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Illustrated Guide to Stages of Jack Pine Cone Development

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ABSTRACT

A self-directed explanation of the reproductive cycle of jack pine, *Pinus banksiana* (Lamb.), is presented. It is mainly intended to facilitate collection of pollen and seed for tree improvement studies of this species. Popular terminology is used wherever possible. An outline of the reproductive cycle and its timing is provided. External appearance and internal anatomy of buds and cones are shown by means of labeled colour photographs of intact and sectioned material.

RÉSUMÉ

Les auteurs de ce manuel donne une explication personnelle du cycle de reproduction du pin gris (*Pinus banksiana* Lamb.); le manuel vise à faciliter la récolte de pollen et de semences pour des études d'amélioration de cette espèce. Un schéma décrit le cycle de reproduction ainsi que sa durée. L'aspect externe et l'anatomie interne des bourgeons et des cônes sont indiqués à l'aide de photographies couleur étiquetées du matériel intact et coupé.

ACKNOWLEDGMENTS

Dr. John Owens (Department of Biology, University of Victoria, British Columbia) provided valuable comments and suggestions, especially with respect to terminology. Dr. George Buchert (Ontario Forest Research Institute, Ministry of Natural Resources, Sault Ste. Marie, Ontario) acted as Scientific Authority for this project on behalf of the Canada-Ontario Forest Resource Development Agreement.

Photographs, except for those on pages 22 and 51, were taken by the senior author. The jack pine silhouette on page 5 was prepared by Don McQuade of Deep River, Ontario.

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Cover photo: Extension growth of a polycyclic terminal bud of jack pine in late May. The red conelets have just been pollinated. Cones from the previous year can be seen at the base of the shoot.

PREFACE

This guide is designed to aid persons involved in research and fieldwork on genetic improvement of jack pine. It could also be a useful adjunct to practical exercises in schools, colleges and universities where the pine life cycle is taught. Throughout the guide, popular terminology is used wherever possible. Technical terms are used only where there is no suitable popular equivalent; such terms are defined in a glossary. A table of technical equivalents of the popular terms is also provided.

Color photographs of pollen- and seed-cones at various stages of development will aid the field worker in locating the best cones and in predicting when they will be ready for collection and/or pollination. A brief outline of the biological processes occurring in the cones during development is provided, but further details should be sought in the literature listed in the bibliography. The timing of developmental stages indicated in the text and in the photographs is that observed at Deep River, Ontario (lat. 46° 0' N, long. 77° 3' W) over a 12-year period. This timing can be expected to vary from season to season and from one region to another. The authors would be pleased to hear of any major deviations in timing, etc., that may be noted by users of this manual and to receive comments or suggestions for its future modification (c/o Department of Biology, University of Ottawa, Ottawa, Ont. K1N 6N5).

Most of the photographs[1] in the manual are of intact structures or hand-cut sections thereof. Some of the illustrations (e.g., page 15), however, are photographs taken through a compound microscope of thin sections of tissue fixed and stained in the laboratory using methodology described elsewhere (e.g., O'Brien and McCully 1981). These are included to illustrate details not readily evident in hand-cut sections of living material.

Except where indicated otherwise, illustrations are of jack pine. In those instances where a particular anatomical feature is difficult to demonstrate with jack pine, white pine (*Pinus strobus* L.) or red pine (*Pinus resinosa* Ait.) have been used for illustrative purposes.

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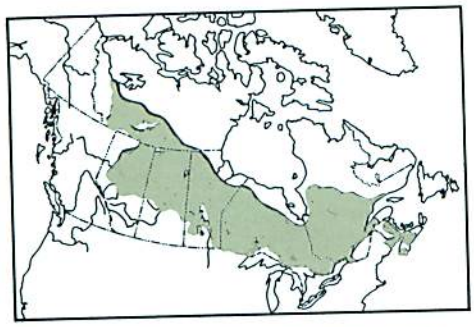
[1]Macrophotographs were taken with a macro lens or bellows using Kodachrome 64 daylight film; Ektachrome 160 tungsten film was used for the microphotographs.

INTRODUCTION

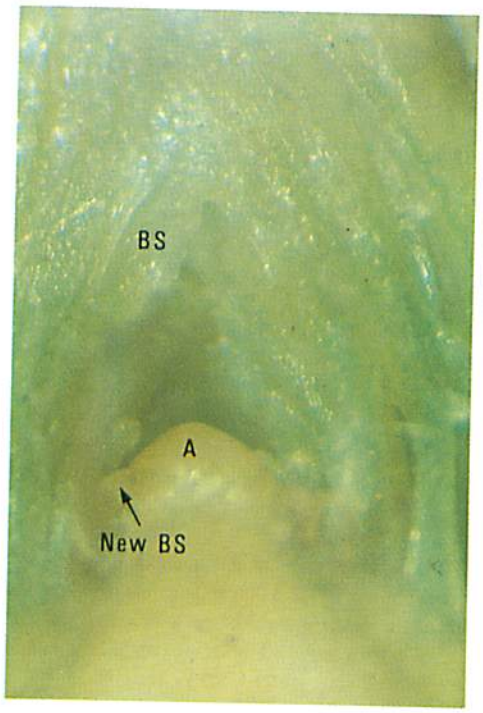
Jack pine, *Pinus banksiana* Lamb., is an important coniferous tree of the boreal forest; it ranges from the maritime provinces in eastern Canada to the Rocky Mountains in the west. It is a valuable source of raw materials for both the pulp and paper industry and for the lumber industry. Because of the economic importance of jack pine, an understanding of its reproductive behavior, including that of pollen and seed production, is essential to facilitate tree-improvement programs.



Distribution of jack pine (after Hosie 1969)

The characteristic shape of the mature jack pine tree, shown in the silhouette on page 5, results from the development of buds found at the end of every branch. These are variously called terminal buds, winter buds or long-shoot buds. Terminal buds consist of a central axis with a growing tip (apical meristem) that is responsible for the production of new tissues, including the bud scales (cataphylls) that pro-

tect the apical region (see photograph below). Where the bud scale and the central axis meet (the bud-scale axil) there is usually a tiny meristem (the bud primordium) that will develop into a lateral bud. However, there are two regions in every terminal bud where lateral buds do not normally form: just below the apical meristem and at the base of the bud. These regions are called "sterile cataphyll zones". Thus, when the central axis of the terminal bud extends in the spring, a short region of the new stem or branch bears only withered bud scales.



A terminal bud of red pine cut longitudinally to show its apical meristem (growing tip - A). Bud scales (BS) surround the meristem, and new ones are being formed at its base.

Silhouette of jack pine

Four kinds of lateral buds may be produced in the axils of bud scales (needle-fascicle buds, branch buds, pollen-cone buds and seed-cone buds). The most common are needle-fascicle buds (dwarf-shoot or dwarf-branch buds), which produce spirally arranged two-needled fascicles along the branches. Jack pine, like most conifers, retains its needles for several years. Terminal buds containing only needle-fascicle buds are typically found at the ends of minor branches.

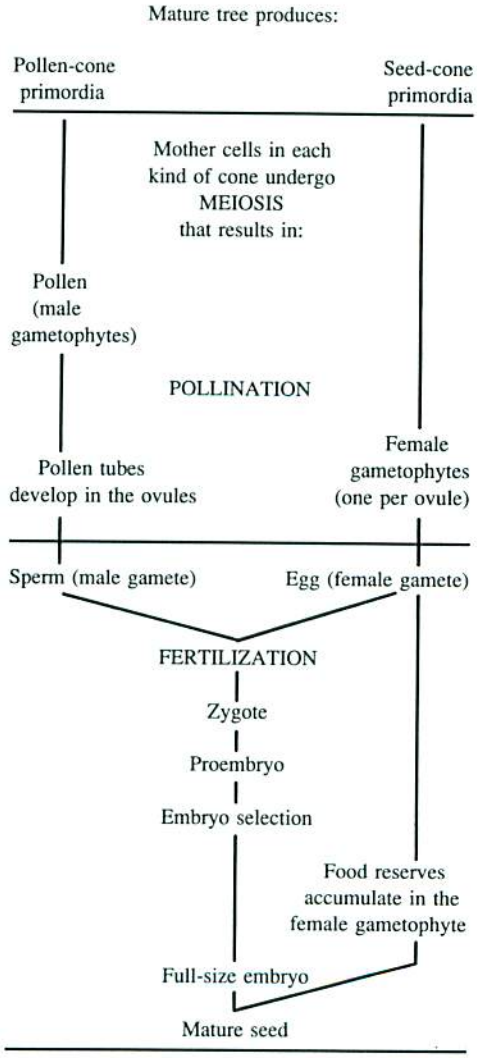
A second common type of lateral bud is the branch bud (long-shoot or long-branch bud), whose structure is the same as that of a terminal bud with only needle-fascicle buds (page 34). Such buds may be produced singly or in whorls of two or more and develop into branches. Jack pine is unusual in that branch buds may be produced at only one position (monocyclic buds) or, more commonly, at more than one position (polycyclic buds) (page 33) along the terminal axis. Above each branch bud position is a "sterile cataphyll zone". Thus, when the central axis elongates, there will again be a region of the stem immediately above the branch(es) with only bud scales present. Such a stem will appear to have two years' growth in one. Typically, the lowest branch buds in a polycyclic terminal bud form first, causing the bud to assume a more or less oval shape (page 29). Those that form just below the "sterile cataphyll zone" at the apex remain inconspicuous until the following season, when they become evident as well-developed buds at the base of the new terminal bud (page 26).

The two types of lateral buds described above are responsible for vegetative growth of the tree and are the only types produced in young trees.

Jack pine trees do not normally begin to produce reproductive structures, i.e., pollen cones and seed cones, until they are at least 3 years old, and then only under ideal conditions. In open-grown trees, pollen and seed cones will often appear at age 5 to 10 years; in closed plantations, 10 to 25 years are needed (Rudolph and Yeatman 1982).

Pollen cones (microstrobili) and seed cones (megastrobili) also begin as lateral buds. Seed cones and pollen cones develop in separate buds at the ends of separate branches. The size of the buds depends on their position in the tree; they are typically larger in the upper crown and at the ends of main branches. Pollen cones form in spirally arranged clusters at the base of the terminal bud; branch buds usually are not present although needle-fascicle buds form above the pollen-cone buds. Terminal buds with pollen-cone buds are typically found on smaller branches lower down in the tree and in more shaded parts of the crown. Seed cones form in whorls of one to five immediately below branch buds. Terminal buds with seed-cone buds are typically found in the upper crown and on larger, unshaded lower branches. As in most pines, three growing seasons are needed to produce a mature seed cone. The chronological development of pollen-cone buds and seed-cone buds is described in the following pages.

Outline of reproductive cycle of jack pine



(Adapted from Weier et al. 1982)

Timing of the major events outlined on the opposite page

Begin to form by July, Year I
(new cone primordia each year)

Meiosis in pollen cone in early May, Year II

Late May, Year II

Meiosis in seed cone by mid-June, Year II

Mid- to late June, Year III

Mid-July, Year III

Mid-August, Year III

September, Year III

Hints for Cone Examination

The external detail of intact buds and related structures can be readily observed in the field with the aid of a good hand lens. For examination of internal structures in the field, a sharp razor or knife blade can be used (with caution!) to make lengthwise or cross-sectional cuts. The cut surfaces can then be studied with the aid of a hand lens, or teased apart with straight pins or a dissecting needle to separate structures such as cone scales. The development of pollen cones, of pollen and, for the first two seasons, of seed cones is easily followed in this way. In the third year of seed-cone development, however, hardening of the cone scales (by August) makes it necessary to use a good pair of pruning shears to cut the cones open. Cones may also be broken in half to remove cone scales and ovules. The events immediately preceding and following fertilization can be observed in hand-cut sections of the future seeds.

To find terminal buds containing pollen-cone buds, look for buds broadened at the base on smaller branches in any part of the tree. For buds containing seed-cone buds, look for the largest buds at the ends of main branches in the crown (closed canopies) or on the side of the tree that gets the most light (open-grown trees), especially on branches that already have cones on them.

Note: For further information on specific cone-preparation techniques, the senior author may be contacted at P.O. Box 159, Deep River, Ont., K0J 1P0.

Pollen-cone Development

In the Deep River area, pollen-cone buds begin to develop in early summer, typically in terminal buds on lower or more shaded branches of the tree. As many as 60 pollen-cone buds (Curtis and Popham 1972), each in the axil of a subtending terminal bud scale, may form in a spiral cluster beginning at the base of the terminal bud. By late August, cone buds are clearly visible as bumps on the terminal bud (page 14). By late September, pollen sacs (microsporangia) have formed on the underside of the pollen-cone scales (microsporophylls), two on each scale (page 15). The buds overwinter in this condition.

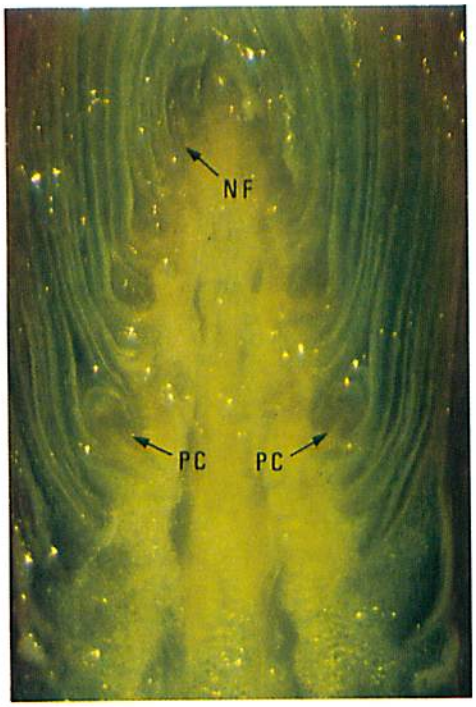
By early May of the following spring, pollen-cone buds begin to emerge from their bud scales (page 18) and microspore mother cells in the pollen sacs undergo reduction division (meiosis) to produce tetrads of haploid cells that soon separate to become individual microspores. Over the course of the next three weeks, each microspore becomes a mature four-celled pollen grain (immature male gametophyte) with two air sacs that enable it to float on the wind. By the time the pollen is shed (page 40), two of the cells have degenerated, leaving one cell (the generative cell) that will later give rise to two sperm cells (male gametes) and a cell responsible for growth of the pollen tube. Further development of the pollen occurs within the seed cones. Once their pollen is shed, the pollen cones wither and eventually drop off.

Pollen-cone Development Year I

Mid-July

- young terminal bud;
- the broadened base suggests that it will produce pollen cones;
- bud scales protect the growing tip (apical meristem) and conceal it from view;
- the two-needled fascicles along the stem developed from buds laid down in the previous year's terminal bud.

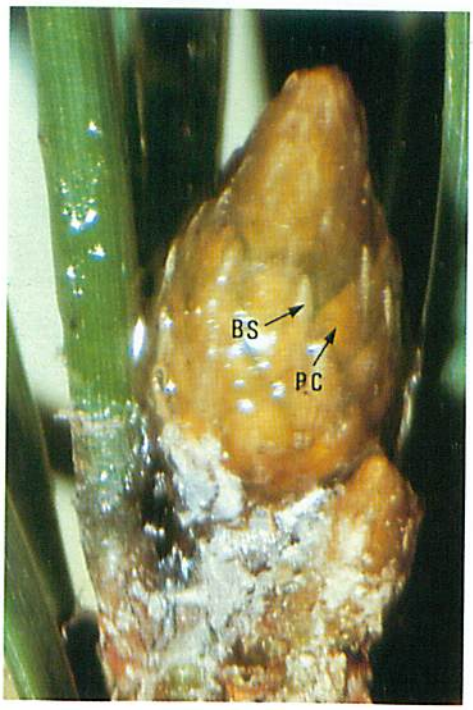
Pollen-cone Development Year I



Mid-July

- young terminal bud cut longitudinally to show developing pollen-cone buds (PC) at the base;
- needle-fascicle buds (NF) will develop at the upper end, below the growing tip.

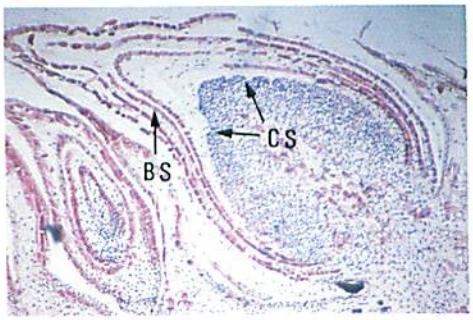
Pollen-cone Development Year I

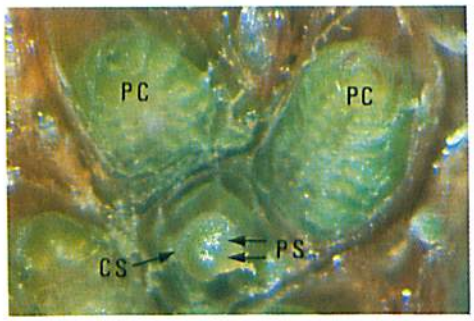


Late August

- terminal bud with pollen-cone buds (PC) visible at the base;
- elongated subtending bud scales (BS) mark the position of each pollen-cone bud;
- the bud is about 1 cm long and coated with a thin layer of clear resin;
- pollen-cone buds become even more prominent by winter.

Pollen-cone Development Year I





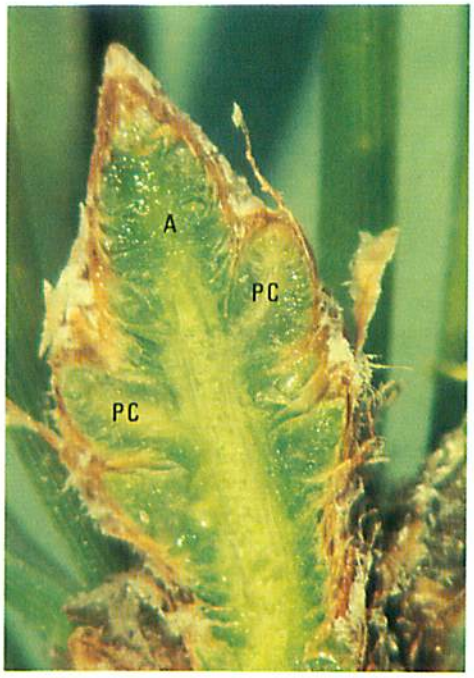
Late August (*top*)

- longitudinal section through a fixed pollen-cone bud surrounded by its own bud scales (BS) showing pollen-cone scale (microsporophyll) primordia (CS).

Mid-September (*bottom*)

- terminal bud cut to show pollen-cone buds (PC);
- pollen sacs are present, with cells that will become pollen grains; two pollen sacs (PS), about 0.2 mm long, can be seen on the cone scale (CS) placed upside down in the center of the photograph.

Pollen-cone Development Year II



February

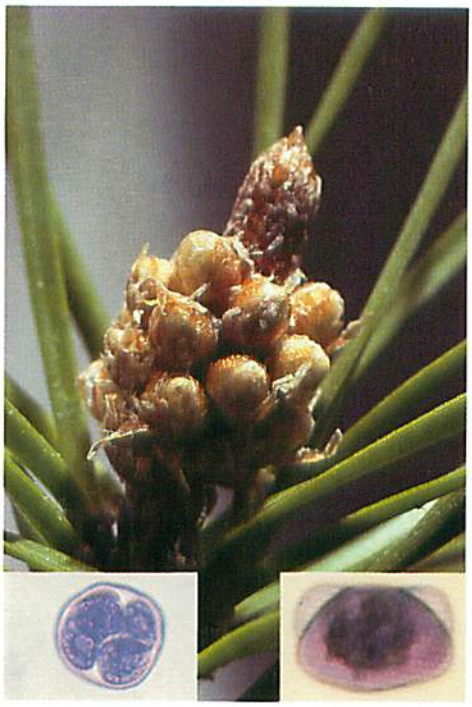
- terminal bud cut longitudinally to show several pollen-cone buds (PC) at its base;
- buds below the growing tip (A) will produce two-needled fascicles in the spring;
- a few bud scales without axillary buds (sterile cataphylls) lie below the pollen-cone buds.

Pollen-cone Development Year II

Early Spring

- expanding terminal bud with pollen-cone buds;
- the resin coating is shed when growth resumes in the spring;
- the bud tip will develop as on page 12, and will probably initiate new pollen-cone buds that will mature in the following year.

Pollen-cone Development Year II



Early May

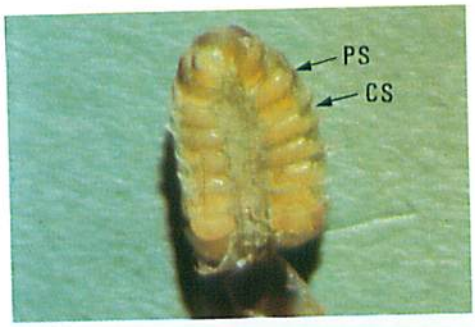
- pollen cones emerging from their bud scales;
- meiosis occurs at this stage to produce a tetrad of haploid cells (*inset left*);
- the tetrads separate into four individual cells (microspores) (*inset right*) that will become pollen grains.

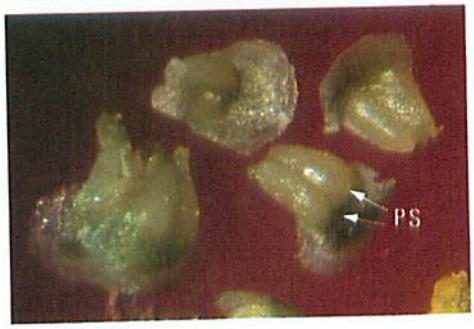
Pollen-cone Development Year II

Mid-May

- pollen cones almost ready to shed pollen;
- cones at the base are usually longer (about 8 mm) than those at the top (about 6 mm);
- pollen grains (*inset*) now have fully developed air sacs and are about twice the size of the original microspore.

Pollen-cone Development Year II





Mid-May

- (*top*) pollen cone cut longitudinally to show the rows of cone scales (CS), each with two pollen sacs (PS) full of yellow pollen on the underside;
- (*bottom*) separated pollen-cone scales to show pairs of pollen sacs (PS).

Pollen-cone Development Year II

Late May

- pollen cones as pollen is being shed; a mature pollen grain is illustrated on page 40;
- the pollen cones are more separated than on page 19 as a result of terminal shoot extension; this will facilitate wind dispersal of the pollen;
- the needle fascicles are beginning to emerge on the terminal shoot.

Pollen-cone Development Year II

Forestry Canada

Early June

- pollen cones after pollen has been shed;
- the scales are now turning brown;
- the old pollen cones will die and drop off, leaving a section of stem without needle fascicles.

Seed-cone Development

Like pollen cones, seed-cone primordia form in the terminal bud during the summer, typically just under branch buds. In a terminal bud with more than one tier of branch buds, those nearest the base appear first (page 27). From one to five seed-cone buds may form at each tier, each in the axil of a terminal-bud scale. By the end of the summer, each seed-cone bud has a well-developed central axis surrounded by its own bud scales (page 31). In the spring, bracts form along the cone axis. Cone-scale primordia form on these bracts (page 36); those at the upper end of the cone bud rapidly enlarge and soon equal or exceed the bracts in size. Two future seeds (ovules) form at the base of each cone scale on its upper surface. By the end of May, the upper half of the seed cone has emerged from its bud scales (page 38). The cone scales separate slightly to permit pollen to drift between them and reach their bases. The opening in the future seed coat (the micropyle) then fills overnight with a sugary solution (the pollination drop), which catches the pollen grains and pulls them through the micropyle as the liquid recedes during the day. When pollen is trapped, the opening closes. The cone scales thicken and the cone is sealed shut. The pollen germinates and pushes a short tube into the tip of the ovule (the nucellus or megasporangium) and then becomes dormant. Meanwhile, a cell deep within the future seed (the megaspore mother cell, page 40) undergoes meiosis to produce four daughter cells, only one of which survives (a megaspore). Over the rest of the summer, nuclear divisions in the megaspore result in a delicate, spherical, multinucleate cell with a large central vacuole

(the young female gametophyte). The cones enlarge somewhat, further emerge from their bud scales, and become brown in color.

In the spring of the third year, expansion of the cones and development of their final elongated tapered shape begins. Within the cones, further nuclear divisions and continued expansion in diameter occur in the female gametophyte. By early June, cell walls are laid down, one or two archegonia form, and each archegonium produces an egg cell. Only then do the pollen tubes resume their growth to deliver two sperm nuclei to each egg cell. The zygote resulting from the fusion of a sperm nucleus and the egg nucleus undergoes four nuclear divisions to form a 16-celled proembryo. Suspensor cells in the proembryo elongate to push the tier of embryo-forming cells into the female gametophyte. Four embryos develop from this tier as a result of a lengthwise split (cleavage polyembryony) and, over a 3-week period (the embryo selection period), compete for space and nutrients. Only one will survive to develop into a mature embryo. A total of eight competing embryos may result if a second egg in the same female gametophyte is fertilized. By the middle of August, embryos have reached their full size, and the female gametophyte occupies most of the space within the seed coat. Maturation of the seeds is indicated by a change in cone color from green to yellow-brown in late August to early September.

Seed-cone Development Year I

Mid-June

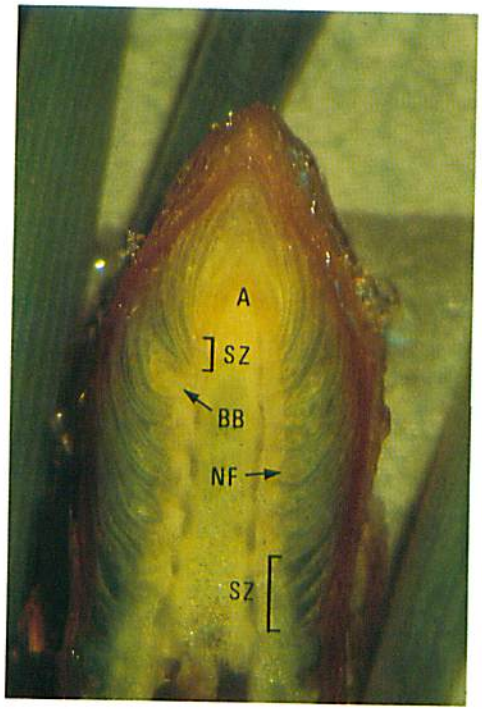
- new terminal bud in right foreground;
- the presence of the pollinated Year II seed cone behind the terminal bud indicates that the latter is likely to produce seed-cone buds.

Seed-cone Development Year I

Early July

- elongated terminal bud, slightly broadened in the middle, possibly by development of new branch buds;
- the pollinated year II seed cone in the background indicates that this terminal bud will likely contain seed-cone buds;
- branch buds (BB), one at the base with bud scales removed, were laid down in the previous year's terminal bud.

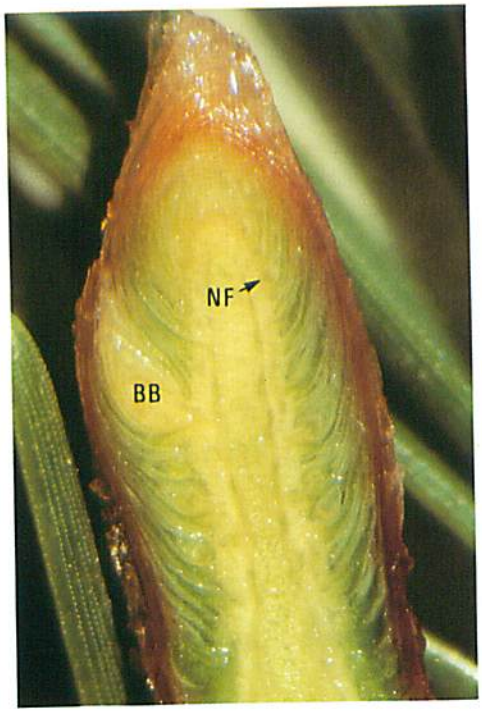
Seed-cone Development Year I



Mid-July

- a future polycyclic terminal bud cut longitudinally to show a prominent branch bud (BB) in the middle;
- seed-cone buds, if present, will be found in the whorl below the branch bud;
- needle-fascicle buds (NF) line the axis below the branch bud;
- sterile cataphyll zones (SZ) are visible at the base of and just above the branch bud;
- new shoot tissues are being produced in the growing tip (A).

Seed-cone Development Year I



Early August

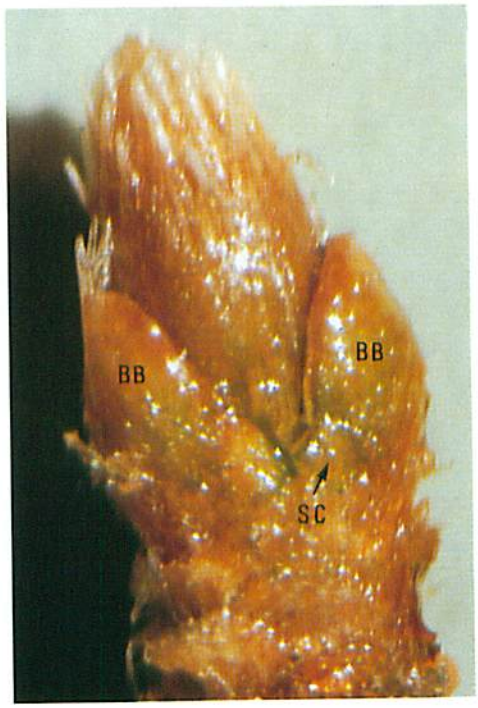
- a nearly fully developed polycyclic terminal bud cut longitudinally to show the extension of the central axis of the bud above the well-developed branch bud (BB) in the middle;
- an upper zone of needle-fascicle buds (NF) is forming.

Seed-cone Development Year I

Late August

- mature polycyclic terminal bud coated with resin;
- the bud is widest in the middle and about 1.5 cm long;
- the subtending branch buds at its base were formed in the previous year's terminal bud.

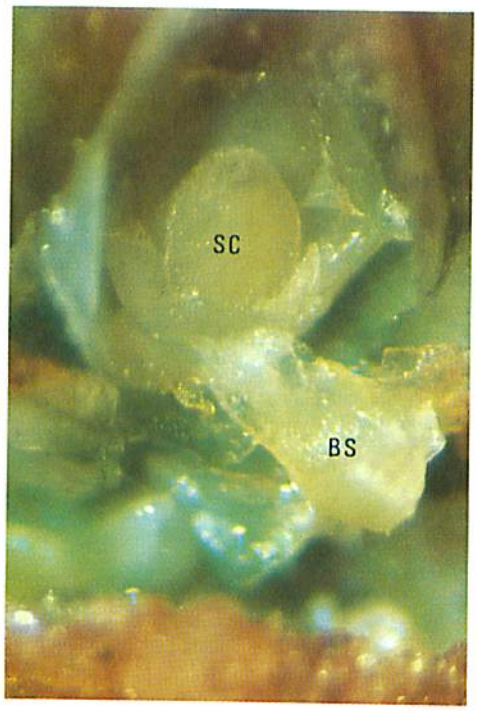
Seed-cone Development Year I



Late August

- the terminal bud on page 29, with resin coating and outer bud scales removed to expose a tiny seed-cone bud (SC) between the two prominent branch buds (BB);
- this preparation shows clearly that branch buds are the reason for the expanded middle of such a bud.

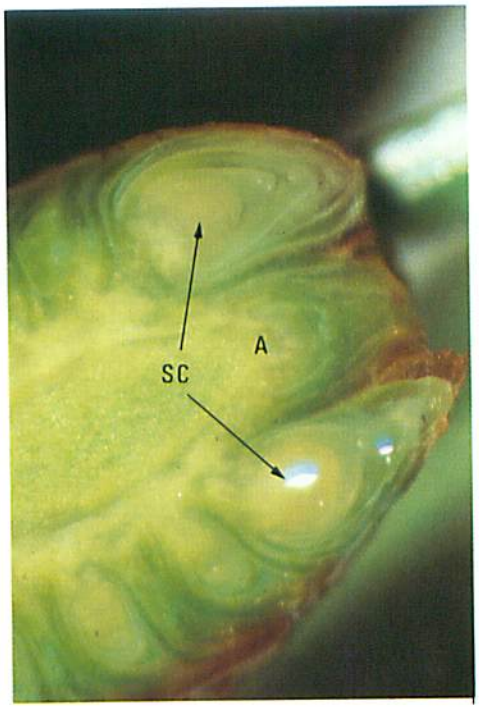
Seed-cone Development Year I



Late August

- seed-cone bud with bud scales (BS) pulled back to expose the tiny (0.8 mm) future seed cone (SC);
- the smooth surface of the seed-cone primordium indicates that bracts have not yet begun to form.

Seed-cone Development Year I



Late October

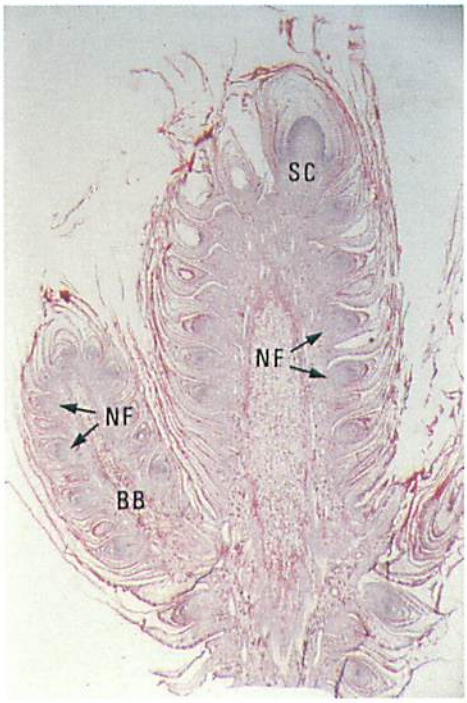
- upper half of a polycyclic terminal bud cut longitudinally to show two seed-cone buds (SC) at the growing tip (A);
- branch-bud primordia may be present above the seed-cone buds;
- a new terminal bud will form at the growing tip during the next summer.

Seed-cone Development Year II

Early Spring

- polycyclic terminal bud beginning to elongate;
- branch buds (BB) show clearly in the middle, and a second tier of branch buds forms the ridge at the top (*arrow*);
- a pollinated seed-cone bud (Year III) is in the foreground.

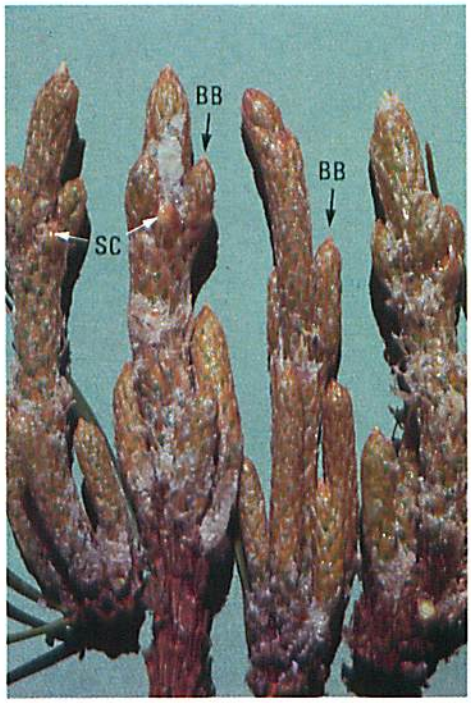
Seed-cone Development Year II



Early Spring

- longitudinal section through the upper half of a fixed polycyclic terminal bud to show a sub-terminal seed-cone bud (SC) and a well-developed branch bud (BB) in the middle;
- needle-fascicle buds (NF) line both the terminal bud and the branch bud.

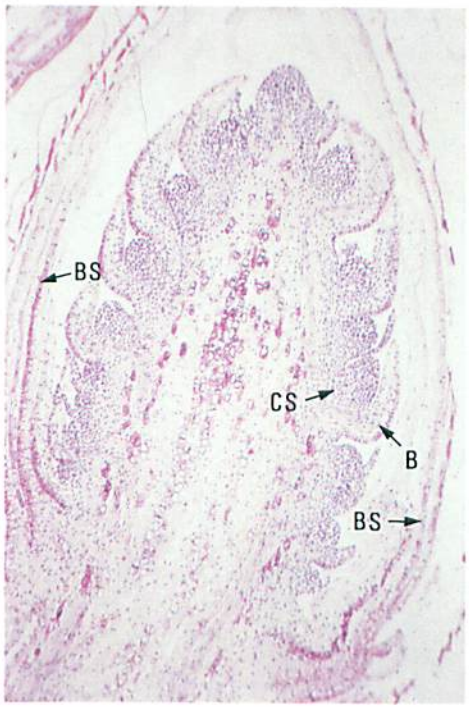
Seed-cone Development Year II



Mid-May

- a collection of polycyclic terminal buds elongated from less than 1.5 cm during dormancy to 6.0 cm;
- seed-cone buds (SC) and branch buds (BB) are ready to emerge from the bud scales that surround them.

Seed-cone Development Year II



Mid-May

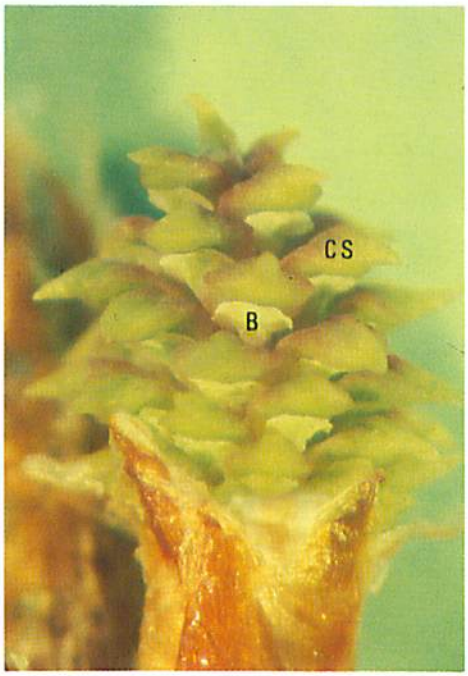
- longitudinal section of a fixed seed-cone bud to show bracts (B) with cone scales (CS) developing on top; the bud is still surrounded by its bud scales (BS);
- the cone scales will enlarge to become the dominant feature; the bracts will enlarge only slightly.

Seed-cone Development Year II

Mid-May

- seed-cone (SC) partly emerged from its bud scales;
- exposed cone scales may be red or green in color;
- two branch buds (BB) and the apical region of the expanding terminal bud will soon emerge.

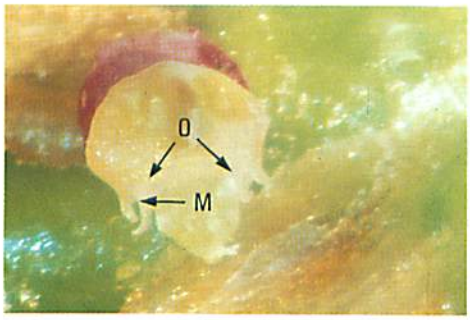
Seed-cone Development Year II

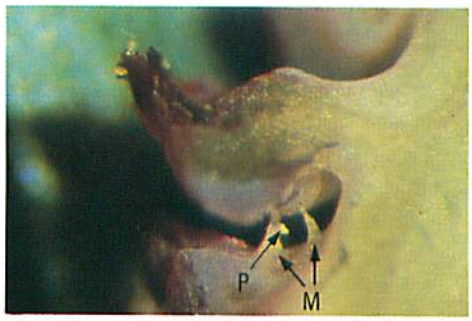


Late May

- young seed cone emerging from its bud scales; only the upper half emerges at this stage and will subsequently produce seed; the sterile lower half will emerge later;
- exposed cone scales (CS), now larger than the bracts (B), are separating and are nearly ready for pollination (i.e., nearly receptive).

Seed-cone Development Year II

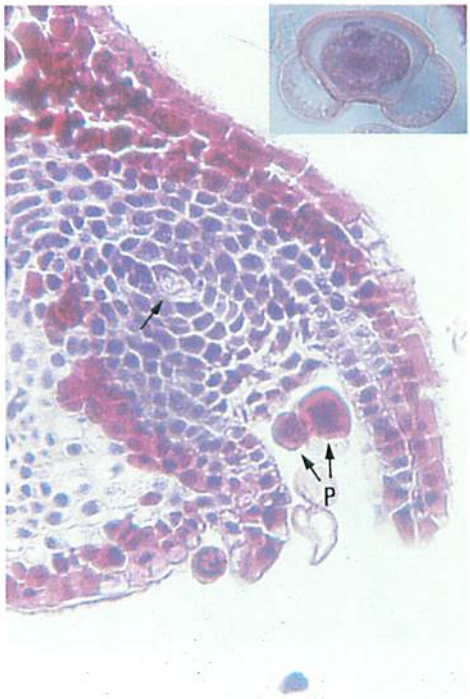




Late May

- (*top*) cone scale from a young red pine cone showing the two future seeds (ovules, O) on its upper surface, each with an opening (the micropyle, M) through which pollen will enter;
- the downward-pointing arms of the micropyles have parted and are nearly receptive.
- (*bottom*) receptive red pine cone cut longitudinally to show pollen grains (P) adhering to the sticky arms of the micropyle (M).

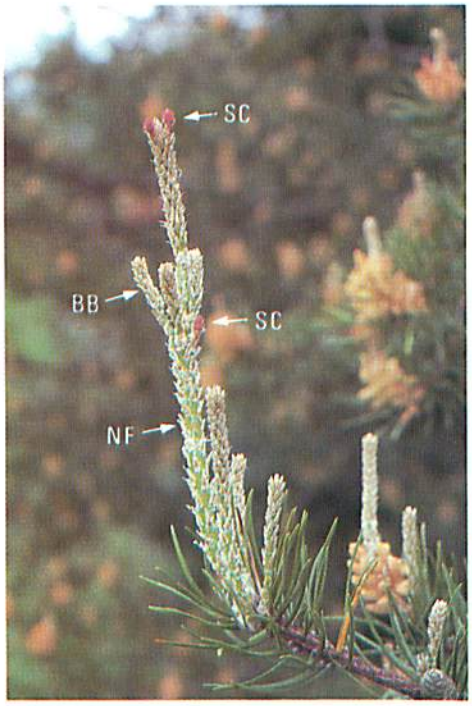
Seed-cone Development Year II



Late May

- longitudinal section of a fixed ovule, showing pollen grains (P) drawn into it by the pollination drop;
- the micropyle will soon close, after which the pollen will send a tube into the ovule and then become dormant;
- in June, a distinct cell in the center (the megaspore mother cell) (*arrow*) will undergo meiotic division (page 23);
- (*inset*) fixed mature pollen grain.

Seed-cone Development Year II



Late May

- new growth produced by a polycyclic terminal bud;
- young pollinated seed cones (SC) are present just below the new terminal bud and just below the expanding branch buds (BB) in the middle of the shoot;
- needle fascicles (NF) are beginning to emerge.

Seed-cone Development Year II

September

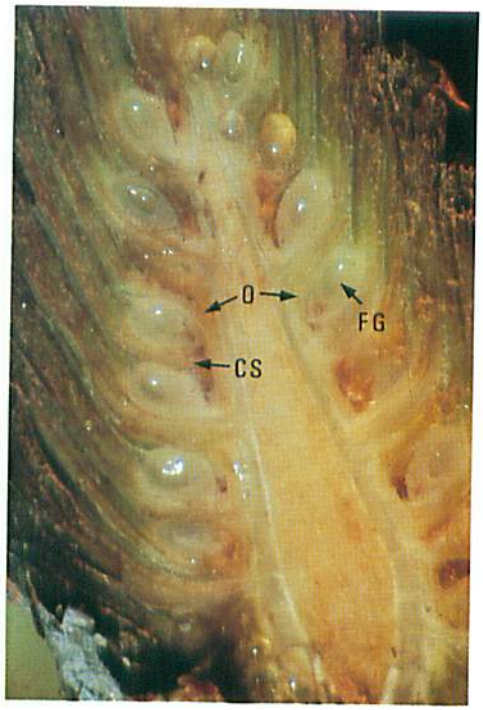
- shoot with two pollinated seed cones (SC), now brown in color and beginning to harden;
- a new terminal bud (TB) and two small branch buds are in the foreground.

Seed-cone Development Year III

Late May

- seed cone (SC) expanding one year after pollination;
- green lines appear between the cone scales;
- the new terminal bud (TB) has expanded and a new cone (*arrow*) is nearly receptive;
- a branch bud (BB) is also developing from the old terminal bud.

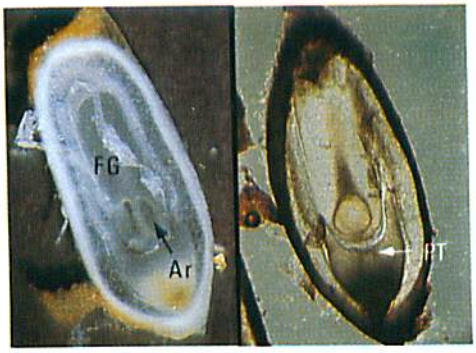
Seed-cone Development Year III



Late May

- seed cone as on page 43, cut longitudinally to expose the future seeds (ovules, O) attached to the cone scales (CS);
- a female gametophyte (FG) is at the center of each ovule;
- at this time, the female gametophyte is a multinucleate cell about 1.0 mm in diameter with a large vacuole; it will soon lay down cell walls, and develop one or two archegonia, each of which will produce an egg.

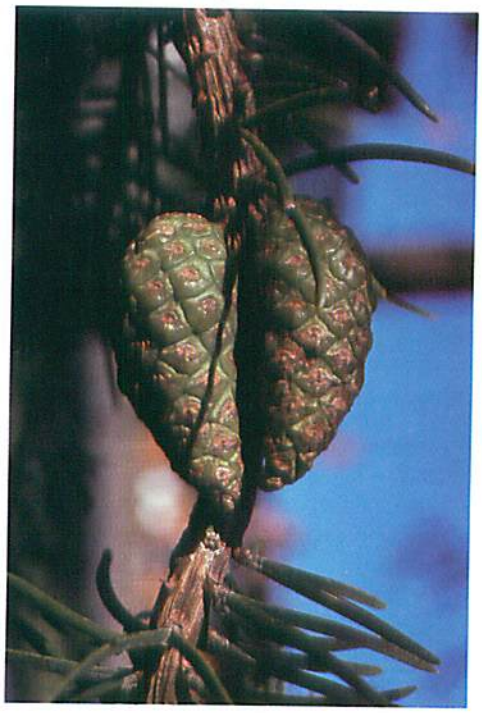
Seed-cone Development Year III



Late June

- developing seeds of white pine before (*left*) and after (*right*) fertilization, both cut longitudinally to show internal detail (the much smaller jack pine ovules have the same anatomy);
- (*left*) the female gametophyte (FG), surrounded by the nucellus, contains two archegonia (Ar);
- (*right*) the ovule has been stained with iodine solution to show starch accumulation ("starch stele") in the dark area below the archegonium;
- appearance of this starch stele coincides with the period during which fertilization normally occurs;
- the paths of two pollen tubes (PT) are visible as two dark lines.

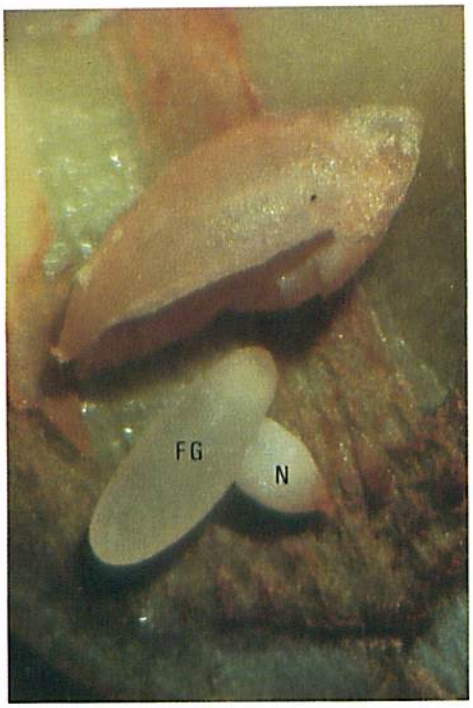
Seed-cone Development Year III



July

- two full-sized cones, still green but becoming woody;
- large, straight cones such as these are desirable for collection (Anon. 1986) because they promise to contain many viable seeds;
- cone size and shape are genetically determined.

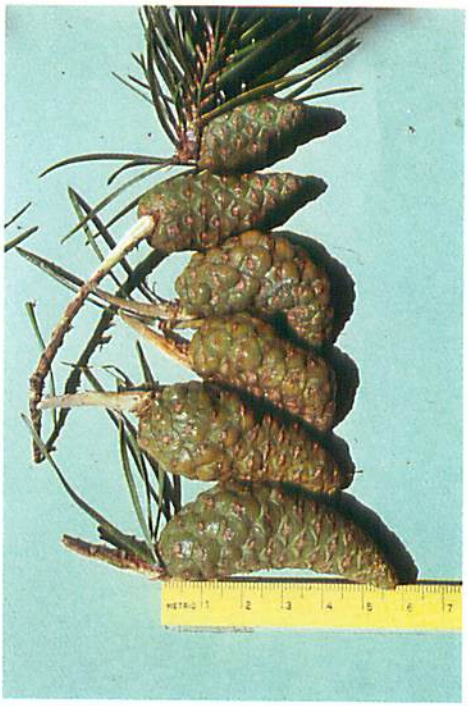
Seed-cone Development Year III



Mid-July

- an opened, immature seed of white pine;
- the brittle, still pale colored seed coat has been separated from the female gametophyte (FG); the remnants of the parent tissue (nucellus, N) lie under the female gametophyte;
- at this stage, the female gametophyte can be cut open to expose four young embryos competing for dominance.

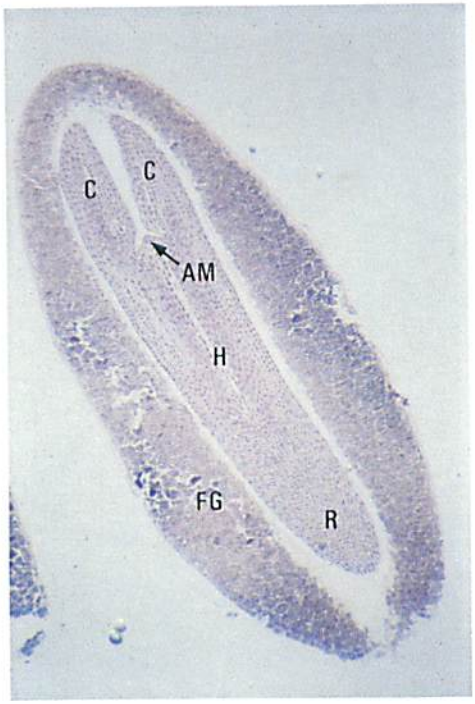
Seed-cone Development Year III



Early August

- full-sized, nearly mature cones from several trees; lengths vary from 3.8 to 6.3 cm and represent a variety of genetic potentials;
- cone scales are sealed shut and woody, and cannot be cut open with a knife;
- the embryos within are at or near full size and can be easily removed from the immature seeds;
- for seed collection purposes, select large, straight cones, which are likely to have larger seeds than short or curved cones.

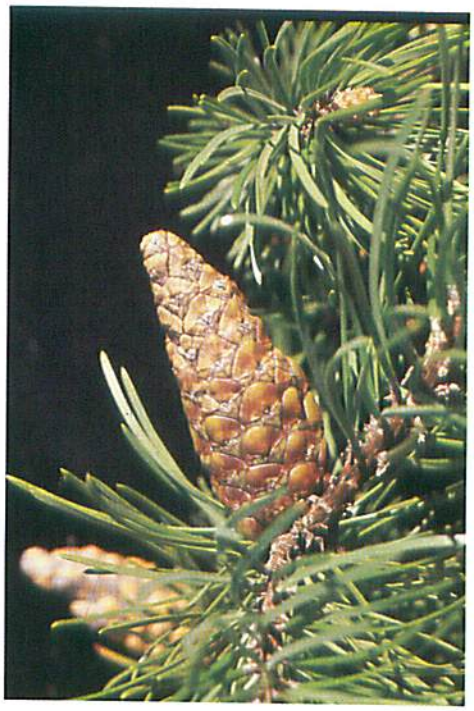
Seed-cone Development Year III



Early August

- longitudinal section of a fixed female gametophyte (FG), showing the embryo;
- the embryo consists of several cotyledons (C) and a hypocotyl (H) with an apical meristem (AM), which will become the shoot; the other end of the hypocotyl (R) will become the root, with its apical meristem protected by the root cap;
- the root initial is nearest the opening in the seed coat (micropyle) and will be the first structure to emerge when the seed germinates.

Seed-cone Development Year III



September

- branch with one brown, woody, mature cone; the change from a green color began by mid-August;
- typically, cones remain closed on the tree for many years (serotinous) and contain at least some viable seeds;
- it is best to collect the most recently matured cones, not those that have become a weathered grey in color (Anon. 1986).

Seed-cone Development Year III

Forestry Canada

October

- (*top*) two mature cones opened by heat; seeds are present in the cone on the left, but have been shaken from the cone on the right;
- (*bottom*) cone scales from a mature cone; those on the left bear seeds with wings attached; the impression of seed wings is visible on the scales to the right;
- typically, seeds in the middle of the cone are larger than those at the top, and scales at the base do not have any seeds;
- jack pine has the smallest seeds of the eastern pines (only 3 to 4 mm long).

Glossary

archegonium - an egg-producing structure of the female gametophyte.

axil - the upper angle between a bud scale and the stem from which it grows.

cataphyll - a bud scale

cleavage polyembryony - the formation of as many as four embryos from a single zygote by separation of the products of cell division; these embryos then compete for dominance, and only one will survive (embryo selection).

embryo selection - see cleavage polyembryony

fertilization - fusion of haploid gametes (sperm and egg) to produce a diploid zygote.

gametophyte - a haploid plant that produces sex cells (gametes). In pines there are two gametophytes; the male (pollen) produces two sperm cells and the female produces one or more archegonia, each with an egg cell.

megasporangium - see nucellus

megaspore mother cell - a single cell in the centre of the ovule that undergoes meiosis to produce four cells, only one of which survives (megaspore) to become the haploid female gametophyte.

meiosis - two successive nuclear divisions in which the diploid chromosome number is halved to produce a haploid.

meristem - a region in a plant where new cells are produced (e.g., at the apex of every terminal bud or branch bud).

micropyle - a passageway in the protective covering (integument) of the ovule that will become the seed coat (testa).

nucellus - tissue in which the megaspore is produced and undergoes further development; also called the megasporangium.

ovule - the structure in the female cone that becomes the seed; technically, a megasporangium covered by an integument.

pollination - the transfer of pollen (by wind, in the case of pines) from the pollen sacs to the ovules.

polycyclic - refers to a terminal overwintering bud with more than one tier of lateral branch and/or seed-cone buds.

primordium (plur. primordia) - precursor of an organ.

proembryo - an organized group of up to 16 cells produced by division of the zygote before organization of the organs of the embryo.

sterile cataphyll - a bud scale (cataphyll) with no axillary bud.

zygote - the diploid cell resulting from fusion of two haploid gametes.

Popular and Technical Terms

Popular term	Technical equivalent
bud scale	cataphyll
cone	strobilus (see pollen cone and seed cone)
conelet	year II megastrobilus
egg	female gamete
endosperm	female gametophyte
flower	receptive megastrobilus
growing tip	apical meristem
pollen cone	microstrobilus
pollen-cone scale	microsporophyll
pollen grain	male gametophyte
pollen sac	microsporangium
seed	matured ovule
seed coat	testa
seed cone	megastrobilus

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