

The Reproductive Cycle of Douglas-Fir

John N. Owens

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Preface

A book by George S. Allen and John N. Owens entitled 'The Life History of Douglas-fir' was published in 1972 by the Canadian Forestry Service, Pacific Forest Research Centre. It gives a comprehensive account of the reproductive cycle of Douglas-fir, from initiation of seed- and pollen-cone buds to shedding of the mature seed.

The book was well received. One frequently expressed response from readers was that a brief and less technical account of the reproductive cycle would be useful and should be made available to students of forestry and

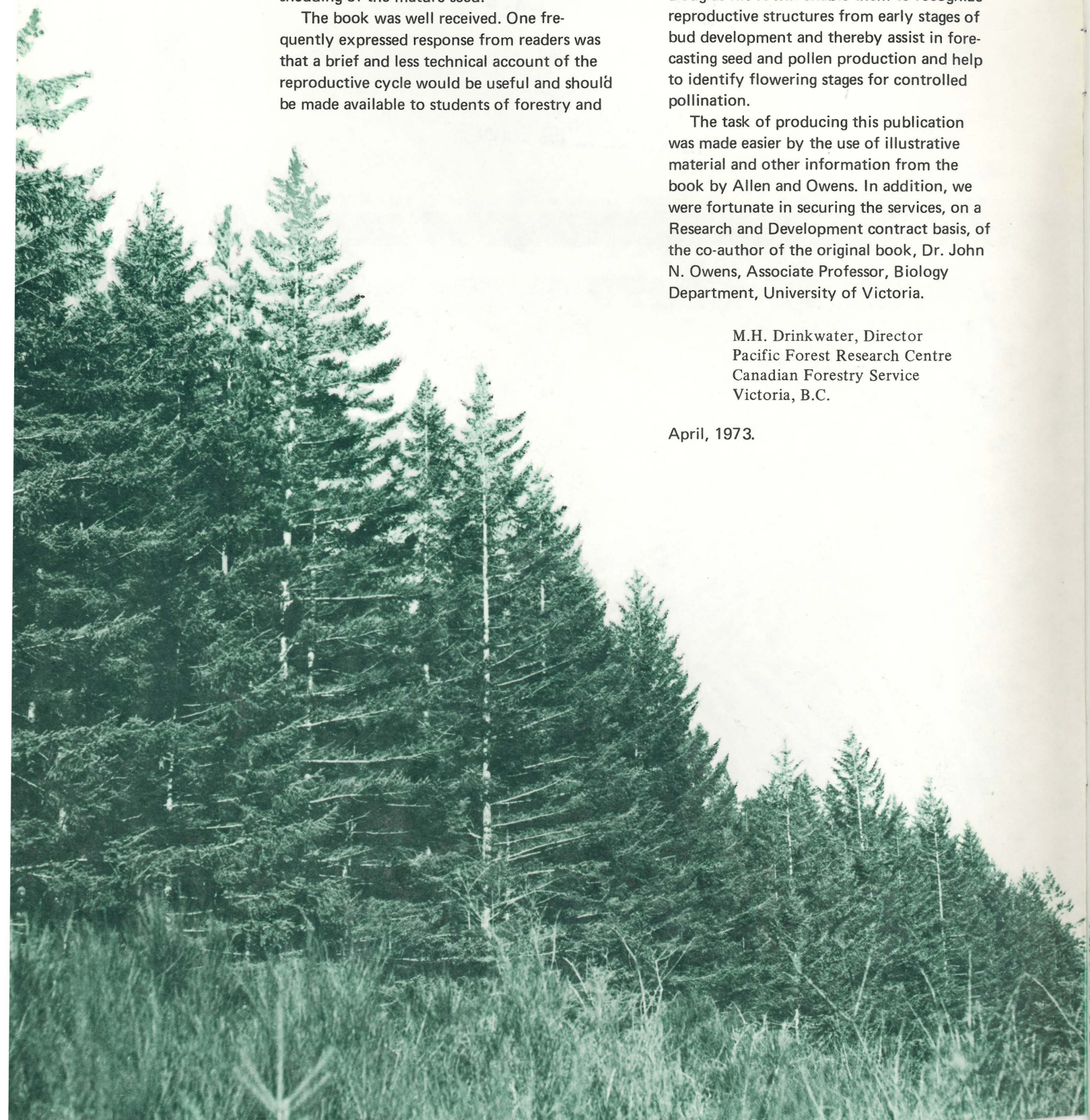
biology, at universities, technical schools and high schools. This book is the result of these suggestions.

Apart from its usefulness in education, the book was prepared so that it would be of practical value to foresters concerned with seed production and tree improvement of Douglas-fir. It will enable them to recognize reproductive structures from early stages of bud development and thereby assist in forecasting seed and pollen production and help to identify flowering stages for controlled pollination.

The task of producing this publication was made easier by the use of illustrative material and other information from the book by Allen and Owens. In addition, we were fortunate in securing the services, on a Research and Development contract basis, of the co-author of the original book, Dr. John N. Owens, Associate Professor, Biology Department, University of Victoria.

M.H. Drinkwater, Director
Pacific Forest Research Centre
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Victoria, B.C.

April, 1973.



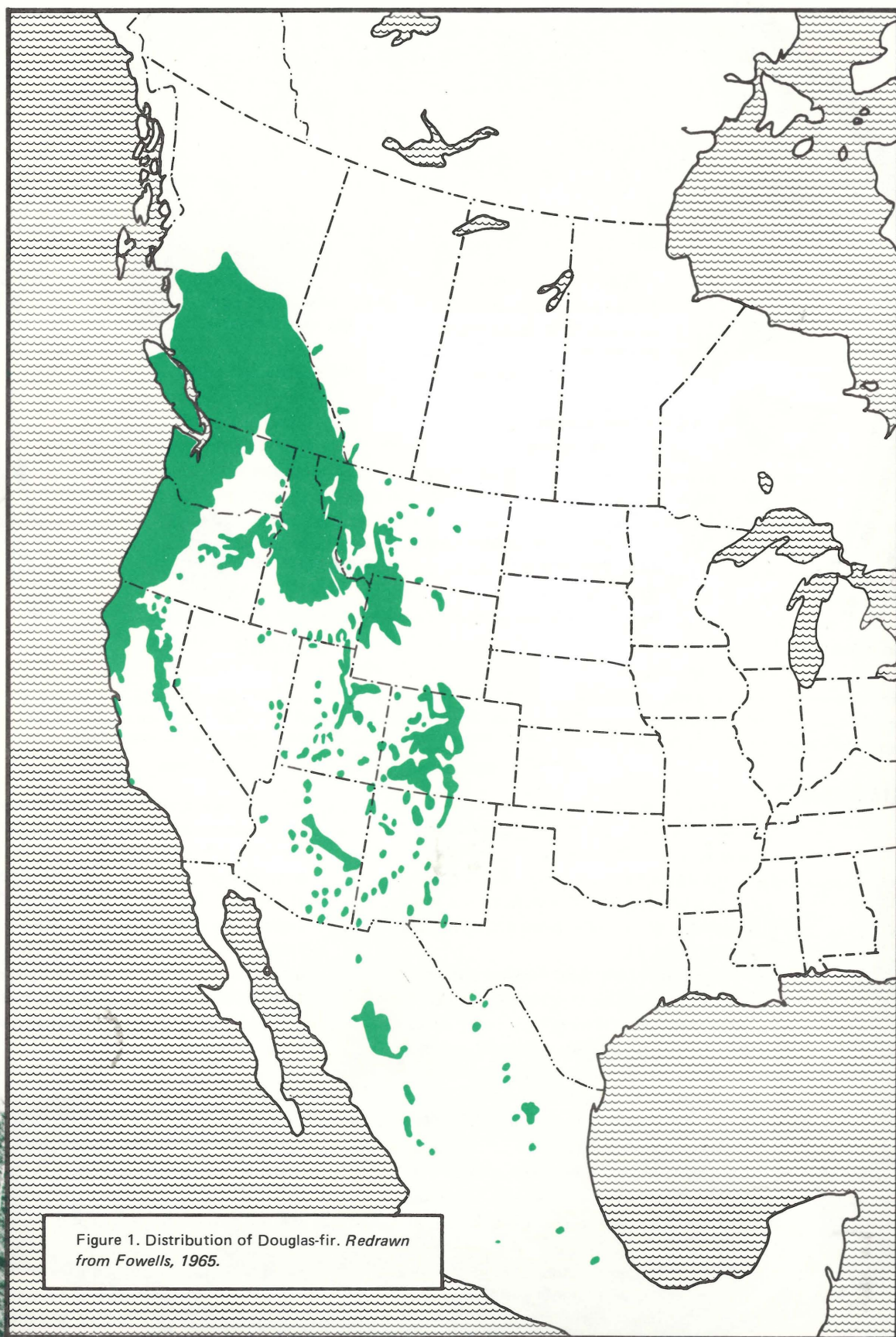


Figure 1. Distribution of Douglas-fir. Redrawn from Fowells, 1965.

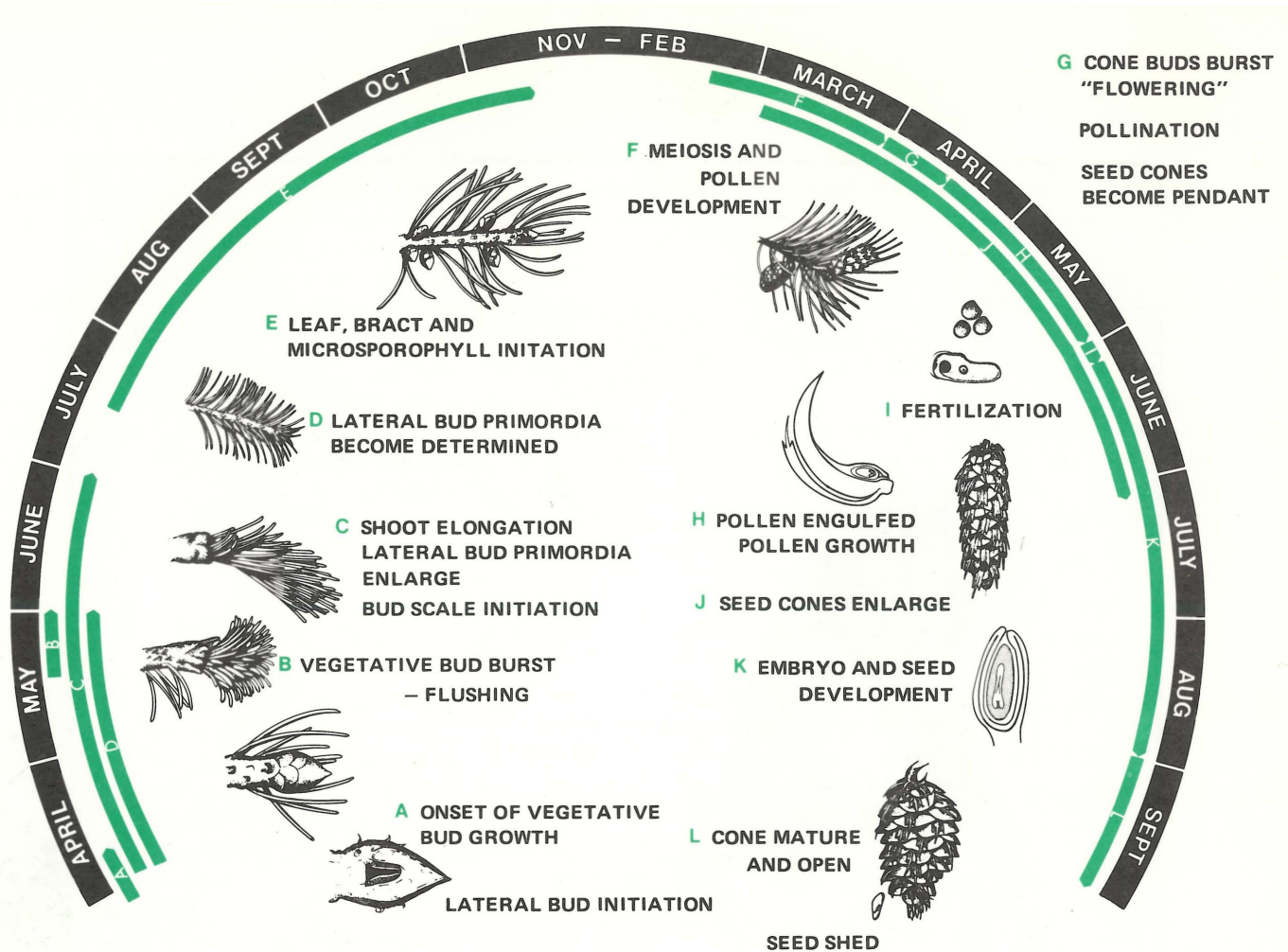


Figure 2. The entire reproductive cycle of Douglas-fir extends over 17 months. Letters A - L represent various stages and a brief description of these stages. The approximate time each stage occupies in the reproductive cycle is represented by the colored arrow. Redrawn from Allen and Owens 1972.

Introduction

Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, is a member of the Pinaceae, the largest family of conifers. Six species of *Pseudotsuga* are recognized: four are native to various regions of China, Formosa and Japan and the other two are native to Western North America.

Douglas-fir, the most familiar and important of these species, consists of two varieties. A coastal form grows on the islands and mainland of the Pacific coast and an interior form is distributed throughout the Rocky Mountain area. The vast north-south range of Douglas-fir extends over 3,000 miles from the southern half of British Columbia, throughout most of the Pacific Northwest and southward along the Rocky Mountains well into Mexico at higher elevations (Fig. 1).

The wide distribution of Douglas-fir and its desirability as a lumber species make it the most extensively harvested forest tree in the Pacific Northwest. Consequently, continuous

reforestation is necessary, but because of the cyclic cone production, seed is not always available for reforestation. In Douglas-fir, a good or heavy cone crop generally occurs about every 5 years but varies from 2 to 7 years at lower elevations and occurs even less frequently at higher elevations. Thus, there is a need for a method of predicting cone crops as far in advance as possible and, even more, a need for eventually controlling cone production.

To understand the problems involved in Douglas-fir reproduction, the phenology or time sequence of the entire reproductive cycle must be thoroughly understood. The phenology will vary as a result of normal variation between individual trees and geographical distribution of the species. However, the sequence of development remains the same and a general description can be given for Douglas-fir growing at the lower elevations of Coastal British Columbia and the Pacific Northwest (Fig. 2).

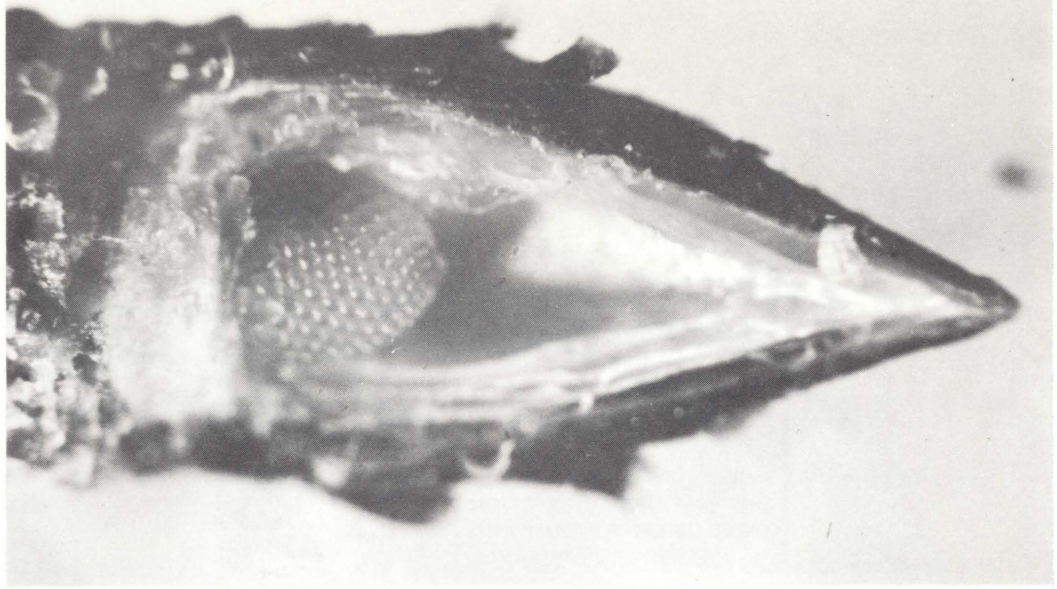


Figure 3. Dissected dormant vegetative bud. X 12. *From Allen and Owens 1972.*

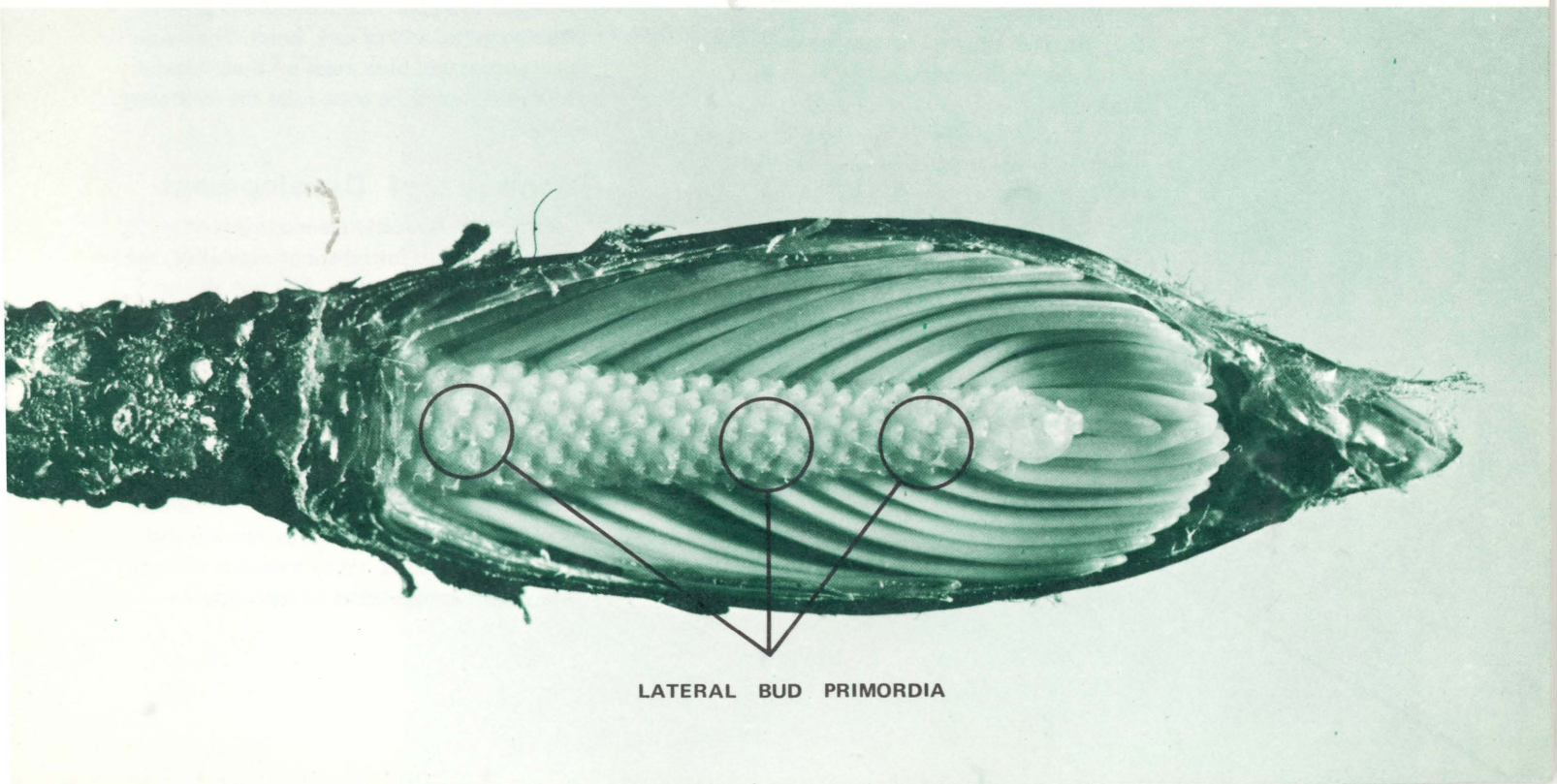
Bud Initiation and Development

Since potential cone buds are initiated within the vegetative bud, the development of the vegetative bud must be examined. Seasonal growth is commonly thought to begin when the vegetative buds burst (flush) about mid-May. However, growth of the telescoped embryonic vegetative shoot usually begins by late March, while it is still enclosed by the brown bud scales (Fig. 3). It is this expanding shoot that pushes the bud scales apart, resulting in flushing and the formation of the new shoot (Fig. 2A - D).

One of the first and most important events to occur inside the vegetative bud when

growth begins in spring is the initiation of lateral buds (Fig. 4). Several bud primordia (rudiments) arise, each from a few dividing cells, about the first of April. The primordia are initiated in the axils of some of the leaf primordia, the axil being the juncture of the leaf primordium and the shoot axis. Considerable lateral bud enlargement and bud-scale initiation and development occur before the vegetative bud, in which they are formed, bursts. These newly formed primordia become the lateral buds which will enlarge and burst the following spring to produce branches or cones.

Figure 4. Dissected vegetative bud collected just before vegetative bud burst (mid-May) showing new lateral bud primordia. X 9.



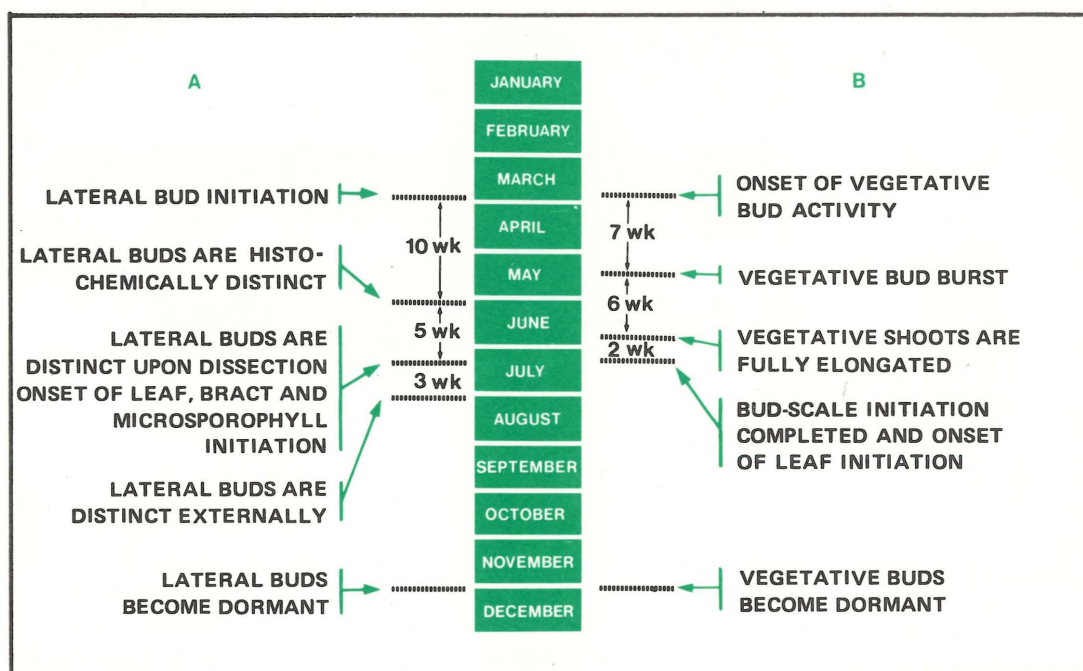


Figure 5. A diagrammatic representation of the growth periodicity in Douglas-fir. Sequence A represents initiation and early development of lateral buds. Sequence B represents vegetative shoot activity. *Redrawn from Allen and Owens 1972.*

Bud Types

The types of buds into which the primordia will develop cannot be distinguished during the first 10 weeks following their initiation. Potentially, they can develop into vegetative buds, seed- or pollen-cone buds. At the time of vegetative bud burst in mid-May, each lateral bud primordium consists only of a tiny mound of rapidly dividing (meristematic) cells termed an apex (or growing tip) (Fig. 4). This apex is enclosed in several bud scales; the outer ones soon begin to turn brown and form the characteristic leathery bud scales so familiar in mature buds. Subsequent enlargement and development of lateral buds occurs while the shoot on which they are borne elongates. This elongation usually ends by late June (Fig. 2B - D).

The type of bud that develops from each primordium can be predicted, based on the position of that primordium along the shoot. The proximal primordia, those closest to the base of the shoot, tend to become pollen cones, while the more-distal primordia become either seed-cone or vegetative buds. At the end of the first 10 weeks of development (Fig. 5), differences can be detected between apices of different bud types by using histochemical staining techniques. By early July,

15 weeks after initiation, all bud types begin to show structural differences by forming their characteristic leaf-like organs. Vegetative lateral buds initiate leaf primordia, while pollen-cone buds initiate microsporophylls, leaf-like structures, that produce the pollen sacs and pollen. Seed-cone buds initiate bract primordia which develop into the trident-like bracts characteristic of Douglas-fir seed cones. Later, during September through November, one ovuliferous scale is initiated in the axil of each bract. The ovuliferous scales will bear seeds on their adaxial surfaces (toward the cone axis) the following season.

Pathways of Development

Studies of the early development of lateral primordia into distinct vegetative, seed- or pollen-cone buds show that not all bud primordia develop to the same extent or at the same rate. Some begin to lag behind within a few weeks after initiation and cease development. These soon degenerate and, in the mature shoots, leave no evidence of their previous existence. They are referred to as aborted buds. Other primordia form most of their bud scales, then cease to develop and become latent buds. These have not become determined as vegetative or reproductive

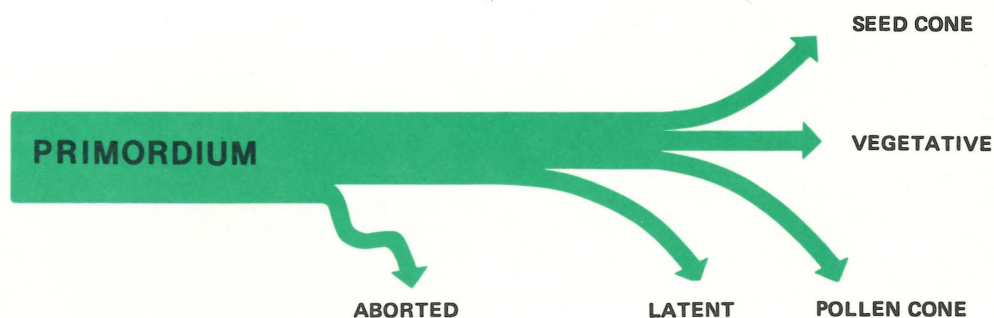


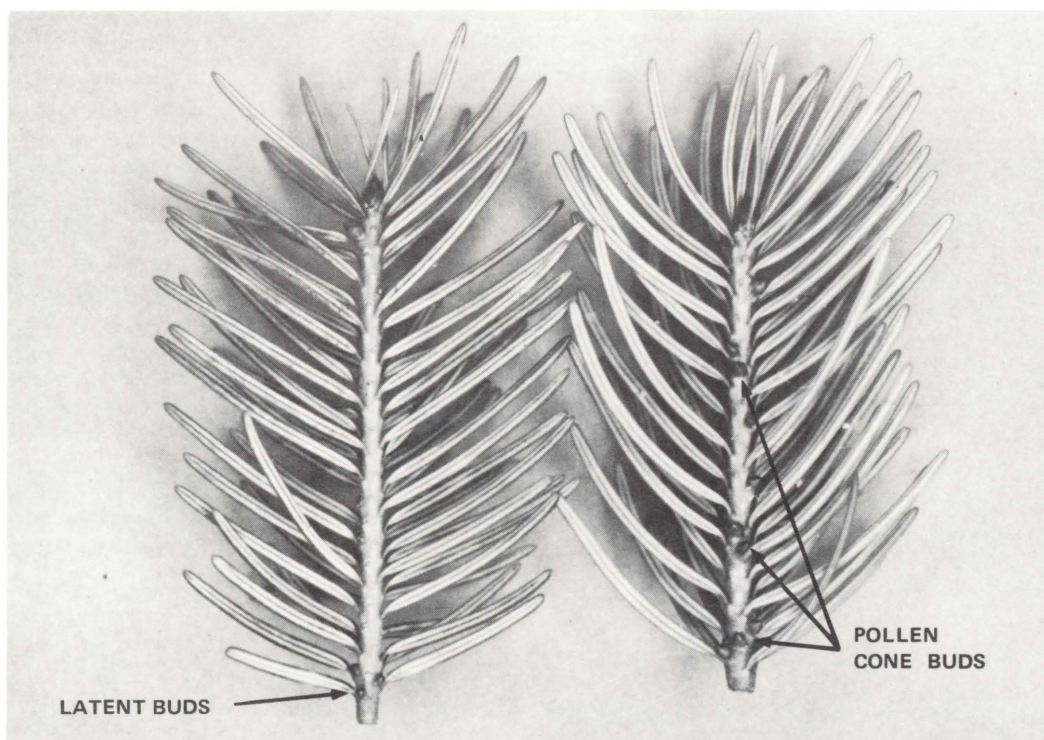
Figure 6. Alternate pathways of lateral bud primordial development. *Redrawn from Allen and Owens 1972.*

buds when their growth stops, and they consist only of a small apex surrounded by numerous bud scales but with no additional foliar primordia. Latent buds can be stimulated to develop by the removal of the terminal vegetative bud on the twig. If this is done, they usually develop into vegetative buds. Bud primordia, which abort or become latent, are commonly the most proximal primordia on the shoot, while those more distal (toward the tip of the shoot) are more likely to develop fully. Thus the development of lateral bud primordia may follow any one of five pathways: (1) abort early and disappear completely within a few weeks of initiation; (2) partially develop and then become undetermined latent buds; (3) develop into vegetative buds; (4) develop into seed-cone buds, or (5) develop into pollen-cone buds (Fig. 6).

Initiation vs. Development

It was believed for many years that the number of cones produced in Douglas-fir and many other conifers was determined by the number of cones initiated, and that if cone production was to be increased, the number of cone primordia that are initiated would have to be increased. This has been shown to be incorrect, at least for Douglas-fir, by comparing the number of lateral bud primordia that were initiated and the number of mature buds that finally developed in successive years. The total number of lateral bud primordia initiated on the shoot of a tree varies little from year to year but the proportion of these primordia that develop along the various pathways does vary. The variation in cone production can be explained by the high pro-

Figure 7. New shoots collected early in July from a tree in which no cones are developing (left) and a tree in which many cones are developing (right). X 1.



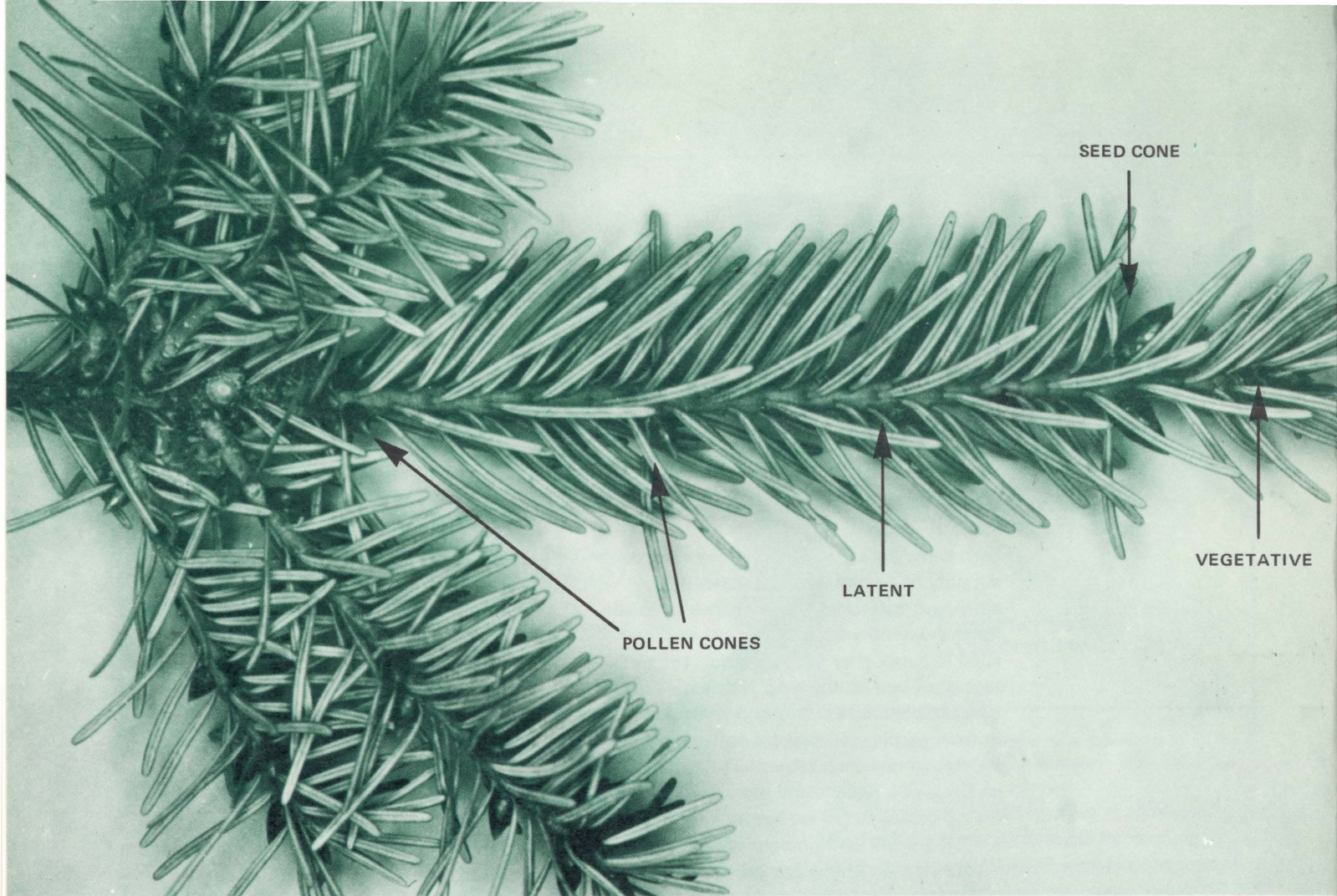


Figure 8. Branch collected in the fall showing position and appearance of bud types. X 1. *From Allen and Owens 1972.*

portion of buds that cease development and abort or become latent in a year that is poor for cone development. Those primordia most likely not to develop are found at the basal region of the shoot, and are those that would otherwise have developed into pollen-cone buds. Although both aborted and latent primordia do occur along the entire length of the shoot in a year when few cone buds develop, they occur infrequently in distal regions where many vegetative buds will develop. Thus it appears that distal undetermined lateral primordia develop as seed cones only under favorable conditions. With unfavorable conditions, a few abort or become latent, but most develop into vegetative buds.

Forecasting Cone Crops

This information not only helps account for the tremendous variation in cone production that can occur on a given tree

from year to year, but it also provides a means of early forecasting of the cone crop. Early forecasting is based on relative numbers of seed-cone and pollen-cone bud primordia. The number of developing lateral bud primordia in the potentially pollen-cone position along the shoot in May (Fig. 4) is a good indication of the number of seed-cone buds that will develop (Figs. 7, 8). This finding is extremely important in planning cone collections, since it allows an additional summer, the year before seed release, to prepare for cone collection and seed extraction if, potentially, there will be a good cone crop for the following year; or, just as important, to realize 16 months ahead of seed release that there will be no cone crop. It should be emphasized that this method can accurately forecast the lack of a cone crop, though not necessarily an abundant crop, because insects, frosts, poor pollination or cone abortion can seriously reduce a potential cone crop between August, when seed cones are easily recognized

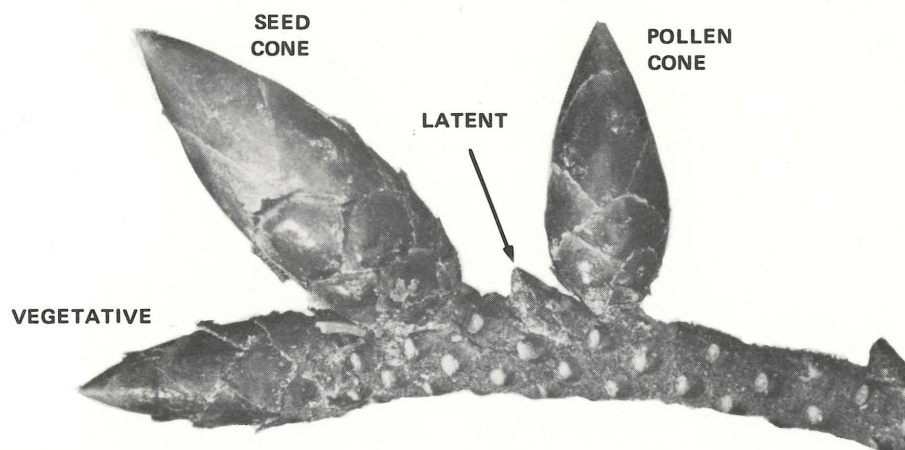


Figure 9. Twig collected in the fall with leaves removed showing vegetative terminal, seed-cone, latent and pollen-cone buds. X 6.

(Figs. 8, 9), and one year later, when the seeds are shed.

The cone crop can frequently be increased by applying nitrate fertilizer to the tree just before vegetative bud burst and during vegetative shoot elongation. This apparently helps prevent bud primordia from aborting or becoming latent during the critical early period of development. Dry, sunny weather at this time also increases the proportion of cone buds that develop.

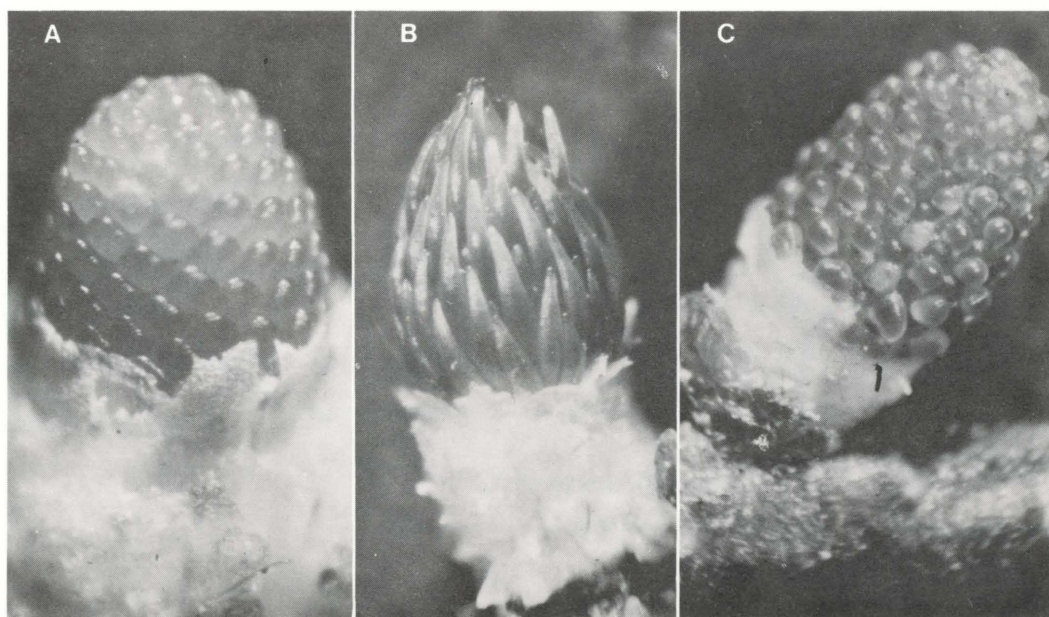
Identification of Buds

Buds are completely formed by October or November and become dormant by December (Figs. 8, 9). If bud scales are carefully removed from the buds anytime after early August, the three bud types can be distinguished (Fig. 10), and by fall the buds are externally distinct (Figs. 8, 9). This is made easier by the more-distal location of vegetative and seed-cone buds, whereas pollen-cone buds

may be found along the entire length of the shoot but are usually more abundant on the proximal portion. Pollen-cone buds are equal in size or somewhat smaller, more globose, lighter brown, and have fewer bud scales and less white resin on the surface of their bud scales than do vegetative buds. Seed-cone buds are longer (about 1 cm long) and broader than either pollen-cone or vegetative buds, but appear much the same as pollen-cone buds in shape and color (Figs. 8, 9).

Dormancy is usually considered to be a period of reduced metabolic activity, but is frequently used with reference to any bud not undergoing visible external changes. As a result, Douglas-fir buds are frequently referred to as "dormant" during late summer and early fall because they appear from the outside to be completely developed (Figs. 8, 9). Actually, cell division and growth continue within the buds until late fall, long after they first appear to be dormant. Metabolic acti-

Figure 10. Dissected dormant (A) vegetative, (B) seed-cone and (C) pollen-cone buds. X 20. *From Allen and Owens 1972.*



Pollen - Cone Development

vity continues within the buds throughout the winter but is considerably reduced. Differences exist between bud types in that

reproductive buds (seed and pollen cones) are more active during winter months than are vegetative buds.

Pollen-cone buds begin growth and further development late in February, 11 months after initiation and 4 to 6 weeks before pollination and the onset of growth in vegetative buds. Growth is not visible externally during the first few weeks, but by mid-March the cones within the bud scales have enlarged enough to cause buds to swell, indicating that pollination will soon occur.

Pollen develops within the pollen cones during the latter half of February and all of March (Fig. 11). Each pollen sac (microsporangium) is filled with many pollen mother cells, each of which, late in February, undergoes meiosis - a special form of cell division that produces four microspores, each with half the original number of chromosomes (haploid). During March, each microspore thus produced divides unequally twice, each time producing a small lens-shaped prothallial cell. The microspore divides unequally again, producing a small generative cell and a large tube cell. The generative cell soon divides, producing a stalk cell and body cell, thus forming the mature 5-celled pollen grain. Shedding of the pollen (pollination) may occur at either the 4- or 5-celled stage (Figs. 11, 13). The body cell divides several weeks

after pollination and just before fertilization, producing two male gametes. During pollen development, the wall of the pollen grain thickens and the pollen grain becomes spheroid but normally has a slight indentation on one side. Mature, dry Douglas-fir pollen is very smooth and, unlike the pollen of many other conifers, lacks wings (Fig. 12).

By the end of March the pollen is mature and the pollen cone has enlarged enough to push the bud scales apart. Elongation of the cone axis causes the cone to bend downward and causes separation of the many pollen sacs, which when dry, split open and release the pollen. To obtain quantities of good pollen, pollen cones should be collected after the pollen cone has pushed the bud scales apart but just before the pollen sacs split open. The pollen cones hang down during pollination, dry out, and most fall from the tree with the first strong wind (Fig. 14). As a result of the large size and absence of wings, only a small portion of Douglas-fir pollen is dispersed further than 5 - 10 times the tree height. However, in years of heavy pollen-cone production and where there are reasonably strong winds, some pollen may be carried for several miles.

Figure 11. Pollen development in Douglas-fir. The body cell divides forming the two male gametes. Haploid tissue is shown in color. *Redrawn from Allen and Owens 1972.*

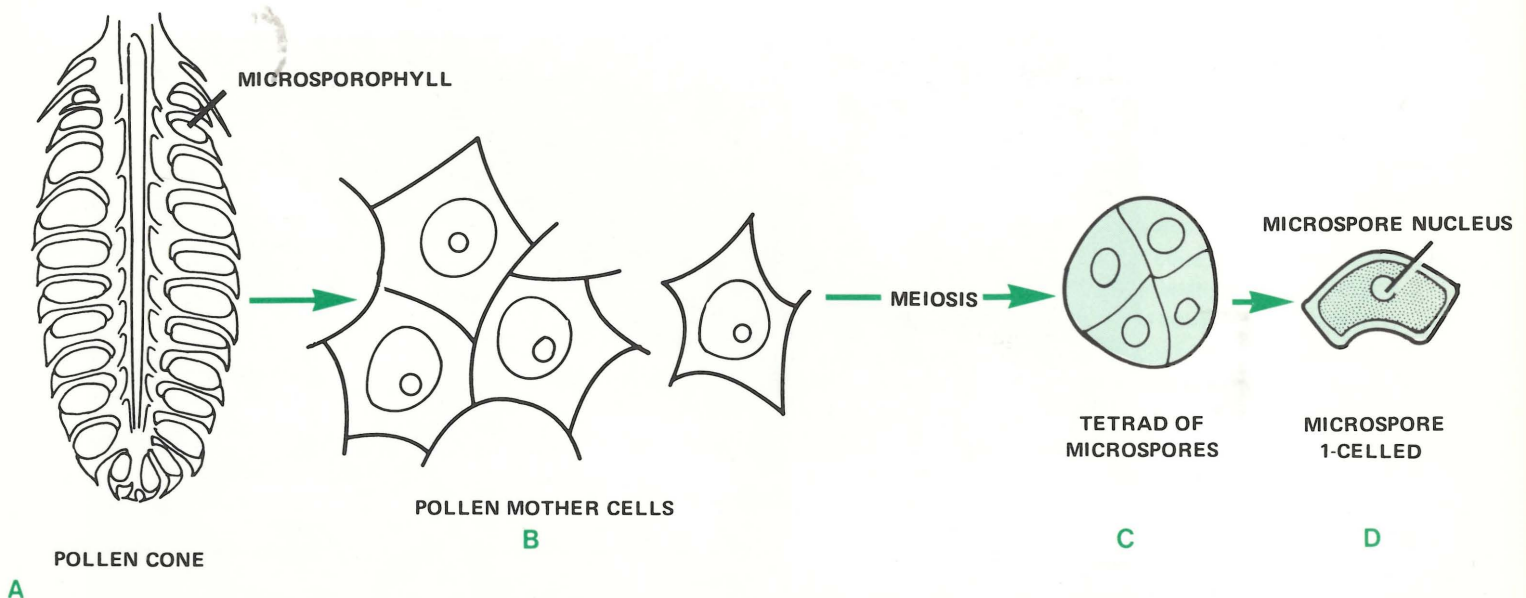
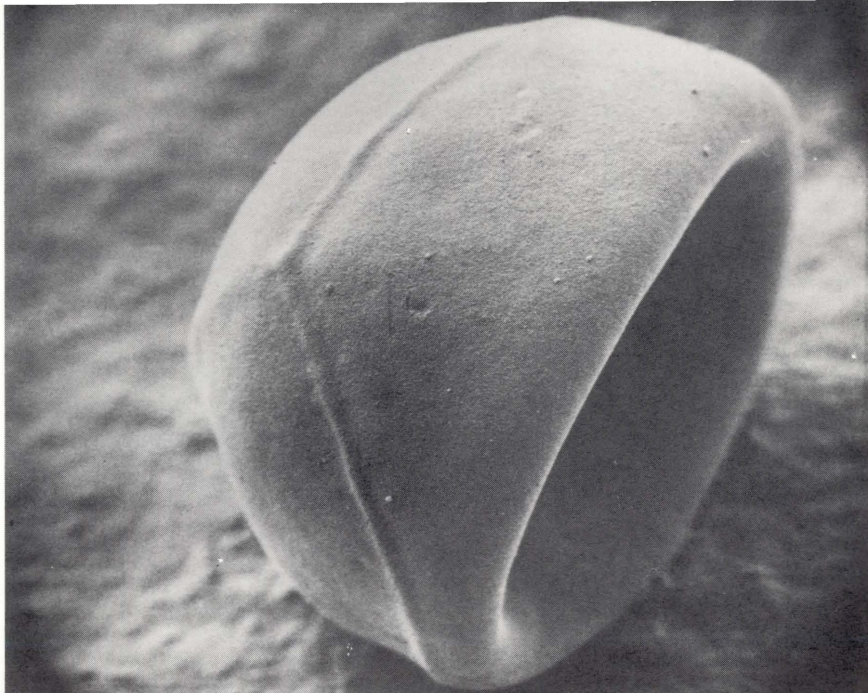


Figure 12. Scanning electron micrograph of Douglas-fir pollen, X 1000. *From Allen and Owens 1972.*



EXINE
INTINE
TUBE NUCLEUS
BODY CELL
STALK CELL
PROTHALLIAL CELLS

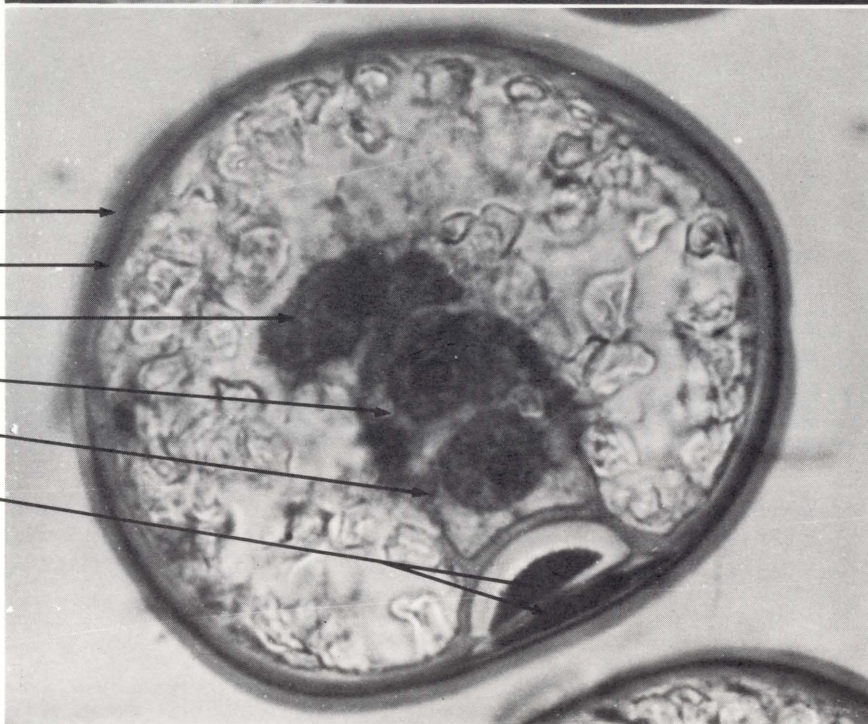


Figure 13. Section of a mature 5 - celled pollen grain. X 1100. *From Allen and Owens 1972.*

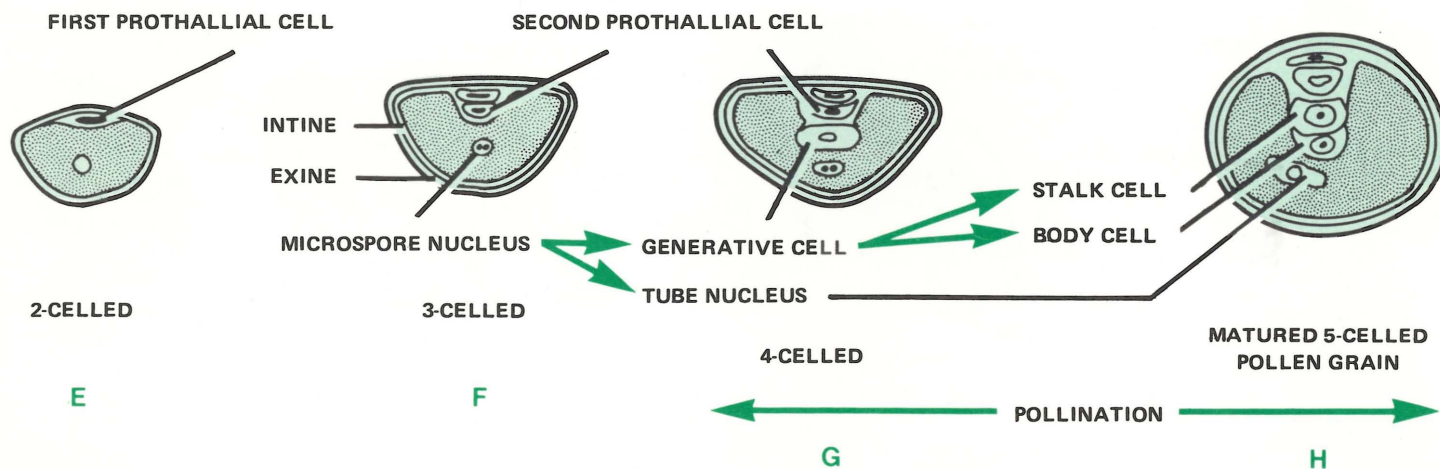
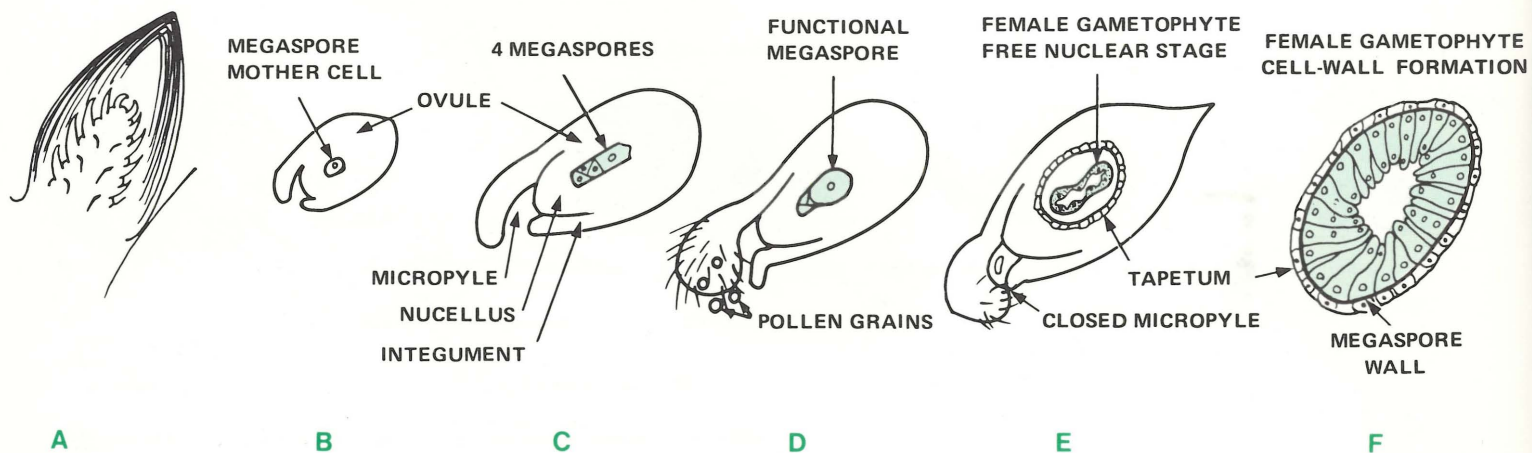




Figure 14. Twig showing pollen and receptive seed cones at pollination. X 2.5

Figure 15. Ovule and female gametophyte development following dormancy. A. represents the dormant seed-cone bud while B - E show a section of the developing ovule. F - H. show only the female gametophyte while I. shows the mature female gametophyte within the ovule. Haploid tissue is shown in color. Redrawn from Allen and Owens 1972.



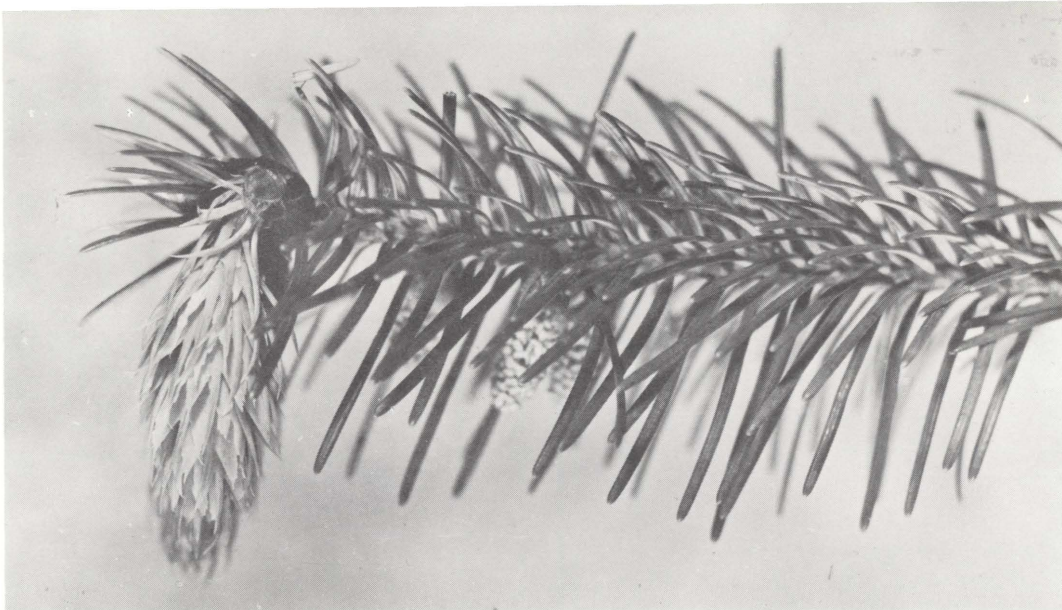


Figure 16. Seed cone after pollination is complete and the cone has bent down. X 1.5.

Seed - Cone Development

Seed-cone buds, like pollen-cone buds, begin growth late in February. Seed cones enlarge within the bud scales and gradually push the bud scales apart, exposing the light brown, inner bud scales at the tip of the bud. The cone axis at the base of the seed-cone bud bends upward so that the bud is nearly upright before the cone pushes through the bud scales. When the seed-cone buds burst, the bracts at first are pressed closely together but they soon bend outward, causing the cone to become fully open and ready for pollination. The seed cone at pollination is upright and about 3 cm long (Fig. 14), but after pollination the cone bends down (Fig. 16).

From mid-February until early June, the seed cone enlarges and the two ovules found on the adaxial surface (the surface facing the

cone axis) of each ovuliferous scale undergo considerable enlargement and development (Fig. 15). Each ovule consists of an integument (ovule wall) enclosing a megasporangium (nucellus). Within each megasporangium, a single, large megaspore mother cell undergoes meiosis early in March, producing four haploid megaspores, each with only one half of the original 26 chromosomes. Three of the megaspores degenerate while the fourth undergoes a sequence of divisions, forming a many-celled haploid female gametophyte. The female gametophyte is enclosed within the nucellus and ovule wall. It contains stored food and produces 4 to 7 archegonia, each containing one egg cell. The female gametophyte consists only of a few cells at pollination but is fully developed at the time of fertilization. (Fig. 15).

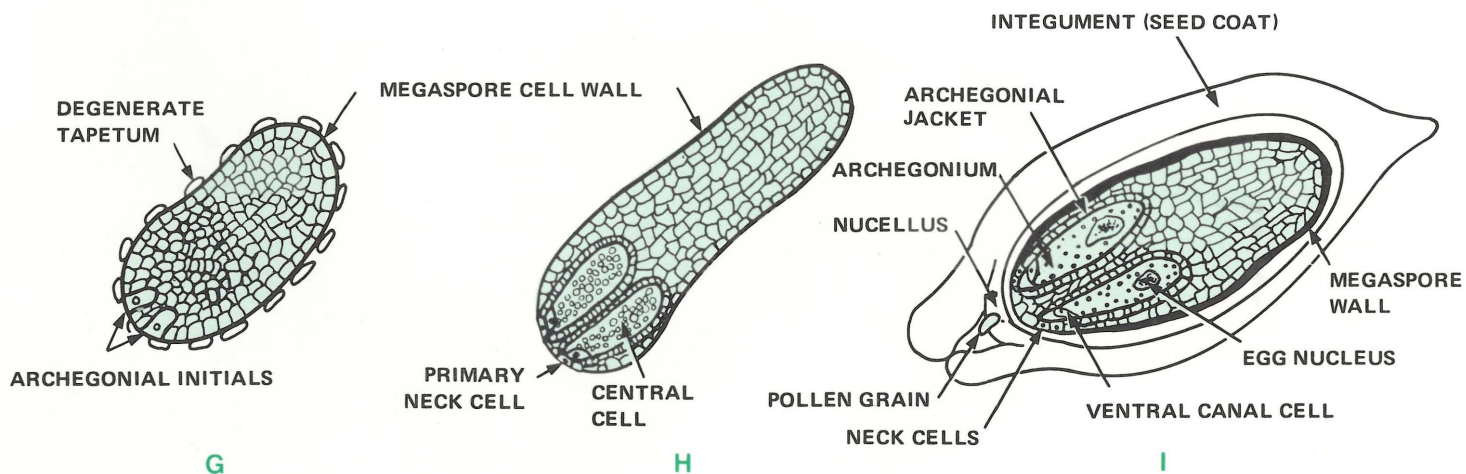


Figure 17. Seed cone during pollination, dissected to reveal the ovuliferous scales and ovules. X 9.

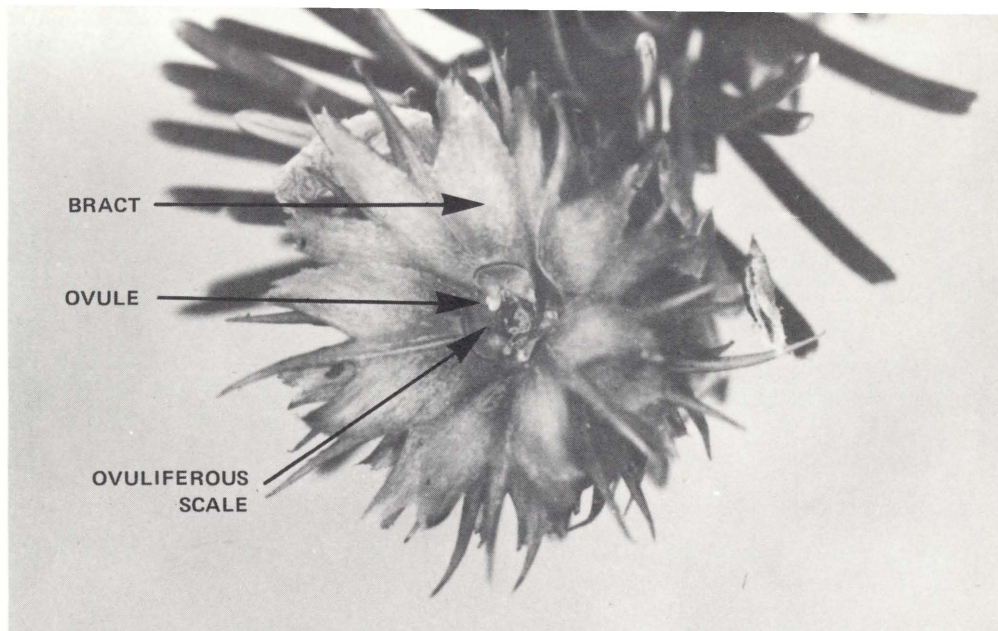
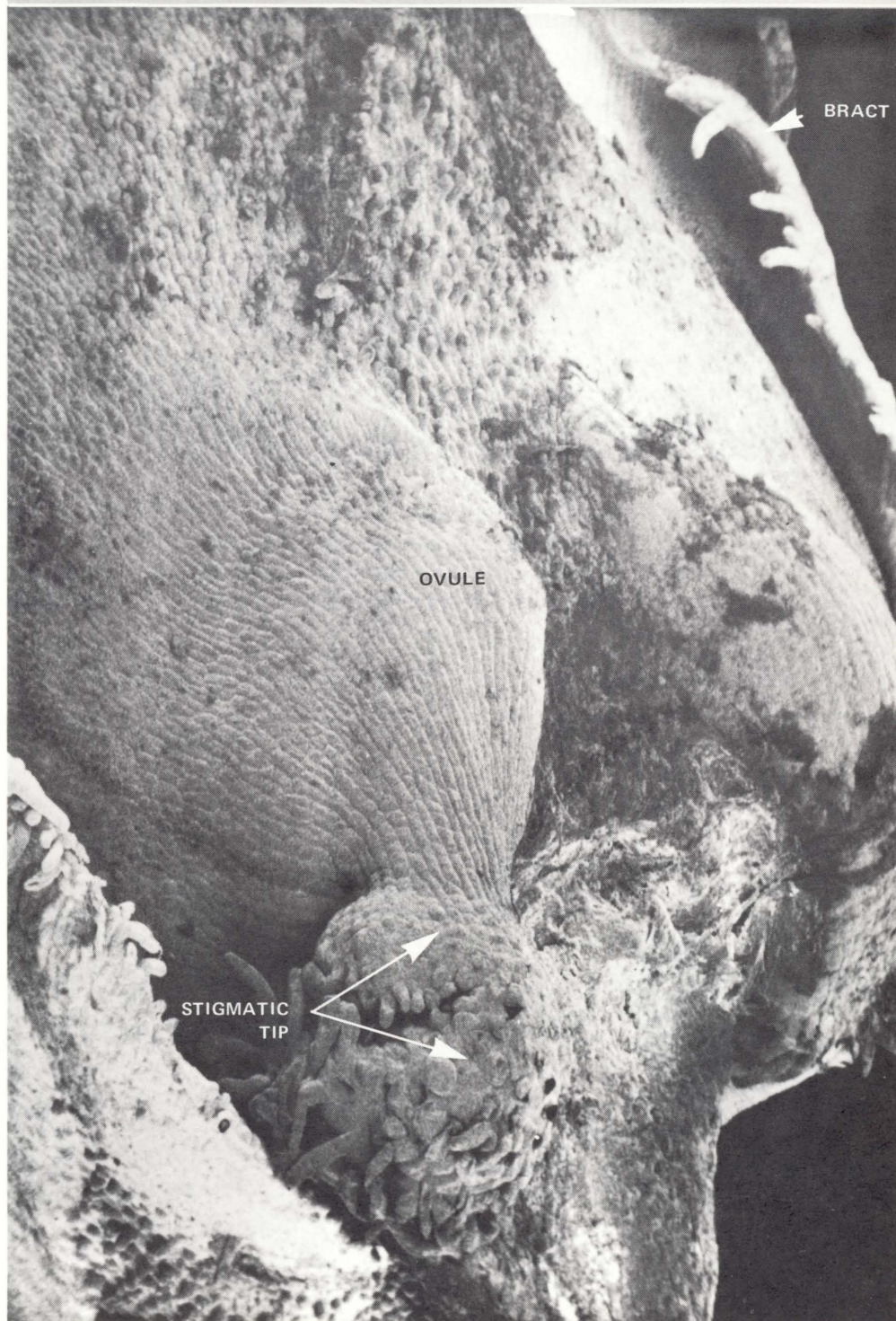


Figure 18. Scanning electron micrograph of the ovuliferous scale during pollination showing the developing ovule and rounded stigmatic tip bearing stigmatic hairs. X 100. From Allen and Owens 1972.



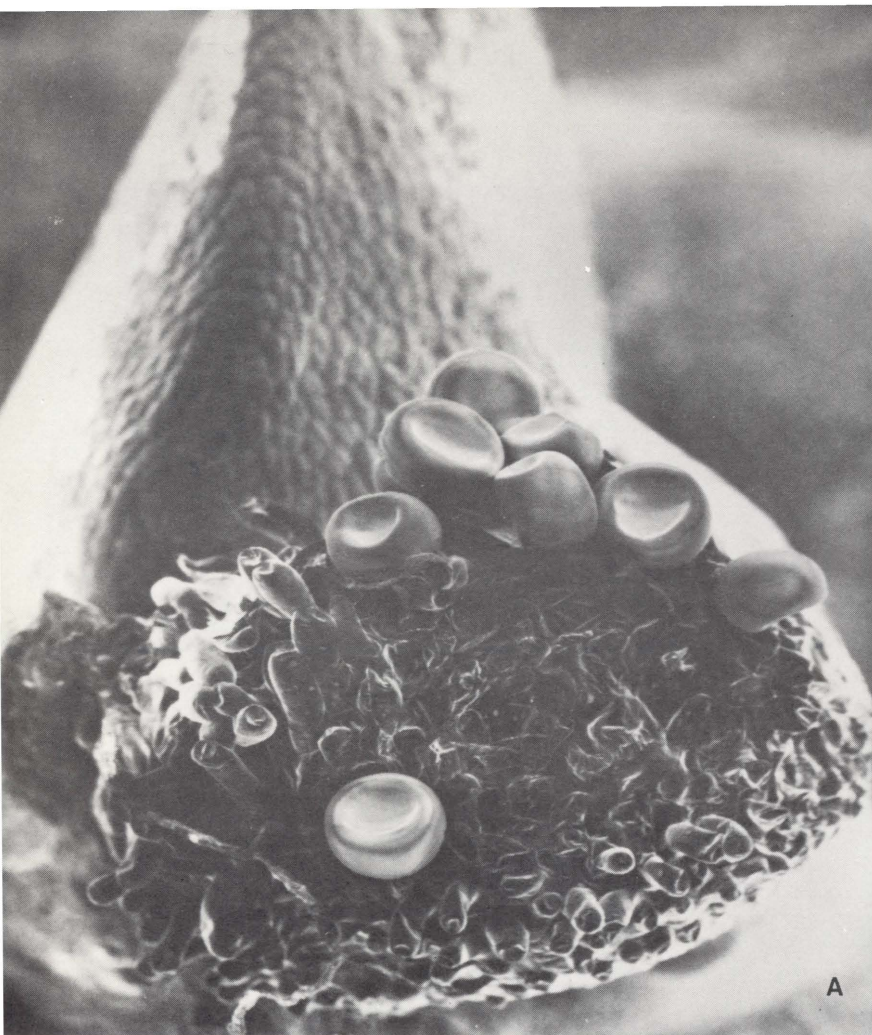


Figure 19. Scanning electron micrographs of: (A) the stigmatic tip with many pollen grains; and, (B) the stigmatic tip engulfing the pollen grains. X 150. *From Allen and Owens 1972.*

Pollination and Fertilization

Pollination and fertilization are distinct but related events that are separated, in conifers, by a considerable amount of time. Pollination is the transfer of pollen from the pollen cone to the seed cone. Unlike flowering plants, it is dispersed in conifers only by wind. Fertilization is the fusion of a male gamete, derived from the pollen grain, with the egg of the ovule.

At the time of pollination, the broad bracts of the seed cone are bent back and remain in this open, receptive condition for about one week (Fig. 14). During pollination, the ovuliferous scales are small and not visible unless the bracts are removed (Fig. 17). If this is done, it can be seen that the development and arrangement of the two structures make them well adapted to effectively capture the available pollen. Bracts narrow toward their base and the margins curve slightly upward to form a funnel-like structure where bract and ovuliferous scale join (Fig. 18). Just above this juncture is the stigmatic tip which is the

elongated neck of the ovule through which the pollen must pass. The stigmatic tip extends beyond the margin of the bract and fills the space between the bract and the ovuliferous scale (Fig. 18). As a result, pollen landing on the bract of the upright cone readily passes down the smooth upper surface of the bract to the base where many pollen grains usually land on the sticky, hairy surface of the stigmatic tip (Fig. 19A). The stigmatic tip consists of two lips which form a slit-like opening (micropyle) that is too narrow for the pollen to pass through. Instead, a different process occurs.

As pollination comes to an end, the two lips of the stigmatic tip grow inward, appearing much like a sea anemone, usually bringing several pollen grains into the micropyle (Fig. 19B). The pollen, once engulfed, is contained within a closed cylindrical chamber (the micropylar canal) and remains attached to the sticky stigmatic hairs.

Within a week or two the pollen grains germinate. They swell and the thick outer

Figure 20. A section through a portion of the ovule tip late in May showing elongated pollen. X 60. *From Allen and Owens 1972.*

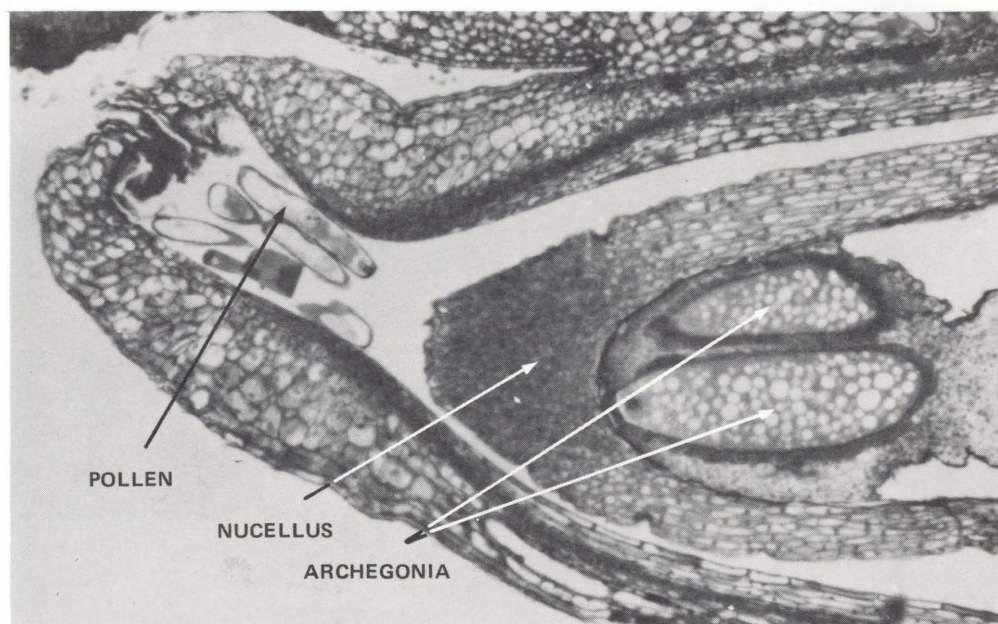


Figure 21. A dissected ovule tip at fertilization early in June showing several pollen grains with pollen tubes penetrating the nucellus. See outlined area in Figure 22. X 250.



wall (exine) splits. Unlike most other conifers, the pollen grains do not form a narrow pollen tube at this time; instead, the entire pollen grain enclosed by the inner wall (intine) elongates, becoming as long as the micropylar canal (Fig. 20). The elongated pollen grains come in contact with the nucellus, which encloses the archegonia. The pollen grain forms a single pollen tube at the point of contact. Pollen growth and pollen-tube formation occur slowly over about two months, from early April until early June, when fertilization occurs (Fig. 2). Usually several

pollen tubes from separate pollen grains penetrate the nucellus and reach the surface of the archegonia (Fig. 21). The pollen tube then discharges its contents, including its two male gametes, into an archegonium.

Fertilization involves the fusion of one gamete with the egg nucleus (Fig. 22). This re-establishes the full complement of 26 chromosomes in the fertilized egg or zygote. The second male gamete as well as other cells from the pollen grain have no function and usually soon become disorganized.

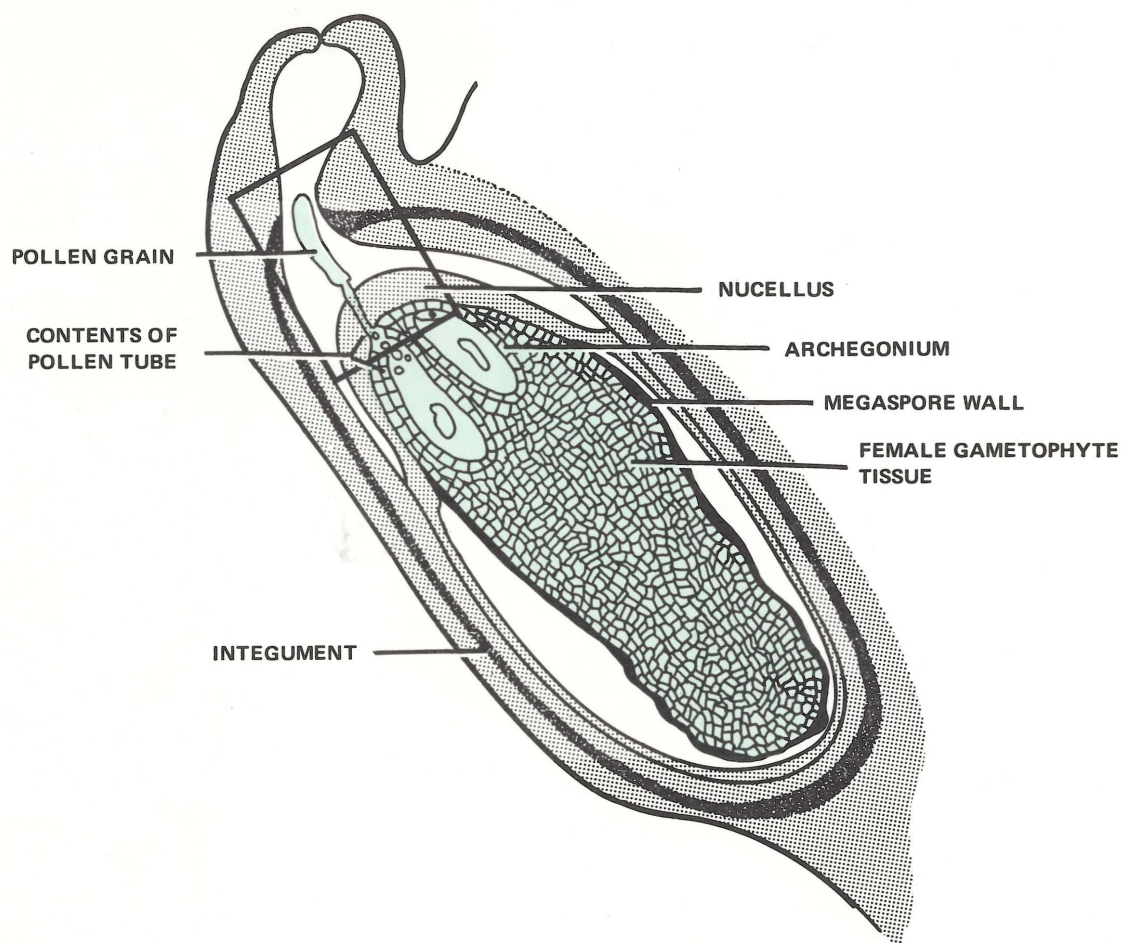


Figure 22. The ovule and mature female gametophyte at fertilization. Haploid tissue is shown in color. Outlined area is shown in Figure 21. *From Allen and Owens 1972.*



OVULIFEROUS SCALE

OVULE

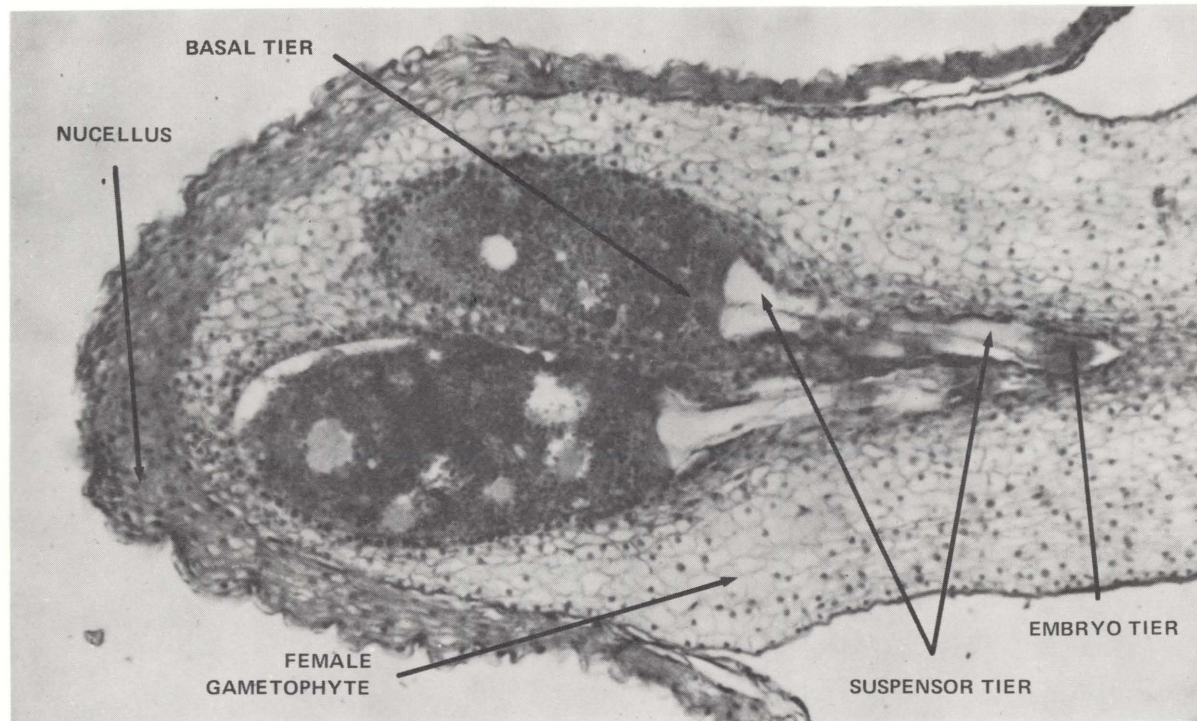


Figure 24. Early development of two proembryos from two archegonia about 2 weeks after fertilization showing the suspensor tier pushing the embryo tier into the female gametophyte. X 85. *From Allen and Owens.*

Embryo and Seed Development

Seed cones show little external change during the period of embryo and seed development from early June until late August. At the time of fertilization in June, the seed cone is at least three-fourths of its final size. Bracts are completely developed and ovuliferous scales are nearly fully enlarged and appear as distinct, spoon-shaped structures in the axils of the bracts. Each ovuliferous scale bears two white ovules on its adaxial surface (Fig. 23). Cone enlargement is complete by early July and mature cones are usually 7 to 8 cm in length. From July to September, differentiation and maturation of tissues occur throughout the cone.

The Embryo

Embryo development begins with the fertilized egg and continues over the next 10 to 12 weeks. Development occurs entirely within the female gametophyte tissue which serves as stored food for the embryo. Development of a relatively elaborate proembryo precedes development of the embryo. The fertilized egg (zygote) divides to form 12 cells arranged in three tiers of

four cells each. The innermost tier of four cells (farthest from the micropyle) is the embryo tier. These are the only cells to develop into the embryo. The middle tier of four suspensor cells elongates greatly and pushes an embryo tier through the archegonium and deep into the female gametophyte. The basal tier has no particular function (Fig. 24). This development takes only 1 to 2 weeks. During embryo development, the female gametophyte continues to store food for the growth of the embryo and as a reserve in the seed.

The embryo tier enlarges by cell divisions and becomes club-shaped (Fig. 25). Not all cells of the embryo tier contribute equally to embryo development, but the 4 cells do not separate and form 4 independent embryos as occurs in many conifers. The club-shaped embryo enlarges, and cells at the distal end form the dome-shaped shoot apex. The root apex forms somewhat below the shoot apex, while the more basal cells form a thick suspensor.

Several proembryos may develop, since each female gametophyte usually contains 4 to 7 archegonia and each may be fertilized

Figure 23. Seed cone and dissected ovuliferous scale at fertilization. X 2.

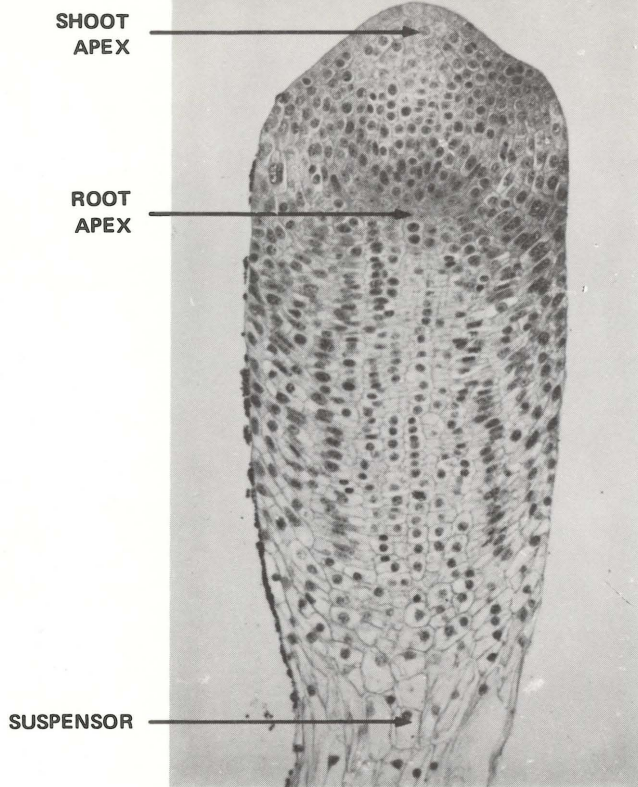


Figure 25. The club-shaped embryo as it appears in July when the root and shoot apex arise. X 100. From Allen and Owens 1972.

by a male gamete from a separate pollen grain. The early development of more than one embryo per ovule is common in conifers. Although more than one and often many embryos begin to develop, a mature seed seldom yields more than a single seedling. All other embryos cease development.

The Seed

Even before fertilization, the seed coat or testa begins to differentiate from the integument. The integument differentiates into three layers (Fig. 26) characteristic of most conifer seeds: (1) The outer layer is continuous with the surface of the ovuliferous scale. This layer changes little during ovule and seed development and forms the thin outer covering of the seed which attaches to the seed wing. (2) Cells of the middle layer remain small, forming a distinct layer up to six cells thick. This layer differentiates into a stony layer. (3) The thin, inner, fleshy layer lies adjacent to the nucellus. Seed wings begin to differentiate at about the time of pollination, when ovuliferous scales are only about 2 mm long. (Figs. 17, 18). The fully developed seed wing consists of two cell layers: an outer epidermis and, below, a layer of greatly enlarged cells. Both layers of the seed wing are

derived from the ovuliferous scale, not from the ovule.

In a mature seed, the embryo is loosely packed within the rather firm, cream-colored, nutritive female gametophyte tissue. This tissue contains abundant stored food and functions as a food reserve for the embryo and very young seedling upon germination. A thin white megaspore cell wall encloses the entire female gametophyte. The grey-colored megasporangium or nucellus, attached to the outside of the megaspore cell wall, is thick and conspicuous at the micropylar end but becomes as thin as the megaspore cell wall at the opposite end. The megaspore cell wall becomes rather hard, forming a distinct brown tip where the micropylar canal and nucellus meet. The female gametophyte tissue and fibrous suspensor are firmly attached to this portion of the nucellus (Fig. 26).

Cone Maturation

Seventeen months elapse between initiation and maturity of the seed cone of Douglas-fir (Fig. 2). The cones are fully elongated by early July of the second season. The months of July and August show little external change in the appearance of the seed cone. Internally, however, seeds develop, and considerable differentiation and maturation occur in tissues of the cone. The final phase in cone maturation involves the drying and death of the vegetative tissues and the resultant opening of the ovuliferous scales and release of the mature seed.

Cone opening is caused by drying, not by growth. During August, ovuliferous scales begin to lose their green color and turn brown (Fig. 27). As drying continues, the ovuliferous scales gradually begin to separate. Dry summers cause rapid drying and earlier opening of the cone. As a result, the time during which most of the seed is shed may vary as much as a month, from year to year. A large zone of mechanical tissue at the base of the ovuliferous scale is responsible, upon drying, for the opening of the ovuliferous scales in the mature cone. About 70 to 90% of Douglas-fir seeds fall during September and October, and most of the remainder be-

Figure 26. Dissected mature seed. X 50. From Allen and Owens 1972.

SEED
COAT

COTYLEDONS

SEED
WING

SHOOT
APEX

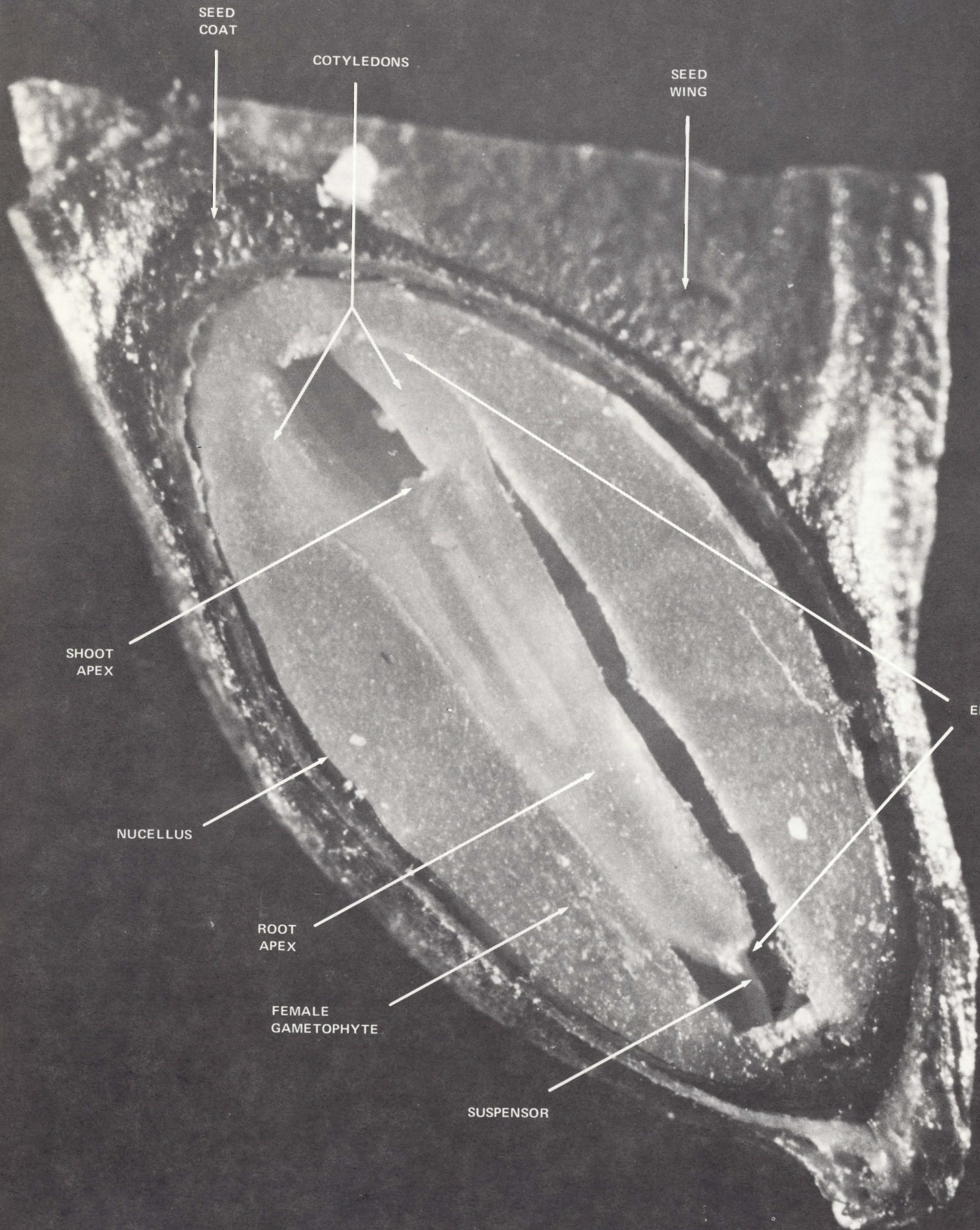
NUCELLUS

ROOT
APEX

FEMALE
GAMETOPHYTE

SUSPENSOR

EMBRYO



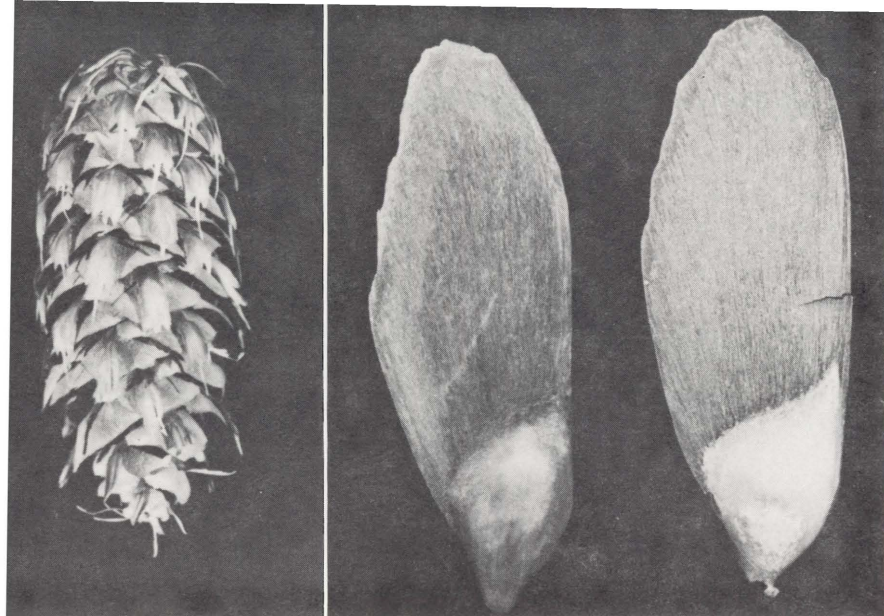


Figure 27. Mature seed cone (X .8) and seed of Douglas fir. X 5. Seed on left shows upper surface and lower surface is shown on the right. *From Allen and Owens 1972.*

tween November and March. The empty cones usually remain on the trees for 1 or 2 years after seedfall. Most seeds fall within 1,000 feet of the parent tree but, in some instances, upward air currents and strong winds have carried Douglas-fir seed as far as a mile.

Seed Production

Seedfall is difficult to estimate and predict from year to year. The number of seeds per cone can vary considerably in Douglas-fir, but the average is usually about 40 seeds per cone. An average mature Douglas-fir tree may produce about one pound or 49,000 seeds per crop. An individual mature tree in an excellent seed year might produce 2,000 to 3,000 seed cones or 2 to 3 bushels of green cones, yielding about one-half pound of seed per bushel. However, since many trees in a forest produce little or no seed even in good seed years, the average seed production is considerably less than one pound per tree, and in a poor or even fair seed year nearly all seeds produced may be lost to insects, birds and rodents.

Since essentially equal numbers of lateral bud primordia are initiated from year to year on a tree, the potential number of cones produced is determined by the percentage of these primordia that develop into vegetative, seed- or pollen-cone buds. The early period of lateral primordial development is of major importance in determining the cone crop, since the absence of a cone crop is more

frequently due to the failure of lateral primordia to develop into cone buds than to failure at any later stage of cone development. Once lateral primordia have developed into distinct seed- and pollen-cone buds, there appears to be little abortion of buds during the rest of the first year's development. Loss of seed cones by abortion is most common for the few weeks during and following pollination. Low temperatures are known to cause much of the abortion at this time, but other unknown factors are also involved.

The ovule and female gametophyte show few irregularities in development that would affect seed production. Exceptions occur in ovules of the most basal and most distal ovuliferous scales, where normal ovule development does not occur. Consequently, most filled seed are obtained from the central portion of the cone. However, even in this portion of the cone, the formation of empty seed is very common in Douglas-fir and may result from the presence of non-viable pollen, a lack of pollen when seed cones are open and receptive, or sterility due to self-pollination. Empty seeds and the cones that contain them look quite normal, since the cone, seed wing and seed coat are almost completely developed before fertilization occurs and are not dependent on the presence of pollen for normal development. Without fertilization, no embryo develops and the female gametophyte tissue degenerates. Consequently, seed that looks good is not necessarily an indication of filled seed. If fertilization occurs and early embryonic stages develop, environmental factors, excluding insects, do not appear to adversely affect later stages of cone and seed development.

Summary

In Douglas-fir, lateral buds are initiated in April; some of them may develop into seed or pollen cones, and release of the mature seed occurs in August or September of the following year. During this 17-month period, many environmental and physiological factors, not fully understood, may affect development of cones and filled, viable seed. Understanding the complete reproductive cycle of Douglas-fir is necessary in promoting and controlling cone and seed production for reforestation.

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