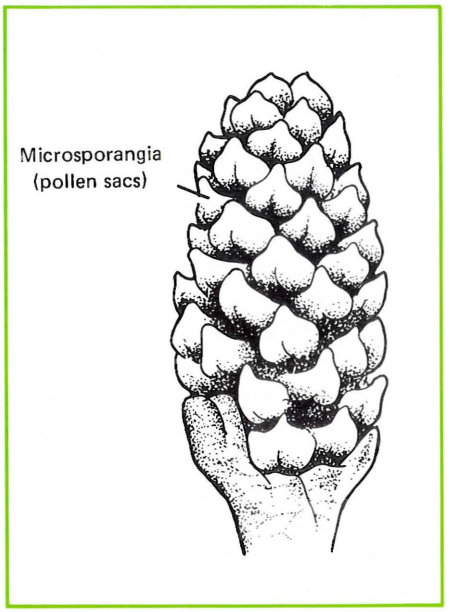


Fig. 5. In spring, the axis of the male strobilus elongates and microsporangia enlarge. Pollen is ready for release.

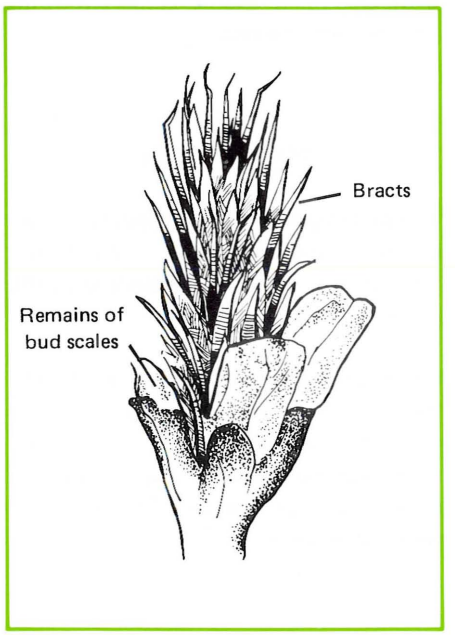


Fig. 6. In female strobilus, the internodes elongate, and bracts separate, enabling pollen to sift down to the ovuliferous scales.

bracts so that pollen can sift down through the spaces to the ovuliferous scales.

Pollen cones are small structures lasting usually for only a few weeks. After pollination, they dry out and fall off. The **megasporangiate** cones are of longer duration. In some genera, they develop in 1 year, as in spruces; in others, as in pines, 2 years are required for full development. After maturity, the cones may fall off, disintegrate or remain on the tree for several years, even after shedding the seeds.

POLLEN

Within the microsporangia or pollen sacs, **microspore mother cells** are produced. By the process of maturation, which involves a **meiotic division**, they give rise to a sphere of four **microspores**. The spores soon separate into individual cells and at this stage are referred to as **pollen grains** or just pollen. Because meiotic division precedes their formation, they have a **haploid** or half number of **chromosomes**. In the spring, pollen is produced in tremendous amounts and appears at maturity as yellow dust.

OVULE

The ovule, located on the upper surface of the scale, consists of a **megasporangium** surrounded by a special covering, the **integument** which later becomes the **seed coat**. In most conifers, the integument covers the ovule as a cuplike overgrowth. At the tip of the ovule, the encircling parts of the integument leave a little opening called the **micropyle** which allows the pollen grain to enter and come in contact with the megasporangium.

The **megasporangium** is the inner tissue of the young ovule. In the young stages, this tissue is undifferentiated, but later, several **megaspore mother cells** are produced at the center. Maturation of a megaspore mother cell includes meiotic division and produces a group of four

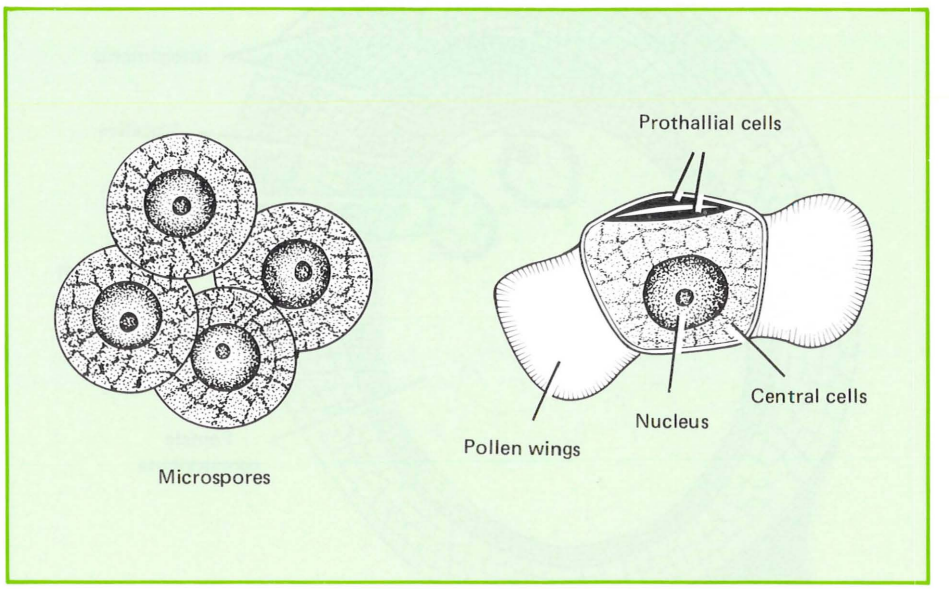


Fig. 7. Microspore mother cell, by meiotic division, gives rise to a group of four microspores having a haploid number of chromosomes. The microspores soon separate and develop wings. At this stage, they are called pollen.

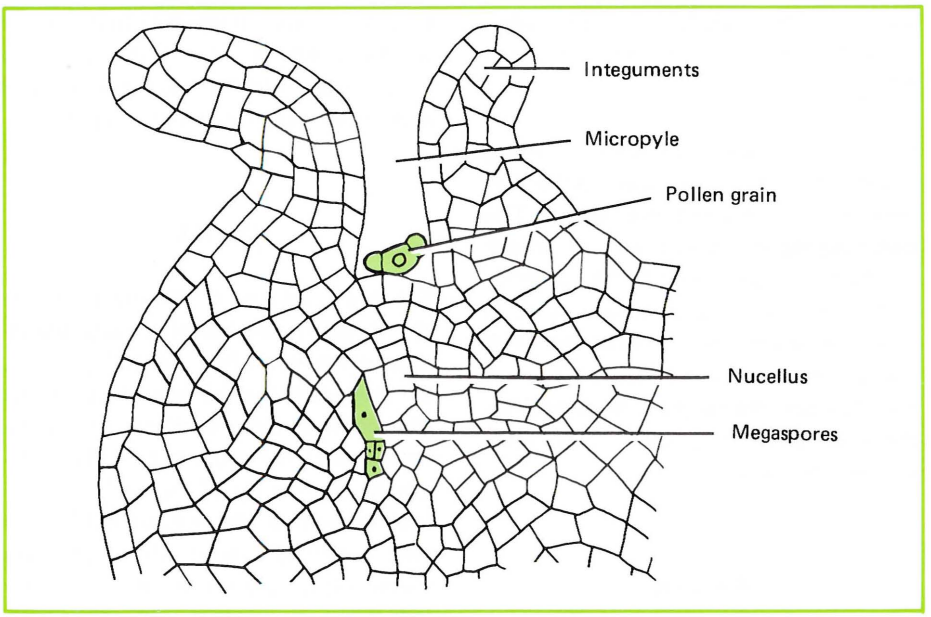
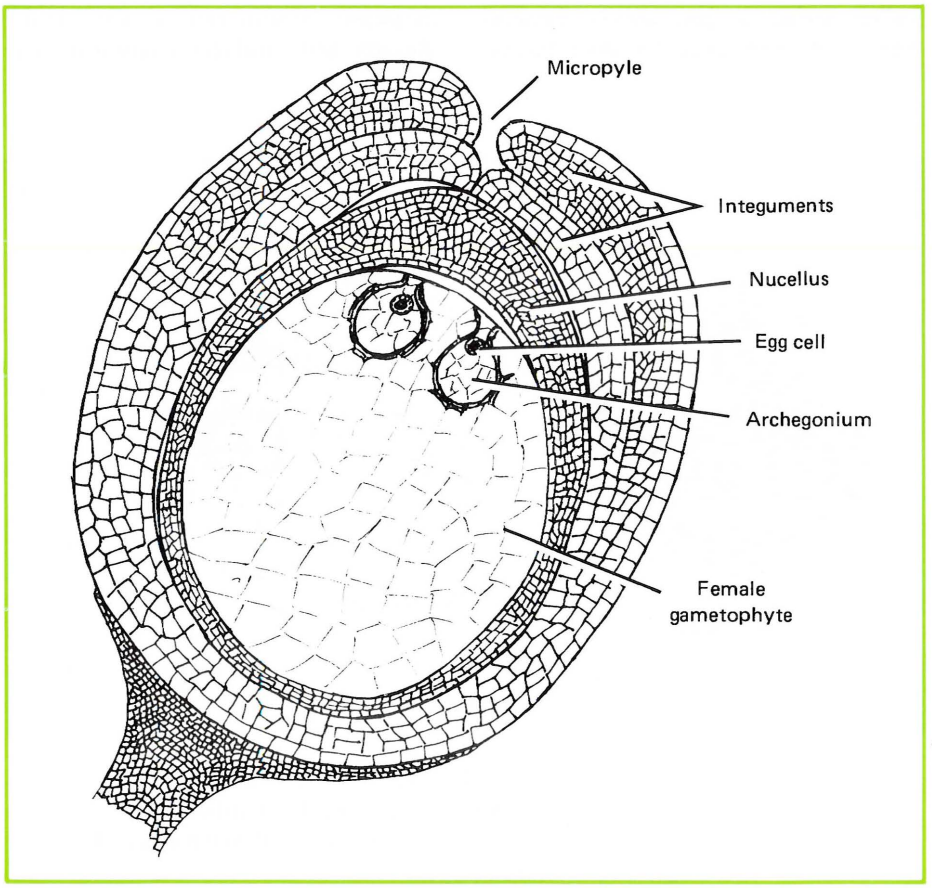


Fig. 8. In most conifers, an ovule is an ovate structure and the integuments cover it as a cuplike overgrowth. At the time of pollination, four megaspores are arranged in the center of the nucellus. Only one, the largest, is functional; the other three degenerate.



◀ Fig. 9. The archegonia are deeply immersed into the female gametophyte. An archegonium consists of an egg cell with nucleus and abundant cytoplasm.

megaspores which, similar to microspores, have a haploid chromosome number.

On germination, the megaspore gives rise to the female gametophyte. The development of the female gametophyte takes place within the megasporangium of the ovule and the gametophyte is entirely dependent for nutrition on the old sporphytic structure.

The digestion of the nucellus results in a vacuole in which the megaspore occupies a central position. Divisions of the megaspore nucleus and an extension of the megaspore cell wall produces a female gametophyte as a multicellular, solid, ovate structure.

Archegonia develop at the micropylar end of the female gametophyte. Each archegonium develops from a single superficial cell of the gametophyte and consists of a short neck, a ventral canal cell, and an egg cell. At maturity, the archegonium is deeply immersed in the female gametophyte.

POLLINATION

The **pollen grains**, or **microspores**, undergo two or more divisions. In most conifers, at this stage of development, the pollen is shed.

Pollination is the term applied to the transporting of the pollen from the male cones to the female cones. In conifers, it is accomplished by the floating of pollen through the air. This is called **wind pollination.**

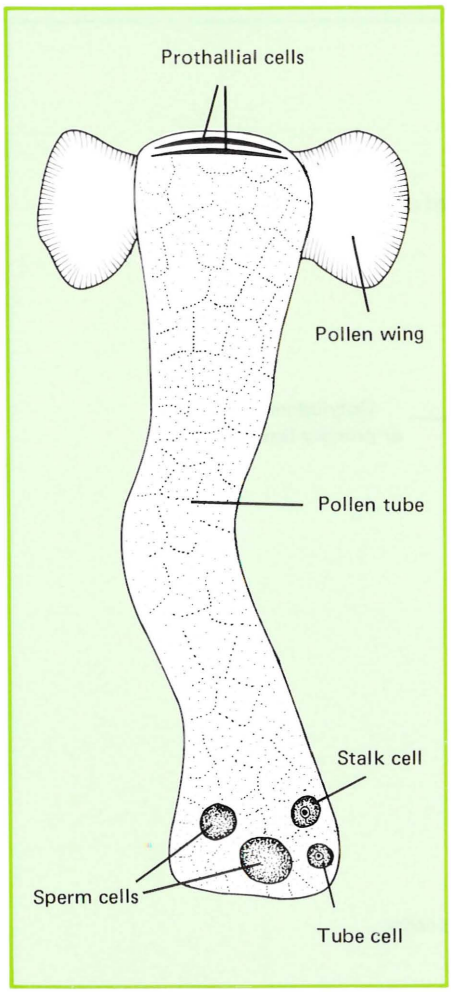


Fig. 10. Shortly before fertilization, the body cell has divided into two male cells or sperms. The stalk cell, the tube cell and the prothallial cells degenerate.

When they reach the female cone, the pollen grains fall down among the scales, reaching the ovules located at their base. When receptive, an ovule secretes a drop of resinous material which eventually dries out and pulls the pollen grains through the micropyle.

After a short period, the **pollen tube** begins to grow, penetrating the tissues of the megasporangium. At this stage, the final division takes place in the pollen grain and two **sperm** are produced.

FERTILIZATION

The fertilization is accomplished by the **fusion** of the **nucleus** of one of the sperm with the nucleus of the megaspore or egg cell. This results in the doubling of chromosomes, which restores their number to that characteristic of the species. In general, where the development of the cone takes 1 year, fertilization occurs in early summer; in those where development of the cones takes longer, fertilization may occur in the spring of the second year.

The fusion of the nuclei doubles the number of chromosomes and initiates the new sporophytic generation.

Soon after fertilization, rapid division of the megaspore nucleus takes place, followed by formation of the cell walls and eventually the complete **seed** is formed.

SEED

The conifer seed is a complicated structure. It consists of an **embryo**, surrounded by a mass of stored food and pro-

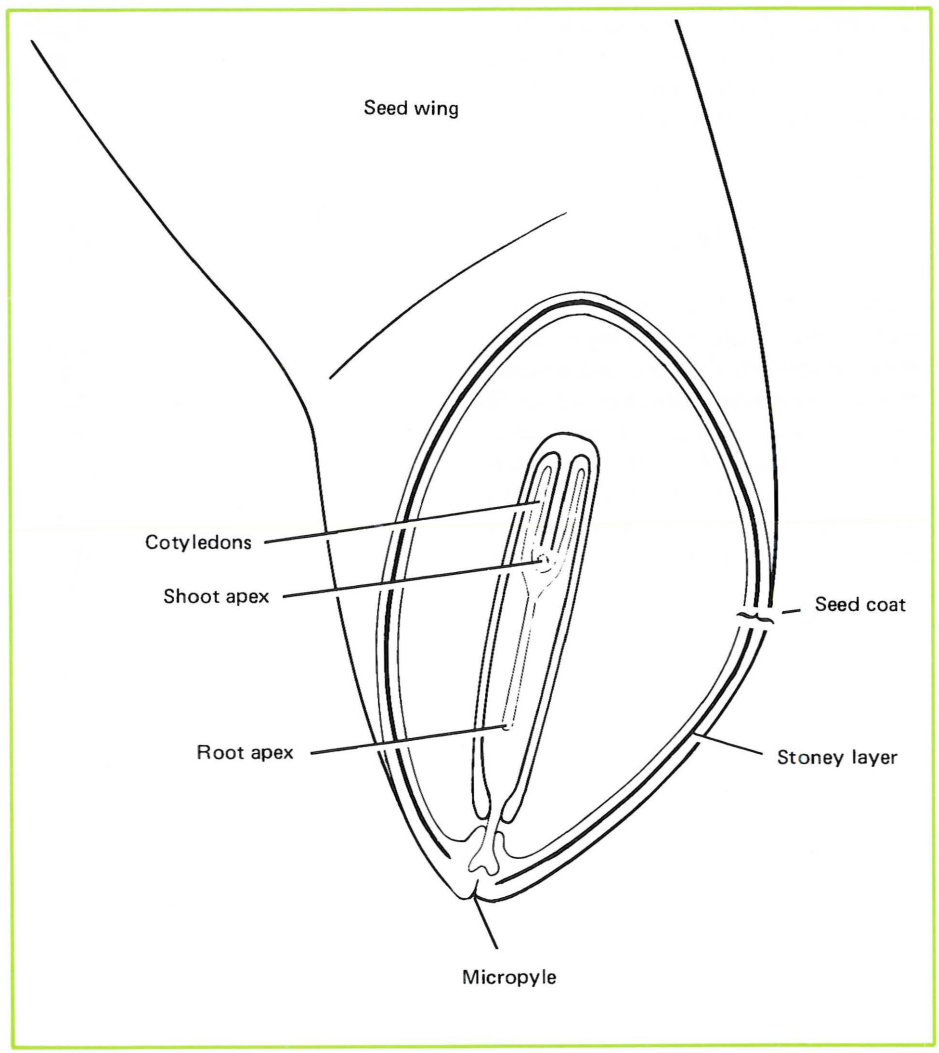


Fig. 11. Seed is a dormant embryo embedded within a female gametophyte which provides food supply for the new growth. All this is covered by a protective, multilayered seed coat.

tected by a thick and usually hard **seed coat**. The embryo is, in a sense, already a complete plant with an elementary **vascular system**, an **axis** with **cotyledons** or primary leaves and a well-developed radicle or root apex. The **shoot apex** is usually only a cone of meristematic cells.

SEEDLING

The seeds of conifers germinate slowly and usually after a prolonged resting period. Upon germination, the **primary root** of the embryo emerges, usually pushing the seed coat up through the ground. Later, the cotyledons are freed from the seed coat and the young seedling begins a long period of growth to develop into a mature tree.

TREE

At first, the seedling produces only vegetative buds. **Sexual maturity** is dependent on species, size, age and environmental conditions. Between 10 to 50 years of age, trees begin also to produce reproductive buds. For a few years these may be only of one sex, but eventually both male and female buds are produced and the reproductive cycle repeats itself.

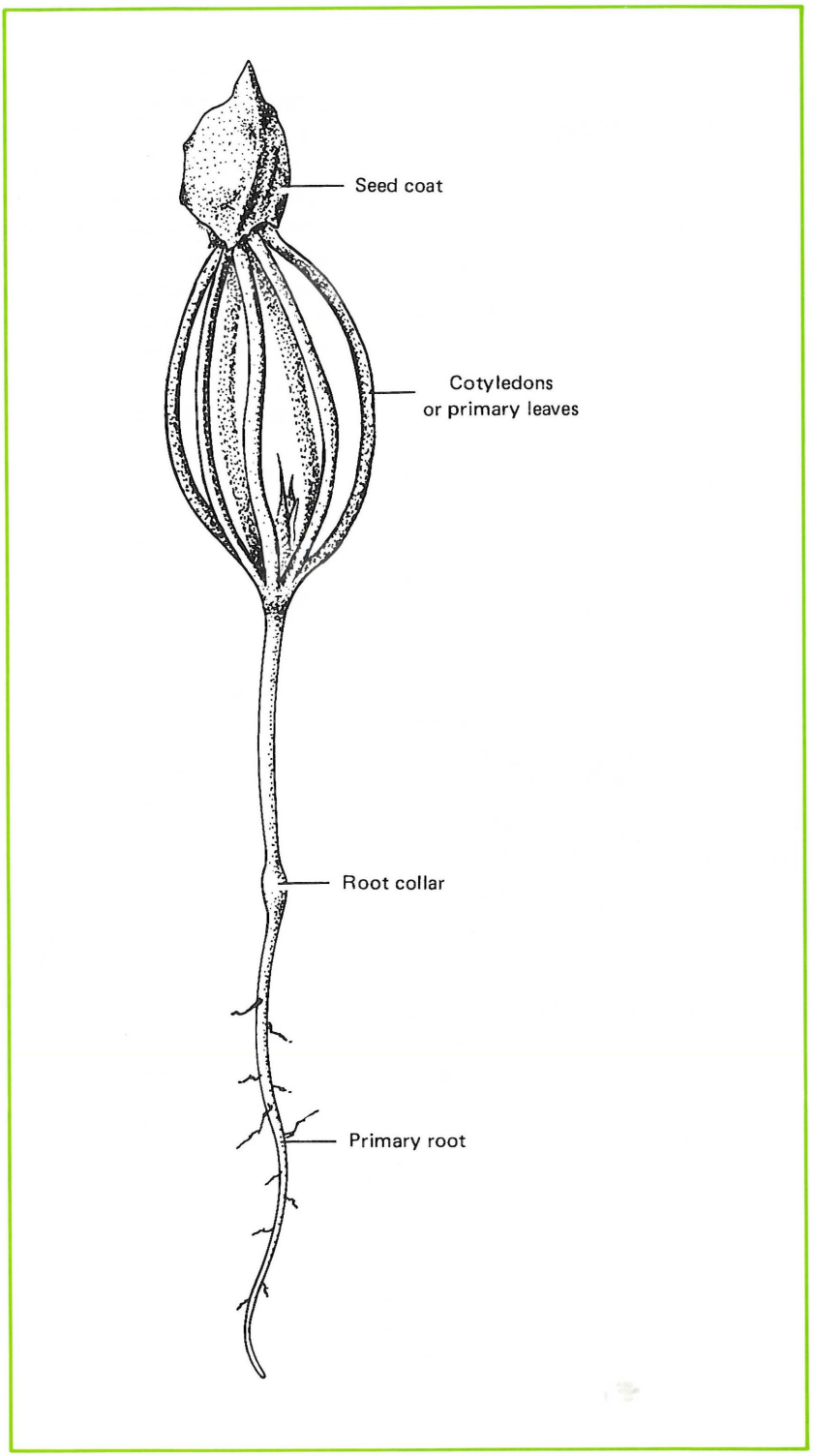


Fig. 12. Upon germination, the embryo elongates, pushing the seed coat up through the ground.

GLOSSARY

adaxial...facing toward the axil.

apex...the growing point of a stem or root.

archegonium...the female sex organ consisting of a neck and a body which contains the ovum.

axil...the angle formed between the axis and any organ that arises from it; e.g., ovule.

axis...an imaginary line, around which the organs are developed.

bract...a vegetative scale of the cone above which lies the seed-bearing scale.

central cell...a cell produced inside the pollen by the first pollen cell division; from this cell in the next division, the tube cell and generative cell are produced.

chromosomes...fibrillar bodies formed during nuclear division, which produce the daughter nuclei.

cotyledon...the first leaves of the embryo.

diploid...having two sets of chromosomes.

distal...remote from the place of attachment, the converse of proximal.

dormant...applied to parts that are not in active life, as buds in winter.

egg cell...the ovum proper apart from any layer of cells derived from it or from other cells.

embryo...the rudimentary plant formed in a seed.

flushing...initiation of growth, as in spring.

fusion...the union of a pair of fertile cells.

gametophyte...the generation that bears the sexual organs.

haploid...the organism with the half number of chromosomes, as in sexual cells.

hybrid...a plant obtained by crossing of two related species.

integument...the covering of an organ or body.

internode...the space or portion of stem between two nodes or whorls of branches.

latent...dormant, usually for a longer period.

megasporangium...the inner tissue of the ovule.

megaspore...a female reproductive cell.

megaspore mother cell...the cell inside the megasporangium which, by meiotic division, produces 4 megaspores.

meiotic division...cell division that includes reduction of chromosomes to haploid number.

meristematic cells...undifferentiated tissue capable of being transformed into special forms, as cambium, etc.

micropyle...the lower part of the tube of the integument, where it expands to join the seed cavity.

microsporangium...receptacle producing microspores or pollen, such as pollen sacs or stamens.

microspore...the male spore in heterosporous plants, applies to the pollen grain.

microspore mother cell...a cell that, by meiotic division, involving reducing of chromosome number, produces microspores or pollen.

microsporophyll...leaflike organ-bearing microsporangia.

mitosis...nuclear division in which the diploid number of chromosomes is retained, as in growth.

monoecious...having unisexual male and female flowers on the same plant.

morphology...the science of form and structure of plants.

nucellus...the body of the ovule or megasporangium containing the embryo.

nucleus...a body inside a cell formed by grouping together of the chromosomes.

ovulate...possessing ovules.

ovule...the organ that, after fertilization, develops into a seed; also, the young seed in the ovary.

ovuliferous scales...inner scales in a cone that bear ovule.

parenchyma...undifferentiated plant tissue which may vary in structure and function and develop into different organs.

pollen, pollen grains...the fertilizing dustlike powder produced by the male flowers.

pollen sac...the microsporangium.

pollen tube...the tube that grows from a pollen grain and that enables passing of chromosomes of the sperm cells to the chromosomes of the egg cells.

pollination...transport of pollen from the microsporangia in male cones to the ovules in female cones.

primary root...the first main root developed from the radicle.

primordium...a member or organ in its earliest condition.

propagation...to cause multiplication of individuals, as of plants.

prothallial cells...two or more cells produced by the first divisions of microspore; they usually degenerate.

proximal...the part nearest the axis, as opposed to distal.

radicle...arising from the root crown, the first root apex.

reproductive...applied to parts that share in reproduction.

root collar...junction between root and stem, usually at the point of germination at ground level.

scale...any thin scarious body, usually a degenerate leaf, sometimes of epidermal origin.

seed...the fertilized and matured ovule.

seed coat...the outer coat of the seed, usually hard and brittle.

shoot...the young growing branch or twig.

shoot apex...the tip of the young growing branch or twig.

sperm cell...usually a minute male active cell whose function is to fertilize a female cell.

sporophyte...the diploid spore-producing phase in higher plants with alteration of generations.

spur shoot...a short lateral shoot, sometimes with a few foliage leaves in a tuft.

stalk cell...the cell arising from division of the antheridial cell in conifers, which does not become the generative cell.

strobilus...an inflorescence largely made up of scales.

subterminal...under or below the terminal or apex.

terminal...proceeding from or belonging to the end or apex.

tube cell...the cell that gives rise to the pollen tube.

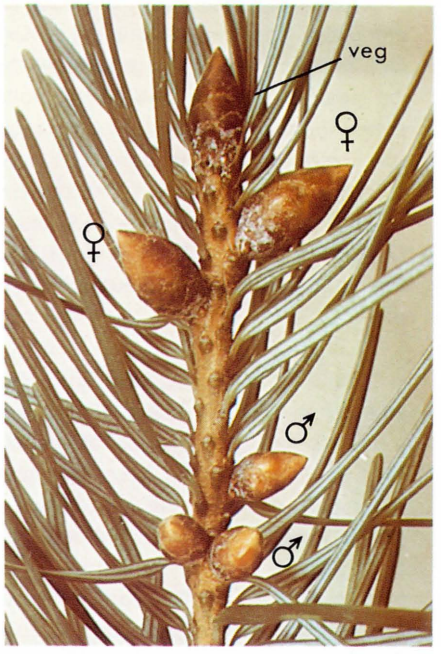
vascular system...vessels adapted for circulation of fluids.

vegetative...stage of growth in plants when reproduction does not occur.

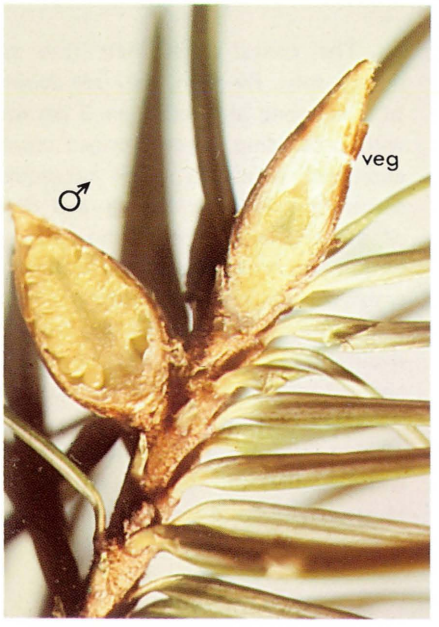
ventral canal cell...a small cell usually without a cell wall within the archegonium.

xylem...the main water-conducting tissue in a plant.

Douglas-fir



1. In heavy crop years, vegetative and reproductive buds of both sexes may occur on the same shoots. The shape and size is indicative of their function, though the size decreases with distance from the tip.



2. Vegetative bud is slim, the male bud ovate and widest in the middle. Microsporophylls can be distinguished from needle primodia.

3. Female bud is ovate and widest at its base. Three-pronged, sharp-pointed, purple bracts differ markedly from microsporophylls or needles.

4. Pollination takes place before vegetative bud break. Male strobili elongate, microsporangia split open and pollen is released. After pollination, male strobili wither and die.

5. At pollination, female strobilus stands erect. Elongation of the axis separates the bracts, allowing for entry of pollen.

6. After pollination, the female cones become pendant and turn green. The three-pronged bracts remain the prominent feature.

7. Seed is about 7 mm long, 3 mm wide and 2 mm thick. There are on an average 90.000 seeds per kg.

Douglas-fir

***Pseudotsuga menziesii* (Mirb.) Franco**

by S.Eis and D.Craigdallie

Douglas-fir begins to produce cones at about 20 to 25 years of age. Preceding light cone crop, the female buds tend to occur mainly at the top and male buds in the middle of the crown; preceding heavy crops, the reproductive buds of both sexes may occur throughout the crown and sometimes even on the same shoots (1). The function of the buds, whether they are vegetative, male or female, can be recognized from their outer appearance from about the beginning of August. If the bud scales are peeled off or the buds are cut open, identification can be made even earlier. Because bud development continues until unfavorable weather forces dormancy in November or December, later identification becomes progressively easier.

The terminal buds are usually vegetative throughout the crown (1). Preceding light crops, the reproductive buds of both sexes occur mainly in subterminal positions (2 and 3), whereas preceding heavy crops, the subterminal positions are occupied by female buds, while male buds are distributed lower along the shoot, sometimes forming a group of three to five at the base of the shoot (1).

BUD DESCRIPTION

The vegetative buds are rather slender (1); reproductive buds are more egg-shaped, somewhat shorter and usually lighter brown, have fewer bud scales and less white resin on the surface of the scales. Both sexes are similar (2 and 3), but the male buds tend to be smaller (1) and broadest near the middle (2), whereas female buds are usually somewhat larger and broadest closer to their base (3).

When bud scales are removed or the buds are cut open, bud recognition becomes easy. The vegetative bud contains the entire following year's shoot, with flanks densely covered with spirally arranged, unelongated, green needles (2). In cross-section, the needles are oblique-angled. This whole structure is only about 2 mm long; the rest of the bud cavity is empty (2). In contrast, the bud cavity of the reproductive buds is completely filled with reproductive structures.

By the time the buds enter dormancy, the male bud contains a well-developed pollen cone, consisting of a simple axis covered with spirally arranged scale-like, blunt and reduced appendages or microsporophylls (2). Each microsporophyll bears, at its lower surface, two yellow or light green microsporangia filled with pollen. The length of the male cone during the winter dormancy is about 4 to 5 mm.

The female cone, during dormancy, is about the same size as the male cone. It consists of an axis bearing a series of spirally arranged, long, pointed trident bracts (3). In the axil of each bract is a small ovuliferous scale which bears at its upper surface two ovules. The scales are visible only upon dissection.

BUD BREAK

The first growth and differentiation occurs in the reproductive buds in late February or early March, about a month or more before any activity takes place inside the vegetative buds.

Inside the male buds, the cone axis elongates and microsporangia enlarge and develop into two large rounded pollen sacs. Following bud burst, pollen cones show a wide range of colors, yellow being most common, but often ranging into green or red. At the time of pollination, the pollen cone is usually pendant and about 2 cm long (4). Soon after pollination, it dries out and breaks off.

Inside the female bud, the bracts and the ovuliferous scales enlarge, with a corresponding elongation of the axis. The lower bud scales become slightly separated, revealing the light-brown or purple inner bud scales. The seed cone buds usually double in length before bud burst. At pollination time, the female cone stands erect and is about 3 cm long. Its appearance is dominated by the large three pronged bracts, which are purple to red (5). After pollination, the female cones turn green and become pendant. Fertilization takes place about 4 to 6 weeks after pollination and initiates the development of the embryo and, subsequently, the seed.

The cones reach their final size during July. By then, they are about 7 to 9 cm long and less than 2 cm wide with protruding, three pronged usually appressed bracts (6). The subsequent maturation involves drying and death of the vegetative tissues and a change of color to brown. In a mature seed, the embryo is loosely packed within a nutritive tissue. Seed wings develop from the ovuliferous scale. The mature seed is about 7 mm long, 3 mm wide and 2 mm thick (7). The seed wing is about 10 to 12 mm long and 5 mm wide. There are about 65,000 to 130,000 seeds per kg. Most seeds are released by late October, the remainder during the winter.

Lodgepole Pine

1. Vegetative buds are long and slim, without swelling at their base.

2. Swelling at the base of a vegetative bud indicates presence of male strobili.

3. Next year's vegetative growth supports spur shoots with needles. At the base of the vegetative growth are clusters of male strobili.

4. The sheath of bud scales which normally covers the male strobili may be entirely missing.

5. Cluster of male strobili are easily noticeable in spring because of their bright yellow color.

6. Female strobili occur on current year's shoots; therefore, they are not visible until late in spring.

7. At pollination time, bracts stand erect or perpendicular to allow for entry of pollen.

8. At the end of the first growing season, conelets are about 15 mm long, almost round and green in color.

9. Mature cones are egg-shaped, pointed and assymmetrical. Their color is light brown. Cones from preceding cone crops are darker.

10. Seeds are about 3 - 4 mm long, ovoid, reddish brown and often mottled. They average about 250.000 per kg.

Lodgepole Pine

Including Shore Pine

***Pinus contorta* Dougl.**

by S. Eis and D. Craigdallie

Lodgepole pine is sometimes divided into two or three subspecies. Since the reproductive organs are practically identical and since there are no reliable needle or cone differences by which they can be distinguished, it would appear that lodgepole pine is morphologically variable, with the two or three described forms constituting a single species.

Lodgepole pine is a prolific seeder and often produces fertile seed before it is 10 years old. However, seed production usually starts at the age of 15 to 20 years, with heavy seed crops at intervals of 2 to 4 years and light crops in most intervening years.

Lodgepole pine bears male and female strobili, usually over the entire crown. The female strobili occur most abundantly in the upper part of the crown, where sometimes the male strobili may be missing. The strobili are lateral in their position; the male strobili are spirally arranged at the base of the current year's growth (4), whereas the female strobili occur near the apex (6). If they occur on the same shoot, the male strobili may be separated from the female strobili by up to 15 cm of vegetative tissue at pollination.

The presence of male strobili becomes evident by late August, but the presence of female strobili cannot be detected visually until after bud break in the spring. Earlier accurate counts can be made only by careful dissections of terminal vegetative buds.

BUD DESCRIPTION

During winter dormancy, the vegetative bud consists of a sheath of semi-transparent, spirally arranged bud scales (1), which enclose an unelongated, following year's shoot, consisting of an axis covered by spur shoots (needle fascicles) with compressed short needles and, at the tip, a group of scales which overarch the apex (3).

If only a few male buds are present, they may be entirely enclosed within the terminal bud scales and appear only as a swelling at its base (2). If numerous male buds were initiated, the bud scales were forced apart, torn and largely shed, exposing the male buds (4). By the time male buds enter dormancy, the sporogenous tissue has considerably enlarged and pollen sacs appear to be in an advanced stage of development (3).

The female strobili develop entirely within the scales of the terminal vegetative bud and, because of their subterminal position on the shoot, their differentiation is delayed until the differentiation of needle fascicles, which progresses acropetally, takes place near the apex of the shoot. During dormancy, the female strobilus consists of a short shoot axis covered with spirally arranged compressed bracts which, at this stage, appear only like lateral outgrowths along its flanks. The whole structure is covered by short hood scales.

STROBILI

At the time of pollination, the male strobili form reddish yellow or brownish yellow clusters at the base of elongated shoots; individual strobili are about 8 to 10 mm long (5). The female strobili occur singly in lateral positions (7) or in groups of 2 to 3 in subterminal positions (6), next to the already formed, next year's vegetative bud. They are about 5 to 6 mm long with a 3 to 5 mm long, thick stalk. The bracts which are the only visible parts, are red to purple with yellow spurs (6 and 7); they stand perpendicular to the axis to allow for the entry of pollen. Despite their small size the strobili are conspicuous because elongation of needles has not been completed.

Pollination is by wind. The male strobili turn brown after pollination, wither and are shed. Within 5 to 7 days following maximum receptivity, the ovulate cones close to form a compact purple conelet. In 2 or 3 weeks, they turn purplish brown or green brown and by the end of the growing season they have grown to about 15 to 18 mm (8). By this time the scales have elongated and thickened and are the only visible parts.

Fertilization occurs about 13 months after pollination, in the late spring of the second year. The development of the seed takes about 3 months and by late August or early September the seed is mature. At maturity, the cones are 2 to 4 cm long, short-cylindrical to egg-shaped and asymmetrical at the base (9). The color changes to lustrous light brown or yellow brown.

Under natural conditions, cones open on hot autumn days when there is usually little wind, so that the range of seed dispersal is not great. The seed release is only partial, as many cones remain closed and attached to the branches for many years. In this manner, large quantities of viable seed are retained.

Seeds are about 4 mm long, ovoid, reddish brown, often mottled with black (10); wings are about 12 mm long. Clean seed averages between 170 000 to 340 000 per kg.

Western Hemlock

1. Vegetative buds are small and slender. They are somewhat angular in cross-section because the outer bud scales have a prominent keel.

2. Female buds occur almost exclusively in terminal or subterminal position. They are spherical or oval, green and pubescent.

3. Male buds may also occasionally occur in terminal position. In such a case, they are not distinguishable from female buds by their outer appearance. Dissection and hand lens is necessary.

4. More frequently, male buds occur in lateral positions along the last year's growth.

5. In heavy crop years, male buds may occur in groups of up to 8 in subterminal position.

6. At pollination, male strobili are about 5 mm long on a thin stalk. The usual color is light purple, but may also be yellow or red. At maturity, pollen sacs are yellow.

7. Female buds are about 1 cm long on a short stalk. The tri-lobed bracts are light blue or light purple; behind them protrude dark-blue ovuliferous scales.

8. The cones are about 25 mm long and 10 mm wide. There are about 7 seeds per cone and 80.000 cones per hl.

9. Seed size is variable. Number of seeds varies from about 0.5 to 1.3 million per kg.

Western Hemlock

***Tsuga heterophylla* (Raf.) Sarg.**

by S.Eis and D.Craigdallie

Western hemlock is a prolific seeder. Seed bearing usually starts between 25 and 30 years of age and some seed is produced every year, with heavy seed crops every 3 to 4 years.

As soon as the buds are formed in summer, their function, whether vegetative or reproductive, can be recognized from their outer appearance, the position on the shoot and the position in the crown.

As in most conifers, in light crop years, female buds occur mainly at the top of the crown and male buds in the middle and lower parts of the crown. In heavy crop years, and especially on open-grown trees, buds of both sexes may occur throughout the crown. The more vigorous shoots in distal positions bear female buds, while those of lower vigor in proximal positions bear male buds.

BUD DESCRIPTION

Even in heavy crop years, most terminal buds are vegetative (1). On vigorous primary branches, they are about 3 to 4 mm long and on secondary lateral branches, about 2 mm long. They are somewhat angular in cross section as a result of the slightly keeled outer bud scales. The bud scales are light brown to dark green and covered with fine hair, like the young shoots. The dormant vegetative bud consists of 20 to 26 bud scales enclosing the next year's growth. The bud is usually obscured by several short needles.

The female buds occur in terminal positions (2). They are borne singly or, rarely, in groups of 2 or 3. They are ovate to obovate and about 3 to 5 mm long and have 20 to 26 bud scales. The outer bud scales are green to light brown, covered with fine hair and extend about three-fourths the length of the bud. Protruding inner bud scales are slightly darker brown, smooth and shiny. Soon after the buds are formed, during the first half of August, bract initiation proceeds up the flanks of the apex and, by the end of August, ovuliferous scales are initiated. During the dormant period, the laterial lobes of the scales overlap the margin on the bracts.

In poor crop years, some male buds may also occupy the terminal positions (3). However, they more typically occupy lateral positions, sometimes singly, but usually as groups of 2 to 4 at the base of last year's shoot (4) or a short distance below the terminal bud (5). They are ovate or obovate and about 2 to 3 mm in length (4). The bud scales are fewer than on female buds, rarely exceeding 20. The outer bud scales are covered with fine hair and are light brown. The pollen cone, tightly packed within the bud scales, often enlarges enough before dormancy so that the tip of the bud is covered by only light-brown inner scales through which the green male strobilus is showing.

When bud scales are removed or the buds are cut open, bud recognition becomes easy; however, because of their small size, a hand lens may be necessary. The vegetative buds contain the next year's shoot with flanks densely covered with green, spirally arranged, unelongated needles. The dormant female bud contains a strobilus with all bracts and ovuliferous scales, although the distal ones may be poorly developed. The male bud has all microsporophylls and pollen sacs.

BUD BREAK

Initiation of activity in the reproductive buds occurs around the beginning of March, about 4 to 6 weeks before any activity takes place in the vegetative buds. In the male buds, the strobilus elongates and microsporangia develop into two rounded pollen sacs. The elongated pollen cone pushes the bud scales apart. At pollination, the pollen cone is light purple, yellowish or reddish, 4 to 5 mm long on a 3 to 4 mm long stalk (6).

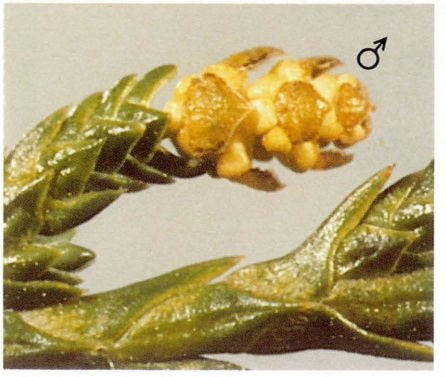
Inside the female bud, the strobilus enlarges, the outer bud scales separate, and the tip which, during dormancy, was covered by brown, shiny inner bud scales, rapidly enlarges. The flanks of the female strobilus are covered with spirally arranged, light blue to purple, tri-lobed bracts, behind which protrude larger, darker blue, two-lobed ovuliferous scales (7). At pollination time, the female cones are about 1 cm long. After pollination, the scales rapidly enlarge, turn green and the cones become pendant. Fertilization takes place about 4 to 6 weeks after pollination.

The cones attain their final size in August, when they are about 2.5 cm long and 1.0 cm wide (8). The subsequent maturation involves drying and death of the vegetative tissues and gradual change of color to brown. Most seeds are released in late September and during October, but sometimes more than 50% are retained and are gradually released until the following spring. The mature seed is about 3 mm long, 1.6 mm wide and 1.1 mm thick (9), but the size range is substantial. The embryo extends about 90% of the seed length. The seed wing is about 8 to 9 mm long and 3 mm wide. The number of seed per kg ranges from about 0.5 to 1.3 million.

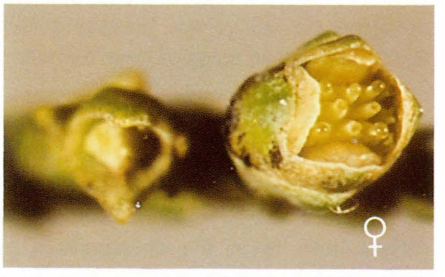
Yellow Cedar

1. In heavy crop years, it is not uncommon to find female and male strobili on the same branches.

2. Female strobili occur at the tips of short shoots near the tip of vigorous vegetative branches. They are about twice the size of vegetative shoot tips and are dark greenish blue or bluish gray.



3. Male strobili enter winter dormancy in an advanced stage of development. They are egg-shaped, about 3 mm long, with green microsporophylls and yellow pollen sacs.



4. At pollination, the fused bract-scale structure separates and exposes the tips of ovules.

5. One-year-old cones are already fully grown. However, they are green and soft to pressure.

6. One-year-old cones are easy to cut. The section is light colored, the seeds small, white and soft.

7. At the end of the second growing season, the cones are hard and brown, with prominent ridges between the scales. There are about 130.000 cones per hl.

8. The seed is about 5 mm long, dark brown with light-brown wings. There are only 7 seeds per cone and about 230.000 seeds per kg. Viability of seed is very variable.

Yellow Cedar

Chamaecyparis nootkatensis **(D.Don) Spach**

by S.Eis and D.Craigdallie

Yellow cedar occurs at high elevations and cool northern slopes. In its natural range, it is rarely a prolific seed producer, though it usually produces some seed every year. Good crops are infrequent and at irregular intervals. In light crop years, female cones are produced on the upper, vigorous branches of the tree, while less vigorous lower branches bear male cones. In heavy crop years, male and female strobili may occur on the same branch: the tip remains vegetative, while short shoots near the end of the main branch bear female strobili and long, proximal shoots bear male strobili.

Yellow cedar does not produce buds or bud scales. Instead, the vegetative apex is enclosed by overarching scale-like leaves and leaf primordia in various stages of development (1). The reproductive structures are produced by a gradual transition of vegetative shoot tips into reproductive tips (2 and 3).

STROBILI

Male strobili (1) are usually far more abundant than female strobili (2) and, in heavy crop years, may occupy almost all the tips of shoots. A new, lateral tip develops a short distance below the male strobilus and, after pollination, when the strobili are shed, grows vegetatively for a few weeks. This new shoot may remain vegetative or produce a male strobilus in the next crop year.

As in all conifers, the initiation of the reproductive structures takes place in summer of the year preceding pollination. At the onset of winter dormancy, the male strobili (3) are egg-shaped and about 3 mm long. The microsporophylls are completely exposed, green to light green, with usually 2, but occasionally 3, microsporangia (pollen sacs) attached to the basal side and extending beyond the microsporophylls. The microsporangia are yellow because pollen is in an advanced stage of development.

Female strobili (2) are produced at the tips of newly formed, short lateral shoots close to the main shoot tip of a branch. Their initial development differs little from the development of male strobili except that no branching takes place, thus these lateral shoots are eliminated for future growth or seed production. During winter dormancy, newly initiated seed cone (2) is about 2 to 3 mm long and the fused bract-ovuliferous scale structures that cover the cone are black. There are usually 3 ovules in the axil of each of the first pair of bract-scales. Occasionally, a second pair of bract-scales is present.

FLUSHING

Little development takes place during the winter. In early spring, the axis of the male strobilus elongates and the pollen sacs enlarge, giving the strobilus a bright yellow color. Pollination takes place during late April. At that time the fused bract-ovuliferous scales structures separate (4), exposing the tips of the ovules. Fertilization occurs in late summer, about 3 months after pollination. By October, the embryo development stops. By this time the cones attain almost their mature size, 7 to 12 mm in diameter (5). They are round, green to purplish green, soft to finger pressure, and the seeds (6) are small, soft, white and immature. They will not germinate, though they usually contain an embryo. At this stage the cones enter winter dormancy.

Embryo development continues in the following spring and by late August of the second year the cones and seeds mature. The cones turn first yellow green and later brown to reddish brown and the lines between the scales become distinct and raised (7). Seed (8) are about 5 mm long, dark brown with light-brown wings, dry and hard. Unlike most other conifers, seed wings do not develop from the ovuliferous scale, but are thin lateral extensions of the seed coat and give the seed an oval shape. Most seeds are shed in late October, but some not until mid-winter.

The seed is variable in size, 150 000 to 400 000 per kg. Germination is usually low and stratification before sowing is recommended.

Larches

1. Vegetative buds are ovate; the remains of the last year's needles usually cover most of the bud.

2. Male buds are hemispherical or broadly ovate and larger; and the bud scales protrude out of needle remains.

3. Female buds are the largest, ovate, and protrude most out of the remains of needles.

4. Needle primoria inside a vegetative bud are green and appressed.

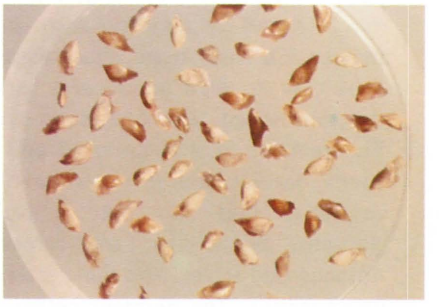
5. Microsporophylls are leaflike with yellow pollen sacs on the abaxial side.

6. Bracts and scales are green, leaflike double structures, though the scale may be small.

7. At pollination, the male cones elongate, thus, separating the microsporophylls.

8. In female cones, the bracts separate to allow for the entry of pollen.

9. At maturity, the color of the cones changes from green to brown.



10. The seeds are triangular and light brown to reddish brown.

Photos 4, 5, and 6 - BCM

Larches

Western Larch, *Larix occidentalis* Nutt.
Alpine Larch, *Larix lyalli* Parl.
Tamarack, *Larix laricina* (Du Roi) K.Koch

by S.Eis and D.Craigdallie

All three species of larch, which are indigenous to Canada, occur in British Columbia. Since there are only a few minor differences between the species, the reproductive structures described are based on the most common—the western larch.

On larches, cones are usually scattered throughout the non-shaded part of the crown. However, as in most conifers, female reproductive structures are more frequent in the upper part of the crown, whereas male reproductive structures occur usually on less vigorous branches in the central or lower regions. Reproductive structures are produced on spur shoots that have changed from the vegetative function (i.e. production of needles) to the reproductive function (i.e. production of strobili). Because spur shoots develop during the second growing season from buds in the axils of needles on new shoots, the strobili are produced on the shoots during the third or subsequent growing seasons and are never near branch tips.

BUD DESCRIPTION

During winter dormancy, vegetative buds (1) are 3 to 4 mm wide and 2 to 3 mm high and, on their short spur shoot, they look broadly ovate. The pubescent, light gray to light gray-brown bark of the spur shoot resembles outer scales. The remains of the appressed previous year's needles appear to overarch the vegetative bud and obscure brown, glabrous, feather-like, and somewhat resinous bud scales. The inner scales are membranous. The dormant pollen-cone or male buds (2) are about 4 mm wide and 3 mm high, and hemispherical or broadly ovate. The brown bud scales protrude much more through the remains of needles than on the vegetative bud. The seed-cone or female buds (3) are 4 to 5 mm wide and 4 to 5 mm high. Since they are longer, they protrude more above the remains of the needles than the male buds. Including the spur shoot, they appear ovate to narrowly ovate.

When the bud is cut open or the scales removed, recognition is easy. A vegetative bud (4) consists of a compressed axis, covered with unelongated, pointed, boat-shaped, green needles. The whole structure is less than 2 mm long, but, because of the small size of the bud, the cavity is entirely filled.

The male bud (5) consists of a short axis densely covered with short, leaf-like microsporophylls on whose lower surface are two large, yellow-green microsporangia or pollen sacs filled with yellow pollen, in an advanced stage of development. During dormancy, the male strobilus is about 3 mm wide and 2 mm high.

The female strobilus (6) consists of a narrowly conical axis reaching almost to the top of the strobilus, covered densely with long, narrow, sharp-pointed green bracts. Each bract bears on its upper, adaxial side a rudimentary ovuliferous scale, visible only with a hand lens. However, a hand lens is not necessary to distinguish the bracts and to identify the female strobilus.

BUD BREAK AND POLLINATION

Reproductive strobili resume development during the first half of March—2 to 3 weeks before any changes take place in the vegetative buds. Vegetative buds swell around the end of March; at that time, the strobili are emerging from the bud scales. However, needles appear to be fully flushed at pollination time, which takes place during the second half of April.

Shortly before pollination, the axis of the male strobilus elongates, separating the microsporophlls (7), which are now fully enlarged and about 5 to 7 mm long on short thin stalks. They are predominantly yellow, but may range from yellow-green to light orange. Pollen sacs split along the thin-walled line on the abaxial side. The pollen is wingless.

During the first half of March, rapid elongation of the axis takes place in the female strobilus as it emerges from the bud scales. By pollination, the internodes have elongated sufficiently to leave large spaces between the bracts, through which pollen enters to the ovuliferous scale. At pollination, the female strobili (8) are 12 to 20 mm long and 10 to 15 mm wide, with bracts perpendicular to the axis. Their color ranges from light green to purple or red.

MATURATION

After pollination, the cones turn green and increase in size. Mature western larch cones (9) measure 20 to 30 mm in length, while tamarack cones rarely exceed 15 mm. As the cones ripen in late August or early September, their color changes from green to brown or brown-purple. Seeds are usually released in early October, but empty cones, which weather to dark brown, may remain on the trees for an indefinite period. Cone collection should take place around the middle of September. There are 10,000 to 15,000 cones per hectolitre, but smaller tamarack cones yield as many as 25,000 per hectolitre.

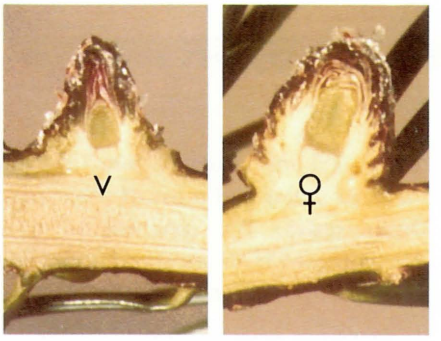
The seeds (10) are winged, nearly triangular in shape, 3 to 4 mm long, 2 to 2½ mm wide, and about 1.2 mm thick (although the size range is considerable) and are light brown to reddish brown. There are 250,000 to 500,000 seeds per kg, but smaller tamarack seeds may yield up to 1,000,000 seeds per kg. Germination is variable.

Grand Fir

1. Terminal buds are always vegetative.

2. Lateral vegetative buds are smaller than female buds and develop into short, weak shoots.

3. Female buds are upward-facing and large.



4. Inside overwintering lateral vegetative buds, the short, next year's shoots do not fill the bud cavity entirely. The cavities in female buds are filled with female strobili.

5. Male buds occur in axillary positions on the lower side of less vigorous shoots.

6. The male strobili enlarge to their full size during April and their color gradually changes to yellow.

7. Female strobili rapidly elongate during April. Only bracts are visible.

8. Cones remain upright. They disintegrate on branches during windy weather, thus, leaving a spikelike axis.

9. The seeds are triangular to oblong and brown or tan.

Grand Fir

Abies grandis **(Dougl.) Lindl.**

by S.Eis and D.Craigdallie

Grand fir starts to produce cones around 50 years of age. After that, the crops are fairly frequent (often every second or third year), though the number of cones is rarely great.

The position of the buds is the best distinguishing feature for the identification of their probable function. The terminal buds are always vegetative (1). Seed cones develop only from upward-facing axillary buds (3) in the top of the crown, whereas pollen cones develop only from axillary buds on the underside of less vigorous branches in the lower part of the crown (5).

Primordia capable of developing into female or male strobili are initiated every year in mature trees. Whether they develop into strobili, produce vegetative shoots, or become latent is probably determined by the preceding environmental factors. Because it is difficult to determine the pathway of development of a potential seed-cone bud from its outer appearance during dormancy, dissection is recommended.

BUD DEVELOPMENT

During dormancy, the vegetative buds (1) are spherical to oval, about 3 mm in diameter, and usually covered with a layer of resin. Terminal vegetative buds (1) have about 35 bud scales; lateral buds, only about 25. Dormant vegetative buds (2) contain a dome-shaped apex about 1.5 mm wide and 1 mm high, with all the next year's growth already initiated (4). Outer bud scales are dark green, brown-green to brown, and leathery, while inner bud scales are green, membranous, and translucent.

Seed cones develop singly or in groups of 2 or 3. During dormancy, the female strobili fill the bud cavity entirely (4). By that time, they are about 2.5 mm wide, 4 mm long, and have all bracts and most of their ovuliferous scales. The spherical to ovoid resin-encased buds are about 7 mm wide and 8 to 10 mm long.

On branches bearing female buds, usually some buds develop only rudimentary zonation; these usually abort. Other buds, identical to female buds in position and outer appearance, initiate only needle primordia and, eventually, produce only short, non-vigorous, vegetative shoots.

Male buds (5) develop from apices in the axils of most of the needles on the abaxial (lower) side of less vigorous shoots. They are smaller than vegetative or potentially female buds and, in late summer, they are dome-shaped. Before dormancy, they increase in size and become spherical. Dormant pollen-cone buds range from light green to blue, blue-black, or brown, are oval or spherical, 3 to 4 mm in diameter, have about 20 bud scales, and are usually covered by a thin layer of resin. Dormant male strobili inside them are about 2 mm long, green to dark green, and have all of their microsporophylls and microsporangia for the next season.

On branches bearing pollen cones, many buds develop only a few bud scales, after which they remain inactive.

BUD BREAK

Around the middle of March, cell division begins in the male and female strobili. The male strobili enlarge first and the buds burst around the beginning of April—2 weeks or more ahead of the female buds and about 3 weeks ahead of vegetative buds. The male strobili (6) are at first purple, orange, or bluish red, but, as the microsporangia enlarge, the color gradually turns light green and then yellow. Pollen is shed about 3 weeks after bud burst. While strobili are shed during fall and winter, the receptacles persist on the twigs for many years.

After bud burst, female strobili (7) rapidly elongate. The bracts increase in length about sixfold over the dormancy size. The elongation of the strobilus axis separates the bracts and, at this stage, around the end of April, female strobili are presumably fully receptive to pollen. Weather permitting, pollen dispersal takes place, usually as soon as this "open stage" is reached. During pollination, the female strobili are about 25 mm long, light green to blue-green or purple-green, and stand erect. After pollination, the bracts reflex upward and become tightly appressed to the side of the cone.

Soon after the receptive stage, the bracts are overgrown by the ovuliferous scales. As a result, the color of the strobili changes from yellow-green or purplish green of the bracts to the gray, dark blue or deep purple of the ovuliferous scales. The cones (8) remain upright. The maximum cone size, about 6 to 7 cm in length and about 3 cm in diameter, is achieved by early or mid-July. During August, the cones gradually turn brown.

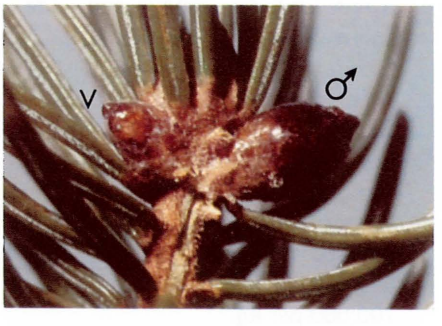
Cones dry out and scales abscise from the axis, allowing the cones to disintegrate as branches are disturbed by the wind. Seed dispersal occurs in late September or early October, leaving the spike-like cone axis, which may persist on the tree for several years.

Mature seeds (9) are typically triangular to oblong, about 6 to 7 mm long, 4 mm wide, 2 mm thick, with large wings. The rather soft seed coat is brown, gray-brown, creamy brown, or tan. Most of the seed is filled with fleshy endosperm and a well-developed embryo may extend the full length of the endosperm. There are 700 to 1,200 cones per hectolitre, yielding about 3 to 4 kg of seeds, with 30 to 60,000 seeds per kg. Germination is extremely variable, 20 to 65 per cent, averaging about 50 per cent.

Interior Spruces

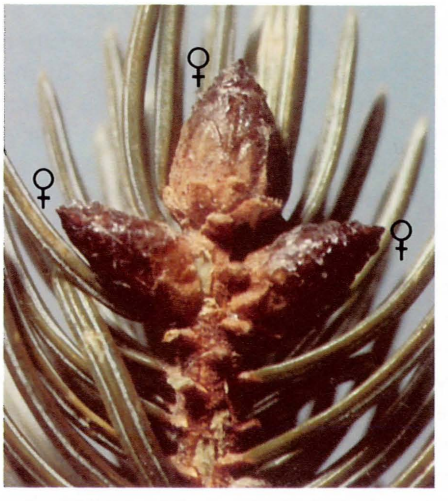
1. Vegetative buds are small and completely covered with green outer scales.

2. Vegetative buds have a large cavity and spirally-arranged needles on a short axis.

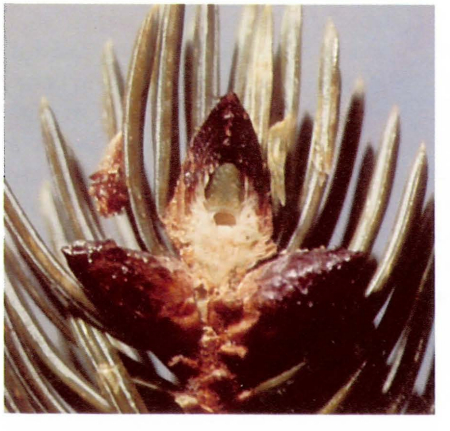


3. Male buds are broad in the midsection.

4. Microsporangia fill the bud cavity.

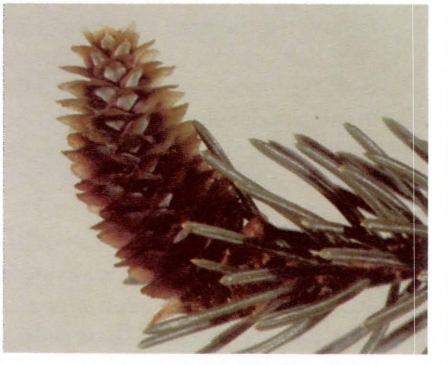


5. Female buds are broadest near the base.



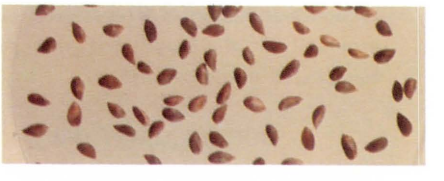
6. Bracts and scales are easily recognized as double structures.

7. By pollination time, microsporangia have developed into rounded pollen sacs.



8. During pollination, the female strobilus stands erect with scales perpendicular to the axis to allow for the entry of pollen.

9. Only cone scales are visible, since the bracts finished their development by pollination.



10. Seeds are about 2.5 mm long, pale brown, and glossy.

Interior Spruces

White Spruce, *Picea glauca* (Moench) Voss
Engelmann Spruce, *Picea engelmanni* Parry

by S.Eis and D.Craigdallie

White spruce and Engelmann spruce hybridize freely wherever the ranges of their distribution overlap, and they are frequently referred to collectively as "interior spruce". Except for cones, their reproductive structures differ only in minute detail and, for the purpose of this publication, they will be treated together.

Interior spruces are sporadic cone producers, good crops occurring about once in 6 years, with usually one or two light crops in between. Cone production starts around 40 years of age, but there is a considerable variation, dependent on the site. As in most conifers, the female reproductive structures occur at the top of the crown and male structures around the middle, with considerable overlap in heavy crop years, when reproductive buds may occur in any position on the shoot. Reproductive buds occur mainly in terminal and subterminal positions, thus ending the terminal shoot growth. This eventually results in seed-producing trees having an irregular and distorted crown shape.

The initiation of the reproductive process in the buds takes place early in the growing season, but buds can rarely be recognized as reproductive before about the middle of September, unless a microscope is used. The development continues until winter dormancy, and recognition becomes progressively easier, especially if the bud is cut open or the bud scales are peeled off.

BUD DESCRIPTION

Bud size generally decreases with distance from the tip of the branch. During winter dormancy, the vegetative buds (1) are smaller, 4 to 6 mm in length, and dome shaped, while the reproductive buds (3 and 5) are larger, 5 to 8 mm, and ovate to obovate. The outer scales on all buds are thick and green and cover the vegetative buds completely. In the reproductive buds, the inner brown and glossy membranous scales protrude over the upper portion of the bud. Female buds (5) are usually more pointed than the male buds (3) and are broadest near the base; the male buds (3) are broadest in the middle. It is often difficult to recognize the sex of the reproductive buds from their outer appearance, and dissection and examination of the appendages with a hand lens may be necessary.

A vegetative bud contains a large cavity (2) and, at its base, a small mound of sharp-pointed, green needle primordia spirally-arranged around next year's shoot. The needle primordia are oblique-angled in cross-section. In contrast, the strobili in reproductive buds (4 and 6) usually completely fill the cavity. In a female strobilus (6), the spirally-arranged appendages are also green, but they are larger and easy to recognize as double structures consisting of bracts and, in their axils, ovuliferous scales, each bearing two ovules at its upper surface. The male bud contains a pollen cone (4) consisting of a short axis covered with spirally-arranged, light green, leaf-like microsporophylls, bearing two yellow-green microsporangia at their lower surface.

BUD BREAK

The time of bud break depends on geographic location and weather and occurs from late April to late May, with vegetative buds breaking about a week or two later than the reproductive buds. Inside the male bud, the pollen axis elongates, thus separating the microsporophylls; the microsporangia enlarge and develop into rounded pollen sacs (7). During pollination, which lasts about 8 to 10 days between the end of May and the end of June, the pollen cone (7) is 12 to 15 mm long, the leaf-like microsporophylls are yellow-green to orange or light purple, and the pollen sacs are creamy yellow. Soon after pollination, the male cone dries, turns brown, and is shed.

Inside the female bud, the seed cone elongates and ovuliferous scales enlarge. At pollination time, the seed cone (8) is 18 to 25 mm long and stands erect. The scales, standing perpendicular to the axis, are purple with light purple or orange fringes. Bracts finish their development around pollination time; they are visible, but shorter than the scales. After pollination, the female cones become pendant and turn green. Fertilization takes place about 4 weeks after pollination.

Cones reach their full size by the beginning of August. They are about 40 mm long and 12 to 15 mm wide, with only the scales visible (9). The seeds appear fully developed by the end of August. Subsequent ripening involves drying and death of the vegetative tissue with a change of color to lustrous light brown. Seed dispersal takes place in September and, by the middle of October, the cones are usually empty, though, in some years, seed is also dispersed on the snow during the winter. Mature seeds (10) are 2.5 to 3 mm long, less than 2 mm wide, and about 1.5 mm thick. The color is pale brown to brown and glossy. The seed wing is about 10 mm long and 4 mm wide, and light brown, with a dark brown stripe along one edge. There are 18,000 to 24,000 cones per hl and 8 to 20 seeds per cone. White spruce has 300,000 to 900,000 seeds per kg, while Engelmann spruce yields 250,000 to 700,000 per kg.

Ponderosa Pine

1. Vegetative buds are slender and long.

2. Male buds are arranged around the base of a vegetative bud.

3. Male strobili are ovoid, yellow or purplish yellow, and about 18 mm long.

4. Female strobili are erect and occupy a subterminal position on the current year's shoots. They are red or purple.

5. Microsporangia open along a predetermined line and pollen is released in early June.

6. Female strobili develop into conelets by the end of the first year.

7. During the second year, the cones rapidly enlarge and change color to lustrous brown or russet brown.

8. The seeds are ovoid to triangular, large, brown to gray-brown, and mottled.

Ponderosa Pine

***Pinus ponderosa* Laws**

by S. Eis and D. Craigdallie

Ponderosa pine starts to produce strobili at the age of 12 to 16 years of age, but seed production is usually sporadic. Collectable seed crops are usually produced at 4- to 6-year intervals.

As in all pines, the male and female strobili occur on the same tree and, in heavy cone crops, even on the same branch. Strobili of both sexes may be produced anywhere in the crown. They are always lateral in their position. Male strobili are spirally-arranged at the base of a vegetative bud or, in the spring, at the base of the current year's shoot. They are grouped in clusters of up to about 20 and are visible by late August. The female strobili occur singly or in groups of two to four near the apex of the current year's growth, but their presence cannot be detected without dissection until the shoot has elongated in the spring.

BUD DESCRIPTION

During winter dormancy, vegetative buds (1) consist of a sheath of spirally-arranged bud scales that enclose next year's growth. This shoot consists of an axis covered with spur shoots (needle fascicles) with compressed shoot needles. The outer bud scales are reddish brown or greenish brown, usually covered with small droplets of resin that gives them a whitish lustre. The inner scales are light brown, semi-transparent, and membranous.

If many male buds are differentiated, then the sheath, which covered them originally, is forced apart and largely shed and then appear as separate buds (2). If only a few were differentiated, then the sheath remains and the appearance is that of a large, broad, vegetative bud. The male strobili undergo considerable development before dormancy. The color of the buds is brown-green or purplish brown.

Female strobili develop entirely within the scales of the terminal vegetative bud and, because of their subterminal position on the shoot, their differentiation is delayed until acropetal differentiation of the needle fascicles takes place near the apex. During dormancy, the female strobilus is less than 1 mm long. It consists of a short shoot axis covered with spirally-arranged bracts, which, at this stage, appear only like lateral outgrowths along its flanks. The whole strobilus is covered by a few short hood-like scales.

While the vegetative buds and male strobili enter a state of dormancy during the winter and further development takes place the following spring, the female strobili continue to grow during late fall and winter.

POLLINATION

Microsporangiate strobili, emerging from the buds in spring, are usually green with a reddish tinge, but, on some trees, they may be red, pale purple, or yellow purple and this color persists until enlarging microsporangia force the microsporophylls apart. Exposed semi-transparent microsporangia, filled with yellow pollen, change the overall color to yellow or purplish yellow (3). Individual male strobili at pollination time are 14 to 20 mm long and 6 to 8 mm wide.

The megasporangiate strobili (4) appear in spring on elongating shoots in subterminal positions. They are deep purple or red with narrow orange or yellow fringes on the bracts; the scales are not visible. The female flowers, excluding a short stalk, are about 8 mm long and 5 mm wide. They stand erect to allow for pollen entry. Despite their small size, they are conspicuous because elongation of the needles has not been completed.

Pollen is mature by the end of May. During dry weather, the microsporangia (5) open along a predetermined abaxial line and the pollen is released. Pollination occurs during the next 2 to 3 weeks.

Soon after pollination, the male strobili turn brown, wither, and are shed, while female strobili close to form a compact purple conelet. This color soon changes to brown or green-brown, and the scales elongate, thicken, and become the only visible part of the cone. Female strobili (6) develop slowly during the first year, reaching about 25 mm in length by the fall. Abortion of the conelet during this period is common and believed to be due to unsatisfactory pollination.

The pollen tube initially develops rapidly, and then rests until spring of the following year. Fertilization takes place during June, which is 13 months after pollination. Conelets enlarge rapidly (7) and reach full size by early September; their color changes from yellow-green or light brown-green to lustrous yellow-brown, green-brown, or russet brown as the vegetative tissues die and dry out. At maturity, the cones are 70 to 90 mm long and, when closed, about 35 mm wide; when opened, they are about 50 to 60 mm wide.

Cones open during hot, dry weather in early October. The seed is heavy and the dispersal range is small.

The seeds are 7 to 9 mm long, 4 to 6 mm wide, 3 to 4 mm thick, ovoid to triangular, brown to gray-brown or pale brown, and usually mottled. The wing is boat-shaped, 18 to 28 mm long, and 8 to 12 mm wide. There are 1 to 3 kg of seeds per hectolitre of cones and 15 to 50 thousand seeds per kg. Seeds have been stored for 18 years without significant loss of viability. Germination varies between 50 and 80 per cent.

Western Red Cedar

1. Western red cedar does not produce buds. Instead, the tip is covered by leaves and leaf primordia.

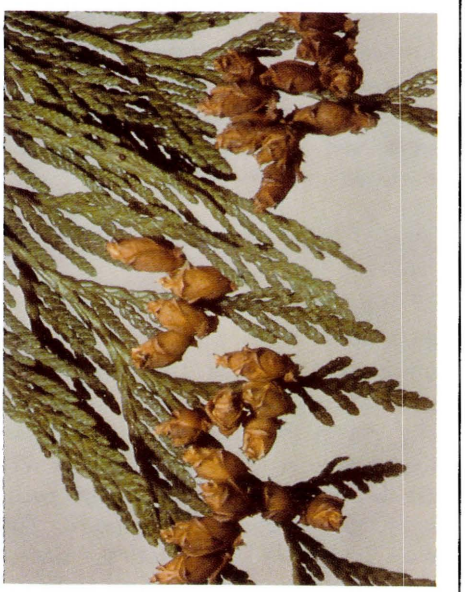
2. Female strobili are oval, bluntly pointed, and brown-green.

3. Male strobili are globose, smooth, and dark brown or black.

4. The female strobilus has 8 to 12 shield-shaped bracts in opposite pairs. At pollination time, the bracts curve outward and give the female strobilus a thorny appearance.

5. The male strobilus is round and has a short stalk. The reddish yellow microsporangia are clearly visible between the brown microsporophylls.

6. The cones remain erect throughout their development. Only 3 or 4 bract-scales in the midsection of the cone bear seeds.



7. Cones may be produced in abundance throughout much of the crown.

8. Seeds are long and narrow, with a pair of papery wings. There are about 500 000 to 1.3 million seeds per kilogram.

Western Red Cedar

Thuja plicata **Donn**

by S.Eis and D.Craigdallie

Red cedar normally starts to produce cones at the age of 20 to 30 years, but on fully exposed trees, cones may be produced a few years earlier. The cones are produced at 2- to 4-year intervals and the cone crop is normally abundant. In heavy crop years on exposed trees, the cones may be distributed throughout the whole crown.

Red cedar does not produce buds. Instead, the vegetative tip (1) is covered by leaves and leaf primordia in various stages of development. The leaves are small and scalelike; the branches are flattened and two-ranked.

SHOOT TIPS

In spring, the shoot tips start to grow about a month earlier than most other conifers. After producing several pairs of leaves, some shoot tips gradually change into rudimentary reproductive structures. The female strobili (2) are initiated near the ends of the main branches on short lateral shoots. The male strobili (3) form from the tips of somewhat longer shoots which, since the onset of growth in the spring, have produced perhaps 30 pairs of leaves and often one short lateral shoot before undergoing transition to the male tip. All the tips on a branch may undergo transition to reproductive strobili or some may remain vegetative. In this case, the vegetative tips are those near the main branch apex; and if both sexes occur on a branch, the distal tips are female strobili and the proximal tips are male strobili.

STROBILI

At the end of the growing season, the vegetative tips remain flattened, bluntly pointed, and covered with green leaves, while the appearance of the reproductive tips changes markedly. Short stalks develop above the last leaf, forcing the reproductive tips slightly above the leaves (2 and 3). The male strobili (3) are globose and have a smooth surface. The color of the outer surface of the microsporophylls gradually changes to dark brown or black. The female strobili (2) are oval, bluntly pointed, and dark brownish green to dark green.

The strobili of both sexes measure about 2 mm in length and, for positive identification before dormancy, a hand lens may be necessary. Both the microsporophylls and bracts are in pairs on the opposite side of the strobilus axis.

In each male strobilus (5), there are 6 to 10 microsporophylls. They are broadly shield-shaped and their bases stand perpendicular to the strobilus axis, with the tips sharply bent to overarch the apex. Each microsporophyll has three reddish microsporangia attached to its abaxial (lower) side.

In each female strobilus (4), there are 8 to 12 shield-shaped bracts. They are similar but somewhat narrower than the microsporophylls in the male strobilus. They stand at an acute angle to the strobilus axis and their tips overarch the apex with a gentle curve. Each bract has, on its adaxial side, a rudimentary scale which remains fused with it; and the rudimentary scale bears, on its adaxial side, two or occasionally three ovules. Of the six pairs of fused bract-scale structures, the proximal (bottom) pair and one or two distal (top) pairs are only partially pigmented; only the three or four pairs at the centre give the cone the green-brown or dark green color. At the end of winter dormancy, the tips of the bracts curve outward, giving the female tip a thorny appearance (4).

Soon after the end of winter dormancy, the male cone axis elongates, separating the microsporophylls (5). The microsporangia enlarge and become clearly visible as reddish yellow lines between the microsporophylls. In the female cone, the axis also elongates, the bract-scales become reflexed to expose the axilliary ovules, and the scale margins curve inward to form a funnel directing the pollen toward the ovules. Of the five or six pairs of the bract-scales, only the three or four pairs in the centre of the cone produce fully developed ovules.

Pollination takes place during a 1- or 2-week period in March. Around that time, meiotic division occurs in the megaspore mother cell. Soon after pollination, the bract-scales elongate and thicken, sealing ovules inside the cone.

FERTILIZATION

The female gametophytes mature during the last week of May; the cones are green and nonwoody and the ovules enlarge to their full size. The pollen, which had been sealed inside the cone, germinates and the pollen tube penetrates into the archegonium. The body cell divides, producing two male gametes. Fertilization normally occurs the last few days of May. By mid-August, fully developed embryos are about 3 to 4 mm long.

Female cones remain erect throughout their development (6). In August, their color changes from green to yellow to cinnamon brown as the tissues dry out. The cones (7) are 12 to 18 mm long and, when closed, 4 to 6 mm wide. Most cones open during the first half of October. Cones that open earlier usually have been damaged by insects.

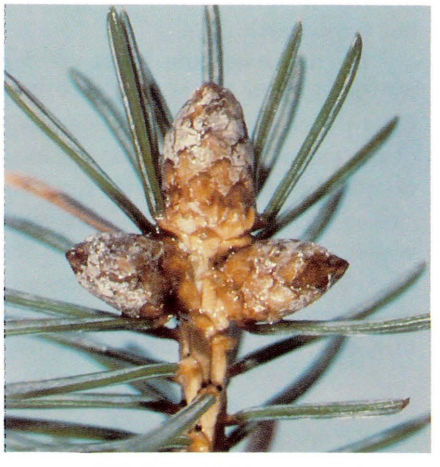
SEEDS

Mature seeds are 4 to 5 mm long, about 1.5 mm wide (8), and eliptical in cross section, with two papery wings about 1.5 mm wide around the seed. In most other conifers, the seed wing develops from the adaxial side of the scale; in the Cypress family, the seed wing develops as a lateral extension of the ovule.

While there are 50 000 to 130 000 cones per hectolitre, they yield only about 150 000 to 500 000 viable seeds. The number of viable seeds per cone is usually 3 or 4. There are 0.5 to 1.3 million seeds per kilogram. A large number indicates a large proportion of them are small, flat, empty, or damaged by insects.

Sitka Spruce

1. Vegetative buds are conical and completely covered with green-brown bud scales.



2. Male buds are oval and broadest in the midsection.

3. Female buds are also oval, but broadest at the base.

4. The male strobilus is globose and large, completely filling the bud cavity. In a vegetative bud, the cavity is not filled and the inner bud scales are loosely packed.

5. The female strobilus is oblong and fills the bud cavity completely.

6. At pollination, the male strobili are yellow and the axes elongate to allow for release of pollen.

7. The female strobili are green and stand erect. The scale is the prominent feature.

8. Mature cones are brown. Seed dispersal starts in early September. Most seeds are released by early October, with a small amount retained until the winter.

9. Seeds are small and light, 300 000 to 900 000 per kilogram.

Sitka Spruce

Picea sitchensis **(Bong.) Carr.**

by S.Eis and D.Craigdallie

Individual open-grown Sitka spruce trees may reach sexual maturity in about 20 years, but cone bearing in stands begins around the age of 25 to 40 years. Except for the northern portion of the range where cone crops are infrequent, good cone crops are produced in 3- or 4-year intervals, with one light crop usually in between.

Generally, vegetative (1) and reproductive (2 and 3) bud size is strongly influenced by the level at which it occurs in the crown. The higher in the crown, the more vigorous the branches and the greater the size of buds.

As in most conifers, female buds occur mainly at the top and male buds in the middle and lower portions of the crown; however, on open-grown trees in years of heavy cone crop, there may be a large overlap. Reproductive buds occur mainly in terminal and subterminal positions, thus periodically ending the terminal shoot growth (2 and 3). This will result in irregular and distorted branch shapes and deformed crowns of the seed-producing trees.

BUD DESCRIPTION

In most other spruces, the vegetative buds can be distinguished from reproductive buds soon after they form in summer. In Sitka spruce, their shapes and sizes are similar until about the middle of September. All the buds are broadly conical, greenish brown to brown, and usually covered with a "bloom" of light grey resinous crystals (1, 2, and 3). Before September, identification of reproductive buds can be made only upon dissection and the use of a hand lens.

Later in the growing season and possibly during the winter, the mounds of tissues in the reproductive buds gradually enlarge and the reproductive buds change their shape from broadly conical to oval, while no visible change occurs in the vegetative buds (1). During winter dormancy, reproductive buds can be distinguished from vegetative buds by their shape, but their sex can only be estimated from their position in the crown. Female buds (3) are about 6 to 8 mm long and oblong to oblong ovate; the male buds (2) are 4 to 6 mm long, ovate, and broader at the top than female buds. Both sexes have a pointed tip and are covered with brown or greenish brown, often glabrous, and usually resinous bud scales. However, dissection makes identification easy (4 and 5). Female strobili (5) are about 4 mm long, oblong, and green, with most of the bracts and all of the ovuliferous scales present; male strobili (4) are about 3 mm long, spherical, light green to yellowish green, and have initiated all microsporophylls and microsporangia. In contrast, the vegetative tip is about 2 mm long, dark green, and contains only needles. A hand lens makes identification easier but is not necessary.

STROBILI

The four-celled, or mature, stage of the pollen is reached by the end of April. By that time, the pollen cones have elongated, separating the microsporophylls. Mature pollen cones are 15 to 20 mm long and yellow, orange-yellow, or yellow-purple (6). Dispersal of pollen occurs around the end of April and lasts about a week.

By mid-April, female strobili gradually elongate and push out of the bud scales, and by the end of April, all but their bases are exposed above the bud scales. The internodal elongation has been completed, resulting in spaces between the bracts and ovuliferous scales through which pollen can sift down to the ovules. During pollination, the ovuliferous scales outgrow the subtending bracts (7). The receptive stage lasts about 10 days or more, since distal ovules are exposed first and proximal ones several days later. After pollination, the growth of the ovuliferous scales fills the internodal spaces and closes the cone. By mid-May, the green cones become pendant, only the broad scales showing. The empty pollen cones wither and die but may persist on a tree throughout the summer.

FERTILIZATION

Pollen germinates about a week after pollination, and by the end of May, the pollen tube has penetrated the nucellus tissue of the ovule and reached the archegonium. Fertilization usually takes place in the first week of June. Any unfertilized egg cells collapse, but by this time, even the unfertilized ovules are fully enlarged and the seed coats are well developed, forming normal appearing, but empty seeds.

By mid-June, the cones are fully elongated, 6 to 10 cm long, and closed (up to 2 cm wide). The differentiation of the tissues and maturation occurs until mid-August. In August, the cones change color from green to yellow to brown (8); dispersal of seeds starts soon after. By the end of October, most seeds have been shed but some are released throughout the winter and early spring.

SEEDS

There are 4 000 to 6 000 cones per hectolitre and sometimes more than 100 seeds per cone, though the average is much less. There are 300 000 to 900 000 seeds per kilogram. Sitka spruce seeds are difficult to distinguish from white spruce or Engelmann spruce. All are about 2.5 to 3 mm long, less than 2 mm wide, and about 1.5 mm thick (9). Sitka spruce seed is slightly flatter on one side and rounder on the opposite. At the micropylar end, it is more beak-shaped and pointed than white or Engelmann spruce seed. The seed wing is slightly larger than in the other species, being 12 to 14 mm long, 4 to 5 mm wide, more pointed at the distal end, and light brown with a darker strip along one edge.

Mountain Hemlock

1. Vegetative buds are small and slender and somewhat angular in cross section, since the outer bud scales have a keel.

2. The mound of needle primordia does not fill the bud cavity and the inner bud scales are loosely packed.

3. Female buds are ovate and somewhat larger than vegetative buds and are red to purple. The outer bud scales have a prominent keel.

4. The female strobilus is well developed, filling completely the bud cavity.

5. Male buds occur in subterminal positions, are ovate and light brown, and have scales without prominent keels.

6. In winter, male buds contain a well developed strobilus which fills the bud cavity.

7. The male strobili are yellow and have long stalks.

8. The female strobili are erect and purple to pink and have prominent sharp-pointed bracts.

9. The cones are 40 to 60 mm long and light purple until maturity. Old cones turn grey-brown.

10. Seed size and weight are variable, ranging from 150 000 to 450 000 per kilogram.

Mountain Hemlock

Tsuga mertensiana (Bong.) Carr.

by S. Eis and D. Craigdallie

On mountain hemlock, seed production generally begins at the age of 30 or somewhat later if trees are shaded. Some seeds are usually produced every year but good cone crops may be 3 to 6 years apart.

Buds can be distinguished as soon as they are fully formed by their location in the crown, position on the shoot, and their shape and size. The female buds occur mainly at the top of the crown on vigorous branches and the male buds occur in the middle and lower portions of the crown on branches of lower vigor. However, on open-grown trees, buds of both sexes may occur throughout the crown.

BUD DESCRIPTION

Even in heavy crop years, most terminal buds remain vegetative (1). On vigorous shoots, they may be up to 4 mm long; on less vigorous branches, they may average only 2 mm. The outer bud scales are keeled and the buds in cross section appear angular. Because of the slow development of the needles inside the vegetative bud, the bud cavity is not completely filled (2) and the innermost, pale green, membranous bud scales are loosely packed. The outer bud scales are leathery, green or brownish green, and covered with fine hair (1). The whole bud is usually obscured by several short, brownish green needles.

Female buds (3) occur in terminal positions on vigorous branches, usually singly, rarely in groups of 2 or 3. They are narrowly ovate and somewhat larger than vegetative buds in similar positions, averaging 4 to 6 mm in length. During winter dormancy, the female strobilus is already well developed (4), filling the bud cavity completely and compressing the inner membranous, light green bud scales. The outer keeled bud scales are red to reddish purple and covered with fine hairs; the rapidly developing female strobilus has forced them apart, so that the lighter reddish brown, smooth scales are showing (3). The bud is almost entirely obscured by several reddish brown needles.

Male buds (5) usually occur in subterminal positions on secondary branches of lesser vigor, forming groups of 3 to 6; or occur in lateral positions, singly or in groups of 2 to 3. They are ovate or obovate and 2 to 4 mm long and have light brown or reddish brown, finely pubescent outer bud scales without prominent ridges. The strobilus fills the bud cavity completely (6), sometimes enlarging enough before dormancy so that the tip of the bud is covered only by smooth, light brown scales.

Bud recognition becomes simple when the bud scales are removed; however, because of their small size, a hand lens may be necessary. The vegetative buds contain the next year's shoot, with flanks densely covered with green, spirally arranged, unelongated, young needles (2). The dormant female bud contains a strobilus with bracts and ovuliferous scales (4). At this stage, the pointed bracts are longer than the round ovuliferous scales. The male bud contains a strobilus with microsporophylls and yellow pollen sacs (6).

POLLINATION

The male strobili have enlarged enough by mid-May to push through the bud scales, exposing the tip of the red strobilus. From mid-May on, the microsporangia enlarge and change their color to yellow, the stalk of the cone extends to about 12 mm, and the cone axis elongates (7).

In the microspore mother cell, the meiotic division with reduction of chromosomes is initiated in the fall and completed in the spring. Tetrads of microspores are present by mid-April. By mid-May, the cells separate and become rounded. By mid-June, the mature five-celled, winged pollen grains are ready for pollination.

Many male buds abort during the winter. There is no visible external difference between living and aborted buds. They can only be distinguished by cutting the bud or removing the bud scales, revealing the brown, dried-out strobilus. The aborted buds are retained on the twig and may be mistaken the following year for developing male buds.

FERTILIZATION

As female strobili emerge, they bend upward. At pollination, they are 16 to 22 mm long, erect with widely separated bracts (8). The ovuliferous scales are small and the ovules appear only as whitish swellings on their adaxial side. Pollen grains remain at the micropyle for about a month. In mid-July, the pollen tube penetrates into the female gametophyte. The broadly ovate, ovuliferous scales enlarge and thicken, filling the internodal spaces between the bracts. Fertilization occurs at the end of July. The cones bend downward. Their color remains purple or brownish purple. They are fully elongated by the end of August, being 40 to 60 mm long and 12 to 15 mm wide (9). The embryo is fully formed by mid-September.

SEEDS

Seed dispersal takes places from late September until early November. There are about 60 seeds per cone but a large proportion may be empty. The seed size varies from 2 to 4 mm long and 1.2 to 2 mm wide (10); the seed wing is 4 to 6 mm long. There are 150 000 to 450 000 seeds per kilogram, with an average of about 250 000.

Western White Pine

1. During the winter, all terminal buds look alike. Male strobili do not show as swellings because they are very small.

2. Male strobili are in the position of needle fascicles and visible only with a hand lens. Female strobili cannot be distinguished from branch buds until spring.

3. Male strobili are formed around the base of the current shoot, often in clusters of up to 20.

4. Female strobili occupy subterminal positions on the current shoot. They are red or pink, about 20 mm long, with a stalk approximately 15 mm long.

5. By the end of the growing season, the conelets have elongated to about 50 mm. Their color has changed to green or brown.

6. After pollination, the growth of scales seals the cone, preventing contamination.

7. The cones mature during late August of the second growing season and turn brown or light brown.

8. Seeds are large and heavy, 30 000 to 50 000 per kilogram.

Western White Pine

Pinus monticola **Dougl.**

by S.Eis and D.Craigdallie

Western white pine is generally a good seed producer. Although male and female strobili occur on the same tree, white pine is precociously female, producing female strobili at 12 to 16 years or earlier on exposed trees. Production of male strobili starts around the age of 20 years. The female strobili are produced most abundantly on vigorous shoots in the upper crown. They occur on the current year's shoots in the subterminal position, sometimes singly, but more often in groups of 2 to 4 (4). Male strobili occur in the lower and middle portions of the crown and are spirally arranged around the base of a current year's shoot in groups often exceeding 20 (3).

In pines, both male and female strobili are initiated within the vegetative buds, but in soft pines (to which white pines belong), their initiation and development is somewhat delayed. The male strobili are initiated at the end of the growing season preceding pollination and occupy lateral axilliary positions (3) where dwarf shoots or needle fascicles would otherwise occur. They are small and difficult to distinguish from needle primordia until the onset of dormancy and the vegetative bud containing them does not show any swelling at its base (1 and 2) as it does in hard pines.

The subterminal primordia, which may develop into female strobili or lateral shoots, are also initiated in autumn. Therefore, the presence of female strobili within the vegetative buds cannot be detected even with a microscope during winter dormancy because of their insufficient development; all subterminal buds appear the same.

STROBILI

The buds appear dormant until about mid-April, when the male strobili (still within the vegetative bud on the flanks of an elongating shoot) begin to grow upward; the microsporophylls become pointed and the shoots bearing male strobili emerge from the bud scales. Meiotic division takes place around mid-May and angular tetrads of microspores are formed soon after. Microsporangia, bulging with pollen, change color from green, reddish green or brownish green to yellow (3). Pollen matures around mid-June. Male strobili are about 8 to 10 mm long and about 5 mm wide.

Subterminal strobili, which remain in the rudimentary stage during winter dormancy, resume growth in early April. In female strobili, bracts are initiated acropetally by early May and reach about 3 mm in length by the time of pollination. They are cordate with irregular margins. By mid-May, ovuliferous scales are initiated in the axils of the bracts and ovules appear as small swellings on their adaxial sides. At the time of pollination, the ovuliferous scales are broad, thick, and half to three-quarters as long as the bracts (4). Female strobili are red or pink, 12 to 20 mm long, and 5 to 7 mm in diameter, with a stalk about 15 mm long, bearing a few bud scales at the base of the strobilus (4).

POLLINATION

At pollination time, the axis of the male strobilus elongates and separation along the line of dehiscence of each microsporangium allows the release of pollen. The axis of the female strobilus also elongates, separating the bracts so that pollen can sift down between the bracts to the micropyle of the ovules.

Pollination occurs around mid-June and is strongly influenced by temperature and humidity. Individual trees are receptive for up to two weeks and variation among trees may extend the pollen flight period to more than three weeks.

After pollination, the male strobili wither, die, and are shed. In the female strobilus, the enlarging and thickening of the scales effectively seals the conelet, preventing contamination (5). Scales soon become the only visible parts of the conelet (6), turning the conelet greenish brown or brown. The bracts finish their growth soon after pollination and remain within the cone as abaxial appendages to the scales. By the end of the growing season, the conelets will reach about 40 to 50 mm in length but little activity takes place, either in the pollen or the ovule, until the spring of the following year.

FERTILIZATION

Pollen tubes resumes growth around mid-May and two nonmotile male gametes, or "sperms", are formed in early June. At about the same time, meiotic nuclear divisions occur in the female gametophyte and eventually a large number of free nuclei is produced. Fertilization occurs around mid-June, about 12 months after pollination.

Cones are fully developed by early August (7). They are 10 to 25 cm long, 2 to 3 cm in diameter, and green, purplish-green, or dark purple. By mid-August, distinct meristematic regions appear in the embryo, hypocotyl, or rudimentary root in the proximal region and the shoot axis in the distal region. In late August, the cotyledons are produced from the short shoulders of the shoot. The incidence of ovules or embryo abortion during development is low.

SEEDS

In early September, the cones begin to dry out and change color to dark beige, brown, or purplish brown. Seeds are shed in late September and early October. There are 250 to 350 cones per hectolitre and each cone yields about 200 seeds, most of them well filled and viable. Seeds (8) are 5 to 7 mm long, 3 to 4 mm wide, and about 2 mm thick. They are light to dark brown, often darkly mottled. Seed wings are 18 to 26 mm long, 6 to 7 mm wide, brown, and darker along the straight edge and tip. There are from 30 000 to 55 000 seeds per kilogram.

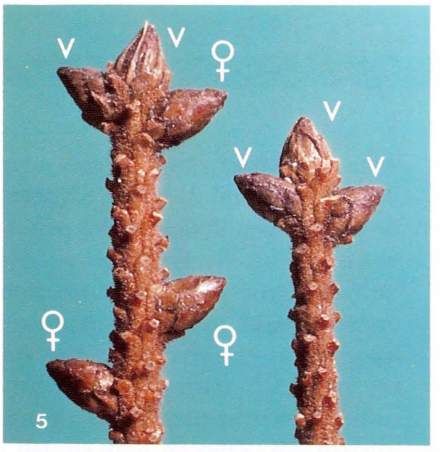
Red Spruce

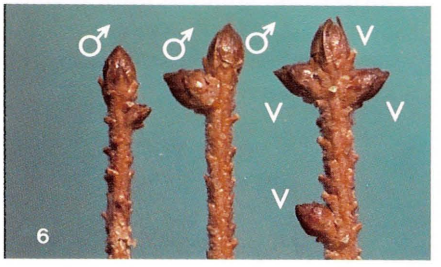
1. Microstrobili push bud scales aside as they grow out in the spring.

2. Each microstrobilus grows erect.

3. Microsporophylls spread apart and the microsporangia they carry split to shed their pollen.

4. After shedding pollen, microstrobili shrivel as they dry; later they fall.

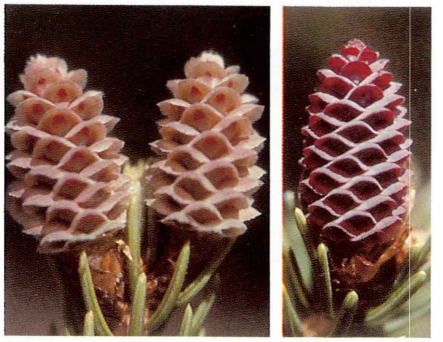




5. and 6. Vegetative buds are conical; megastrobilus buds are ovoid-conical, often with smooth bud scales showing near their apices; and microstrobilus buds are globular-conical.

7. A full-grown maturing megastrobilus is greyish or greenish in color, but with pinkish-brown hues which darken as ripeness approaches.

8. Open mature megastrobili are ovoid and reddish brown.



9. Megastrobili at the receptive stage range in color from greenish through pink to purple. Small bracts subtend the larger reflexed ovuliferous scales which serve to direct pollen into the interior of the structures.

10., 11., and 12. The ovuliferous scales bend upwards to close the growing megastrobilus (10) which then turns through a horizontal position (11) to become pendent (12).

13. Seeds are equipped with a terminal wing attached to the seed in a clasping manner; the wing detaches readily.

Red Spruce

Picea rubens **Sarg.**

by G.R. Powell

Stand-grown red spruce starts to produce strobili about 30 years from release, but vigorous, open-grown trees may produce strobili from 15 years of age. Healthy trees bear large crops of strobili at intervals of 2 to 8 years. Megastrobili occur in the uppermost parts of the crown, and microstrobili in a zone below this—sometimes extending to the base of the crown in open-grown trees.

BUDS

Terminal and lateral buds are initiated before the shoots on which they form burst from their buds. Bud differentiation occurs when shoots stop elongating. Buds in either terminal or lateral positions may differentiate reproductively (6), but whether or not terminal buds do so depends on the relative vigor, and position on the branch, of the shoot on which they occur. On relatively vigorous shoots in either the megastrobilus or microstrobilus zone, the reproductive buds tend to be proximally or medially situated, but on relatively weak shoots they tend to be distally or terminally situated (5, 6).

The zonal and on-shoot patterns of bud distribution are helpful in identifying buds of different types because the types of buds are not very distinctive (5, 6). Overwintering vegetative buds are broadly conical, megastrobilus buds are ovoid-conical and microstrobilus buds are globular-conical. Bud sizes vary with position and shoot vigor, so are not particularly helpful, but microstrobilus buds tend to be smaller than megastrobilus buds.

Internally, the buds are readily distinguishable. The shoot primordium in a vegetative bud has uniformly green, blunt-tipped leaf primordia arranged in spirals around its axis. The megastrobilus has broad, green bracts arranged in spirals around its axis. Each bract has a whitish ovuliferous scale, about the same size as the bract, on its adaxial surface. The smaller, and more globular microstrobilus has broad, green microsporophylls arranged in spirals around its axis. Each microsporophyll has two whitish microsporangia on its abaxial surface. So, although both strobili have green and whitish coloration, the arrangement of the structures of different colors is reversed.

BUD BURST AND RECEPTIVITY

As the reproductive buds begin to swell 4 to 6 weeks before they burst, the two kinds become more distinctive. The megastrobilus buds become more long-pointed as smooth, inner bud scales become visible near the buds' tips, and the microstrobilus buds become more globular and then ovoid-cylindrical. When the microstrobilus buds burst, the bud scales tend to be pushed aside (1); whereas, when the megastrobilus buds burst, a cap of bud scales is frequently carried upward by the growing megastrobilus.

The microstrobili grow rapidly to erect lengths of 15 to 23 mm by axial extension within and below the strobili (2, 3). The erose-margined, leaflike but yellowish to purple, upward-oriented, tips of the microsporophylls are spread apart (3) and the yellow microsporangia on their proximal abaxial surfaces split to shed pollen. The microstrobili then shrival (4), turn brown and eventually abscise, leaving the bud scales on the shoots.

The megastrobili grow erect rapidly, and concurrently the ovuliferous scales grow upward and outward and their tips become reflexed as the stage of full receptivity is reached (9). The megastrobili range from 15 to 24 mm long and from 10 to 14 mm wide, and are ovoid-cylindrical at that time. A small greenish or reddish bract occurs beneath each ovuliferous scale. The scales range in color, by tree, from green (occasionally) to pink and to purple with a bluish bloom. Pollen enters the megastrobilus through the openings between the scales and is channelled to the paired outgrowths of the integuments which are oriented downwards over the inner margins of the ovuliferous scales. Continued growth and thickening of the ovuliferous scales, and especially upturning of their tips closes the openings in the megastrobilus and ends the period of receptivity (10).

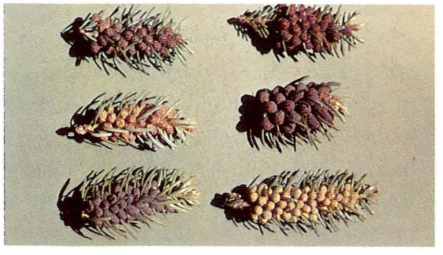
MEGASTROBILI AND SEEDS

As the megastrobili close, their color changes as the greyish abaxial surfaces of the ovuliferous scales are exposed. Then the axis at the base of the strobilus bends and the megastrobilus becomes first horizontal (11), and then pendent (12). It is at about the horizontal stage that vegetative buds burst. Megastrobilus growth continues until mid-July. By about the end of June, the ovules reach full size, fertilization occurs, and embryo development follows in fertilized seeds. The full-grown megastrobili are dull greyish or greenish (7), 25 to 45 mm long and 13 to 24 mm wide. In August and early September, they gradually dry and turn reddish brown. Then, the scales bend outwards in dry weather, thus opening the strobili and permitting seed dissemination (8). About 75 percent of the seed falls within 8 weeks of strobilus ripening; the rest falls over a more protracted period into the winter. The megastrobili usually fall within one year of ripening.

Red spruce seeds are 2 to 3 mm long and 1 to 2 mm wide. A pale brown wing, 8 to 10 mm long, is attached to each seed in a clasping manner, but is easily and totally detached (13). Empty "seeds" have less mass than full seeds and are therefore removable by mechanical or flotation procedures. Thus, lots of cleaned seeds can contain mostly full seeds. On average, there are 306 000 seeds per kg.

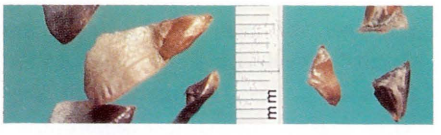
Balsam Fir

1. Microstrobilus buds occur in large numbers on the abaxial surfaces of shoots in the microstrobilus zone of the crown.

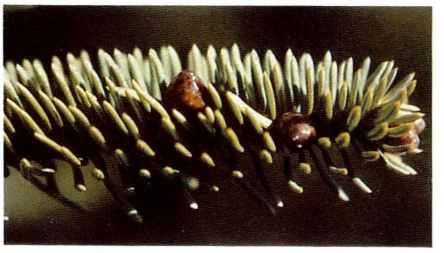


2. After bud burst, microstrobili range in color, by tree, from bluish purple through purple, red, and orange to yellow.

3. As pollen is shed, the axes of the microstrobili elongate to carry the strobili clear of the bud scales. The strobili then shrivel and gradually abscise.



4. Seeds are equipped with purple or brown terminal wings held in wrap-around fashion. This and pockets of resin between wing base and seed make complete removal of wings impracticable; instead, only the blades of the wings are broken off.



5. Large, broadly ovoid-conical megastrobilus buds occur in axils of only a few leaves on adaxial shoot surfaces.

6. Megastrobili burst through their bud scales by pushing the latter aside.

7. Receptive megastrobili are usually yellowish green. Large bracts, which subtend small ovuliferous scales, serve to direct pollen into the interior of the structure.

8. to 13. Megastrobili remain erect throughout their development. The receptive stage (8) ends as ovuliferous scales grow out between the bracts (9) which are overgrown (10) as growth to full strobilus size (11) occurs. Resin is exuded near the strobilus tip. The strobili dry, the scales spread apart (12) and are then shed, with the seeds (13), leaving the upright, woody axes on the shoot.

Balsam Fir

Abies balsamea **(L.) Mill.**

by G.R. Powell

Stand-grown balsam fir starts to produce strobili about 30 years from release, but vigorous, open-grown trees may produce strobili from 15 years of age. Healthy trees tend to bear strobili biennially. Megastrobili are borne on the upper 3 to 6 whorls of nodal branches and on the internodal branches between, and microstrobili are borne in the 1 to 4 m of crown below this. These zones are usually separate, but may overlap slightly when crops are heavy.

BUDS

All buds are initiated before the shoots on which they form burst from their buds, but differentiation occurs when shoot elongation ceases. Buds in any position may fail to differentiate and remain latent. Terminal and subterminal buds only differentiate vegetatively, so reproductive buds are always laterally situated. Lateral buds in the megastrobilus zone arise on adaxial surfaces of the shoots in axils of only a few leaves. Commonly, 1 to 3 megastrobilus buds form per shoot: they become the largest buds on the shoot (5). From late summer, these broad buds are distinguishable from the shorter, narrower, more conical, lateral vegetative buds. Lateral buds in the microstrobilus zone arise almost exclusively on the abaxial surfaces of the shoots in axils of most of the leaves. They differentiate as ellipsoidal to globular microstrobilus buds, and there may be many per shoot (1).

Both megastrobilus and vegetative buds have thick masses of brown, resin-coated bud scales surrounding loosely packed, thin white or purplish inner bud scales which overarch the strobilus or shoot. Microstrobilus buds have a thin covering of bud scales. The dormant megastrobilus is 1.0 to 1.5 mm long and almost as broad. It consists of long-pointed bracts arranged in spirals around its axis, and a small apex. Each bract has an ovuliferous-scale primordium on the lower quarter of its adaxial surface. The dormant microstrobilus is less than 1 mm long and consists of short, blunt, microsporophylls arranged in spirals around its axis. Each microsporophyll has two microsporangia projecting bulbously from its abaxial surface. The primordial shoot in a vegetative bud has, spirally arranged around its axis, blunt-tipped leaf primordia devoid of surficial or axilliary structures.

BUD BURST AND RECEPTIVITY

The overwintered strobili inside the buds start expanding 6 to 10 weeks before bud burst. This soon results in swelling of microstrobilus buds, but megastrobilus buds swell only after the spaces within the buds have been occupied. Vegetative-bud swelling lags behind megastrobilus-bud swelling. Microctobilus buds burst 2 to 3 weeks, and megastrobilus buds burst (6) about 10 days before vegetative buds.

The microstrobili grow rapidly to lengths of 4 to 7 mm, and then the microsporangia split and release their pollen (3). The axis below the microstrobilus also elongates and pushes the strobilus beyond the bud scales. Before shedding pollen, the microstrobili range in color, by tree, from bluish purple through purple, reddish purple, red, and orange, to yellow (2). After shedding pollen, the microstrobili shrivel, turn brown, and abscise, leaving the bud scales on the shoots.

The megastrobili grow rapidly to erect lengths of 2 to 3 cm and then stop elongating for 4 to 8 days. These receptive megastrobili are generally pale green or yellow-green (7, 8), but some trees bear orangish or purplish megastrobili. The color is that of the bracts, which form the bulk of the receptive strobilus. The bracts are spread apart forming rhombic openings through which pollen enters. By this time integments from the ovules which have formed on the ovuliferous scales extend over the inner edges of each bract lamina and flare into downward-facing funnelform structures to which pollen adheres. Pollen shedding and reception of pollen occurs at the time of vegetative-bud burst.

MEGASTROBILI AND SEEDS

Rapid elongation of the megastrobilus resumes as the ovuliferous-scale growth rate increases. The grey to purple scales are soon visible as they grow between the bracts and seal the openings (9). Scale and strobilus growth continues until mid-July (when shoot elongation also stops) when the strobili are 4 to 7 cm long and 15 to 28 mm wide. Generally, the scales overgrow the bracts (10, 11), but in bracted balsam fir the tips of the bracts remain exserted. During growth, white resin is copiously exuded from the tops of the strobili (9-11). Fertilization occurs in late June and rapid embryo growth ensures in the seeds.

The megastrobili dry and turn brown during August. The scales then spread apart (12) and abscise as wind action breaks up the strobili and disseminates the scales and seeds (13). The axes remain on the shoots for many years.

The seeds are 3 to 6 mm long, 2 to 3 mm wide, and 1.5 to 2.5 mm thick (4). Each has a purple to brown wing attached to it in wrap-around fashion—and resin visicles occur between the wing base and the seed. This makes removal of the whole wing impracticable, so only the blade of the wing is removed for seed storage (4). Empty "seeds" develop a thick, hard wall and a mass similar to that of full seeds. This makes mechanical separation of full seeds difficult, so "cleaned" lots of seeds (averaging 131 000 seeds per kg) may contain many empty "seeds". This contributes to the low germination sometimes ascribed to balsam fir seeds.

Alpine Fir

1. Terminal positions on the shoots always contain vegetative buds.

2. Vegetative buds may also occur in lateral positions. They are smaller and narrower than megasporangiate buds.

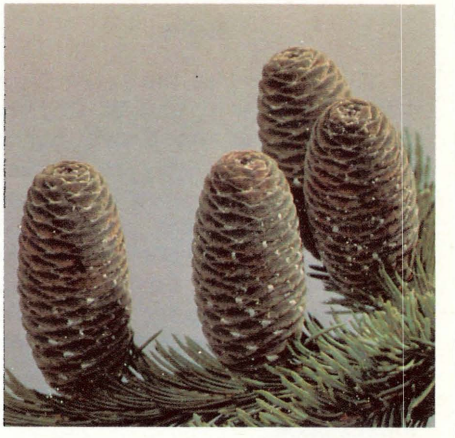
3. Megasporangiate buds are always in lateral positions. They are larger and broader and occur only as a few top whorls.

4. The vegetative apex only partially fills the bud cavity and the inner scales are loosely packed. The megasporangiate buds are completely filled with the developing strobilus.

5. The microsporangiate buds are clustered on the underside of shoots in the lower parts of the crown.

6. The developing pollen cones (strobili) are bluish-purple. As their axes elongate, yellow pollen sacs protrude gradually among the sporophylls.

7. Developing seed cones are purple with only the sharp-pointed, appressed bracts showing. During pollination the bracts stand perpendicular to allow for entry of pollen.



8. In the seed cones, the scales overgrow the buds. The cones stand erect. In October they disintegrate.

9. Seeds are 5 to 7 mm long and 2 to 3 mm wide. The papery wing is wrapped around the seed and in closing only the blade is removed.

Alpine Fir

Abies lasiocarpa **(Hook.) Nutt.**

by S. Eis and D. Craigdallie

The minimum age for production of seed cones on alpine fir is about 25 years and for pollen cones about 35 years. Cone crops occur in two- to five-year intervals, but good cone crops are infrequent. Seed cone buds are located on a few top whorls. They occur singly on the upper side of the shoots and stand erect. Pollen cones develop on the lower side of the shoots in large clusters in the lower half of the crown. The two zones rarely overlap.

BUDS

On a given tree, the coloring of all buds is similar (2 and 3). On most trees the buds are brown, but on some trees they may be reddish-brown, purplish-brown or light brown. All buds are covered with semi- transparent, often crystalized layer of resin about 1 mm thick which gives them a silvery sheen. The brown color of the outer leather-like scales gradually changes to the green color of the thin, paper-like inner scales.

The terminal buds are always vegetative (1). At the top of the crown they are in groups of three, in the lower part of the crown they may be in groups of up to six. They are orbicular to ovate, 4 to 5 mm in diameter. Inside buds, oval apices are about 3 mm high and 2 mm wide. During dormancy the appendages can be recognized as needles by their simple structure and short needle-like shape.

While vegetative buds also occur in axillary positions (2), reproductive buds develop only in axillary positions. The megasporangiate buds (3) develop on the adaxial (upper) side of a few top whorls of branches, usually one to three on each shoot. During the winter dormancy, they are about 8 mm high and 6 mm in diameter, globose to ovate. The apex is 4 to 5 mm high and 2-3 mm in diameter and completely fills the bud cavity. By the onset of dormancy all bracts and most ovuliferous scales are present. Marginal growth at the base of the bract gives it a lanceolate shape with a broad base and a narrow, sharp tip. Compared to bracts, the scales are small protruberances in the axils of the bracts.

Buds are produced in typical megasporangiate bud positions every year. In some years, however, they are somewhat smaller and more conical, and the apex inside them is vegetative (2 and 4). These buds will produce weak shoots. Even in good crop years some of these buds occur among the reproductive buds. Also, in good crop years, some reproductive buds are somewhat smaller and the apex is not as advanced as in the larger buds. These smaller buds may live for a short while but they eventually abort.

The microsporangiate buds (5) develop in the lower and middle part of the crown in clusters on the abaxial (lower) side of the shoots. In the dormant stage, they are globular, 3 to 4 mm in diameter, have only about 20 bud scales. The bud cavity is completely filled with the apex, which is about 2 to 3 mm long. It contains spirally arranged microsporophylls bearing well developed microsporangia. As is the case with seed cone buds, many pollen cone buds abort even in seed years.

POLLINATION

The elongation of the strobili in spring begins at the end of April and the reproductive bud break takes place around the middle of May. At an early stage, the developing pollen cones are bluish-purple but, as their axes elongate, the yellow pollen sacs protrude gradually among the sporophylls (6). At pollination, the pollen cones are 13 to 15 mm long, including a stalk about 4 mm long.

The emerging seed cones are purple to bluish-purple, or greenish-purple. Before pollination, the bracts become deltoid, showing only long, sharp-pointed, purple tips (7). Later, the extension of the axis exposes pale green or grayish-green broad base. Because of the wide geographic distribution, pollination may take place from the middle of May to the middle of June. At that time the scale is still only a small outgrowth in the axil of the bract.

CONES

After pollination the pollen cones shrivel, turn brown and are shed; the bud scales remain on the shoots for many years. The seed cones (8) keep enlarging. The scales through marginal growth seal the openings between bracts and, because the bracts stopped growing, the scales soon become the only visible parts of the cone. They soon change their color to dark purple-blue, dark greyish-purple or sometimes dark greenish-purple. By the middle of August they attain their mature size, about 6 to 12 cm in length and 2 to 4 cm in diameter. Seeds mature around the end of August. In mid-September the cones dry, turn brown and the scales spread apart. During windy days in October, the cones break apart and scales and seeds are disseminated. The spike-like axes remain on the shoots for several years.

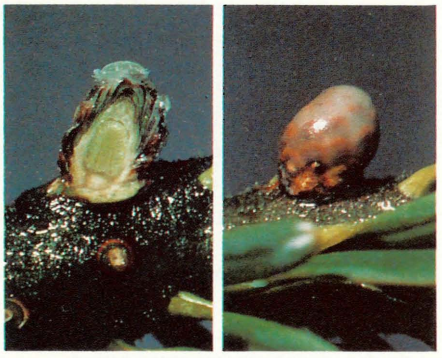
SEEDS

The seeds (9) are about 5 to 7 mm long, 2 to 3 mm wide and about 2 mm thick. The papery greyish-brown wing is about one-and-a-half times as long and as wide as the seed. It is wrapped around the seed and attached to it firmly by resin, so that in cleaning only the blade is broken and the part wrapped around the seed remains on it. Empty seeds are indistinguishable from filled seeds and have a similar specific gravity.

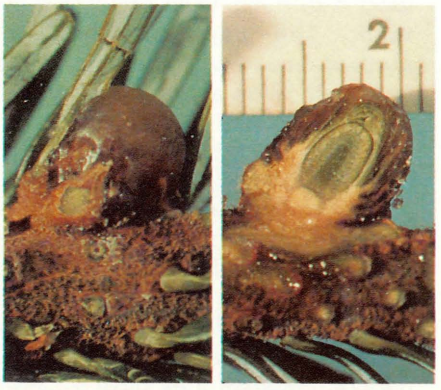
There are 700 to 1100 cones per hectolitre, 2.3 Kg of seeds per hectolitre of cones, and 50 000 to 120 000 seeds per kilogram. Germination is usually low. It is difficult to break the seed dormancy uniformly.

Amabilis Fir

1. Terminal buds are always vegetative.



2. Vegetative buds in lateral positions are smaller than megasporangiate bud and the apex does not fill the bud cavity.



3. Megasporangiate buds are larger and broader than vegetative buds and the apex completely fills the bud cavity.

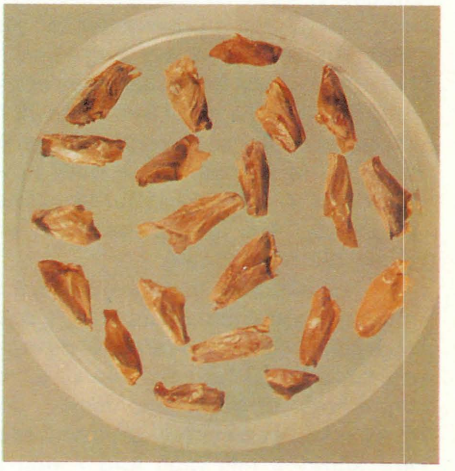
4. Microsporangiate buds are clustered on the underside of branches in the lower half of the crown. The apex fills the bud cavity completely.

5. Before pollination the pollen strobili are red or purplish red.

6. Elongation of the strobili exposes the yellow pollen sacs.

7. Emerging seed cones show only red, sharp pointed appressed bracts, elongation exposes their yellowish brown or green bases.

8. After pollination, the scales overgrow the bracts and seal the cone. The cone turns dark purplish gray.



9. Seeds are about 12 mm long and 5 mm wide. The wing is firmly attached to the seed and cleaning the seed separates only the blade.

Amabilis Fir

Abies amabilis (Dougl.) Forbes

by S. Eis and D. Craigdallie

In heavy cone crop years, open-grown trees may produce a few cones before the age of 20, but good cone crops rarely begin before the trees are about 35 years old. Cones are often produced in two- or three-year intervals and good crops occur once in about five or six years. Seed cones develop on the top five to seven whorls and pollen cones in the lower part of the crown. The two zones rarely overlap.

BUD DESCRIPTION

Apart from its position on the tree, bud location on a branch is the most important distinguishing characteristic of its probable function. The coloring of all buds is the same — brown to greenish brown; but they are covered with a semitransparent, silvery, often crystalized layer of resin, 1 to 2 mm thick. The outer scales are leather-like, the inner scales progressively greener and more paper-like.

The terminal buds (1) occur in groups of three on vigorous branches and up to six on branches of low vigor, usually on lower branches of old trees. They are globose, average 5 or 6 mm in diameter and have 33 to 40 bud scales, and are always vegetative. The apices are about 3 mm high and 4 mm wide. During winter dormancy the green needles are easily distinguishable.

Reproductive buds are always in axillary lateral positions. The megasporangiate (female) buds (3) develop on the adaxial (upper) side of a few top whorls of branches, usually one to three on each shoot. Dormant, they are about 9 mm high and 7 mm in diameter and are oblongly globose to broadly ovate. The megasporangiate apex completely fills the bud cavity, measuring up to 5 mm high and about 3 mm broad. By the onset of dormancy, all bracts and most ovuliferous scales are present. Marginal growth at the base of the bract gives it a lanceolate shape with a broad base. Compared to bracts, the scales are small, and are about twice as wide as they are high.

Even in good seed years, not all buds in megasporangiate bud positions produce cones. Some are small and usually covered with less resin; they will become latent and will eventually abort. Other buds, somewhat smaller than megasporangiate buds, have a more conical or narrowly oval shape (2); these will produce weak vegetative shoots. In winter, the vegetative apex only partially fills the bud cavity and needles are readily recognizable on the flanks of the apex.

The microsporangiate buds (4) differentiate on less vigorous branches in the lower part of the crown, in the axils of most of the needles on the abaxial (lower) side of the shoots. The dormant buds are globular, about 4 mm in diameter, have only about 20 bud scales and are covered with a thin layer of resin. Many microsporangiate buds become latent and eventually abort.

POLLINATION

The strobili inside the buds begin to elongate around the end of April and emerge from the bud scales around the beginning of May. Before pollination, the pollen cones (5) are dark purplish-red, red or pale-red, but as their axes elongate, the yellow pollen sacs protrude (6). Around the middle of May, the cones elongate to about 14 to 17 mm and become pendant.

Seed cones (7) emerging from the buds are usually red or purplish-red, occasionally green and stand erect on the upper side of the shoots. Before pollination, the bracts become deltoid with a broad pale green or brown base and a long, sharp-pointed red tip. As the axes of the cones elongate to allow for entry of pollen, the bract bases become progressively more visible. Pollination takes place during the second half of May, 10 to 14 days before vegetative bud break. At pollination, the scale is still only a small, flat appendage, twice as broad as it is high.

CONES

Soon after pollination, the pollen cones shrivel, turn brown and are shed, but the bud scales remain on the shoots for many years. The seed cones (8) keep enlarging. The scales, through rapid marginal growth, seal the openings between bracts, overgrow the bracts and become the only visible parts of the cone. The cones turn dark purple-gray to dark bluish-purple. By the middle of August they reach their mature size of about 9 to 13 cm in length and 4 to 6 cm in diameter.

Cones need to be picked in late August or early September because, as they dry out, they become brittle. In late September and during October, the scales spread apart and wind action breaks them up and disseminates the scales and the seeds. The spike-like axes usually remain on the shoots for several years.

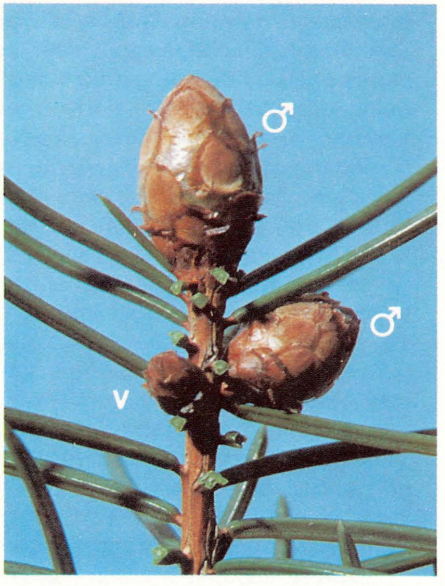
SEEDS

The seeds (9) are 10 to 12 mm long, 4 to 6 mm wide and 3 to 4 mm thick. The papery, translucent, purplish-brown wing is about one-and- half times as long and as wide as the seed and is attached to it in wrap-around fashion with a layer of resin. In cleaning, the blade is broken off, but the proximal part remains on the seed. Empty seeds — often more abundant than filled seeds — are well developed and not readily distinguishable from viable seeds. Separation of empty and filled seeds may be difficult because they have a similar specific gravity.

There are 500 to 800 cones per hectolitre, about 350 seeds per cone and 20 000 to 40 000 seeds per kg. Germination is low, often only 30%.

Norway Spruce

1. Vegetative buds on the verge of bud break are long and cylindrical in shape.



2. At the same time, male buds are globular in shape and their scales remain appressed to each other.

3. More globular than the vegetative buds, female buds are cylindrical and ogival in shape.

4. Male strobili change from purple to yellow; two weeks after their appearance, they release pollen.

5. After pollen is released, the male strobilus dries out and eventually falls off.

6. After pollination, female cone scales close and fertilization soon follows. The cone grows more pendant, its red colour changes to green. Three to four weeks after bud break, the female cone is already 5 cm long.

7. Mature cones are pendant, cylindrical, rigid and about 10 to 18 cm in length. The harvest must be carried out from early September to mid-October.

8. Seed length varies from 3 to 5 mm. There are 120 000 to 140 000 seeds per kg.

Norway Spruce

Picea abies (L.) Karst.

by A. Corriveau

Norway Spruce begins to produce commercial seed crops at about 30 to 40 years of age. Peak seed crops occur every 4 to 8 years, although seed production remains at modest levels.

The species is monoecious. Male cones may be scattered throughout the crown, but occur primarily in the middle and lower sections and even on the very lowest branches when there is sufficient sunlight. Female cones are produced later in the life of the tree and are spread through the upper third of the crown.

BUD DESCRIPTION

In winter, vegetative buds are oval-conical in shape, with a pointed apex, and measure 5 to 9 mm in length. Their scales are brown to reddish brown and nonresinous; the side exposed to sunlight is duller and darker in colour. Terminal scales may be curled in buds that have been exposed to heat for an extended period during dormancy. Dissection shows that unextended shoots occupy little space overall, being entirely confined within a conical green mass about 2 mm long. covered with spirally-arranged protuberances (needle primordia). When the scales (modified leaves) covering male or female reproductive buds begin breaking, vegetative buds are long and cylindrical in shape, measuring about 1.5 cm or less (1) according to whether they are near the top or beside reproductive buds.

Male buds are positioned laterally along the previous year's growth and, on occasion, in a subterminal or terminal position. Unlike vegetative buds, which remain narrow when ready to break (1), they are quite globular and their protective scales remain appressed to each other as the reproductive structure grows (2). At this stage, a yellowish liquid flows when the male bud is pressed. A lengthwise section shows that tissue differentiation has created the following arrangement: a series of microsporophylls arranged in a spiral around a central axis, each with two pollen sacs on the abaxial side.

Female buds are less numerous than male buds and are found in only the terminal position on certain shoots spread throughout the upper third of the tree, with the exception of the final half-metre. When ready to break, they are slightly globular in shape, although the overall configuration is rather cylindrical and ogival, and are covered with bud scales set closely together (3). A lengthwise section shows that the interior organization of female buds is similar to that of male buds, except that the megaspores are on the adaxial side and that, under the ovuliferous scale (megasporophyll), a second type of scale exists (the axillant scale or bract) that will remain small in size. Formation of the three types of buds begins in June of the year before bud break and their differentiation continues through July and August of that same year.

BUD BREAK

The growing season begins in early or mid-May, when vegetative and reproductive buds increase in volume following the differentiation of parenchymatous cells and overall lengthening. Reproductive buds open fully one to two weeks after the start of this physiological activity, while vegetative buds require three to four weeks to open.

The male bud thus produces a strobilus 1 to 2 cm in length, oval in shape and attached to a stalk 3 to 5 mm in length. Purple-tinged upon its appearance (4), it turns yellow by the time it reaches maturity after one to two weeks. Subsequently the colour becomes duller (5) and the male strobilus falls off after having released its pollen to the air through the dehiscence of pollen sacs.

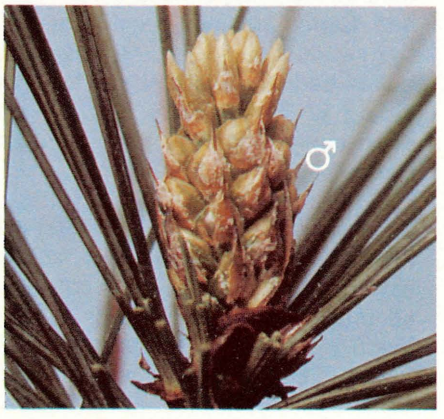
The development of male and female buds is synchronized. Each female bud produces a pliable, sessile strobilus made up of about 200 purple ovuliferous scales. As in the majority of other conifers, these scales bend into perpendicular position during pollination, i.e., the cone opens for this period of maximum receptiveness. Pollen grains, which are deposited deep inside the cone, are held by a secretion from the ovule which, as it dries, directs the pollen toward the micropylar chamber. The scales close after pollination and the cone continues to grow. Less than two weeks after pollination female conelets measure close to 5 cm (6), the same as new shoots. After dissection the future seed is easily seen because of its whitish tinge; the wing is being differentiated from the upper surface of the ovuliferous scale. During the same growing season, fertilization occurs, the embryo is formed, and the cone reaches maturity and starts releasing its seeds.

In the final stage, cones are pendant, cylindrical, rigid and 10 to 18 cm long (7). Greenish in colour during the maturation period, they may persist in the tree until the following spring; seed dispersal extends from September to April, depending on periods of hot, dry weather. The cone harvest must be carried out from early September to mid-October.

Mature seeds are reddish brown, approximately 3 to 5 mm in length, and sharp on the micropyle side (8). Each is covered entirely on one side by a seed wing 15 to 20 mm long. The average seed tree produces 175 g of seeds. There are 120 000 to 140 000 seeds per kg. Close to 700 cones are needed to make one hectolitre and this volume contains about 1 kg of seed. The mean germination rate is approximately 70 percent.

Eastern White Pine

1. From the second or third week following the start of the growing season vegetative shoots are cylindrical and thin.



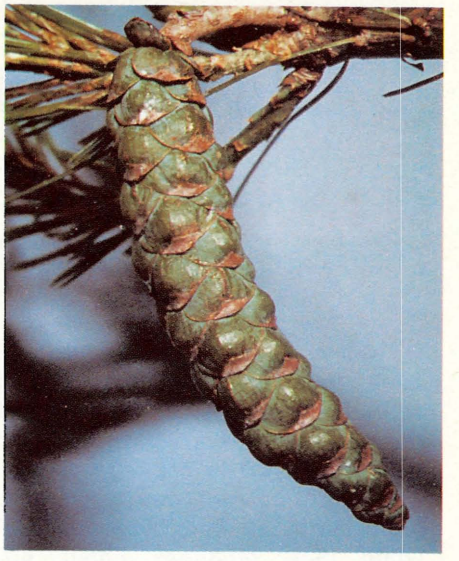
2. Male strobili are globular in shape and grouped in the lower portion of new shoots.

3. Male strobili reach maturity less than 3 weeks after bud break.

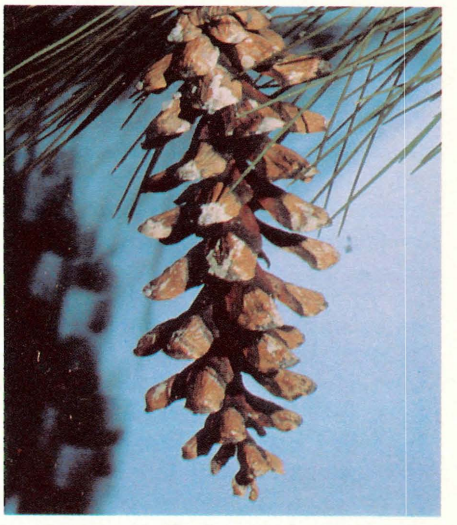
4. Female strobili are conical in shape and occupy a subterminal position on new shoots.

5. Female strobili spread their scales apart for the period of maximum receptiveness.

6. During the dormant period, conelets measure approximately 2 cm.



7. Conelets, or cones by then, reach a length of 7 cm by the time new strobili are ready to be pollinated.



8. This brown and lignified cone has just released its seed and will break off during the next winter or spring.

9. The mean germination rate is approximately 85 percent, and there are 60 000 to 80 000 seeds per kg.

Eastern White Pine

***Pinus strobus* L.**

by A. Corriveau

White pine begins to produce cones between the ages of 5 to 10 years. Production of viable seed crops, however, does not begin until trees reach 20 to 50 years of age. Abundant pollen cone production often starts 10 to 20 years later. A white pine produces about 400 cones annually and produces peak crops every 3 to 10 years.

BUD DESCRIPTION

Vegetative buds are yellowish brown and oval-oblong. They have long, reddish brown pointed scales. Their surface is nonresinous, although there is a translucent wax covering. Terminal buds normally measure 5 to 10 mm and, in general, are longer than subterminal buds.

Although their differentiation dates back to the previous growing season, male buds are practically unobservable during dormancy. In fact, they consist of nothing more than tiny primordia camouflaged by the scales of certain terminal vegetative buds. A lengthwise section of appropriate terminal buds, however, shows the unextended microscopic pattern of next year's male cones in the lower section and of foliar structures in the upper section.

Similar careful observation is required to locate female cone primordia, which are in a subterminal position inside certain terminal buds whose remaining cells are vegetative.

BUD BREAK

In early May, buds and conelets pollinated in the preceding year start to extend. After 2 to 3 weeks of development, the new tissue is completely out in the open and foliar growth may be readily differentiated from male or female strobilus growth.

In an exclusively vegetative terminal bud or emerging shoot (1), there is a series of long, thin, cylindrical structures (the needles) spirally arranged around a central axis, which is the future shoot. If the terminal bud also contains male strobilus primordia, these can be seen as rather globular structures in the lower portion of the new growth (2). These will form groups of 10 to 20 oval-shaped, yellowish green strobili surrounding the base of the new annual growth. Each male strobilus measures 6 to 8 mm and comprises a multitude of microsporophylls arranged spirally around the central axis; the abaxial side of each scale carries two microsporangia containing microspores, each of which will become a pollen grain.

As male strobili develop they become more pliable and somewhat elongated. Their color changes from greenish yellow to pale yellow (3). Less than 5 to 6 weeks after the start of the growing season, the male strobili reach maturity and release a vast quantity of pollen grains that are transported on the wind. Afterwards, male cones dry out and break off. Their former presence is marked by a needle-free area covered with scars.

Female strobili may be found at the subterminal position on certain new shoots about 2 to 3 weeks after the start of the growing season, at which time they are almost 5 mm long and may be distinguished from foliar growths by their conical shape and larger size (4). After another 2 to 3 weeks, the female strobili are green, cylindrical and stalked. Its structure follows the pattern set by the male strobilus except that the mother cells are on the adaxial side of the ovuliferous scales. The female conelet is usually solitary, but groups of two or more may occur; in some cases, branches are so heavily laden as to resemble grape clusters.

Less than a week after its appearance, the female strobilus spreads its scales and may be pollinated (5). After pollination, the scales close and the conelet and its peduncle extend to a length of about 2 cm each. At the end of its first growing season, the conelet is still aligned in the same axis as the shoot that carries it, and is purplish brown (6).

Fertilization does not occur until the spring following pollination. Because the seed integument starts forming prior to fertilization, the fertilization process may be thwarted and sterile seeds produced.

At the start of the second growing season, female conelets measure about 7 cm — and can be called cones (7). The cones continue to extend, reaching 8 to 20 cm in length and approximately 2.5 cm in breadth by mid-summer. As they develop, cones become pendant and take the shape of long, green, stalked and often curved cylinders that are spotted with resin (8).

The cone has 50 to 80 thin scales that are truncated at the extremity, rounded and not very lignified. In August, these scales begin to turn brown and progressively lignify. This is a clear indication of cone maturation. Soon after reaching maturity, the cones open to release seed; they break off during the winter or the following spring.

Seeds are reddish brown to gray mottled with brown or black; they are 6 to 8 mm in length (9). The narrow seed wing about 20 mm in length extends the sowing radius to approximately 60 m. This wing is easily detachable, since it surrounds the seed by means of just two very small lateral appendages.

The average seed tree produces 200 g of seed annually. The germination rate is in the neighborhood of 85 percent, and there are 60 000 to 80 000 seeds per kg. About 1 600 cones are needed to make one hectolitre, and this volume contains about 700 g of seed.