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Growth and Development of Trees

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Volume I

Seed Germination, Ontogeny, and Shoot Growth



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T O M A U D E

PREFACE

This two-volume treatise characterizes important features of growth and development of trees and other woody plants during their life cycles. The need for this work was indicated by greatly accelerated research and a rapidly expanding body of information on the nature and control of growth of woody plants. These volumes were planned as text or reference material for upper level undergraduate students, graduate students, investigators, and growers. The content is sufficiently interdisciplinary to make it useful to academics as well as those involved in the practice of growing trees and other woody plants for fruit crops or wood as well as for esthetic reasons. The subject matter will be of interest to arborists, foresters, horticulturists, plant ecologists, plant physiologists, plant anatomists, tree breeders and geneticists, plant pathologists, entomologists, soil scientists, meteorologists and landscape architects.

The viewpoint in these books is largely developmental, with strong ecological and physiological overtones throughout. In organizing the chapters, an attempt was made to adhere to the following central objectives: (1) To present a comprehensive treatment of the current state of knowledge of the important events in growth of the perennial woody plant. (2) To highlight the significant changes which take place in vegetative and reproductive growth as woody plants progress from juvenility to adulthood and, finally, to a senescent state. Such an emphasis seemed especially important because ontogenetic changes often have not been treated in depth or have been overlooked in the literature on tree growth. (3) To interpret the effects of external and internal controls of vegetative and reproductive growth. Considerable attention is given to important spatial and temporal variations in growth. Among the reasons for this emphasis was my realization that cambial growth generally has been described in terms of an "annual ring" at a single stem height. As cambial growth varies markedly with stem height the need was evident for dealing with the developmental architecture of a tree axis in three dimensions. To this end particular stress has been placed on variations in production and maturation of cambial derivatives at different stem heights and along branches.

(4) To present significant reference material selected from the world literature so as to make the work authoritative and well documented.

Despite the explosive accumulation during recent years of research data, both controversies and deficiencies exist in information on several aspects of growth of woody plants. When possible an attempt was made to present conclusions that seemed most reasonable in the light of available data. Nevertheless, certain interpretations must be considered tentative, and some of the conclusions presented may be reinforced and others revised as new information becomes available.

I wish to express a debt of gratitude to a number of friends and colleagues who contributed in various ways. Particularly, I acknowledge the help of J. Johanna Clausen who read the first draft of most chapters and made many valuable suggestions. Individual chapters were also reviewed by R. F. Evert, W. E. Hillis, B. F. Kukachka, P. R. Larson, A. C. Leopold, G. C. Marks, J. D. Matthews, Daphne J. Osborne, Diana M. Smith, G. R. Stairs, R. G. Stanley, E. L. Stone, H. B. Tepper, T. A. Villiers, Y. Waisel, P. F. Wareing, H. E. Wilcox, and S. A. Wilde. To all I express my sincere appreciation for their generosity and kindly counsel.

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Chapter 1

STRUCTURAL AND GROWTH CHARACTERISTICS OF TREES

Introduction

Trees and other woody plants are lignified perennating structures usually, though not always, formed from many apical meristems and a sheathing meristem throughout their stems, branches, and major roots. Because woody perennial plants are the largest and oldest living organisms, they are unique objects for biological study. Trees over 300 ft tall and more than 5000 years old have been described.

This chapter will discuss general structure and growth of trees. Structural characteristics of trees will be considered first as an important prelude to understanding their growth.

Structure of Trees and Other Woody Plants

A mature woody plant consists of vegetative organs (leaves, stems, and roots) and reproductive organs (flowers, fruits, and seeds). A woody plant, like all other multicellular organisms, grows by accumulating new cells. Whereas meristematic cells remain alive and functional throughout the life of a perennial woody plant, most of its other cells have a relatively brief life span. Many living tissues such as leaves, flowers, fruits, and young roots are shed periodically and other persistent tissues eventually die. Hence, a massive old tree consists of an accumulation of dead cells numbering in the billions, and a very small percentage of living cells which carry on its vital metabolic activities.

Crown Form

The shapes of tree crowns are extremely variable, but two general forms, excurrent and deliquescent, are widely recognized. In most gymnosperms and a few angiosperms the terminal leader grows more each year than the lateral branches below it, resulting in a conical crown and a single central stem. This pattern of branching results in an excurrent tree form. In most angiosperm trees, the lateral branches grow almost as fast as, or faster than, the terminal leader, resulting in a growth habit described as decurrent or deliquescent. For example, the deliquescent crown form of elms is traceable to loss of terminal buds and branching and rebranching of lateral buds, causing loss of identity of the main stem in the crown (Kramer and Kozlowski, 1960). Hence, the differential elongation of buds and branches determines the shape of a tree.

Open-grown deliquescent trees tend to develop characteristic shapes for genera or species (Fig. 1.1). The most common form is an ovate to elongate crown (e.g., *Fraxinus*, *Fagus*, *Quercus*). In some species (e.g., *Tilia*, *Prunus*) the crowns may be more broad than high (e.g., *Malus*), and in still others they are vase shaped (e.g., *Ulmus*).

Whereas open-grown trees have large crowns, those growing in stands tend to have small crowns. During the development of a community of closely spaced trees intense competition occurs for light, moisture, and minerals, resulting in stratification of trees into different crown classes. In a young, even-aged stand all trees may have more or less similar crown shapes. However, with increasing tree age, competition intensifies as the crowns begin to close. Some trees become suppressed, whereas others express dominance to become the largest and most vigorous trees. The least vigorous trees tend to occupy low positions in the canopy. Foresters find it useful to use the following standard classification for crowns of trees in even-aged stands (D. M. Smith, 1962):

Dominant Trees. Crowns are above the level of the crown cover and receive full light from above and partly from the sides. Dominant trees are larger and more vigorous than average trees in the stand. The crowns are well developed but they may be crowded on the sides.

Codominant Trees. Crowns form the level of the crown cover and receive full light from above but little from the sides. These median-sized crowns are somewhat crowded from the sides.

Intermediate Trees. These are shorter than either dominant or codominant trees. The crowns, which extend into the crown cover formed by codominant

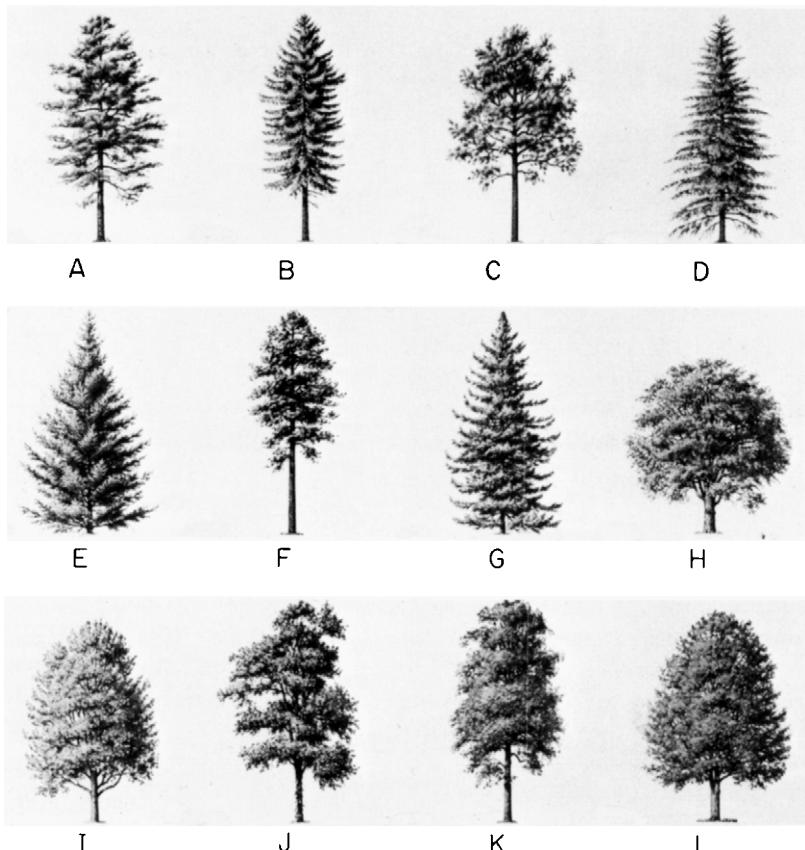


FIG. 1.1. Variations in form of open-grown trees. (A) *Pinus strobus*; (B) *Pseudotsuga menziesii*; (C) *Pinus palustris*; (D) *Tsuga heterophylla*; (E) *Abies balsamea*; (F) *Pinus ponderosa*; (G) *Picea glauca*; (H) *Quercus alba*; (I) *Liquidambar styraciflua*; (J) *Carya ovata*; (K) *Liriodendron tulipifera*; (L) *Acer saccharum*. (Photo courtesy St. Regis Paper Co.)

and dominant trees, receive little light from above and none from the sides. Crowns are small and usually crowded on the sides.

Suppressed (Overtopped) Trees. Crowns, which are below the level of the crown cover, do not receive direct light either from above or below.

Useful systems have also been devised for classifying crowns of forest trees in uneven-aged stands. For example, Dunning (1928) classified forest trees into seven classes which correlated vigor, age class, and seed production with the appearance of trees in each class. Another more complicated system of classifying gymnosperm trees is that of Keen (1936, 1943), which involved 16 classes based on four stages of maturity and groups of crown vigor. For a

good discussion of crown classification of forest trees the reader is referred to D. M. Smith (1962).

Leaves

Trees develop very extensive leaf areas. For example, an acre of forest with a stem basal area of only 60 ft² produced an aggregate leaf surface area of more than five acres (Rothacher *et al.*, 1954). Cummings (1941) found that a single open-grown *Acer saccharinum* tree had 177,000 leaves comprising a leaf blade area of over a sixth of an acre. Some idea of the great extent of annual leaf production by forests may be gained from data of Bray and Gorham (1964). They reviewed many studies of collections made during the period of leaf maturity and preceding defoliation. Data for various species were compared on an annual production basis in order to allow for comparison of data for angiosperms and gymnosperms. Leaf crops of gymnosperms were similar to those of angiosperms. Mean angiosperm leaf production was 2.8 metric tons per hectare per year, and for gymnosperms it was 2.9 tons. Some variations in leaf production were noted among genera. The mean leaf crop in tons per hectare per year for closed-canopy angiosperm forests was 3.7 for eleven *Quercus* sites; 3.0 for three *Fagus* sites; 2.9 for two *Salix* sites; 2.6 for two *Ulmus* sites; 2.5 for two *Fraxinus* sites; 2.5 for three *Populus* sites; and 2.4 for eight *Betula* sites. On five *Pinus* sites, the leaf crops averaged 2.8 tons per hectare per year and 3.0 tons for two *Larix* sites.

Species vary greatly in the number of leaves they produce, with gymnosperms producing many more leaves than angiosperms of comparable age. Whereas angiosperm trees bear leaves in the thousands, individual gymnosperm trees often have several million leaves. For example, MacDougall (1938) showed that an 18-year-old *Pinus radiata* tree had approximately three million needles. According to Fraser *et al.* (1964) a 36-year-old *Picea glauca* tree had over five million needles, with slightly more than a million needles produced during each of the last two years (Table 1.1).

In general, leaf sizes and leaf numbers of trees are negatively correlated. For example, a 21-year-old *Catalpa* tree had 26,000 large leaves (Turrell, 1934), whereas a citrus tree that was only 12 years old had over 90,000 small leaves. Similarly, *Cornus florida* trees with small leaves had over 50,000 leaves, whereas large-leaved *Carya* trees of comparable diameter had fewer than 5000 leaves (Table 1.2). Nevertheless, the total leaf area of *Carya* trees was much greater than in *Cornus*.

The distribution of foliage within tree crowns is extremely variable. This is specially emphasized by several studies on *Pinus resinosa*, a species

TABLE 1.1

NUMBERS AND DRY WEIGHT OF NEEDLES^a PRESENT ON A 36-YEAR-OLD *Picea glauca* TREE^b

Year	Number of Needles	Dry wt (gm)
1961	1,050,000	2,558.4
1960	1,050,000	2,700
1959	803,000	2,406
1958	681,000	1,937
1957	555,000	1,550
1956	405,000	1,152
1955	297,000	872.2
1954	219,000	630.3
1953	116,000	348.1
1952	29,700	93.96
1951	4,980	15.68
1950	845	2.779
1949	420	1.433

^a By year formed.^b From Fraser *et al.* (1964).

TABLE 1.2

VARIATIONS IN NUMBERS OF LEAVES BORNE BY TREES OF DIFFERENT SIZE IN SEVERAL SPECIES^a

	Diameter at breast height (in.)	
	2	8
<i>Quercus alba</i>	2,880	35,900
<i>Quercus velutina</i>	996	13,100
<i>Quercus stellata</i>	1,140	9,800
<i>Carya</i> sp.	588	4,860
<i>Oxydendron arboreum</i>	2,720	18,600
<i>Cornus florida</i>	3,030	51,900

^a From Rothacher *et al.* (1954).

known to have little genetic variability. Stiell (1962) found that foliage weight of plantation-grown *Pinus resinosa* trees increased from the top downward, tended to remain more or less constant for four to five whorls of branches, and then diminished toward the base of the crown. In most trees these few whorls contained between half and three-fourths of the total foliage. The main stem and a zone around it occupied a needle-free core up the center. There were gaps between the foliage of successive branches, both horizontally

and vertically, and the weight of foliage varied erratically from one branch whorl to another. Hall (1965) also emphasized extreme diversity among five dominant, 50-year-old *Pinus resinosa* trees. The lengths of live crown varied among these trees from 18 to 24 branch whorls and the dry weight of foliage from 6.6 to 14.5 kg.

STRUCTURE OF ANGIOSPERM LEAVES

The typical foliage leaf of angiosperms is composed mainly of primary tissues. The blade, or lamina, usually broad and flat and supported by a petiole, contains ground tissues, or mesophyll, enclosed by an upper and lower epidermis. Mesophyll is composed of varying amounts of palisade

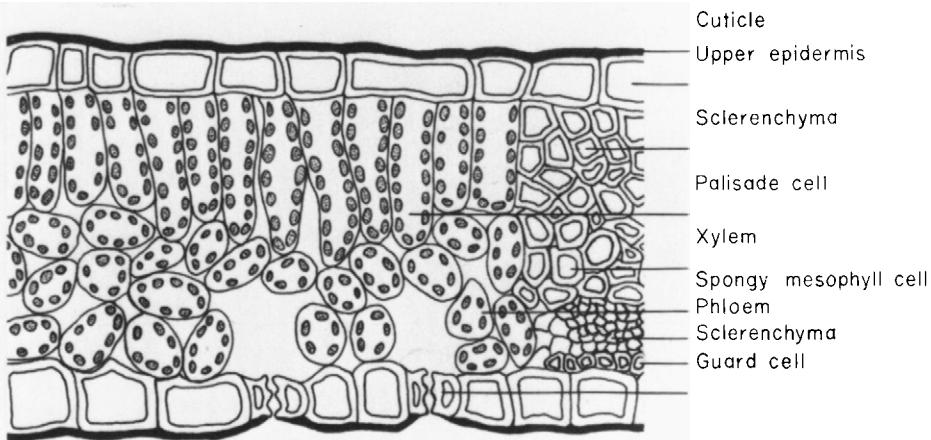


FIG. 1.2. Transection of a portion of a leaf blade from an angiosperm tree.

tissue and spongy parenchyma. The columnar, regularly-shaped palisade cells below the upper epidermis (and sometimes above the lower epidermis), are easily distinguished from the irregular-shaped spongy parenchyma cells adjacent to the lower epidermis (Fig. 1.2). There may be only a single layer of palisade cells perpendicularly arranged to the upper epidermis, or there may be as many as three layers. When more than one layer is present, however, the cells of the outermost layer are longest, and those of the innermost layer may grade in size to resemble the spongy parenchyma cells. When the difference between palisade and spongy cells is very distinct, most of the chloroplasts are localized in the palisade tissues. The mesophyll tissue has abundant intercellular spaces which are connected to the outer atmosphere by stomatal

openings in the epidermis. The internal exposed surface of mesophyll cells is much greater than the external leaf surface.

In leaves of many plants, both angiosperms and gymnosperms, the loss of water by cuticular transpiration is prevented by waxy coatings. The cuticle is considered to be the noncellular membrane which lies over the epidermis cells. The cuticle extends out into stomatal openings, where they occur, as a thin lining of the subsurface cavities. The cuticle, a layer of cross-linked hydroxy fatty acids, usually is bounded by a layer of wax (Fig. 1.3). The amount of surface wax varies greatly among species and in some may represent up to 15% of leaf dry weight. Surface waxes of plants represent a wide range of organic compounds. Those examined in detail are complex mixtures of long-chain alkanes, alcohols, ketones, aldehydes, acetols, esters, and acids (Eglinton and Hamilton, 1967). The degree of waxiness apparently affects wettability of leaves much less than does the physical form of the wax. When the wax is composed of crystalline or semicrystalline masses it presents an uneven, strongly water-repellent surface. However, when present in an amorphous noncrystalline form its surface is smooth and easily wetted (Martin, 1966).

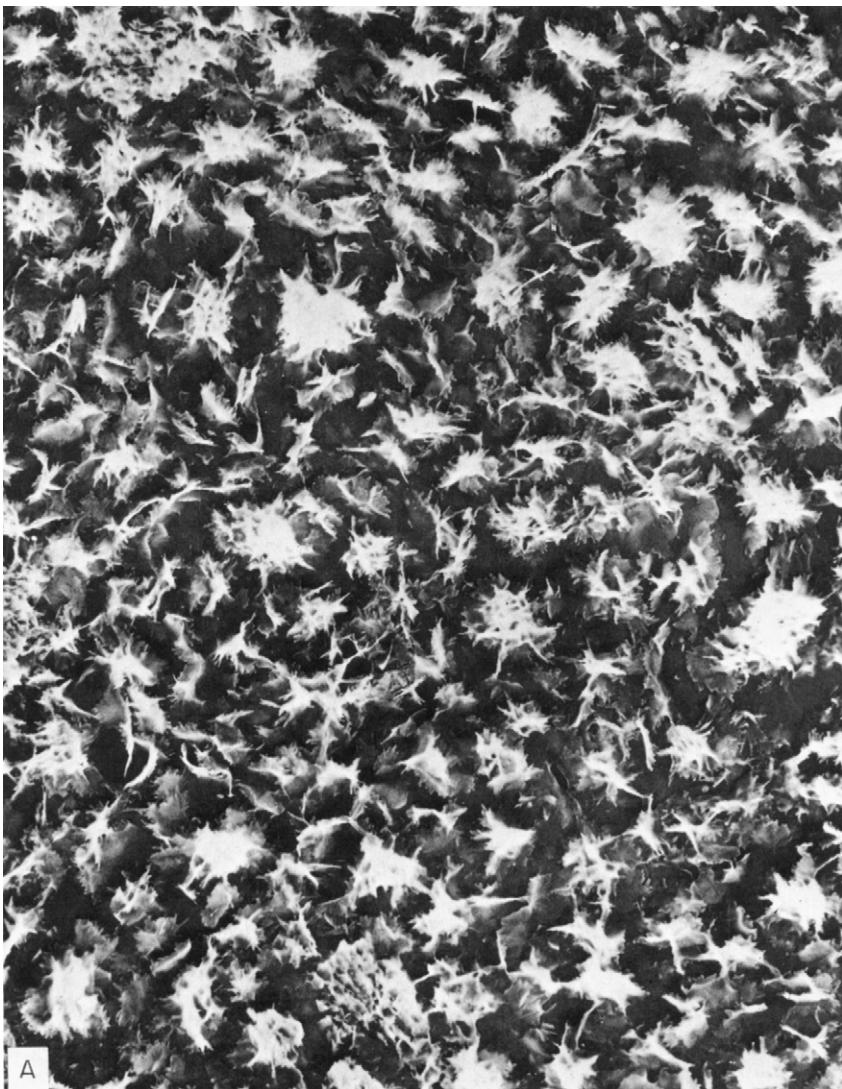
STRUCTURE OF GYMNOSPERM LEAVES

Except for a few genera, the leaves of gymnosperms are evergreen. Most gymnosperm leaves are linear or lanceolate and bifacially flattened, but other shapes occur also. For example, the leaves of *Podocarpus*, *Picea*, and occasionally *Larix*, are tetragonal in cross section. Scalelike leaves are characteristics of *Sequoia*, *Cupressus*, *Chamaecyparis*, *Thuja*, and *Libocedrus*. Broad, ovate, and flat leaves are found in *Araucaria* (de Laubenfels, 1953).

In *Abies*, *Cunninghamia*, *Dacrydium*, *Sequoia*, *Taxus*, *Torreya*, *Ginkgo*, *Araucaria*, and *Podocarpus*, the leaf mesophyll is differentiated into palisade cells and spongy parenchyma. The leaves of the latter two genera have palisade parenchyma on both sides (Esau, 1965b). In pines the mesophyll is not differentiated into palisade cells and spongy parenchyma.

Pine needles, which are borne in fascicles, are hemispherical (two-needed species), triangular (three-needed species) or circular in cross section, (one-needed species, e.g., *Pinus monophylla*) (Fig. 1.4). Sometimes the number of needles per fascicle varies from the typical condition. This often is a response to unusual nutritional conditions, injury, or abnormal development. The predominantly three-needed *Pinus ponderosa* had more two-needed fascicles when young than when old (Haller, 1962).

In *Pinus banksiana*, three-needed fascicles were more common on lamas shoots than on normal shoots. Whereas 42% of the fascicles were three-needed on lamas shoots, only 22% of the normal shoot tips had such



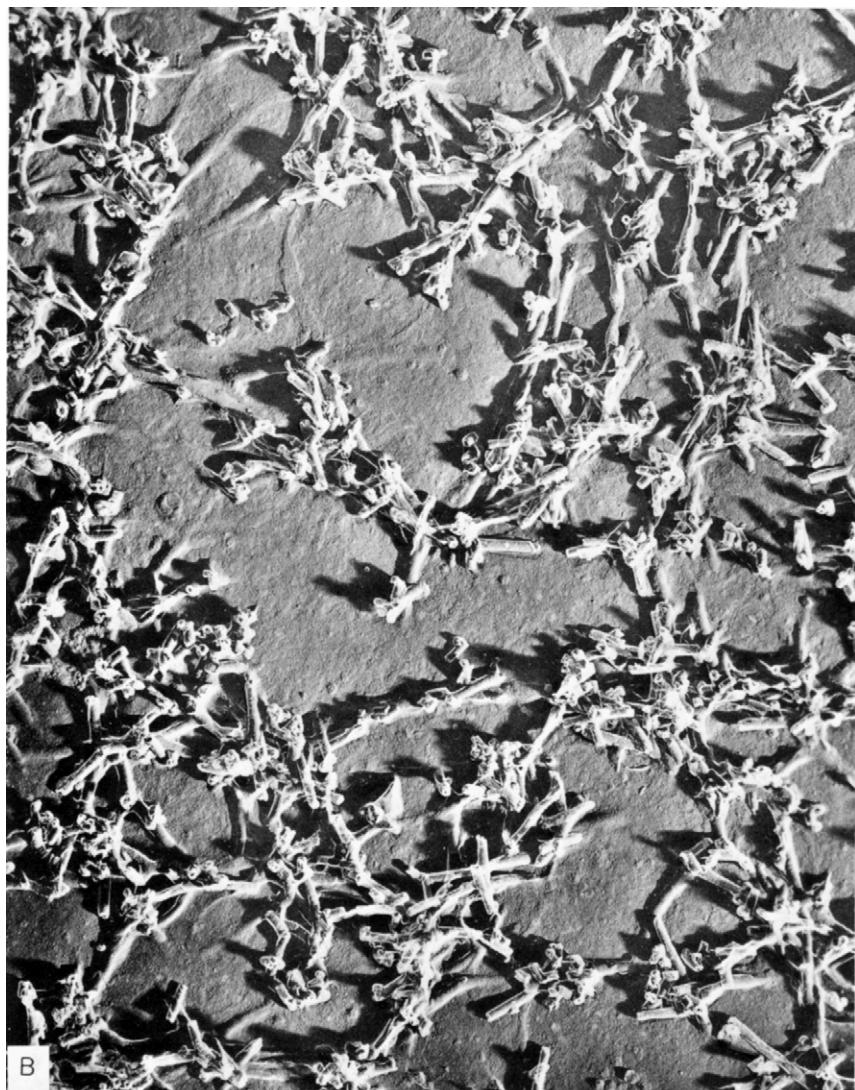


FIG. 1.3. Electronmicrograph showing waxy deposits on upper surface of *Eucalyptus cloeziana* leaf ($\times 5250$) (A) and on *Picea abies* needle ($\times 14,000$) (B). [From Eglinton and Hamilton (1967)].

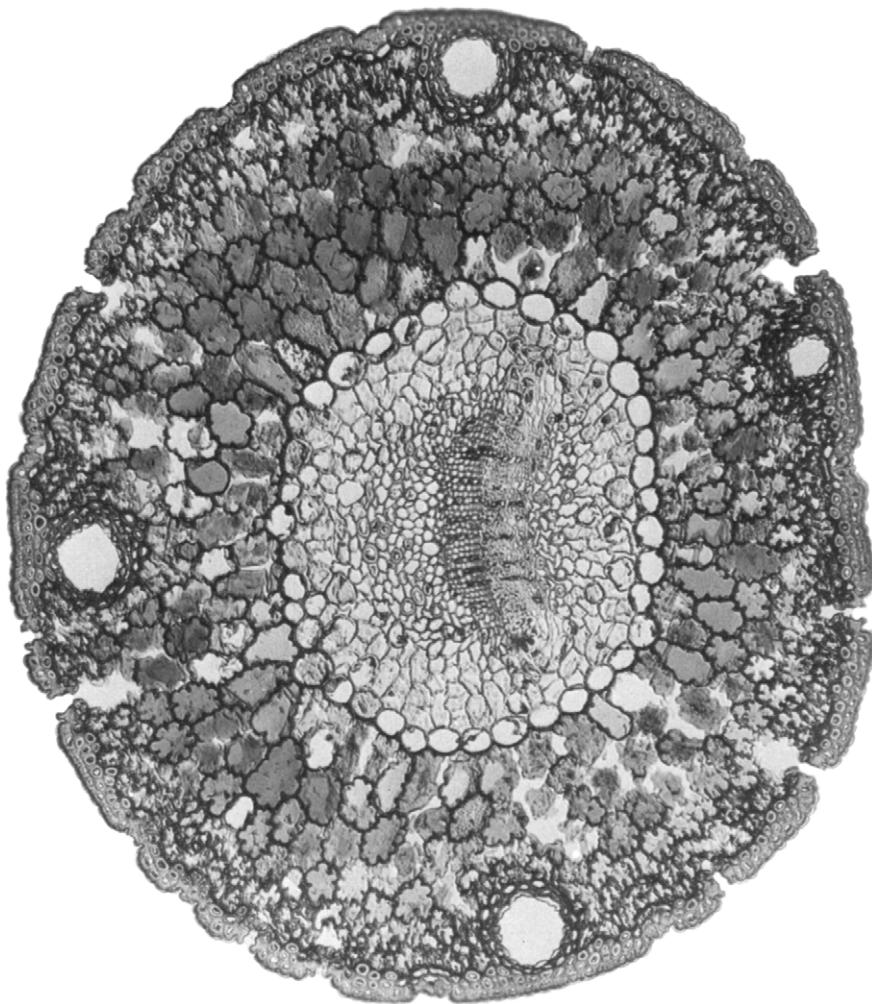


FIG. 1.4. Transection of needle of *Pinus monophylla*. (U.S. Forest Service, Forest Products Laboratory photo.)

fascicles. Three-needed fascicles also were more common close to the tip of young normal shoots than a short distance from the apex. The occurrence of supernumerary needles appeared to be governed by gradients of apically produced growth regulators (Ghent and Thomas, 1960).

The epidermis of pine needles has a heavy cuticle. The deeply sunken stomates are arranged in rows. Below the epidermis and surrounding the mesophyll is a thick-walled hypodermal layer. Parenchyma cells of the

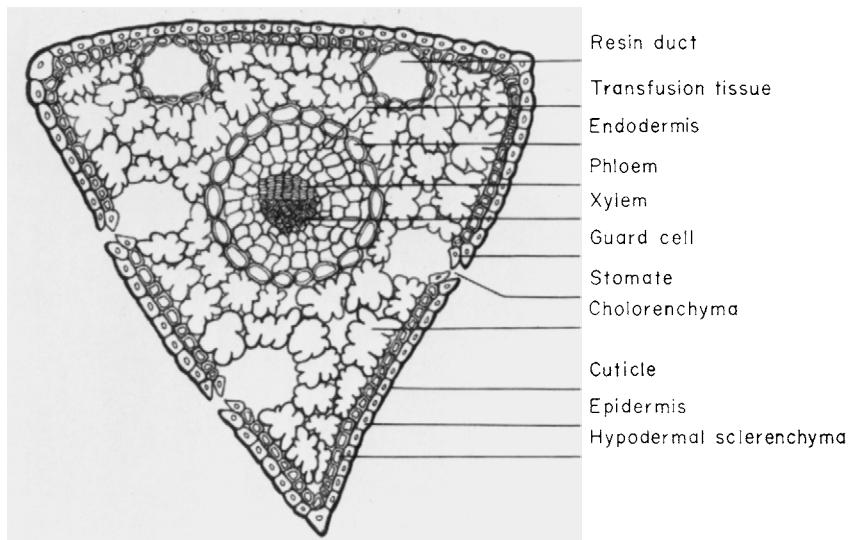


FIG. 1.5. Transection of secondary needle of *Pinus strobus*.

mesophyll are deeply infolded. The one or two vascular bundles per needle are surrounded by transfusion tissue consisting of dead tracheids and living parenchyma cells. The cells of the endodermis, which surrounds the transfusion tissue, are rather thick-walled (Fig. 1.5).

Variations in Structure of Leaves

The ultimate development of leaves may vary greatly within a species and in different parts of the same tree. Leaf size often is variable from year to year because of environmental variations. That final expression of leaves of deciduous trees is not determined at the bud stage was shown by Isonogle (1944), who shaded one bud of each of opposite pairs and left the other one of each pair as a control. The latter developed normal leaves whereas the ultimate leaf structure of shaded buds varied greatly with the degree of shading to which they had been subjected. The internal anatomy of gymnosperm leaves appears to be less variable than that of angiosperm leaves.

The size and structure of leaves often vary with location on the tree, as in sun and shade leaves (Chapter 8). Leaves of sprout shoots usually are larger than those on shoots of nonsprout origin (Chapter 7). Variations also occur between juvenile and adult leaves (Chapter 3), early and late leaves of

heterophyllous species, and between leaves of normal, early-season shoots, and those of late-season lammas or proleptic shoots (Chapter 5).

LEAF VENATION

Food, water, and minerals are supplied to and removed from the leaves through veins which penetrate the mesophyll tissues. The vascular system of leaves may vary from a single vein as in many gymnosperms to a multiveined system as in angiosperms and in some gymnosperms (e.g., *Ginkgo* and *Gnetum*). In angiosperms, leaf venation may be netted as in dicotyledons or parallel as in monocotyledons. In parallel venation the veins are connected laterally by numerous small bundles. In dicotyledon leaves, in which venation may be pinnate or palmate, veins vary greatly in size. The vascular bundles of major veins are imbedded in parenchyma tissue and isolated from the mesophyll. In contrast, the minor veins usually are located in the upper part of the spongy parenchyma, and divide the mesophyll into small sections called areoles. The extensively branching vascular system thoroughly penetrates the mesophyll. Plymale and Wylie (1944) found, for example, that the total length of veins averaged 102 cm for each cm^2 of leaf blade.

Stems

The tree stem is made up mostly of wood or xylem, which is surrounded by a very thin meristematic sheath of cambium and enclosed by a relatively thin layer of bark (Fig. 1.6). Stem cells are primarily vertically oriented, with transversely oriented components present. The woody stem axis of a tree in the Temperate Zone consists of firmly joined annual increments of xylem added one on top of another in a series of firmly joined hollow cones (Fig. 1.7). As will be discussed in Volume II, Chapter 2, these overlapping xylem sheaths vary in thickness at different stem heights. Xylem cells possess lignified cell walls.

SAPWOOD AND HEARTWOOD

Young xylem or sapwood conducts sap (primarily water), strengthens the stem, and to some extent serves as a storage reservoir for food. The living parenchyma cells in the sapwood, which are very important because they store food reserves, consist of transversely oriented ray cells and, in many trees, of vertically oriented axial parenchyma as well. On the average only about 10% of the cells in the sapwood are alive. As the xylem ages, however, all the living cells die and usually change color as a result of deposition of various substances such as oils, gums, resins, and tannins. As a result, adult trees possess a central cylinder of dead tissue, called heartwood, which

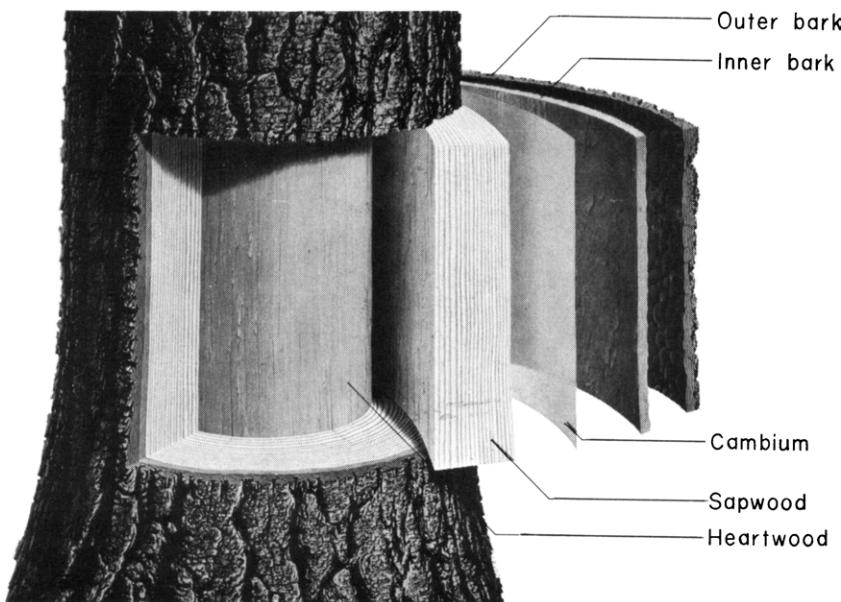


FIG. 1.6. Generalized structure of a tree stem showing orientation of major tissues including outer bark, inner bark, cambium, sapwood, and heartwood. (Photo courtesy St. Regis Paper Co.)

provides mechanical support and is not involved in metabolic processes. Once true heartwood begins to form it continues to increase in diameter throughout the life of the tree. Conversely, sapwood is relatively wide in the stem cross section of a young tree and narrow in an old tree.

Species vary greatly in the amount and color of their sapwood (Table 1.3).

TABLE 1.3
VARIATIONS IN THICKNESS OF SAPWOOD AMONG ANGIOSPERMS^a

	Number of xylem rings in sapwood
<i>Catalpa speciosa</i>	1-2
<i>Robinia pseudoacacia</i>	2-3
<i>Juglans cinerea</i>	5-6
<i>Maclura pomifera</i>	5-10
<i>Sassafras officinale</i>	7-8
<i>Aesculus glabra</i>	10-12
<i>Juglans nigra</i>	10-20
<i>Prunus serotina</i>	10-12
<i>Gleditsia triacanthos</i>	10-12

^a From Sargent (1926).

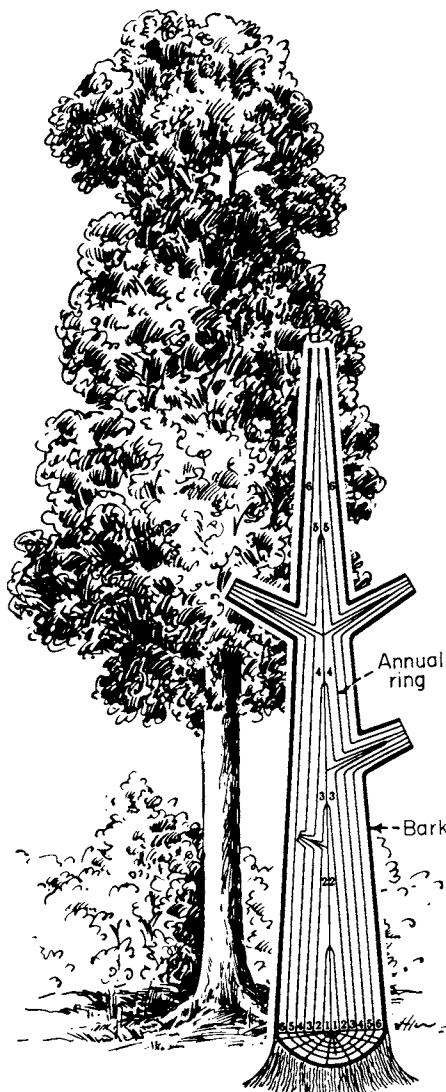


FIG. 1.7. Diagrammatic median longitudinal section of a tree showing pattern of annual xylem increments in the stem and major branches.

Practically all of *Ceiba* wood may be sapwood. Certain characteristically "sapwood" trees, such as species of *Ilex*, *Abies*, *Picea*, *Tsuga*, and *Populus*, often show little or no difference in the color of their sapwood and heartwood. In contrast, species of *Robinia* and *Larix* form a wide, dark, visibly differentiated heartwood core. Some species have a rather definite transition zone

between the sapwood and heartwood. This transition zone often is drier and lighter in color than typical core heartwood and has fewer living cells than the sapwood. Such transition zones have been described for *Pseudotsuga menziesii*, *Taxus baccata*, and *Pinus radiata*, among other species (Harris, 1954). Sometimes light colored streaks of "included sapwood" are found within normal heartwood zones. Included sapwood does not contain living cells.

To account for species differences in heartwood characteristics various classification schemes have been advanced. One useful classification is that of Hillis (1965):

1. NORMAL OR DRY HEARTWOOD in which moisture content is appreciably lower than in the sapwood and the content of extractives is higher. An example is *Pinus sylvestris*.

2. RIPEWOOD in which moisture content is lower than in the sapwood and the cytological characteristics are similar to those in normal heartwood. The absence of color suggests a low content of extractives. Examples are *Picea abies*, *Acer campestre*, and *Abies alba*.

3. RED HEART, which has a lower average moisture content than the sapwood, but the decrease at the sapwood-heartwood boundary is slight. An example is *Fagus sylvatica*.

4. WET HEARTWOOD, which has a higher moisture content than the sapwood. Examples are *Carya* spp. and *Fraxinus excelsior*.

Some examples of heartwood in different species are shown in Figs. 1.8 and 1.9. The formation of heartwood is discussed further in Chapter 4.

WOOD OR XYLEM OF GYMNOSPERMS

In most gymnosperm stems the longitudinal elements of the xylem consist mainly of tracheids and a few axial parenchyma and epithelial cells (Fig. 1.10). Whereas axial parenchyma cells occur in *Sequoia* and *Thuja* xylem, they are absent in *Pinus*. The transversely oriented elements, which are relatively few, include ray tracheids, ray parenchyma cells, and epithelial cells. Interspersed also are longitudinally and transversely oriented resin canals which are intercellular spaces of postcambial development rather than cellular elements. Resin is secreted into these canals by epithelial cells. Resin canals are a normal feature of *Pinus*, *Picea*, *Larix*, and *Pseudotsuga*. In addition, traumatic resin canals may occur together with normal resin canals, or they may be found in woods lacking normal resin canals such as *Cedrus*, *Tsuga*, and *Abies*.

Longitudinal Elements

As much as 90% of the wood or xylem of gymnosperms is made up of vertically stacked, overlapping tracheids, arranged in rather uniform radial

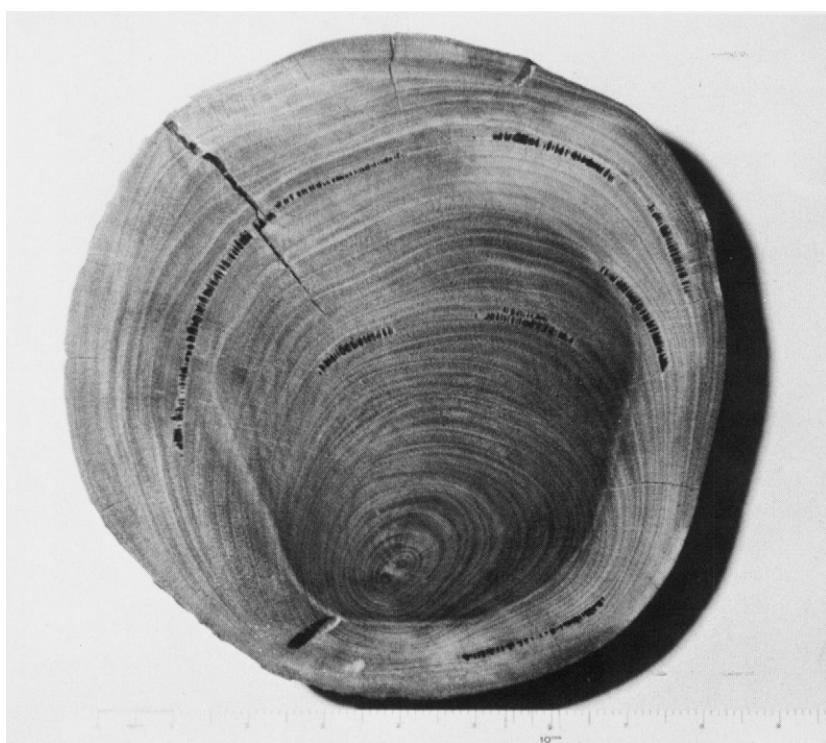


FIG. 1.8. Eccentric stem of *Angophora costata* showing kino veins, grub hole, heartwood, and intermediate zone which do not correspond to xylem growth rings. [From Hillis (1962)].

rows. These four- to six-sided, thick-walled, tapering cells often are as much as 100 times longer than wide. They may vary in length from about 3 to 7 mm, but in most Temperate Zone gymnosperms they average 3 to 5 mm long. Those formed early in the growing season are larger in cross section and have thinner walls than those formed later. The transition from large, earlywood cells to small, latewood cells may be gradual as in *Pinus lambertiana*, or it may be abrupt as in *Pinus taeda* or *P. palustris*.

Walls of longitudinal tracheids have various types of pits that allow for transfer of materials to adjacent cells. These include pit pairs between a longitudinal tracheid and a ray tracheid, between a longitudinal tracheid and a ray parenchyma cell, or between two adjacent longitudinal tracheids. Pits on tracheid walls occur predominantly on radial surfaces in the area where tracheids overlap. Bordered pit pairs have a common membrane of primary walls and a lamella. In such a pit pair the secondary wall of each adjacent cell arches over the pit cavity. The pit in most gymnosperms has a

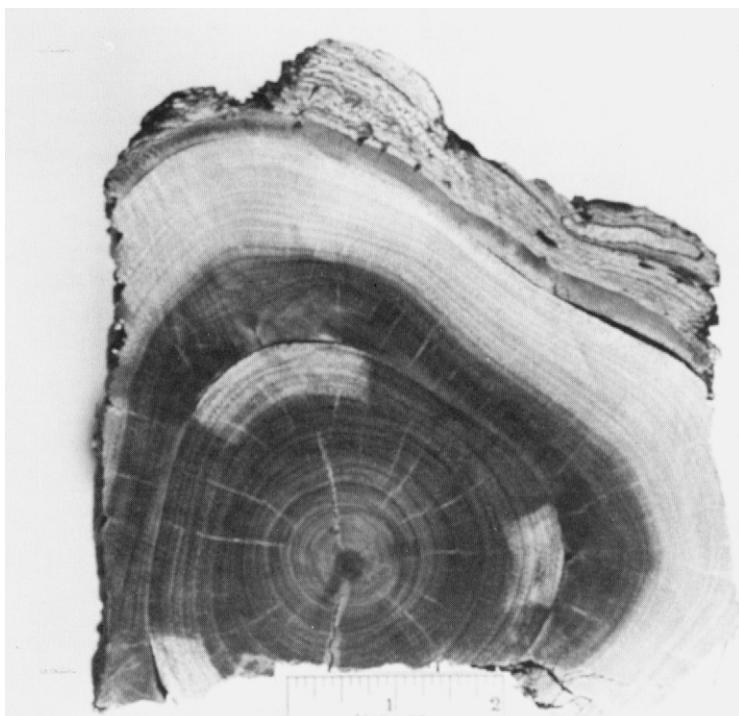


FIG. 1.9. Transection of *Eucalyptus* stem showing included sapwood. [From Hillis (1962)].

thickened torus surrounded with a thin margin called the margo. The membrane of bordered pits is made up of cellulose strands which radiate from the torus to the margin of the pit cavity. Liquid moves readily through the pores in the margo of the pit membrane when the torus is in a medial position. However, when the pit is aspirated (the torus displaced laterally against the pit membrane), the flow of liquid is greatly restricted.

Perforations in membranes of bordered pits of gymnosperm xylem vary from a few angstrom units to several microns in the same pit. Pit diameter also varies greatly among species. The bordered pits of gymnosperms are more numerous and much larger in earlywood than in latewood of the same annual ring. There appears to be much more resistance to water transport in latewood than in earlywood (Kozlowski *et al.*, 1966).

When present in gymnosperms axial parenchyma occur as long strands. Axial parenchyma is relatively abundant in *Sequoia* and *Taxodium*, sparse in *Larix* and *Pseudotsuga*, and absent in *Pinus*. As viewed in cross section, axial

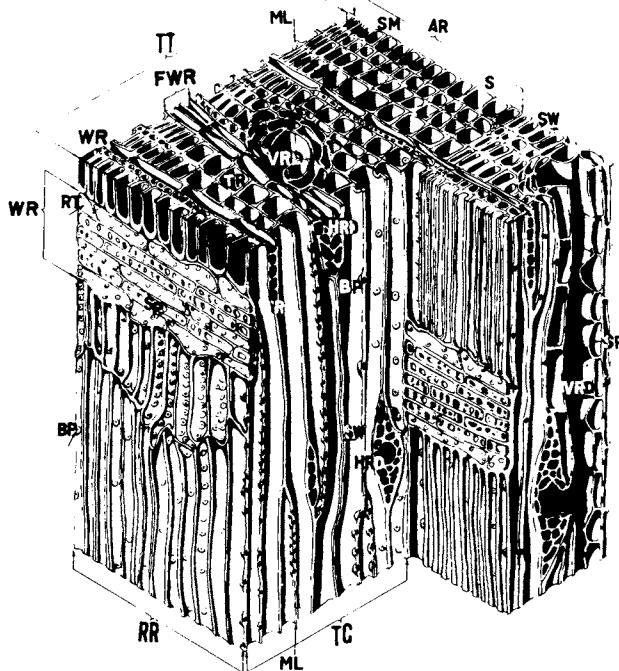


FIG. 1.10. Anatomy of gymnosperm wood. TT, transection; RR, radial section; TG, tangential section; TR, tracheids; ML, middle lamella; S, earlywood; SM or SW, latewood; AR, annual ring; WR, wood ray; RT, ray tracheid; FWR, fusiform wood ray; SP, simple pit; BP, bordered pit; HRD, horizontal resin duct; VRD, vertical resin duct. (U.S. Forest Service, Forest Products Laboratory photo.)

parenchyma of gymnosperms may be widely scattered among the tracheids in a growth ring (diffuse parenchyma), in a tangential band within a growth ring (banded parenchyma), or confined to the beginning or end of a growth ring (terminal or marginal parenchyma).

Transverse Elements

The wood rays comprise the major transversely oriented elements of gymnosperm wood. These ribbon-shaped aggregates of cells radiate in a stem cross section like wheel spokes. Two types of rays occur in gymnosperms (1) narrow usually uniseriate rays and (2) wide fusiform rays when transverse resin canals are present.

In the majority of gymnosperms the narrow rays are only about 10 to 15 cells high, yet in some species (e.g., *Taxodium distichum*) they may be up to 60 cells high.

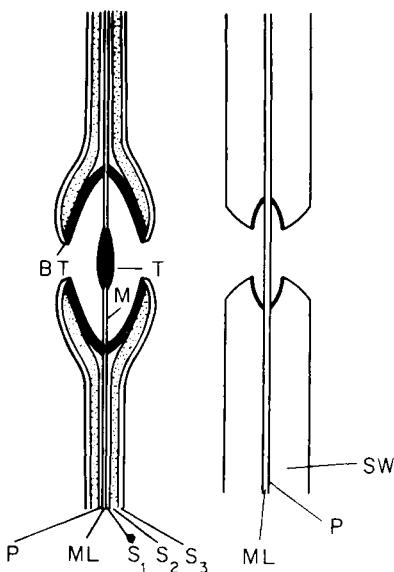


FIG. 1.11. Pit of gymnosperm wood (left) and angiosperm wood (right). For the gymnosperm wood: ML = middle lamella; P = primary wall; S₁ = outside layer of secondary wall; S₂ = middle layer of secondary wall; S₃ = inner layer of secondary wall; M = pit membrane; T = torus; and B.T. = initial border thickening. For the angiosperm wood: ML = middle lamella; P = primary wall, and S.W. = secondary wall. [From Wardrop 1962].

Individual rays of gymnosperms are made up of either ray parenchyma cells or of ray parenchyma cells and ray tracheids as well. Ray tracheids always occur in *Pinus*, *Picea*, *Larix*, and *Pseudotsuga*, and are less commonly found in other genera such as *Abies*, *Taxodium*, *Sequoia*, *Thuja*, *Libocedrus*, and *Juniperus*. When the prosenchymatous ray tracheids are present they may occur in rows at ray margins or among layers of ray parenchyma cells. A ray may even consist exclusively of ray tracheids. Ray parenchyma cells have thin walls and living protoplasts when they are located in the portion of the ray which is in the sapwood. Ray tracheids have thick lignified walls. The ray tracheids of hard pines are described as dentate because of the presence of toothlike projections on their inner walls.

Pit pairs between adjacent ray tracheids, or between ray tracheids and longitudinal tracheids, are bordered, whereas those connecting ray tracheids with ray parenchyma cells are half-bordered. In a half-bordered pit the part of the ray tracheid side is typically bordered (Fig. 1.11) while that on the ray parenchyma side is simple. The membranes of half-bordered and simple pits of gymnosperms lack openings and do not have a torus. Ray parenchyma

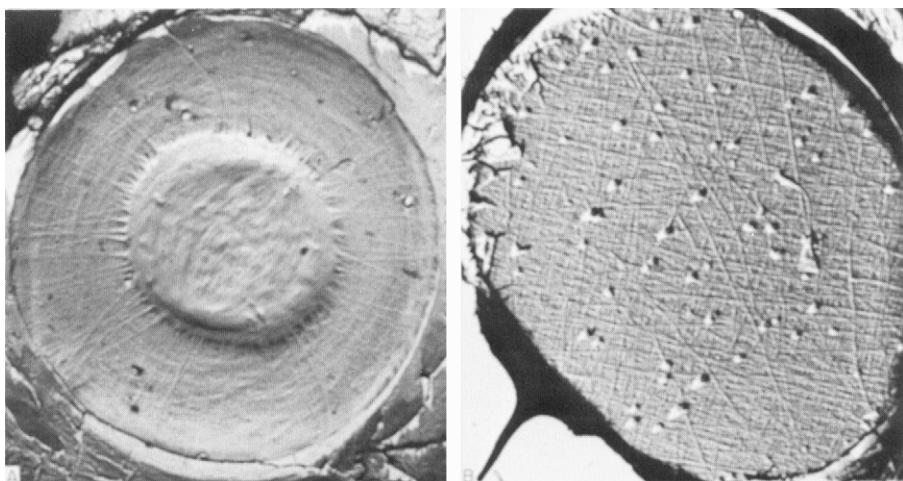


FIG. 1.12. Variations in orientation of microfibrillar strands in bordered pits of gymnosperms and angiosperms. (A) Radiating strands of pit in xylem of *Pseudotsuga macrocarpa*, $\times 6150$; (B) Randomly arranged strands of pit membrane surface in *Tilia*, $\times 25,000$. (Photo courtesy of W. A. Coté, Jr.)

cells are characteristically longer than ray tracheids, and they can be identified by their simple pitting.

Fusiform rays, which may be found in *Pinus*, *Picea*, *Pseudotsuga*, and *Larix*, consist of marginal ray tracheids, ray parenchyma cells, and epithelial cells around a horizontally oriented resin canal. The resin-secreting ray epithelial cells form by splitting of the middle lamella of ray parenchyma daughter cells. Fusiform rays are proportionally few in number and do not exceed 5% of the total number of rays present.

ANGIOSPERM WOOD OR XYLEM

Angiosperm wood consists of longitudinal prosenchymatous components (vessels, tracheids, and fibers), parenchymatous components (axial parenchyma), and epithelial cells (Fig. 1.13). As a rule angiosperms lack transversely oriented prosenchymatous cells. Their transverse elements include ray parenchyma and, infrequently, epithelial cells. Whereas longitudinal or transverse resin canals occur normally in various tropical angiosperms, they are conspicuously absent in virtually all Temperate Zone species.

Longitudinal Elements

As pointed out earlier, there are more cell types in the xylem of angiosperms than in gymnosperms. Most conspicuous are vessels, which are the

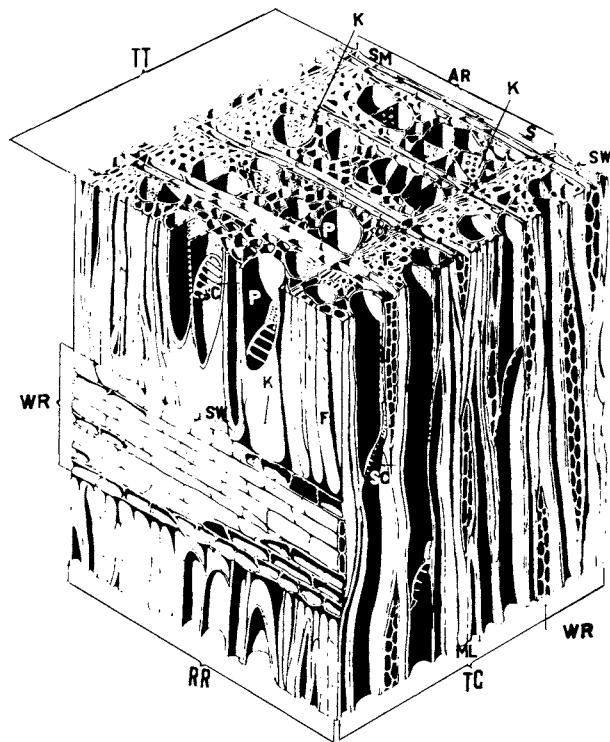


FIG. 1.13. Anatomy of angiosperm wood. TT, transection; RR, radial section; TG, tangential section; P, vessel; SC, perforation plate at end of vessel; F, fibers; K, pit; WR wood ray; AR, annual ring; S, earlywood; SM or SW, latewood; ML, middle lamella (U.S. Forest Service, Forest Products Laboratory photo.)

chief water conducting components. Vessels are made up of vessel members, single cells from which end walls have disintegrated. Vessel members are superimposed one above another to create a tubular structure that may vary in length from a few centimeters to several meters. Some angiosperm genera such as *Acer*, *Betula*, and *Populus* have vessels of relatively small diameter interspersed rather uniformly throughout each annual ring. Such species are considered to have diffuse porous wood. In contrast, ring porous genera, such as *Quercus*, *Fraxinus*, and *Carya* have vessels of very large diameter in the earlywood. In ring porous woods the earlywood vessels may have diameters of the order of a hundred times as great as that of latewood vessels.

In transection most vessels are oval in shape but in woods of the more primitive species the vessels tend to be angular. Vessel arrangements are fixed and therefore very useful in wood identification (Fig. 1.14). For example,

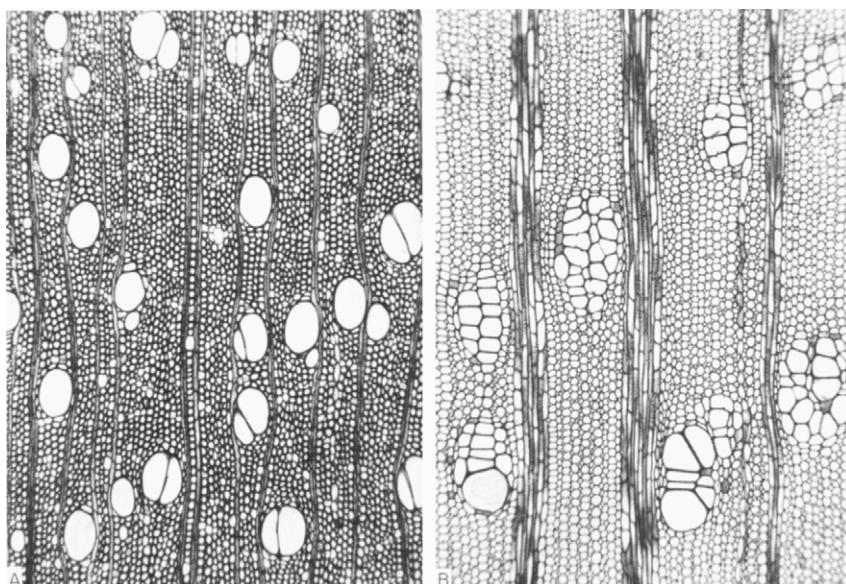


FIG. 1.14. Vessel arrangement (A) *Warburgia ugadensis*, with solitary pores. The apparent pairs of pores are due to overlapping of oblique end walls of vessel members, (B) *Ailanthus altissima*, with pore clusters in the latewood. [From Brazier and Franklin (1961). Reproduced by permission of the Controller of Her Britannic Majesty's Stationery Office.]

vessels may be arranged in pore multiples (*Acer*, *Betula*, *Populus*), chains (*Ilex*), or as groups in the latewood in concentric wavy bands (*Ulmus* and *Celtis*).

Tracheids are individual cells and are smaller than vessels. Two types of tracheids may occur in angiosperms, vascular tracheids and vasicentric tracheids. Vascular tracheids are imperforate cells resembling small vessel members in form and position. Vasicentric tracheids are short, irregularly formed tracheids in the immediate proximity of vessels and not forming part of definite axial rows.

The bulk of the xylem of angiosperms usually consists of fibers. These resemble tracheids somewhat but they have thicker walls, fewer pits, and smaller lumens.

Xylem elements of angiosperms lack the orderly radial alignment characteristic of gymnosperm tracheids. The seemingly random distribution of elements in angiosperms results from extensive diameter growth of vessel members after they are cut off by the cambium. This forces other cells out of orderly alignment and causes narrow rays to bend around large vessels. This random arrangement is also partly caused by lesser tendency for division of cambial initials opposite rapidly expanding vessels than of initials in a region where no large earlywood vessels form (Panshin *et al.*, 1964).

In angiosperm xylem, liquids move vertically through the perforated vessels. Lateral movement of liquids occurs through bordered and half-bordered pits. Pits of angiosperms may connect fibers to fibers, vessels to fibers, fibers to ray cells, and vessels to ray cells. The membrane of bordered pit pairs of angiosperms is the primary lamella of adjacent cells. There are no openings in this membrane which is made up of randomly arranged microfibrils rather than centrally radiating ones as in gymnosperms (Fig. 1.12).

The amount of axial parenchyma in wood of most angiosperms is considerably greater than in gymnosperms. In some tropical trees as much as half of the wood volume may consist of axial parenchyma. However, in most Temperate Zone trees axial parenchyma makes up less than 50% of the wood volume, and in some only a few percent. In *Populus* the amount of axial parenchyma is negligible.

The fact that the pattern of arrangement of axial parenchyma is relatively constant for various genera is of considerable value in wood identification. The two major classifications of axial parenchyma of angiosperms are (1) apotracheal (arranged independently of pores or vessels), and (2) paratracheal (associated with vessels or tracheids). Apotracheal parenchyma may be further subdivided as marginal (found singly or as a band at the growth ring boundary), diffuse (distributed as single cells in no characteristic pattern), or banded (in concentric bands).

The arrangement of paratracheal parenchyma may be vasicentric (forming a complete sheath around a vessel), scanty (a few cells around a vessel), aliform (extending laterally from the vessels in winglike projections), and confluent (aliform parenchyma so arranged as to coalesce into irregular tangential or diagonal bands). Some examples of arrangement of axial parenchyma are shown in Fig. 1.15.

Transverse Elements

The rays of angiosperms vary much more in width, height, and spacing than do the rays of gymnosperms (Fig. 1.16). Usually the rays of angiosperms are two or more cells wide and in some genera, such as *Quercus*, they may be up to 30 cells wide. Some species of angiosperms have rays of two size classes with the smaller rays being only one cell wide. A few genera (e.g., *Alnus*, *Carpinus*, *Corylus*) have "aggregate" rays which consist of groups of narrow, closely spaced rays with intervening tracheary tissue (Fig. 1.17). These aggregates often appear to be a single, very wide ray. Ray height is also extremely variable in angiosperms. The lowest rays are only a few microns high and the tallest ones may exceed 2 in. in height. As an extreme case, ray height may be equivalent to internode length of several inches, as in *Piper*.

Rays of angiosperms are made up exclusively of parenchyma cells. Ray cells are variously classified. They may be radially oriented (procumbent) or

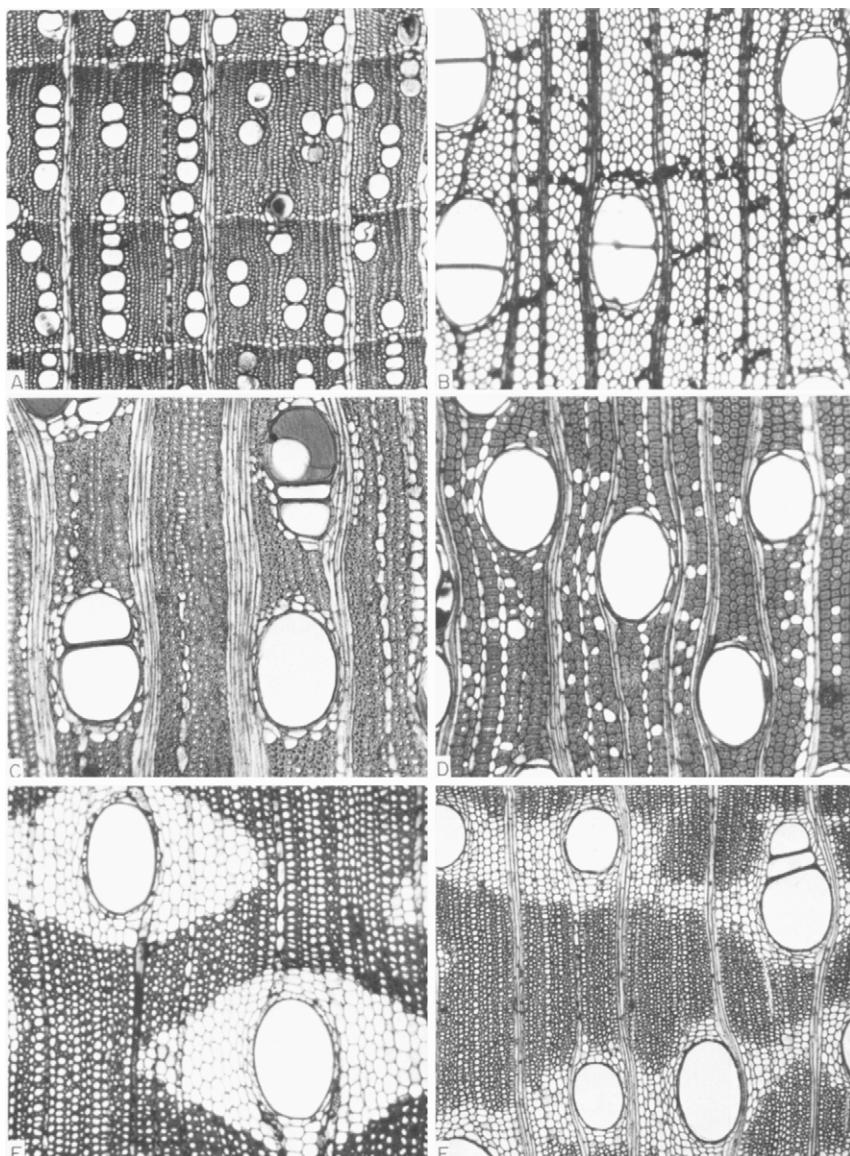


FIG. 1.15. Variations among species in arrangement of axial parenchyma. (A) *Fagara flava*, parenchyma apotracheal, marginal; (B) *Juglans regia*, parenchyma, apotracheal, diffuse in aggregates; (C) *Khaya grandifoliola*, parenchyma paratracheal, vasicentric; (D) *Gouania glabra*, parenchyma paratracheal, scanty; (E) *Berlinia grandiflora*, parenchyma paratracheal, aliform; (F) *Chlorophora excelsa*, parenchyma paratracheal, aliform and also locally confluent. [From Brazier and Franklin (1961). Reproduced by permission of the Controller of Her Britannic Majesty's Stationery Office.]

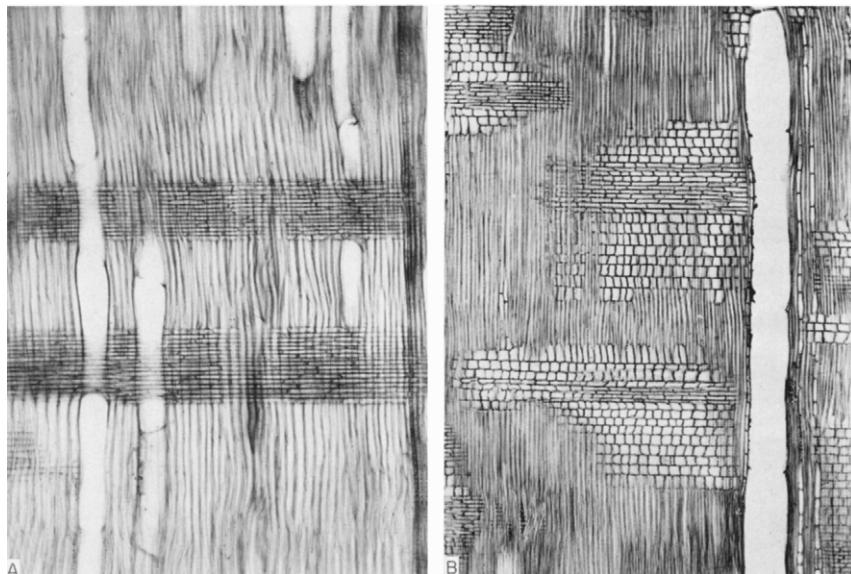


FIG. 1.16. Variations in ray structures. (A) *Acer campestre* with ray tissue homogeneous in which rays are composed entirely of procumbent cells; (B) *Nauclea didderichii*, with rays composed of procumbent, upright, and square cells. [From Brazier and Franklin (1961). Reproduced by permission of the Controller of Her Britannic Majesty's Stationery Office.]

vertically oriented (upright). Rays are classified as homocellular when comprised of parenchyma cells of similar size and shape, and heterocellular when cell size and shape are dissimilar (Fig. 1.16). The structure and size of pits in ray parenchyma cells, which may be simple to bordered, is used as a diagnostic feature in wood identification.

BARK

The bark is a much more complex tissue system than the wood. In a mature tree the bark includes all tissues outside the cambium (the inner living phloem and dead outer tissues called rhytidome). More specifically, in tissues which have gone into secondary thickening, bark tissues include primary and secondary phloem, cortex, and periderm. However, in stems not yet undergoing secondary thickening, only the primary phloem and cortex are included in the bark.

Phloem Structure

Phloem tissues may be classified as primary or secondary. The primary phloem, which was initiated in the embryo, differentiates from procambium.

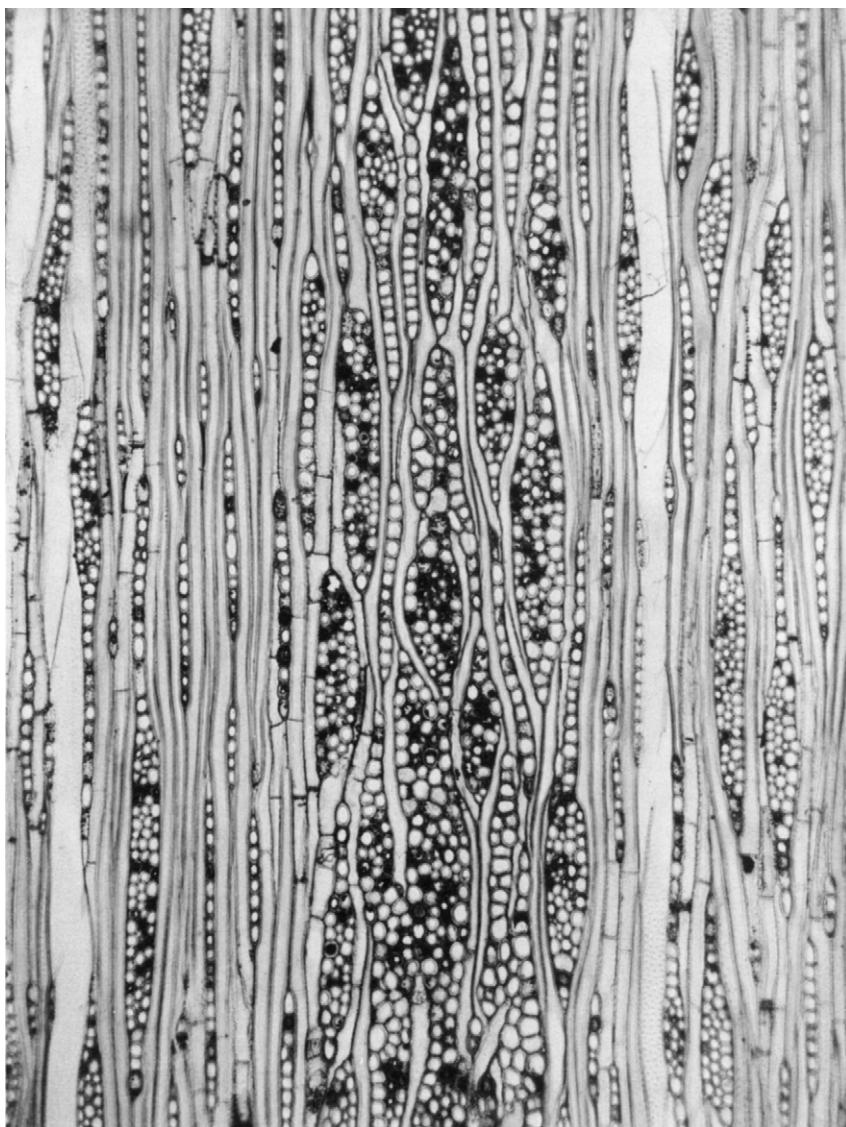


FIG. 1.17. Part of an aggregate ray of *Carpinus betulus*. [From Brazier and Franklin (1961). Reproduced by permission of the Controller of Her Britannic Majesty's Stationery Office.]

Production of secondary phloem by cambial activity results in pushing the primary phloem outward until it eventually becomes crushed and is sloughed off from the periphery of the tree.

The cambium-produced secondary phloem consists of vertically and transversely oriented systems of cells. In gymnosperms the secondary phloem is relatively simple, consisting only of vertically oriented sieve cells, parenchyma cells and, often, fibers. The transversely oriented, generally uniseriate rays contain only parenchyma or parenchyma and albuminous cells. Vertical parenchyma often has resins, crystals, and tannins.

The secondary phloem of angiosperms is much more complicated and variable among species than the phloem of gymnosperms. Angiosperm phloem consists of vertically oriented sieve tubes, usually with companion cells, parenchyma cells, and fibers. The rays may be uniseriate, biserrate, or multiseriate. The axial and transverse systems may also have sclereids, laticifers, secretory elements, idioblasts, and crystals.

Bark Formation

In most species the epidermis of young stems cannot increase in diameter as the stem increases in girth. Hence, the epidermis splits and disintegrates, usually during the first year. However, sometime prior to the loss of the epidermis secondary tissues called periderms form, usually in the cortex beneath the epidermis or, less commonly, from the epidermis or pericycle. Periderms are three layered and consist of (1) the cork cambium (phellogen), a secondary lateral meristem, and its derivative tissues, (2) pheloderm cut off to the inside and (3) phellem (cork) to the outside (Fig. 1.18). As the stem subsequently increases in diameter, new periderm layers form in deeper cortical tissues and eventually in the secondary phloem. In many species the initial periderm appears in stem transections as a cylinder, but subsequent periderms develop as short arcs. Tissues outside the periderms soon perish as they are isolated from food and water by the impermeable layers of cork in the periderm. Periderm formation is discussed in more detail in Volume II, Chapter 1.

In an adult tree the layer of inner bark stays of about the same thickness because old inner bark becomes outer bark about as rapidly as new inner bark is formed. The bark is thinner than the wood because (1) more xylem than phloem cells are cut off annually by the cambium; (2) phloem cells, unlike xylem cells, collapse usually after the first year; and (3) variable amounts of dead outer bark are sloughed off, whereas all xylem cells are retained. Bark patterns vary among species from smooth to scaly to deeply fissured ones. Reasons for these variations are discussed in Volume II, Chapter 2.

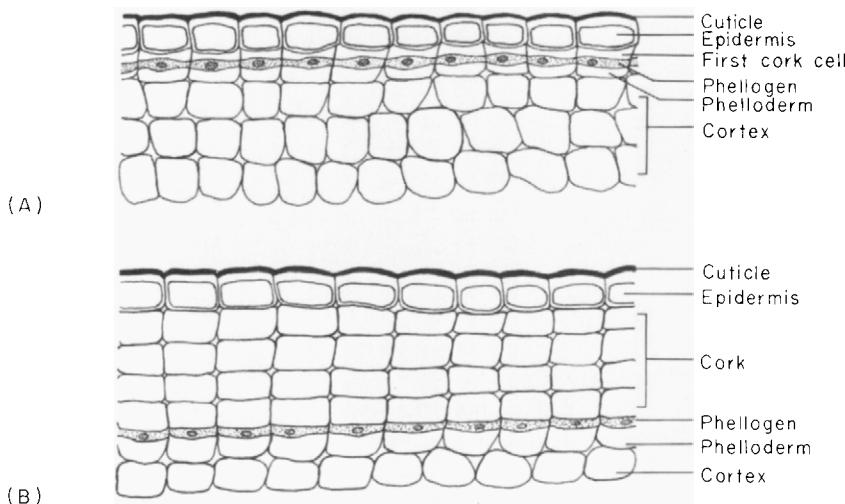


FIG. 1.18. Transection of stem portion showing origin of phellogen (A) and development of tissues by division of phellogen cells (B).

Roots

It is difficult to classify rooting characteristics of different species of trees because site and soil conditions sometimes modify root growth so much that species characteristics are obscured. One system of nomenclature which is used in Europe for the different parts of a root system is given in Fig. 1.19. Recently emerged seedlings of forest trees have a positively geotropic radicle which subsequently either becomes a taproot, is suppressed, or dies back (Aldrich-Blake, 1929). Whereas oaks and hickories retain taproots the initial taproot of basswood (*Tilia americana*) is replaced in the early years by a root system with predominantly lateral roots (W. C. Ashby, 1962). Old trees usually can be classified into those with deeply penetrating taproots or those with slowly growing primary roots and very extensive, fast-growing laterals (Kramer and Kozlowski, 1960).

As tree seedlings age their root form often is altered by environment, but, as mentioned, there is wide variation among species in root plasticity. For example, the root system of *Acer pseudoplatanus* consists of a taproot with evenly spaced, short laterals. Its form is not altered substantially under a variety of environmental conditions. In contrast, *Fraxinus* seedlings have long or short taproots and varying numbers of lateral roots, depending on the environment (Majid, 1954). Numerous examples of changes in root

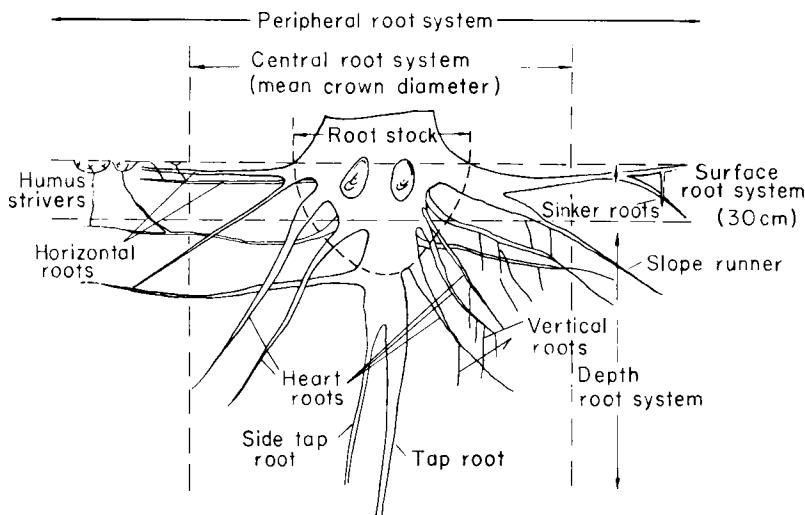


FIG. 1.19. Schematic representation of a root system of a mature tree. [From Lyr and Hoffmann (1967)].

type in different environments exist and only a few will be cited. The extreme plasticity of roots of *Pinus sylvestris* was described by Vomperskij (1959) who divided roots of seedlings of this species into five distinct types associated with differences in soil drainage. The types ranged from a root system with a vertical taproot and horizontal spreading roots at its lower end and a rooting depth of 30 to 55 cm, to one with no taproot and a rooting depth of 15 to 20 cm. In *Malus*, excessive soil moisture decreased the amount of absorbing roots to about 10% of that present under favorable moisture conditions. Drought also caused a marked reduction in the number of absorbing roots (Ermeev, 1960).

Species of *Eucalyptus* in dry areas develop a long taproot with few, poorly developed laterals. On good sites, however, they develop a shallow, fibrous root system (Zimmer and Grosse, 1958). *Eucalyptus* is said to have three types of roots in the same root system. First there are descending "heart" roots. Branching from these, or from the stem base, are horizontally extending roots. Finally, there are small branch roots. In general, the more favorable the environment for root growth, the greater the number of small branch roots (W. R. Day, 1959). *Acer rubrum* is rather plastic and develops shallow, lateral roots in swamps and deep taproots in upland soils (Kramer and Kozlowski, 1960). *Pinus contorta* roots also show considerable environmental amplitude. They show diversity with soil conditions as well as between individual trees in the same soil. Although a taproot is maintained in *Pinus*

contorta it sometimes is bent or stunted and may be obscured by many "sinkers" descending vertically from the bases of lateral roots. Before the polewood stage is reached, at about 40 years, there is a tendency for sinkers to develop, giving the entire root system a heart-shaped form, but variations from this pattern frequently occur. Most of the lateral roots are in the upper few inches of soil. Predominant in modifying the hereditary pattern of the *Pinus contorta* root system are soil texture or structure, soil moisture, and fertility (K. W. Horton, 1958a). In the unique basalt-pumice soils of the Blue Mountains of Northeastern Oregon a very high proportion of *Pinus contorta* roots were found in the surface pumicite layer, probably in response to readily available moisture there (Bishop, 1962). *Robusta* coffee trees have a straight taproot up to 90 cm long, but it becomes physiologically less important with increasing age. In older trees a superficial root system of laterals and secondary roots forms a rather dense and uniform network around the stem over an area of 7 to 8 m² (Hatert, 1958).

HETERORHIZY

Most pines have a "heterorhizic" root system made up of long and short roots (Aldrich-Blake, 1930; Kozlowski and Scholtes, 1948; Wilcox, 1964, 1968). The long roots consist of the main root and fast growing laterals of the first and second order which account for the overall development of the root system (Figs. 1.20-1.22). Long roots are considered permanent and they increase in diameter by cambial growth. The ephemeral and slow growing short roots which occur along the long roots have an apical meristem but not a true rootcap. Short roots lack secondary growth and most disappear during their first or second year. They commonly are converted to mycorrhizae (Volume II, Chapter 6). The long roots of pines, which are important in developing the framework of the root system, have been further subdivided into "pioneer" and "mother" roots by Noelle (1910) and Aldrich-Blake (1930). Wilcox (1964) added a third category of "subordinate mother roots" for *Pinus resinosa*. Pioneer roots, the largest-diameter members of the pine root system, were so named by Noelle (1910) because they accounted for rapid extension of the root system. Pioneer roots are never abundant and generally can be found during the late spring and late summer when root growth is most active (Wilcox, 1964). Mother roots, so named because of their profuse branching, are smaller in diameter and shorter in length than pioneer roots. The subordinate mother roots of *Pinus resinosa* that were described by Wilcox (1964) were finer and of smaller diameter than mother roots. They were comparable to second-order laterals of two-year-old seedlings (Table 1.4).

As Wilcox (1962) explained, forestry literature in the past tended to

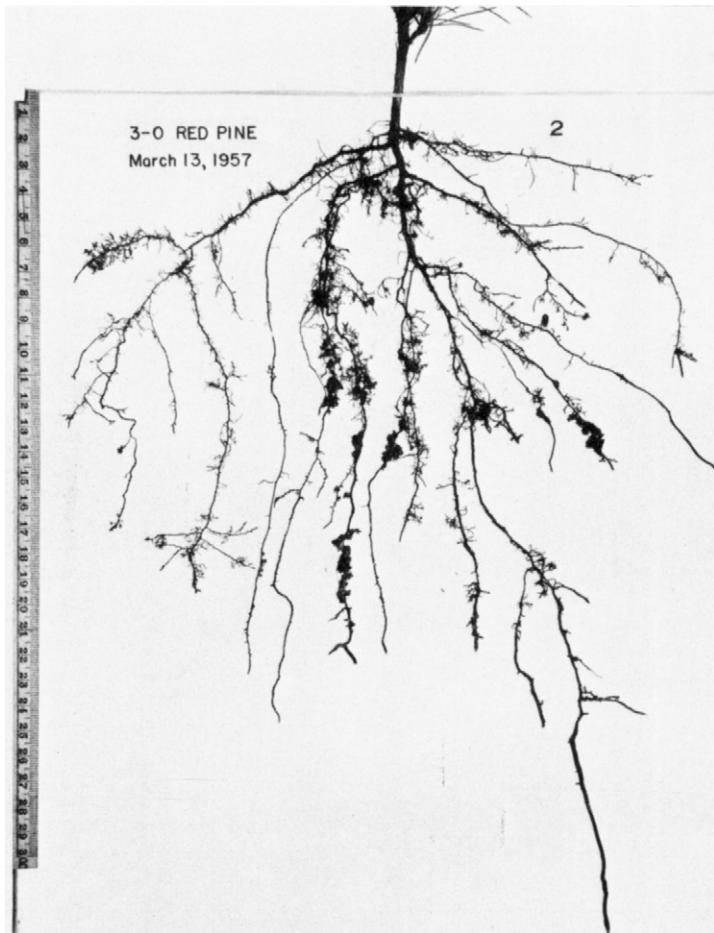


FIG. 1.20. Morphological features of roots of *Pinus resinosa*. Heterorhizic roots of *Pinus resinosa*. (Photo courtesy H. Wilcox.)

oversimplify in implying that both long and short roots are present in tree root systems, probably because of the association of short roots with mycorrhizae. Although short roots occur throughout the Pinaceae, Betulaceae, Fagaceae, and a few other gymnosperms, they are absent in many woody plants. *Libocedrus*, for example, like other plants in the Cupressaceae, does not develop a heterorhizic root system.

The system of classification based on long and short shoots is not always useful because, as Leshem (1965) noted, short roots eventually may be converted into long roots, or into thickened anchor roots capable of absorbing water at or near the tips.

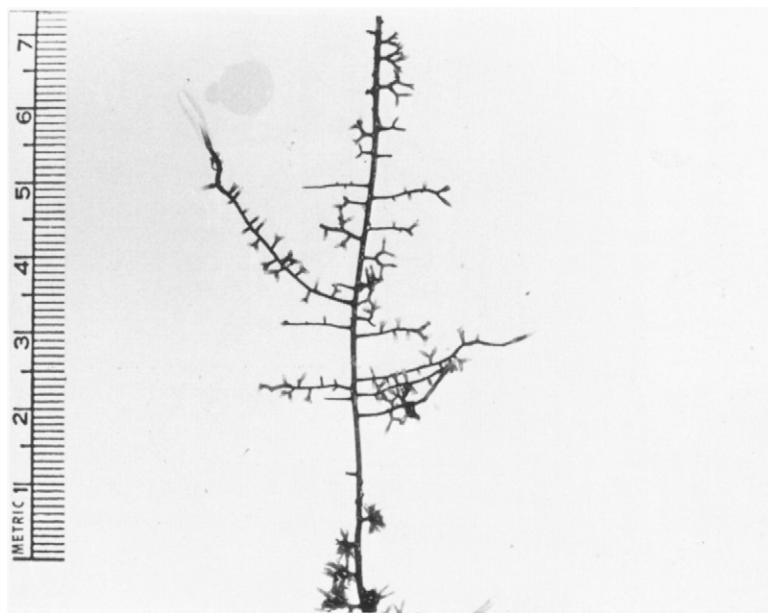


FIG. 1.21. Morphological features of roots of *Pinus resinosa*. Root portion of a first-order lateral. (Photo courtesy of H. Wilcox.)

TABLE 1.4

CLASSIFICATION, DISTRIBUTION, AND DIAMETERS OF ROOTS OF 2-YEAR-OLD NURSERY SEEDLINGS AND ADULT *Pinus resinosa* TREES^a

Class of roots	Number of roots	Diameter (mm)			
		Mature Trees		Seedlings	
		Average	Range	Average	Range
Pioneer	10	1.66	(1.32-1.81)		
Mother	26	0.85	(0.74-1.21)		
Subordinate mother	37	0.54	(0.36-0.71)		
Short roots	207	0.42	(0.23-0.50)	0.34	(0.26-0.41)
Primary				1.03	
First-order laterals				0.99	
Second-order laterals				0.55	

^a From Wilcox (1964).

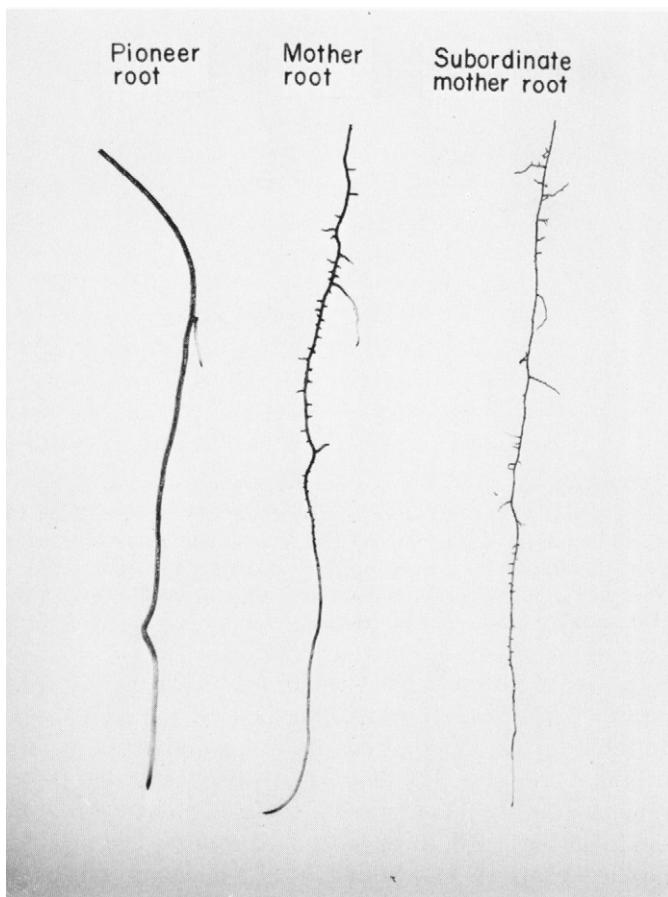


FIG. 1.22. Morphological features of roots of *Pinus resinosa*. Terminal portions from various classes of long roots from 30-year-old trees. [From Wilcox (1964)].

WOODY AND NONWOODY ROOTS

Clowes (1950) and Lyford and Wilson (1964) considered the classification of roots as long or short to be inadequate for certain angiosperms. Lyford and Wilson (1964) preferred to classify *Acer rubrum* roots as woody or non-woody. They viewed a mature root system as a framework of permanent woody roots bearing many fans of relatively short-lived, nonwoody roots. The woody roots extended from the stem base in essentially straight lines, tapering rapidly near the stem to ropelike structures, with relatively small

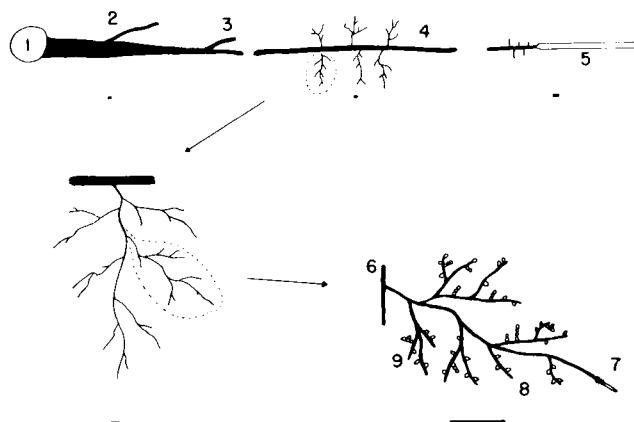


FIG. 1.23. Relationships of woody and nonwoody roots in *Acer rubrum*. 1, Stem; 2, adventitious roots in zone of rapid taper; 3, lateral root; 4, nonwoody root fans; 5, tip of woody root and first-order, nonwoody roots; 6, second- and higher-order nonwoody root emerging from first-order nonwoody roots; 7, uninjected tip of second-order nonwoody root with root hairs; 8, third-order nonwoody root with bead-shaped mycorrhizae; 9, fourth-order nonwoody root with mycorrhizae. [From Lyford and Wilson (1964).]

diameters (up to 2.5 cm) and great length (up to 25 m). At approximately 1–5 m intervals, lateral woody roots branched off the main root. The first nonwoody roots emerged at right angles to a woody root at intervals of 1 to 3 cm behind its root tip. The first-order woody roots and those of higher order springing from them comprised a complex pinnate “root fan” about 20 to 40 cm long (Fig. 1.23). Such short-lived root fans became less frequent on old and thick roots. As shown in Table 1.5 diameters of tips and lengths

TABLE 1.5
CHARACTERISTICS OF *Acer rubrum* ROOTS^a

Root type	Approximate tip diameter (mm)	Approximate final length	Frequency of laterals per cm of length	Frequency of mycorrhizae
Woody	2.0	10–25 m	0.3–1	None
Nonwoody				
First order	0.5–1.0	20–40 cm	2–3	None
Second order	0.5–1.0	10–15 cm	3–10	Low
Third order	0.3–0.5	1–2 cm	3–10	High
Higher than third order and mycorrhizae	0.2–0.3	1–10 mm	—	Almost all

^a From Lyford and Wilson (1964).

of nonwoody roots decreased in successively higher orders, but distribution of mycorrhizae and lateral roots increased.

SUBERIZED AND UNSUBERIZED ROOTS

Individual roots of trees may continue to grow for several weeks and produce lateral roots or they may stop growing after only a few weeks. The outer cortical tissues of roots remain white for a short time which in *Malus* may vary from 1 to 4 weeks during the summer and up to 3 months in the winter (Head, 1966). The outer tissues then turn brown and degenerate. The remaining central cylinder may or may not undergo secondary thickening. The onset of browning is associated with suberization.

As root systems age an increasing proportion of the total surface becomes suberized. Only the most recently formed roots are unsuberized and their total surface area is exceedingly small in comparison to the surface of the total root system. Kramer and Bullock (1966) followed seasonal changes in proportions of growing and suberized roots in *Pinus taeda* and *Liriodendron tulipifera* trees growing in North Carolina. The surface area of growing, unsuberized roots usually amounted to only a fraction of 1% of the total root surface area (Table 1.6). It exceeded 1% at only one sampling time

TABLE 1.6

SEASONAL VARIATION IN PERCENTAGE OF SURFACE AREA IN UNSUBERIZED AND SUBERIZED ROOTS UNDER A 34-YEAR-OLD *Pinus taeda* STAND IN NORTH CAROLINA^a

Date	Growing tips (%)	Mycorrhizal (%)	Total unsuberized (%)	Total suberized (%)
March	0.06	0.53	0.59	99.41
	0.15	1.20	1.35	98.65
	0.13	1.18	1.31	98.69
	0.13	1.64	1.77	98.69
	0.13	2.06	2.39	97.61
April	0.43	2.27	2.70	97.30
	0.39	5.09	5.48	94.52
	0.53	2.77	3.30	96.70
	0.34	5.30	5.64	94.36
May	0.72	5.76	6.48	93.52
	0.30	3.95	4.25	95.75
June	0.25	6.06	5.31	93.69
	0.48	3.05	3.53	96.47
	0.38	3.00	3.38	96.62
July	0.22	3.00	3.22	96.78
	0.54	2.38	2.92	97.08
	1.36	2.81	4.17	95.83
Nov. 11	0.61	2.84	3.55	95.83

^a From Kramer and Bullock (1966).

following a heavy rainfall in July. Most of the unshrubized root surface consisted of mycorrhizae, but the surface provided by growing tips plus mycorrhizal roots never exceeded 7% during the growing season. The total shrubized root surface area varied from more than 93–99% at various times during the year.

Although much emphasis has been placed on the importance of unshrubized roots in absorption of water and solutes, evidence is available that water can be absorbed through shrubized roots (Kramer and Bullock, 1966). The water absorbed by shrubized roots apparently enters through lenticels, crevices around branch roots, and openings left by death of branch roots (Addoms, 1946; Kramer, 1946).

SPECIALIZED ROOT SYSTEMS

In addition to the normal types of roots discussed here many interesting specialized and modified tree roots occur. Among these are various forms of aerial and adventitious roots, grafted roots, nodulated roots, root buttresses, "knee" roots and pneumatophores, and mycorrhizal roots. These are discussed in Volume II, Chapter 6.

Generalized Growth Characteristics

In its simplest form growth of woody plants involves addition of tissues to roots, stems, and leaves, as well as reproductive structures, through cell division and production of new protoplasm. Trees grow both in length and in girth through the activity of meristematic tissues which make up a very small fraction of their mass. Extension growth results from bud expansion through activity of many terminal growing points distributed over the stem, branches, and twigs. Growth in length of roots also occurs from many terminally located meristems. Such apical growing points contain meristematic cells which divide to produce new cells. Actually growth consists of several sequential phases which include division, elongation, differentiation, and maturation of cells. These occur in order at various distances from the tips of shoots and roots. The formation of appendages such as buds, leaves, branches, and fruits is also traceable to apical growth (Kramer and Kozlowski, 1960).

Shoot growth usually, but not always, encompasses both growth of leaves and expansion of internodes. Duration of these two aspects of shoot growth may or may not be correlated. In some shoots bud opening is followed by maturation of leaves with no appreciable internodal growth. When internode elongation occurs, it may or may not be correlated with leaf growth. For example, in some pines internode expansion ceases long before leaves stop

growing. Such variations in shoot growth are discussed in more detail in Chapters 5, 6, and 7 of this volume.

Growth in thickness of trees is primarily traceable to a vascular cambium located between the bark and wood and extending from the tips of all twigs, branches, and main stem into the roots. The cambium is a very thin sheath of meristematic tissue which each year gives rise to additional xylem cells to the inside and phloem cells to the outside. Layers of new xylem and new phloem (inner bark) are thus inserted annually between older layers of the same kind, causing the stem to increase in girth. A small amount of increase in thickness is traceable to activity of a cork cambium (phellogen).

The prominence of annual rings of wood as seen in cross sections of stems and branches of trees of the Temperate Zone is the result of variations in cell size and density of wood within each annual growth increment. The relatively dense wood produced late in the growing season abuts against the less dense wood formed early in the following season, producing a line of demarcation between annual growth increments. As pointed out in more detail in Volume II, Chapter 2, many tropical trees, in contrast to Temperate Zone trees, do not enter extended periods of dormancy and hence do not produce distinct annual rings.

Various parts of trees grow at different rates and often at different times of the year. For example, the seasonal duration of shoot growth usually is less than that of cambial growth in the same tree, and growth in length of roots lasts longer than either of these (Fig. 1.24). Also, the amount and duration of cambial growth vary between the stem and major roots. Hence,

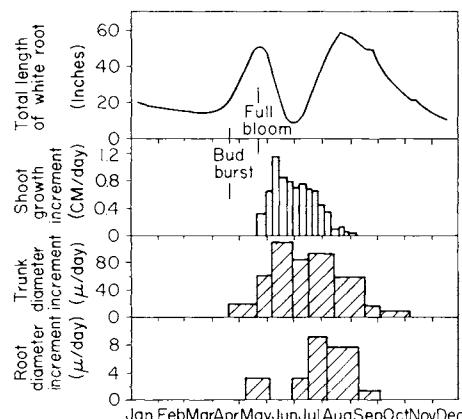


FIG. 1.24. Seasonal variation in amount and duration of root and shoot elongation and diameter growth of the trunk and roots of Worcester Pearmain apple trees. [From Head (1968).]

the general conclusions drawn about the nature of tree growth and its control will depend to a large extent on what is measured—increase in length of terminal or lateral shoots, increase in root length, increase in diameter in various parts of a woody axis, growth of reproductive tissues, or dry weight increment of parts of trees, whole trees, or stands. It makes considerable difference also if the architecture of a tree stem is evaluated in terms of the varying pattern of xylem increment during each succeeding year of growth or only the pattern of addition of the xylem sheath within a single growing season. Furthermore, specific growth responses are conditioned by aging of trees. Such growth characteristics as balance between increment in reproductive and vegetative tissues and amounts of vegetative growth, as well as distribution of new tissues throughout the tree, vary greatly among young and old trees. The effects of maturation and aging on growth of trees are discussed further in Chapters 3 and 4 of this volume.

Viewed broadly, the growth of a tree as a whole is exceedingly intermittent whether considered for several years, within a year, or even within a single day. Trees of the Temperate Zone fluctuate annually from a state of endogenously controlled, deepseated winter dormancy, to active meristematic activity during the growing season. But even during the frost-free season in the Temperate Zone, trees fluctuate from periods of active and variable growth to ones of inactivity or quiescence. Whereas many tropical trees have been reported as growing more or less continuously throughout the year, close examination shows that their rates of growth vary greatly with time. Hence, they too grow somewhat spasmodically. This is discussed in more detail in Chapters 5 to 8 of this volume and Chapters 1 to 5 of Volume II.

Unfortunately many published growth curves tend to represent shoot growth or cambial growth as essentially a continuous process characterized by a smooth sigmoid curve over the growing season. Such curves usually are based on averaged observations rather widely spaced in time and taken on a large number of trees. When observations are taken frequently on individual trees, however, they emphasize variability and intermittency of tree growth. Whereas typical sigmoid growth curves are very valuable for general studies of trends in productivity, they are not always useful in biological studies of growth characteristics because they may obscure short-time fluctuations in growth of individual trees. The reader is cautioned that the literature is replete with reports of growth characteristics of trees based on observations taken only on parts of trees. It cannot be emphasized too strongly that the perennial woody plant is a three-dimensional structure which grows intermittently in length and girth, with some of its parts often growing while others are inactive.

Among the most interesting features of growth of woody plants are variations in rates and patterns of growth of different species. Much of this

variability is genetically controlled and some of it is traceable to variations in response to environmental stress as a result of different morphological characteristics. For example, deep-rooted species often survive drought more successfully than shallow-rooted ones, because of better internal water relations of the former. But whatever the specific reasons for differences in growth characteristics among species, it is clear that communities of trees such as plantations or natural forests are complex and dynamic ecosystems whose components undergo severe competition. The growth of individual members of such complex plant communities often is inhibited, and many trees are eliminated by competition. Therefore, the ultimate species composition of forests reflects variations in capacity for maintaining high rates of growth for a long time (Winget and Kozlowski, 1965b).

GROWTH REQUIREMENTS

To survive and grow woody plants require such materials as water, foods, nitrogenous compounds, mineral salts, hormonal growth regulators, vitamins, and possibly other substances. Internal control of growth of both vegetative and reproductive tissues involves close interdependency between roots and shoots as sources of essential growth controlling factors. Roots depend on leaves for both sugars and hormonal growth regulators. Shoots, in turn, depend on roots for supplying water and mineral elements. In addition, the roots play an essential role in protein synthesis. In apple trees, for example, nitrate reduction occurs primarily in the fine roots. The amino acids, which form in roots, are translocated to shoots where they are used in protein synthesis. As the shoots lack nitrate reductase they cannot utilize nitrates. Similarly, shoot growth in peach trees depends on organic nitrogen compounds supplied by the roots (Luckwill, 1959). Throughout its life span a tree is supplied by its leaves and roots with essentials for growth over increasingly longer translocation paths. This necessitates a delicate balance between organs and precise correlations in rates of physiological processes especially photosynthesis, hormone synthesis, respiration, nitrogen and fat metabolism, enzymatic activity, translocation, and assimilation. The amount of growth which occurs over a given time depends to a considerable extent on important regulatory mechanisms of food conversion in addition to food synthesis.

In large woody plants rapid translocation of various growth requirements must occur through the stem, between the mutually interdependent and widely separated roots and shoots. The principal conducting tissues are xylem and phloem. These vascular tissues traverse the woody plant, extending as they do from the small roots through the stem and branches to the tiny veins in leaves and reproductive structures.

Carbohydrates are translocated through sieve elements of the phloem or inner bark. Sieve elements differ from the water conducting elements of the xylem in containing cytoplasm and in lacking cell walls. The efficiency of food translocation in woody plants is quite remarkable because the avenue for carbohydrate translocation is a layer of phloem only a fraction of a millimeter thick (Kozlowski and Keller, 1966).

Water is translocated largely through the lumens of fully differentiated xylem vessels in angiosperms and tracheids in gymnosperms. Essential to water transport through the xylem are various types of openings including intercellular spaces, disintegrated end walls, cell lumens, and pits. The latter two allow passage from one cell to another.

Suggested Collateral Reading

- Browning, B. L., ed. (1963). "The Chemistry of Wood." Wiley, New York.
- Büsgen, M., and Münch, E. (1931). "The Structure and Life of Forest Trees" (transl. by T. Thomson). Wiley, New York.
- Coté, W. A., Jr., ed. (1965). "Cellular Ultrastructure of Woody Plants." Syracuse Univ. Press, Syracuse, New York.
- Coulter, J. M., and Chamberlain, C. J. (1917). "Morphology of Gymnosperms," Univ. of Chicago Press, Chicago, Illinois.
- Desch, H. E. (1968). "Timber, its Structure and Properties." Macmillan, New York.
- Eames, A. J. (1961). "Morphology of the Angiosperms." McGraw-Hill, New York.
- Esau, K. (1960). "Anatomy of Seed Plants." Wiley, New York.
- Esau, K. (1965). "Plant Anatomy." Wiley, New York.
- Fahn, A. (1967). "Plant Anatomy." Pergamon Press, Oxford.
- Foster, A. A., and Gifford, E. M., Jr. (1959). "Comparative Morphology of Vascular Plants." Freeman, San Francisco, California.
- Jane, F. W. (1956). "The Structure of Wood." Black, London.
- Jane, F. W. (1963). Botanical aspects of wood science. *Vistas Bot.* **2**, 1-35.
- Kozlowski, T. T., ed. (1962). "Tree Growth." Ronald Press, New York.
- Kozlowski, T. T. (1963). Growth characteristics of forest trees. *J. Forest.* **61**, 655-662.
- Kramer, P. J., and Kozlowski, T. T. (1960). "Physiology of Trees." McGraw-Hill, New York.
- Lyr, H., Polster, H., and Fiedler, H. J. (1967). "Gehölzphysiologie." Fischer, Jena.
- Panshin, A. J., De Zeeuw, C. E., and Brown, H. P. (1966). "Textbook of Wood Technology," Vol. I. Structure Identification, Uses, and Properties of the Commercial Woods of the United States. McGraw-Hill, New York.
- Romberger, J. A. (1963). Meristems, growth, and development in woody plants. *U.S. Dep. Agr., Tech. Bull.* **1293**.
- Sinnott, E. W. (1960). "Plant Morphogenesis." McGraw-Hill, New York.
- Stamm, A. J. (1964). "Wood and Cellulose Science." Ronald Press, New York.
- Thimann, K. V., ed. (1958). "The Physiology of Forest Trees." Ronald Press, New York.
- Zimmermann, M. H., ed. (1964). "The Formation of Wood in Forest Trees." Academic Press, New York.

Chapter 2

SEED GERMINATION AND SEEDLING DEVELOPMENT

Introduction

Growth of a tree begins with germination of its most important propagule, the seed. However, the chance that an individual seed will actually become a mature tree is very slim indeed. The stages of greatest mortality risk are those of the ungerminated embryo in the seed and of recently germinated seedlings. Under natural conditions remarkably high losses of seeds are traceable to lack of seed viability, seed dormancy, and injury or consumption of seeds by fungi, insects, and various higher animals. The seedbed itself often is unsuitable for germination of viable seeds, but if a seed should germinate the plant is subjected throughout its existence to possible attacks by various organisms and to environmental stresses. Many trees which survive the dangerous seed germination and seedling development stages also fail to reach maturity because of increasingly intense competition among plants (Kozlowski, 1949).

Lawrence and Rediske (1962) made a detailed appraisal of the fate of sown *Pseudotsuga menziesii* seeds. Pregermination losses amounted to 46%, with fungi 20%, insects and other invertebrates 10%, rodents 8%, and birds 3%, all contributing to early seed losses (Fig. 2.1). During the first year, 27% of the seeds failed to germinate, with damping-off fungi the primary agent causing seedling mortality. Gashwiler (1967) found in another study that, from the beginning of seed fall until the end of germination, only 12% of *Pseudotsuga menziesii* seeds survived, with 63% of the loss attributed to ground feeding birds and small mammals, and 25% to other agents. Birds and mammals showed a distinct preference for *Pseudotsuga* seeds over those of *Tsuga heterophylla* or *Thuja plicata*. Only about a fourth as many *Tsuga* seeds as *Pseudotsuga* seeds were taken, and only very small amounts of *Thuja* seeds.

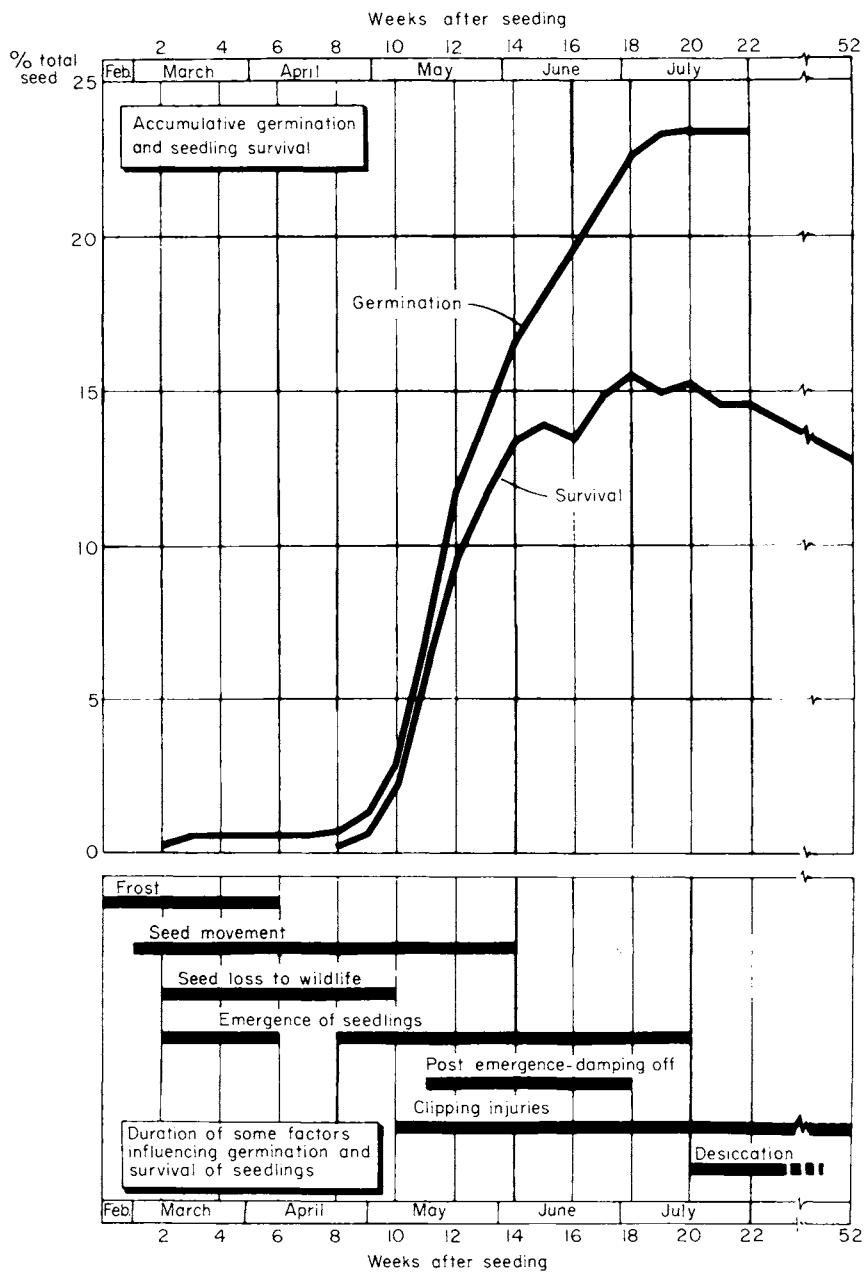


FIG. 2.1. Variations in germination and survival of *Pseudotsuga menziesii* seeds during one growing season. Duration of various factors influencing the ultimate fate of seedlings is given below. [From Lawrence and Rediske (1962).]

In some areas rodents account for very large seed losses. In Massachusetts, mice and moles consumed more pine seeds than could be sown economically by direct seeding. Rodents were capable of eating and storing all the naturally produced seeds except those which they failed to detect (Abbott, 1961). In East Texas, Stephenson *et al.* (1963) found that rodents were able to consume most of the 0.5 to 1 lb of pine seed per acre that normally was seeded directly. However, rodents did not interfere seriously with natural regeneration in good seed years, when 15 to 20 lb of seed per acre were available.

Germination of *Eucalyptus* seeds under favorable conditions in Australia may be as high as 80 or 90%, whereas survival under natural conditions often is less than 1% (Jacobs, 1955). The newly emerged seedling in the field shows sensitivity to drought, flood, frost, and insects. Its food reserves from the seed are low and its roots must become established quickly to absorb sufficient water and nutrients to enable the new leaves to photosynthesize efficiently. The primary cause of mortality of young *Eucalyptus* seedlings in Australia appears to be desiccation. Hot, dry days following germination produce spectacular losses of newly emerged seedlings. A significant percentage of seedlings survive behind obstructions such as stones and logs which protect them from direct insolation. These few examples emphasize the improbability of both seed germination and seedling survival. This chapter will discuss the nature and control of seed germination and seedling development.

Seed Structure and Composition

The seed is a ripened ovule consisting of an embryo and, in many seeds, an endosperm all enclosed in an envelope (Fig. 2.2). The embryo is a miniature plant made up of a radicle, a plumule or epicotyl, one or more cotyledons or first leaves, and a hypocotyl connecting the plumule and radicle. As may be seen in Fig. 2.3 the size of the embryo varies greatly in seeds of different species. In mature seeds of some species the embryo is a rudimentary structure whereas in other species it almost fills the seed (Fig. 2.3). Seeds of most woody angiosperms have two cotyledons. Those of gymnosperms have from two cotyledons to as many as eighteen (Table 2.1). Cotyledons usually either store foods or synthesize them. Cotyledons of some genera, such as *Juglans* and *Quercus* store foods which the growing seedling utilizes until secondary leaves become photosynthetically active. In other species, such as *Cornus*, the cotyledons store little food but become photosynthetically active shortly after they emerge from the ground. In the latter group, food storage in the seed occurs inside the embryo, usually in endosperm. Cotyledons may also absorb food stored in the endosperm and act as protection for the epicotyl during germination in species in which the cotyledons emerge from the seed.

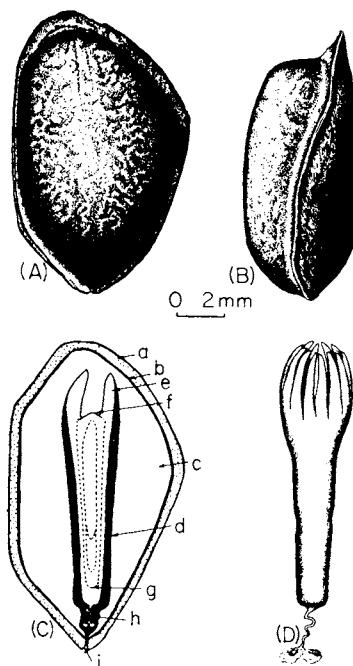


FIG. 2.2 Structure of mature seed of *Pinus lambertiana*. (A), (B) Exterior view of two planes. (C) Longitudinal section: *a*, seed coat; *b*, nucellus; *c*, endosperm; *d*, embryo cavity; *e*, cotyledons; *f*, plumule; *g*, radicle; *h*, suspensor; *i*, micropyle. (D) Embryo. [From Woody Plant Seed Manual (Anonymous, 1948).]

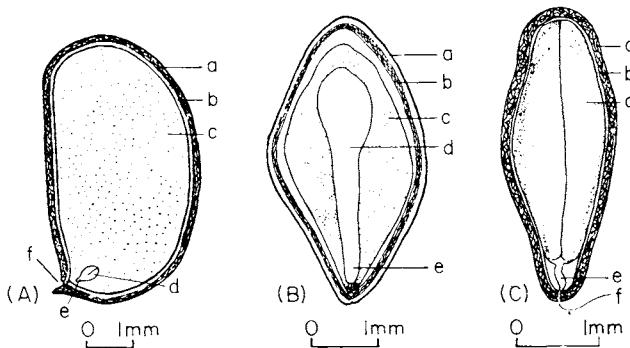


FIG. 2.3. Variations in seed structure. (A) *Aralia nudicaulis*, with large endosperm and small embryo; (B) *Tsuga canadensis*, with large embryo surrounded by endosperm; (C) *Amelanchier*, with no endosperm and embryo almost filling the seed cavity. *a*, Outer seed coat; *b*, inner seed coat; *c*, endosperm; *d*, cotyledon; *e*, radicle; *f*, micropyle. [From Woody Plant Seed Manual (Anonymous, 1948).]

TABLE 2.1
VARIATION IN NUMBER OF COTYLEDONS IN VARIOUS GENERA OF GYMNOSPERMS^a

Genus	Range in number of cotyledons	Average number of cotyledons
<i>Abies</i>	2-10	5.9
<i>Cedrus</i>	5-13	9
<i>Larix</i>	3-8	5.7
<i>Picea</i>	2-15	6.4
<i>Pinus</i>	3-18	8.1
<i>Pseudotsuga</i>	4-12	6.8
<i>Tsuga</i>	2-7	3.7

^a From C. R. Chowdhury (1962).

The seed coats, which provide the embryo with protection from desiccation or attacks by various pests, usually consist of an outer hard coat, the testa, and a thin and membranous inner coat. However, considerable variation occurs in seed coat characteristics. For example, in *Populus* and *Salix* the testa is very soft, whereas in *Crataegus* and *Ilex* it is very hard. In *Ulmus* both the inner and outer seed coats are membranous. The rather simple seed coats of gymnosperms vary from hard in *Pinus* to soft in *Abies*.

CHEMICAL COMPOSITION OF SEEDS

Seeds contain variable quantities of all three classes of foods, including carbohydrates, fats, and proteins. The proportions of these vary greatly among seeds of different species, with carbohydrates or lipids usually predominating. Whereas seeds of *Quercus* and *Acer* are noteworthy for high carbohydrate content, those of *Aleurites* and *Pinus* have high fat contents (Table 2.2). Although some seed proteins, such as enzyme proteins and nucleoproteins, are metabolically active, a large proportion is inactive. In addition to proteins, the nitrogenous material in seeds includes free amino acids and amides. The amides usually are glutamine and asparagine. Some alkaloids also occur. Other seed constituents include variable quantities of minerals, organic acids, phytosterols, phenolic compounds, vitamins, and growth regulators.

Environmental Control of Seed Germination and Seedling Establishment

As mentioned previously, nondormant seeds often are prevented from germinating by unsuitable environmental conditions. Among the most

TABLE 2.2
RELATIVE CARBOHYDRATE, FAT, AND PROTEIN CONTENTS OF TREE SEEDS^a

Species	Percentage of air-dried seeds		
	Carbohydrates	Fats	Proteins
<i>Acer saccharinum</i>	62.0	4.0	27.5
<i>Aesculus hippocastanum</i>	68.0	5.0	7.0
<i>Castanea vesca</i>	42.0	3.0	4.0
<i>Quercus pedunculata</i>	47.0	3.0	3.0
<i>Quercus alba</i>	58.4	6.8	7.4
<i>Aleurites moluccana</i>	5.0	21.0	62.0
<i>Pinus strobus</i>	4.8	35.4	30.2
<i>Pinus palustris</i>	4.5	31.7	35.2

^a From Mayer and Poljakoff-Mayber (1963) and Woody Plant Seed Manual (Anonymous, 1948).

important environmental factors controlling seed germination are water, temperature, light, oxygen supply, and biocides. Even if seeds germinate many young seedlings are killed because of environmental stresses which subsequently develop as well as attacks by fungi, insects, and higher animals. Some of the major factors controlling seed germination and environmental requirements for seedling establishment will be discussed briefly.

WATER

Seeds do not resume physiological activity until they imbibe a certain amount of water. Hence, water availability often controls seed germination (Figs. 2.4 and 2.5). Lack of dormancy in seeds with short life-spans often precludes germination in dry soils. In Arizona, for example, the phreatophyte *Tamarix* produces seeds abundantly from April to October but seed viability is retained for only a few weeks. Fresh seeds germinate rapidly, often in less than 24 hours. Germination depends on saturated soils. Receding spring and summer flows are ideal for germination. The young seedlings are very sensitive to drying and their survival depends on saturated soils for 2 to 4 weeks after seed germination occurs (J. S. Horton *et al.*, 1960).

Satoo (1966) studied effects of soil moisture availability on germination of seeds of *Pinus densiflora*, *P. thunbergii*, and *Chamaecyparis obtusa*. As soil moisture content decreased from field capacity, seed germination of all three species decreased but germination of *Chamaecyparis obtusa* seeds was about three times as sensitive to drying soil as were seeds of either pine. When soil moisture contents were converted to diffusion pressure deficits (DPD) germination of *Chamaecyparis obtusa* seeds decreased by about 6% for each

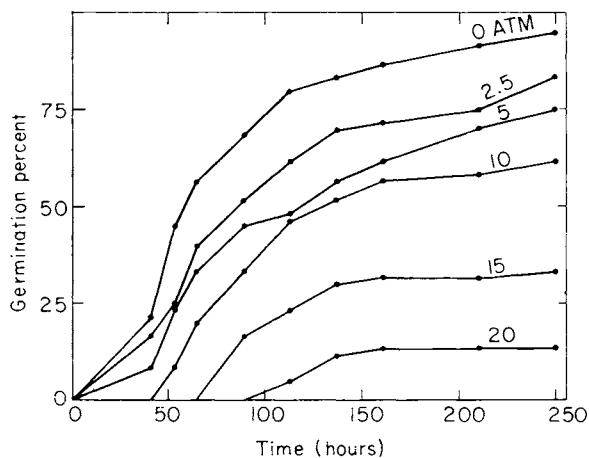


FIG. 2.4. Cumulative germination of *Quercus palustris* acorns in sucrose solutions with various osmotic stresses. [From F. T. Bonner (1968).]

1 atm increase in DPD. Corresponding decreases were 2.5% for *Pinus densiflora* seed and 1.5% for *P. thunbergii* seeds. Soil moisture contents in excess of field capacity inhibited seed germination of all three species but seeds of *Chamaecyparis* tolerated excessive soil moisture (or deficient soil air) much better than did seeds of either of the pines.

Both total germination and rate of germination of *Quercus palustris* acorns were decreased by increasing osmotic stress with sucrose solutions and impeding water uptake (Fig. 2.4). When acorns were placed in the sucrose solutions their moisture content averaged 45%. Those in solutions with low osmotic stress germinated first. Their moisture contents were 65–75%. By comparison, the few acorns that germinated in solutions of 20 atm osmotic pressure had moisture contents of only 45–49% (F. T. Bonner, 1968).

G. S. Allen (1962) showed that a high threshold level of hydration was effective for stratifying dormant *Pseudotsuga menziesii* seeds. He recommended bringing the initial moisture content of seeds up to 70%. Such seeds could be dried, after stratification, at room temperature for 24 hours and stored at 0° to 2°C in closed containers for long periods without loss of germinative capacity or decreased germination rate. Seeds that initially were drier showed sensitivity to further drying.

It should be remembered that the seed coats of hard-coated seeds, such as those of legumes, often act as a barrier which prevents inner tissues from absorbing water. Hence, they often do not germinate readily in soil with a high soil moisture content.

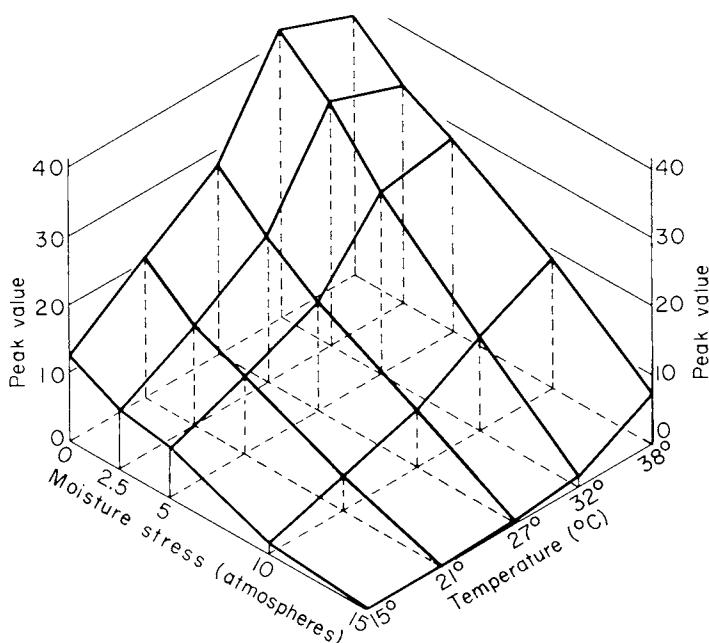
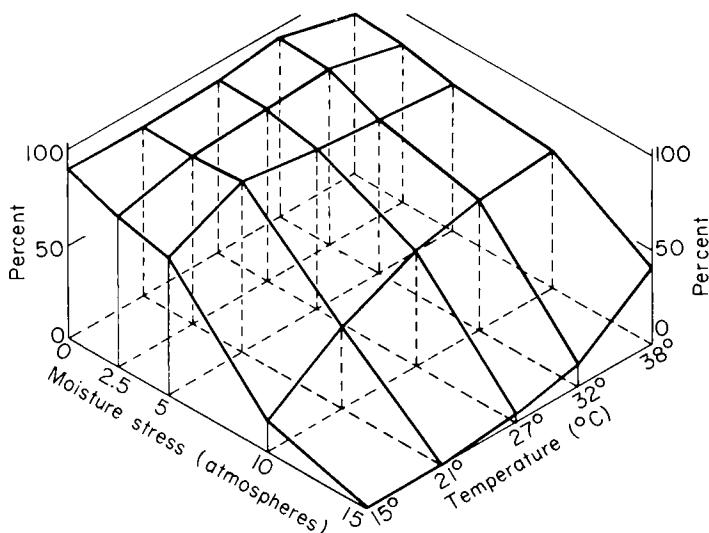


FIG. 2.5. Effects of water deficit and temperature on peak values (left) and final germination percent of fresh *Populus deltoides* seeds. [From Farmer and Bonner (1967).]

TEMPERATURE

Although seeds of many species will germinate over a rather wide temperature range, those of some species have rather definite temperature requirements. Whereas *Fagus* seeds germinate at temperatures slightly above freezing, those of other species require much higher temperatures. Seeds of *Pinus contorta* germinate at about the same rate at 20°C as at 30°C (Critchfield, 1957). Among seeds which germinate well only over a specific temperature range are those of *Acer negundo*. Roe (1941) found that seeds of this species showed 67% germination as temperatures alternated between 50° and 77°F, but only 12% germinated as temperatures alternated between 68° and 86°F. *Acer platanoides* seeds germinated best between 41° and 50°F.

Seeds of many species will germinate at constant temperatures, while others require diurnal temperature fluctuations, with the majority of species falling into the latter group (Hatano and Asakawa, 1964). For example, after seeds of *Fraxinus mandshurica* var. *japonica* were first exposed to moist, low temperature treatment and then placed in a constant temperature of 25°C, only a few germinated. At a constant temperature of 8°C seed germination



was greatly delayed. By comparison, alternating temperatures between 8°C for 20 hours and 25°C for 4 hours each day greatly accelerated seed germination (Asakawa, 1956). Germination of *Pinus densiflora* and *P. thunbergii* seeds also was accelerated by diurnal thermoperiodicity (Asakawa, 1959). The favorable influences of fluctuating temperatures may reflect a balance of intermediate compounds of respiration at the high temperature period of the cycle which inhibit germination at the high temperature but promote it at a lower one (E. H. Toole *et al.*, 1956).

LIGHT

Light affects seed germination of many species of trees. Whereas light intensity has relatively minor effects, photoperiod and wavelength often have pronounced effects. Seeds usually germinate at low light intensities, with those of *Picea* requiring only 0.08 lux; *Betula*, 1 lux and *Pinus*, 5 lux. Seeds of a few species require up to 100 lux for germination (L. R. Jones, 1961).

Photoperiod

For seeds of most species of forest trees the maximum total germination and speed of germination occur in daily light periods of 8 to 12 hours. Interrupting the dark period with a short light flash or increasing temperature usually give the same effect as lengthening the duration of exposure to light. A few examples of variation in photoperiodic requirements among species will be given. In *Tsuga canadensis* 8- or 12-hour days induced maximum

seed germination with no added response by increasing daylength to 14 or 20 hours (Olson *et al.*, 1959). Eucalyptus seeds germinate well in 8-hour days and those of *Betula* in 20-hour days. Seeds of *Pseudotsuga menziesii*, however, germinated in continuous light or 16-hour days, but not in 8-hour days (L. R. Jones, 1961). An interesting effect of temperature on the light effect in germination of *Betula pubescens* was shown by Black and Wareing (1955). At 15°C there was a requirement of several cycles of long day treatment for germination of *Betula* seeds. At 20°C, however, the seeds would germinate after a single light exposure and at 25° to 30°C germination would occur in the dark.

Wavelength

Germination of some species of forest trees is sensitive to wavelength, with red light (about 650 m μ) stimulating germination and far red light (about 730 m μ) inhibiting it. If seeds are given red and far red light successively, the occurrence or failure of germination depends on which irradiation was given last. The influence of red light in promoting germination is multiplied if it is followed by infrared. If, however, infrared is followed by red light then germination follows (Table 2.3).

Among the species whose seeds have been shown to be sensitive to the red and far red reactions are species of *Abies*, *Alnus inokuma*, *Betula pubescens*, *Fraxinus mandshurica* var. *japonica*, *Picea glehnii*, *Pinus thunbergii*, *P. strobus*, *P. taeda*, *P. virginiana*, and *P. sylvestris* (Hatano and Asakawa, 1964).

The light sensitivity of seeds usually is influenced by temperature pretreatment. With an increase in duration of cold pretreatment, seed germination in darkness increases, and sensitivity to far red light decreases (Hatano and Asakawa, 1964). The light requirement for germination also varies with amount of water imbibition pretreatment. For example, V. K. Toole *et al.*

TABLE 2.3

INFLUENCE OF ALTERNATING RED AND FAR RED IRRADIATION ON
GERMINATION OF *Pinus virginiana* SEEDS^a

Character of irradiation ^b	Percent germination
Dark control	4
R	92
R + FR	4
R + FR + R	94
R + FR + R + FR	3
	93

^a From V. K. Toole *et al.*, (1961).

^b R = Red; FR = Far red.

(1961) noted that promotion of germination with red light of *Pinus virginiana* seeds occurred faster after a 20-day period of imbibition. Maximum germination of seeds promoted by red light was greater when they absorbed water at 5° than at 25°C.

It is clear that metabolic activity and mitoses in embryos are stimulated by red light and inhibited by far red light in light-sensitive seeds. This was shown by Nyman (1961) by alternating red and far red treatments to *Pinus sylvestris* seeds and observing their effects on respiration, mitosis, and germination. The time of response varied with the process measured. Significant increases in respiration were induced by red light after imbibition for 24 hours, whereas, mitotic activity was stimulated after 36 hours of imbibition. Rootlets did not protrude until after more than 48 hours of imbibition.

Oxygen Supply

As stimulation of respiration is an essential phase of germination it is not surprising that oxygen supply affects germination. The oxygen requirements of different seeds vary rather widely, but most tree seeds can germinate at oxygen tensions below atmospheric concentrations.

Seeds of many species will not germinate in waterlogged soils. By comparison, seeds of some bottomland species, such as *Nyssa aquatica* and *Taxodium distichum* appear to have low oxygen requirements and can endure prolonged inundation without loss of viability. Hosner (1957) found no appreciable effect of soaking seeds, for as long as 32 days, on germination of six bottomland species.

The seed coats appear to be a barrier to oxygen uptake in some species. Removal of seed coats of *Pinus strobus* seeds markedly accelerated oxygen uptake. Exposure of intact seeds to high oxygen concentration also greatly accelerated their rate of oxygen uptake. Removal of seed coats, followed by exposure of seeds to high oxygen concentrations, resulted in higher rates of seed respiration than did either removal of seed coats or exposing seeds to high oxygen (Kozlowski and Gentile, 1959).

Oxygen plays a primary role as the electron acceptor in catabolism. In some species it may also be involved in inactivation of an inhibitor. Germination of isolated embryos of *Betula pubescens* and *B. verrucosa* species was prevented by aqueous extracts of seeds and such inhibition could be modified by light (Black and Wareing, 1959). It appeared that the intact seed coat prevented germination in the dark by reducing oxygen supply below a critical level. Nevertheless isolated embryos germinated in low concentrations of oxygen. Hence, the embryo appeared to have a high oxygen requirement only when the seed coat was present. The data suggested that the inhibitor increased

the oxygen requirement of the embryo or that oxygen above a threshold level was required to suppress the action of the inhibitor. Black and Wareing (1959) stated that light, chilling, and gibberellic acid were all effective in breaking dormancy of *Betula* seed, possibly by overcoming the influence of the inhibitor on the embryo.

Biocides

A variety of naturally occurring and applied chemical substances decrease the number of germinants either by suppressing the seed germination process or by being toxic to recently emerged seedlings. Such biocides include insecticides, fungicides, herbicides, and fertilizers as well as various chemical inhibitors found in leaves or roots of plants. The influence of biocides on seed germination varies greatly with the specific chemical; the rate, method, time and number of applications, the species, soil type, weather, and other factors (Kozlowski, 1960). A few examples of effects of biocides on germination will be given.

Insecticides and Fungicides

A number of insecticides (e.g., dieldrin, aldrin, parathion, DDT, toxaphene, Dilan, chlordane, heptachlor, and octamethyl), at concentrations used to control white grubs in forest nurseries, were nontoxic to growth of pine roots. In contrast, as little as 1 ppm of crude benzene hexachloride and 8 ounces of gamma (in crude benzene hexachloride) per acre in solution and in sand caused root malformations in *Pinus resinosa* seedlings (Simkover and Shenefelt, 1952).

Captan is an example of a fungicide which reduced the number of normal germinants of *Picea glauca*, *Pinus banksiana*, or *P. resinosa*. This was the result of injury to root tips shortly after seeds germinated. Satisfactory germination was obtained by covering seeds with soil whereas surface-sown germinants were largely abnormal (Cayford and Waldron, 1967).

Methyl bromide fumigation can kill or injure gymnosperm seeds which have a high moisture content at time of treatment (L. Jones *et al.*, 1964). However, when seeds with a low moisture content are properly fumigated with methyl bromide and aerated for 24 hours, they usually maintain viability during subsequent cold storage (L. Jones and Havel, 1968).

Herbicides

Many herbicides decrease the number of germinants. The inhibitory effect may be exerted by direct suppression of seed germination, subsequent toxicity to young seedlings, or both (Sasaki and Kozlowski, 1967, 1968b). Although it generally is assumed that the toxic component of commercial

herbicide formulations resides wholly in the "active" ingredients, toxic effects sometimes are also exerted by the "inert" ingredients and by interactions of active and inert ingredients (Sasaki and Kozlowski, 1968c,d).

Some herbicides markedly inhibit seed germination whereas others have no obvious or appreciable effects. Herbicides such as NPA, CDEC, CDAA, EPTC, and 2,4-D variously suppressed early or final germination of *Pinus resinosa* seeds (Sasaki and Kozlowski, 1968b; Sasaki *et al.*, 1968; Kozlowski and Sasaki, 1970). At comparable dosages monuron, DCPA, and the s-triazine herbicides (e.g., atrazine, simazin, propazine, ipazine) did not affect seed germination appreciably (Kozlowski and Kuntz, 1963; Kozlowski and Torrie, 1965; Kozlowski *et al.*, 1967a; Sasaki *et al.*, 1968; Kozlowski and Sasaki, 1968a). However, the triazine herbicides were very toxic to young seedlings shortly after germination occurred. Many herbicides check photosynthesis rapidly and reduce the rate of dry weight increment as a prelude to killing seedlings (Winget *et al.*, 1963; Kozlowski, 1965).

The effects of herbicides on seed germination under natural conditions often are masked by the manner in which they are applied. Thus, it is important to maintain a clear distinction between real and apparent herbicide toxicity. The absolute toxicity of many herbicides to seed germination cannot be determined in soil cultures because the soil is a barrier between a seed and the applied chemical. Soil-applied herbicides often are lost to seeds by evaporation, leaching, microbial or chemical decomposition, and irreversible adsorption on the soil.

High absolute toxicity of 2,4-D and CDAA to seed germination has been demonstrated (Kozlowski and Sasaki, 1970). When these herbicides were placed in direct contact with *Pinus resinosa* seeds in petri dishes they inhibited seed germination at concentrations as low as 50 ppm (Kozlowski and Sasaki, 1968b). However, germination was inhibited much less when *Pinus resinosa* seeds were pretreated for 24 hours with 2,4-D or CDAA at concentrations as high as 1000 ppm, and then planted in soil (Sasaki *et al.*, 1968). When CDAA was applied at dosages as high as 16 lb/acre to the soil surface and then incorporated in soil in which *Pinus resinosa* seeds were planted, it had little influence on seed germination (Kozlowski and Torrie, 1965), further emphasizing large losses of herbicides to seeds under some conditions of application.

As some herbicides are rather volatile they affect germination much more when incorporated in the soil than when applied to the soil surface. Kozlowski *et al.* (1967b) applied EPTC, CDEC, and CDAA to the surface of soil in greenhouse flats. Several days later the soil and herbicide were mixed together, after which *Pinus resinosa* seeds were planted in the mixture. Subsequent observations of seed germination did not demonstrate strong herbicide toxicity. The apparent lack of toxicity of these herbicides was caused by their rapid losses by volatilization.

Inhibitors

In addition to the dormancy promoting effect of endogenous inhibitors, which are discussed in the section under seed dormancy, many laboratory tests have identified compounds present in leaves or roots which appreciably inhibit germination of seeds of neighboring plants (Ooyama, 1954; Lerner and Evenari, 1961; Cannon *et al.* 1962). For example, water extracts of leaves of *Myrus communis*, *Eucalyptus rostrata*, *Laurus nobilis*, and *Pinus halepensis* variously impeded seed germination (Yardeni and Evenari, 1952). Leaf extracts of *Myrus* were most effective as germination inhibitors. Those of *Eucalyptus* were less effective and those of *Pinus* least effective. As may be seen in Table 2.4, water extracts of both woody and nonwoody species associated with *Pinus banksiana* variously inhibited germination of its seed. In fact extracts of *Prunus pumila* and *P. serotina* completely inhibited germination of *Pinus banksiana* seeds.

As emphasized by Lerner and Evenari (1961), laboratory data showing drastic inhibition of seed germination by chemicals washed out of leaf litter should be interpreted with caution with respect to ecological significance. Although leaves of *Eucalyptus rostrata* contained substances which inhibited seed germination, tests of soil from beneath *Eucalyptus* trees indicated that the inhibitors present in the leaves did not accumulate in the soil to inhibitory concentrations. Cannon *et al.* (1962) presented convincing evidence that substrates prepared from milled leaves, or extracts of plants which often are

TABLE 2.4

EFFECTS OF WATER EXTRACTS OF NEIGHBORING PLANTS ON GERMINATION OF *Pinus banksiana* SEEDS^a

Species	Plant part extracted	Percent germination after 14 days
Control		82
<i>Boletus edulis</i>	Fruiting bodies	37
<i>Cladonia cristatella</i>	Plants	24
<i>Sphagnum capillaceum</i>	Plants	22
<i>Salix pellita</i>	Leaves	9
<i>Prunus pumila</i>	Leaves	0
<i>Prunus serotina</i>	Leaves	0
<i>Gaultheria procumbens</i>	Leaves	21
<i>Solidago juncea</i>	Flowers	11
<i>Solidago juncea</i>	Leaves	9
<i>Solidago uliginosa</i>	Leaves	2

^a From R. T. Brown (1967).

used to show "antibiotic" effects, are not comparable with substrates of intact leaves. In laboratory tests, extracts of *Backhausia* leaves hindered germination of *Araucaria* seeds. In the field, however, germination of *Araucaria* seeds was higher on litter enriched with *Backhausia* leaves than on natural litter. Nevertheless, R. T. Brown (1967) found that the presence of plants in the field, whose extracts strongly inhibited germination in the laboratory, also inhibited germination in the field. It undoubtedly is true that the ecological significance of inhibitors from neighboring plants sometimes has been overemphasized because of results obtained in the laboratory. Yet there is evidence of some ecological significance of inhibitors of adjacent plants. Further field experiments are needed to quantify the inhibitory effects of plant chemicals on seed germination of various species.

SEEDBED CHARACTERISTICS AND SEEDLING DEVELOPMENT

Regeneration of trees varies greatly on different seedbeds because of wide differences in temperature, water availability, ability of rootlets to penetrate a seedbed, and nutrient availability. Heat and drought effects often are related because heat inhibits germination and growth by drying the seedbed surfaces. D. M. Smith (1962) considered the most crucial features of seedbeds on regeneration to be the amount of overhead shade, proximity to competing vegetation, and physical characteristics of seedbeds.

On many sites mineral soil provides excellent conditions for regeneration because of its high infiltration capacity, suitable aeration, and close contact between soil particles and the imbibing seed. Mineral soil warms faster than loose organic matter and offers little resistance to penetration by roots. Litter and duff often are much less suitable media because they inhibit root penetration, prevent seeds from contacting the soil, and shade out small, recently emerged seedlings (Place, 1955). Suitability of litter as a seedbed often varies with its thickness and many species fail to become established because roots cannot penetrate a thick layer of litter before the surface layers dry out. Regeneration of *Picea glauca* in Manitoba was better on thin than on thick litter (Phelps, 1948). Thick litter appears to be more of a barrier to some species than to others. For example, roots of *Abies balsamea* were more successful than *Picea* roots in penetrating thick layers of hardwood or softwood litter because of more rapid growth of the former (Place, 1955).

Although sphagnum moss offers suitable conditions for germination because of its high water-holding capacity it may subsequently smother seedlings. Upland mosses of the genus *Polytrichum* often are beneficial to regeneration on dry, sunny sites because they protect the young plant against the injurious effects of high temperatures. On very wet sites, however, *Polytrichum* moss grows very rapidly and may smother young plants.

Decayed wood provides excellent seedbed conditions for many species primarily because of its high water-holding capacity. This was emphasized by Place (1950) who found that, whereas the moisture content of humus remained below wilting point for extended periods, that of immediately adjacent decayed wood remained slightly below field capacity.

Variations in Regeneration of Different Seedbeds

Natural reproduction of many trees is hindered by lack of a suitable medium for seed germination or subsequent seedling establishment. Regeneration of a species often is difficult because the conditions which favor germination and survival often are not ideal for vigorous early growth of the established seedling. For example, seed germination and seedling survival of *Betula papyrifera* were highest on mineral soils and at shaded positions

TABLE 2.5

AVERAGE SEED GERMINATION AND FIRST-YEAR HEIGHT GROWTH OF SEEDLINGS OF *Betula papyrifera*^{a,b}

Seedbed	Germination					
	Sun		Shade		Height growth (inches)	
	1959	1960	1959	1960	Sun	Shade
Leaf-litter	15	16	8	21	4.6	0.9
Humus	40	41	72	115	4.9	2.0
Mineral soil	192	39	279	106	2.0	1.6

^a From Marquis *et al.* (1964).

^b Number of seedlings per seedspot.

whereas first-year height growth was greatest on organic seedbeds and in direct sunlight (Table 2.5).

Voluminous data are available which show superiority of certain seedbeds over others for regeneration of trees and only a few examples will be cited. *Polytrichum* moss and moist mineral soil seedbeds were better for germination and early survival of *Pinus strobus* than were litter of the same species, lichens, or dry mineral soil (D. M. Smith, 1951). The variable influences of these seedbeds were restricted to areas exposed to direct sun and were fundamentally caused by differences in heat dissipating characteristics. Seedbeds which lost heat slowly attained high surface temperatures, causing extreme desiccation and suppression of germination. Furthermore, recently emerged seedlings were killed by the high temperatures. Some examples of differences in seed germination on various seedbeds are shown in Fig. 2.6.

In southern Canada natural seedbeds generally were suitable for regeneration of *Picea rubens*, *P. abies*, *P. glauca*, and *Abies balsamea* (Place, 1955). Germination usually was high on mineral soil but growth was restricted on either leached A₂ horizons or cold wet soil. Moist heavy mineral soils in the open were subject to frost heaving, and in the shade they were too cold and wet for seedling establishment. Sandy soils were unsuitable because they tended to dry out in the open. Place (1955) found it much easier to establish seedlings under a forest stand and then to harvest the stand than to establish seedlings in the open after the stand had been cut.

Winget and Kozlowski (1965a) compared germination and seedling growth of yellow birch (*Betula alleghaniensis*) for various types of naturally occurring seedbeds (Fig. 2.6). Maximum rates of germination were reached earlier on moist H-layer humus and on decayed hemlock (*Tsuga canadensis*) wood seedbeds than on mineral soil, but total germination eventually was similar on all. Important differences in rooting also were found in the different seedbeds. As rootlets of seeds germinating on humus or sandy loam readily penetrated the rooting medium the seedlings grew upright. In contrast, rootlets of seeds germinating in litter tended to grow horizontally over the leaf mat. Often the main rootlet was completely exposed with only fine



FIG. 2.6. Variations in development of *Betula alleghaniensis* seedlings on different seedbeds 91 days after seeding. *Upper left:* sandy loam mineral soil. *Lower left and upper right:* moss covered decayed *Tsuga canadensis* wood. *Lower right:* humus-litter over sandy loam mineral soil. [From Winget and Kozlowski (1965a).]

secondary rootlets penetrating the leaves. The seedling stems often were prostrate, or nearly so, with only a few millimeters of their stem tip oriented vertically. Occasionally, the levering action of a rootlet against the leaf surface overturned the seedling, thereby exposing the roots and causing eventual desiccation of the plant.

Much more rapid height growth of seedlings and greater dry weight increment occurred on seedbeds of exposed, intact humus over mineral soil profiles than on sandy loam, silty mineral soil, or decayed hemlock wood. Drought resistance of established seedlings was greatest on humus seedbeds. This probably was related to favorable root development and efficient use of available water. Newly germinated seedlings developed rapidly, soon penetrating the thin humus layer, which had abundant available nutrients, and developing roots in the mineral soil below. The critical length of time between germination and onset of summer drought would be shortened considerably with such a two-phased system (humus over mineral soil). In contrast, a seedling rooted only in mineral soil had a stable water supply but lacked necessary mineral nutrients to attain maximum early growth rates.

Germination of oil palm seed varies greatly with site. High germination rates occurred in open areas and none in a forest (Rees, 1963a). As may be seen in Fig. 2.7 germination for each of four sites showed a peak at the beginning of the rainy season and then rapidly fell to a negligible value until the beginning of the rainy season of the following year. Two years after

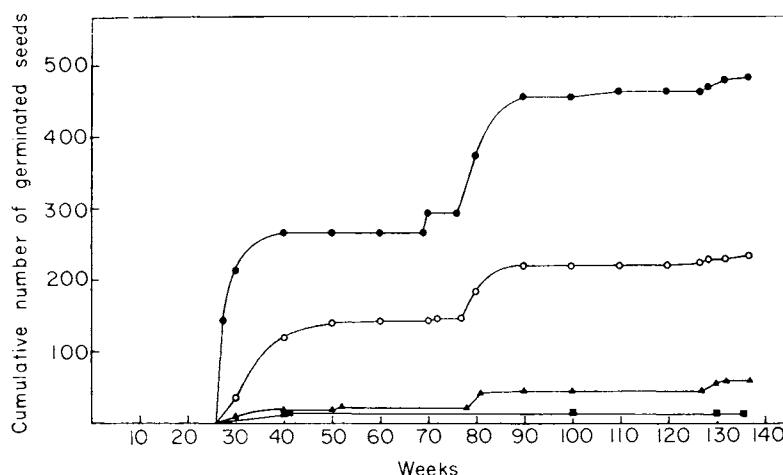


FIG. 2.7. Effect of seedbed on germination of oil palm seeds planted at the end of the wet season (November 1959) until June 1962 in West Africa. Closed circles, grass plantings; open circles, bare soil planting; triangles, palm plantation; squares, high forest. [From Rees (1963a).]

planting oil palm seeds, Rees (1963a) recovered and examined the ungerminated seeds for damage and viability. Under the conditions of the very seasonal germination observed, the loss of viability amounted to 70–90%. The losses were greatest under forest conditions, where all but a few percent of the seeds were nonviable because of insect and fungal activity and, less importantly, because of rodent damage (Table 2.6). The greatest damage to

TABLE 2.6

CONDITION OF UNGERMINATED OIL PALM SEEDS AFTER 2 YEARS ON 4 SITES^a

Condition of seed	Percent of total for each site			
	Bare soil	Grass	Plantation	Forest
Eaten by rodents	7.3	6.4	7.7	8.4
White, delignified	4.3	6.5	16.2	14.6
Perforated by beetles	3.0	1.3	74.7	74.9
Unperforated	85.4	85.8	1.5	2.2
Viable	3.0	10.0	3.5	1.0

^a From Rees (1963a).

seeds that did not germinate early was caused by a beetle (*Coccotrypes congonus*). In general, activity of this insect was inversely related to the amount of incident light reaching the site (Rees, 1963b).

Physiology of Seed Germination

LONGEVITY OF SEEDS

Woody plants intermittently produce large seed crops. Hence, seed longevity is extremely important for regeneration of plants by direct seeding or for production of nursery stock. The life-span of seeds varies greatly among species, and the literature is rich with examples of both long- and short-lived seeds. For example, seeds of *Populus* and *Salix* live a very short time under natural conditions. Engstrom (1948) found rapid loss of viability of *Populus* seeds within two days after harvest. In contrast, seeds of certain genera of *Leguminosae* have a life-span of 50 to 150 years. *Mimosa glomerata* seeds are very long-lived. Becquerel (1934) ran germination tests on very old seeds of this species and concluded they had a confirmed longevity of 81 years and a probable longevity of 221 years. *Albizia* and *Mimosa* seeds also are long-lived and retain viability for as much as 50 years (Ewart, 1908). It should be remembered that the life of any seed usually can be greatly prolonged by appropriate storage, and species comparisons are really valid

only if the data for each species are based on similar storage environments prior to viability tests.

Many tree seeds with extremely short life-spans under natural conditions may live for a long time under controlled environment storage. For example, the characteristically short-lived seeds of *Ulmus americana* retained viability for 15 years with appropriate storage pretreatment (Barton, 1961). *Fraxinus* seeds usually are considered short-lived, but Barton (1945b) found that at moisture contents of 7–10% and a storage temperature of 5°C their life-span could be prolonged to at least seven years (Table 2.7). Janisevskii and

TABLE 2.7

INFLUENCE OF STORAGE CONDITIONS ON LONGEVITY OF *Fraxinus pennsylvanica* SEED^a

Storage conditions	Percent moisture ^b	Percent seedling production after years of storage						
		0	1	2	5	7	8	9
Laboratory								
Open	3.9		36	2	0			
Sealed	6.8	68	75	45	2			
Over CaO	0.4		1	0	1			
5°C Room								
Open	13.3		26	0	0			
Sealed	7.6	68	83	55	51	63	39	0
Over CaO	2.3		65	49	36	45	34	

^a From Barton (1945b).

^b After 1 year of storage. Percentages based on dry weights of fruit lots used.

Pervuhina (1941) greatly extended the life of *Salix caprea* seeds from their normal 30–40 days in open storage. Both drying and storing at 6–9°C were beneficial. Although oak acorns generally have a short life-span under natural conditions, their germination capacity was maintained for ten months when they were stored in sand in airtight cans at 32–40°F (Gardner, 1937; Mirov, 1943). The relatively short-lived seeds of *Cinchona ledgeriana* retained viability for at least 4 years if their moisture content was 9% of dry weight and they were kept at temperatures between 5°C and –4°C (Barton, 1947).

Gymnosperm seeds generally have a short life-span in open storage but they can be kept alive for many years by sealed cold temperature storage. A few examples will be given. Baldwin (1934) noted rapid loss of viability of *Picea rubens* seed stored in duff. In airtight storage, however, germination decreased only by 10% each year for three years. According to K. E. Clausen and Rudolph (1958), seeds of *Pinus resinosa* will retain viability for at least 30 years if stored at low temperatures.

In open room storage germination of *Pinus taeda* seeds decreased greatly after 1 year and only a few seedlings were subsequently produced. In contrast, when stored in sealed containers at low temperatures, the seeds produced large numbers of seedlings for 7 years (Barton, 1935). Seeds of *Pinus ponderosa*, *Picea excelsa*, and *Picea glauca* stored at low temperatures (-4° to -15°C) retained their viability for 4 to 6 years. According to Barton (1953) the life-span of *Pinus* seeds was decreased faster by laboratory temperatures than by 5°C . However, *Pinus echinata* and *P. taeda* seeds kept better at -4°C than 5°C .

Seeds of several species of *Pinus* which have serotinous cones may retain viability for many years as long as they are not removed from the cone. This includes seeds of *P. contorta*, *P. attenuata*, *P. pinea*, *P. chihuahuana*, *P. banksiana*, *P. pungens*, and *P. serotina*. Seeds of *Pinus contorta murrayana* that had remained in the cone for 30 years still showed approximately 30% germination (Blumer, 1910). According to the Woody Plant Seed Manual (Anonymous, 1948) the life-span of *Pinus banksiana* seeds in cones on trees was tripled over storage of seeds removed from cones and stored at 32° – 41°F . In *Pinus contorta* longevity of seeds in cones was quadrupled over seeds separated from the cones.

Seeds of many tropical trees deteriorate rapidly. Genera whose seeds have a characteristically short life-span in open storage include *Theobroma*, *Coffea*, *Cinchona*, *Erythroxylon*, *Litchii*, *Montezuma*, *Macadamia*, *Hevea*, *Thea*, and *Cocos* (Crocker, 1938, 1948; Barton, 1961). By temperature and humidity adjustments during storage, the life of many tropical seeds can be prolonged from a few weeks or months to at least a year (Marrero, 1943). For example, germination of *Montezuma speciosissima* seeds was greatly reduced within 2 weeks in ordinary storage. However, with a moisture content of as high as 33% of fresh weight, viability of seeds was retained for a month in sealed storage at 5°C . Drying at laboratory temperature to 10% moisture content and storing at -5° , 5° or 20°C decreased germination percentage by half, but this lowered germination capacity was retained for at least 6 months (Table 2.8). For detailed information on extending viability of seeds of various species through control of storage environment the reader is referred to the Woody Plant Seed Manual (Anonymous, 1948) and the book by Barton (1961).

Causes of Seed Deterioration

Seed longevity appears to be controlled by both environmental and genetic factors. Ample evidence has already been presented that moisture and temperature control are the most important external factors influencing life-span of seeds.

Loss of seed viability has been attributed to various internal changes. It

TABLE 2.8

INFLUENCE OF STORAGE CONDITIONS ON LONGEVITY OF *Montezuma speciosissima* SEEDS^a

Moisture	Temperature (°C)	Moisture content		Percent germination after storage (months)					
		Fresh wt. (%)	Dry wt. (%)	0	0.5	1	3	6	9
Moist	-5				0	0	0	0	
	5	33.1	49.6	66	68	50	20	0	
	20				10	0	0	0	
Dried 6 hours	-5				0	0	0	0	
	5	21.1	26.7	68	32	28	0	0	
	20				28	8	0	0	
Dried 24 hours	-5				12	32	18	20	
	5	10.4	11.6	30	38	30	20	24	14
	20				24	30	16	16	
Dried 48 hours	-5				28	22	18	24	33
	5	8.3	9.1	16	22	24	8	14	24
	20				20	12	18	14	

^a From Barton (1945a).

appears that species vary in internal requirements as shown by different environmental optima for extending the life-span of various seeds. Some seeds are particularly sensitive to desiccation. *Acer saccharinum* seeds, for example, had a moisture content of 58% when shed and were killed when they dried to a moisture content of 30–34% (H. A. Jones, 1920). Examples of seeds sensitive to desiccation are those of *Liriodendron* and *Quercus*. Citrus seeds vary widely in this respect, with sour orange and rough lemon seeds able to withstand much greater desiccation than seeds of grapefruit or sweet orange (Barton, 1961).

Loss of viability often has been attributed to depletion of food supply of the embryo. However, most old seeds in dry storage contain large amounts of stored foods long after loss of vitality. According to E. C. Stone (1957), loss of viability may be linked to exhaustion of a metabolic substrate. A closely related view is that seed reserves are altered chemically so they no longer furnish the nutritional requirements of the embryo. An increase in free fatty acids of oily seeds accompanies loss of viability (Mirov, 1944).

It has been suggested that seed deterioration may be linked to gradual coagulation of embryo proteins or decrease in enzymes. Barton (1961) presents a good review of data which show no simple relationships between enzyme activity and aging of seeds.

Considerable emphasis has been given to genetic aspects of seed aging.

Gradual dislocations occur in the chromosome apparatus of aging embryo cells. It is not clear, however, whether such changes are the cause or effect of the deterioration during aging. Harrison and McLeish (1954) observed a low incidence of chromosome breaking as plants become older and concluded that cytological changes were the result rather than the cause of seed deterioration.

CHANGES DURING SEED GERMINATION

Seed germination may be considered to be resumption of embryo growth which causes seed coat rupture and emergence of the young plant. Both cell division and cell elongation are involved in embryo growth, with cell division occurring first in some species and cell elongation in others. For example cell division preceded cell elongation in embryo growth in *Pinus thunbergii* seeds (Goo, 1952). In *Prunus cerasus*, however, there was more or less simultaneous occurrence of cell division and cell elongation in embryonic organs (Pollock and Olney, 1959). In early stages of growth following germination, the embryo is wholly dependent on stored foods. In angiosperm seeds the food is stored either in the cotyledons or in endosperm. In gymnosperm seeds the food storage tissue is the female gametophyte (megagametophyte). Reserve foods in the seed sustain the growing embryo until leaves expand to provide photosynthetic surface and roots develop to supply water and minerals, thereby making the young plant physiologically self-sufficient.

Among the essential steps in seed germination are the following: (1) absorption of water, (2) initiation of cell enlargement and division, (3) increased enzymatic activity, especially food digestion, (4) translocation of foods to growing regions, (5) increase in respiration and assimilation, (6) increase in cell division and enlargement, and (7) differentiation of cells into tissues and organs of seedlings (Kramer and Kozlowski, 1960). The specific sequence of these events is not consistent and several of them overlap. Ching (1959) considered the normal course of germination of *Pseudotsuga* seeds to occur in four major sequential stages. These included:

Stage 1. The imbibition phase, which usually was short and characterized by almost linear increase of respiration and water uptake. This phase usually provided adequate hydration for enzymatic activity.

Stage 2. The antephase of mobilization phase, which was characterized by a constant respiratory rate and respiratory quotient, and temporary cessation of water uptake.

Stage 3. The preemergence phase, which was characterized by a gradual increase of water uptake and respiratory rate, and rapid rise of the respiratory quotient to approximately 1.15 at the time of radicle emergence. This stage

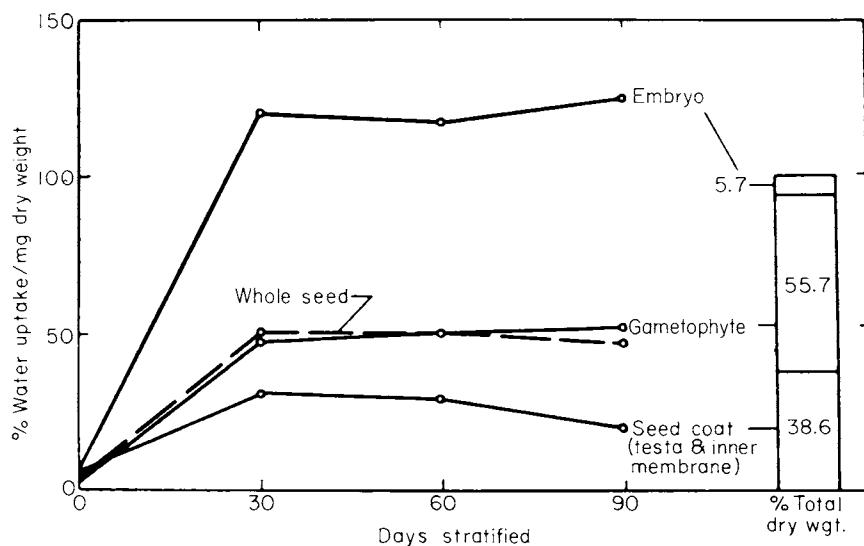


FIG. 2.8. Water uptake by various parts of *Pinus lambertiana* seeds during stratification. [From Stanley (1958).]

involved active mobilization of the energy source and cellular components preparatory to later stages of germination which were accompanied by growth in terms of cell number, cell size, and tissue differentiation.

Stage 4. Postemergence phase characterized by increase in respiration and water uptake. Although respiration and water uptake were increased, the respiratory quotient declined in the seedling and attached, partially digested gametophyte. This stage appeared to indicate a remobilization for cotyledon emergence.

Hydration

Water must be imbibed by seeds to increase protoplasmic hydration as a part of the germination process. Early germination of seeds often can be stimulated by increasing the length of immersion of seeds in water.

When seeds of *Pinus lambertiana* were exposed to conditions favorable for germination, imbibitional water uptake took place. Thereafter, moisture content remained fairly constant for periods which varied with the way in which the seed had been treated (Stanley, 1958). As duration of stratification was increased the subsequent rate of water uptake by seeds was greatly enhanced. Stanley (1958) found high correlation between the water content of the embryo and time of radicle emergence. Germination of *Pinus lambertiana* seed at 30°C occurred when the embryo had a moisture content of approximately 23%. Goo (1952) found a critical moisture content of 26%

necessary for germination of *Pinus thunbergii* seeds at room temperature.

The amount of water taken up by various parts of seeds during germination varies greatly and does not appear to be correlated with size (Fig. 2.8). For example, in *Pinus lambertiana*, the embryo, which was the smallest seed component, absorbed most water as a percent of its dry weight. The endosperm absorbed much less water than was taken up by the embryo and the seed coat absorbed the least amount. The rate and pattern of water uptake by embryos are strongly influenced by dormancy-breaking treatments such as stratification. For example, in embryos of *Pinus lambertiana* seeds, the percentage of moisture absorbed was greater as stratification time under moist conditions was increased (Fig. 2.8). Embryos of unstratified seeds absorbed some water during the first 12 hours of exposure to moist conditions and for approximately 50 hours thereafter they absorbed very little additional water. Then they showed a further increase in water uptake. Such a plateau of inhibited water uptake appeared later and was shorter in seeds stratified for 60 days than in unstratified seeds. Seeds stratified for 90 days did not show any lapse but absorbed water at approximately a linear rate for 72 hours (Fig. 2.9).

Respiration

Germinating seeds utilize oxygen as the terminal electron acceptor in catabolism. Oxygen uptake of seeds increases soon after water is imbibed,

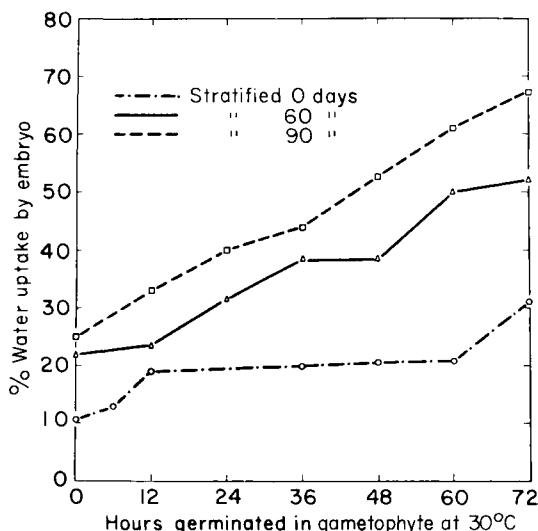


FIG. 2.9. Effect of stratification of *Pinus lambertiana* seed on absorption of water by embryos germinated in the gametophyte (without testa or papery membrane). [From Stanley (1958).]

and respiratory activity generally follows the pattern of water uptake. Following an increase in respiratory activity during an incipient stage of germination, a plateau of oxygen uptake is achieved which may be maintained for a few days. Thereafter, respiratory activity suddenly increases markedly. Stanley (1958) suggested that such changes in respiratory activity were correlated with metabolic changes in which carbohydrates were utilized as metabolic and respiratory substrates in early stages of germination, whereas organic acids were preferentially used in later stages. The rate of oxygen uptake on a unit dry weight basis varies for different seed components during germination, with higher inherent respiratory activity in the embryo than in the megagametophyte (Stanley, 1958; Hatano, 1963).

Stanley (1957) showed that nutritive tissue which sustains initial seedling development contains a mechanism for aerobic respiration similar to that in the mature sporophyte. In *Pinus lambertiana* seeds all necessary respiratory enzymes were present in the megagametophyte. During early germination significant changes in enzyme activity took place. The capacity of megagametophyte mitochondria to oxidize citrate increased five times and their

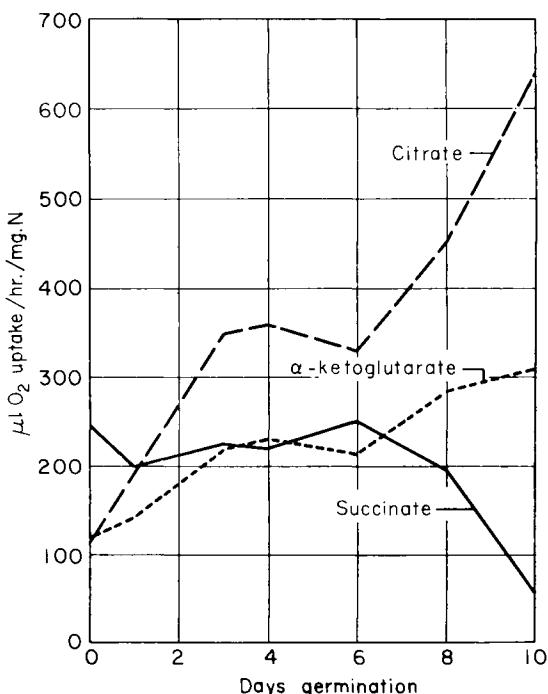


FIG. 2.10. Changes during seed germination in rate of substrate oxidation by gametophyte of *Pinus lambertiana*. [From Stanley (1957).]

TABLE 2.9

EFFECT OF SOAKING SEEDS ON OXIDATIVE ACTIVITY OF MITOCHONDRIA OF MEGAGAMETOPHYTE
OF *Pinus lambertiana* SEED^a

Time of soaking (hr)	Water content of megagametophyte (%)	Substrate oxidized ($\mu\text{l O}_2/\text{hr} \times \text{mg N}$)		
		Succinate	α -ketoglutarate	Citrate
0	3	37	11	0
2	32	86	33	32
6	57	246	118	112

^a From Stanley (1957).

capacity to oxidize α -ketoglutarate doubled (Fig. 2.10). Oxidation of succinate stayed at a constant level for 6 days and then decreased sharply.

The importance of water uptake early in germination is emphasized by Table 2.9 which shows that initial oxidative activity was related to the amount of water imbibed. Mitochondria from megagametophytes of seeds soaked for 6 hours (water content 57%) showed 10 times the activity of mitochondria from megagametophytes of unsoaked seeds (water content 3%).

Stanley and Conn (1957) showed that mitochondria from megagametophytes of nonstratified, ungerminated seeds of *Pinus lambertiana* had higher Krebs cycle enzyme activity than mitochondria from germinated seedlings (Table 2.10). Stanley and Conn (1957) suggested several possible hypotheses

TABLE 2.10

OXIDATIVE ACTIVITY OF MITOCHONDRIA FROM *Pinus lambertiana* EMBRYOS AND SEEDLINGS
AS INFLUENCED BY GERMINATION AND STRATIFICATION^a

Substrate	Concentration ($\mu\text{moles}/$ vessel)	Seed treatment			
		Unstratified		Stratified ungerminated	
		Ungerminated	Germinated 5 days	60 days	120 days
Succinate	20	880	330	720	310
Citrate	30	410	180	300	220
α -Ketoglutarate	30	470	200	210	210
L-Malate	20	330	180	320	150
L-Malate	2	80	55	100	50
Pyruvate	17	140	10	120	40
Pyruvate + L-malate	17 + 2	420	220	310	160

^a From Stanley and Conn (1957).

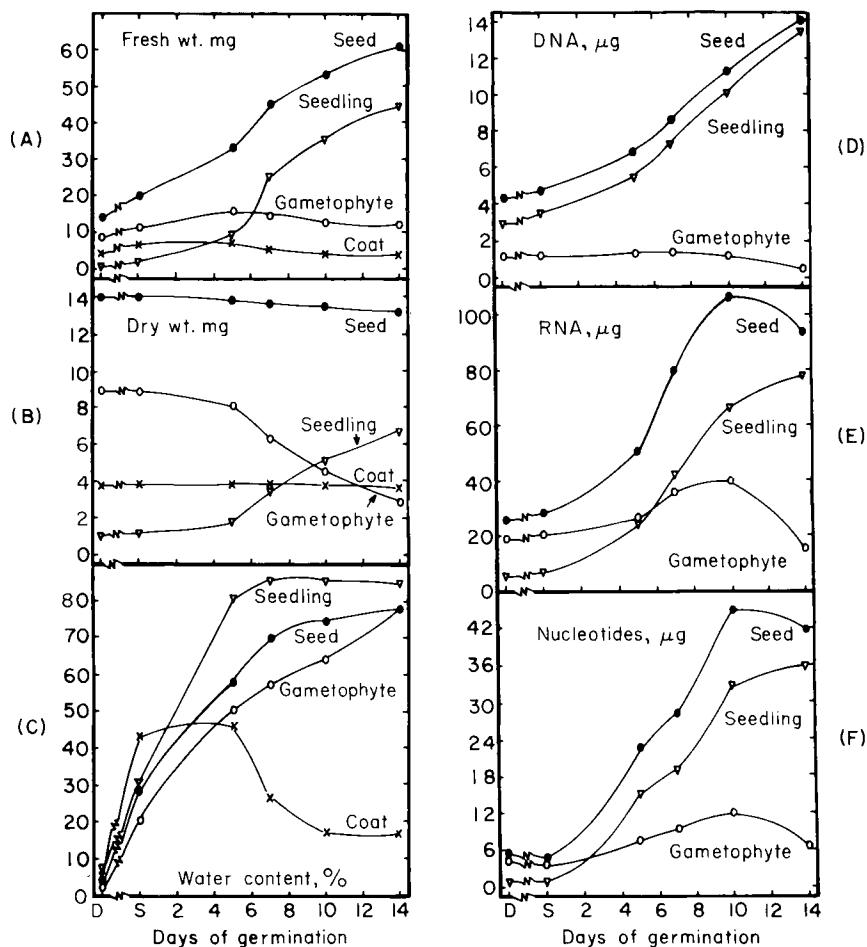
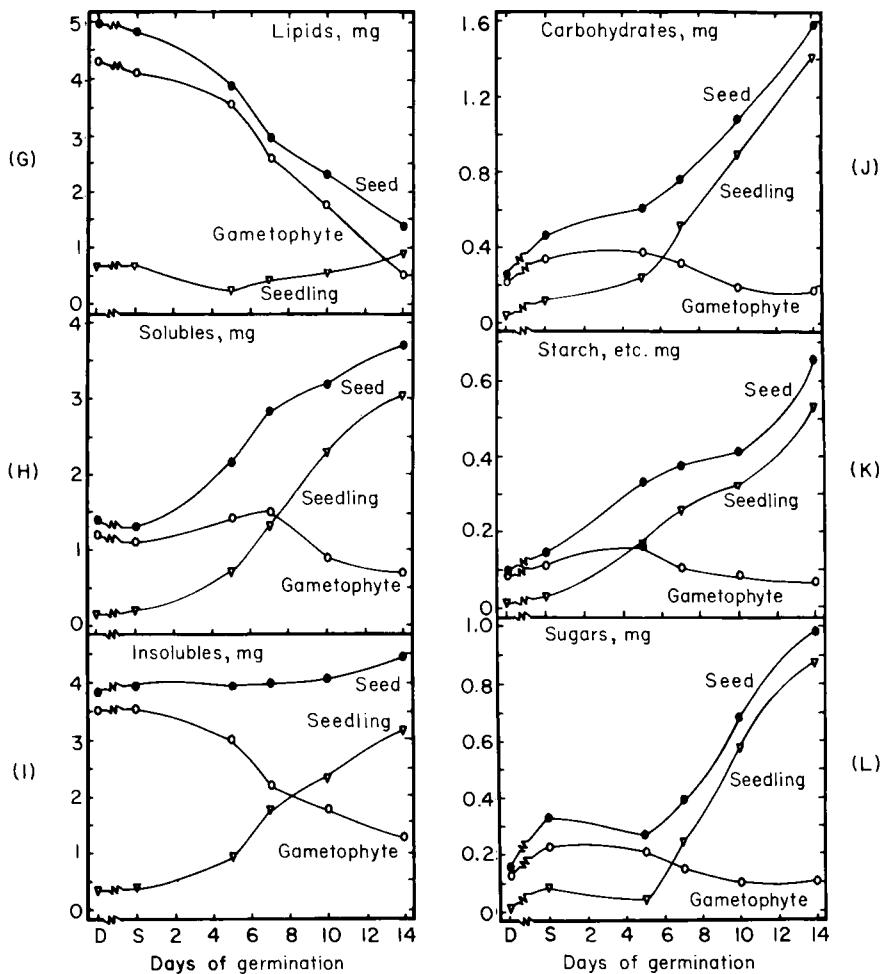


FIG. 2.11, A-R. Changes in weight and composition of embryo, female gametophyte, seed coat, and whole seed of *Pseudotsuga menziesii* during germination. D = air-dried seed, S = stratified seed. [From Ching (1966).]

for decreased mitochondrial activity with germination or stratification. These included: (1) decrease in enzymes in mitochondria during germination or stratification, (2) increase in fragility of particulates during germination, (3) accumulation of metabolic inhibitors, (4) increase in proteins or nitrogen containing macromolecules sedimenting with mitochondria, and (5) decrease in an essential cofactor.



Compositional Changes

The changes in composition during germination are rather similar for seeds of both angiosperms and gymnosperms. Major events include degradation of reserve lipids, proteins, and phosphorus compounds as well as transport of these compounds to the embryo where cellular components are synthesized.

During germination of fatty seeds, rapid depletion of fats occurs through the action of lipases. For example, total fats decreased from 36 to 12% of the dry weight during germination of *Pseudotsuga menziesii* seeds. Glycerides were used during germination and a decrease of 86 to 59% of the total fats

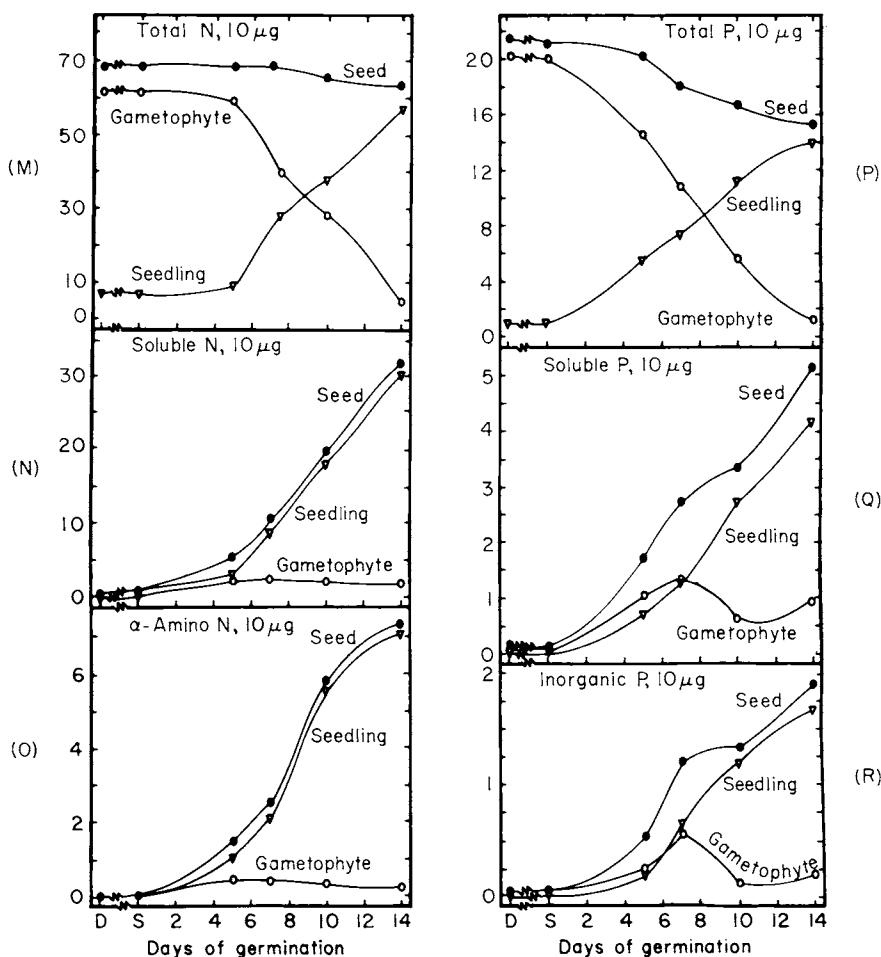


FIG. 2.11 (contd.). Changes in composition of embryo, female gametophyte, and seed without coat of *Pseudotsuga menziesii* during germination. D = air-dried seed, S = stratified seed. [From Ching (1966).]

occurred. Acetone-insoluble phospholipids increased gradually during early phases of germination, and more rapidly at later stages. Phospholipids increased from 5–25% of total fats. Twenty-two fatty acids were identified during germination, with linoleic, oleic, palmitic, and arachadic acids the major components of free fatty acids. Linoleic, oleic, and palmitic acids were the major components of phospholipids (Ching, 1963a,b).

Intense nitrogen metabolism also is characteristic of germinating seeds.

As proteins are degraded, there often is an increase in the amount and number of amino acids and amides followed by synthesis of new proteins in the growing part of the embryo (Koller *et al.*, 1962). Another general characteristic of germination is rapid metabolism of glutamic acid and presence of enzymes involved in transamination.

Storage carbohydrates often are broken down during stages of germination and activity of amylases and phosphorylases increases. Carbohydrates often are transported from endosperm or cotyledon tissues to growing parts of the embryo.

Some idea of the nature and magnitude of compositional changes occurring in *Pseudotsuga menziesii* seeds during germination may be gained from the work of Ching (1966) as summarized in Fig. 2.11, A to R. During seed germination the dry weight of the embryo increased by 600% and that of the gametophytic tissue decreased by 70%. The DNA content of the embryo increased slightly during stratification, doubled during the radicle emergence stage, and increased by 450% toward the end of germination. RNA synthesis also increased in seedlings, whereas in the gametophyte it decreased. Changes in soluble nucleotides were similar to those of RNA. The changes in DNA, RNA, and soluble nucleotides indicated that nucleic acids were being synthesized.

Although normally it would be assumed that the manufacture of RNA is a prerequisite for protein synthesis some evidence indicates that production of RNA is not essential for germination. Dure and Waters (1965) demonstrated that actinomycin D did not prevent the formation of protein in imbibing seeds and also did not block early stages of seed germination. As actinomycin D prevents formation of mRNA, it was concluded that formation of mRNA was not essential for early stages of germination and that there was a form of stored mRNA already present in the resting embryo. Marcus and Feeley (1964) reported that the resting embryo contains abundant ribosomes which become active in protein synthesis shortly after nondormant seeds imbibe water. Villiers (1968) noted that abscisic acid (ABA) maintained embryos of *Fraxinus excelsior* in a state of dormancy and also blocked RNA synthesis. Villiers concluded that ABA maintained seed dormancy by inhibiting production of specific types of mRNA and, therefore, the formation of specific proteins.

Lipids, the major food reserves, originally made up 48 and 55% of the dry weight of the gametophyte and embryo, respectively. During germination the lipids in the gametophyte decreased greatly, whereas those in the seedling decreased initially and subsequently increased. During germination lipids and insoluble residues were used for embryo development (Fig. 2.11).

Reserve fats in seeds usually are converted to sugars which, in turn, are translocated to the growing seedling where they are utilized in growth. Total

carbohydrates accumulated slowly during stratification of *Pseudotsuga* seeds, remained relatively constant before radicle emergence, and then increased rapidly. At first the increase occurred in both the embryo and gametophyte. In later stages of germination a rapid increase in total carbohydrates was observed in seedlings.

Total nitrogen declined slightly during germination but rapid translocation of soluble nitrogen occurred from the gametophyte to the seedling. Characteristic changes occurring first in the gametophyte and later in the seedling included solvation of insoluble protein, activation of existing enzymes, breakdown of storage protein, and active transport and synthesis of new protein.

Total phosphorus in the seed was reduced almost 30% by the end of seed germination. Soluble phosphorus compounds in the seed increased by 4000% and inorganic phosphate increased similarly.

Seed Dormancy

Seeds of only a few genera of trees, such as *Rhizophora* and *Bruguiera*, are viviparous and have a relatively continuous development of the fertilized egg into an embryo and then into a seedling. In contrast, the seeds of most trees exhibit some degree of dormancy and will not germinate even if placed under the most favorable environmental conditions (Kramer and Kozlowski, 1960). Seed dormancy can be both a disadvantage and an advantage. It is especially troublesome in forest nurseries where prompt seed germination is desirable. On the other hand, seed dormancy often is advantageous in correlating germination with the environment. In nature a chilling requirement often postpones germination until after winter. In this way many seedlings that might not survive the winter are protected until after the cold of winter breaks dormancy. A variable depth of dormancy of seeds in the same provenance, and associated spread of germination over a period of time, provide for several chances of reestablishment should some disaster eliminate previously emerged seedlings. As Wareing (1963) emphasized, adaptive mechanisms in seeds also operate in hot and dry areas. In deserts, for example, inhibitors in seed coats of some species prevent seed germination until sufficient rain falls to wet the soil thoroughly and at the same time leach out germination inhibitors. The requirement of afterripening also delays germination and gears it to a particular season.

CAUSES OF SEED DORMANCY

From a practical viewpoint it usually is desirable to break the interruption of growth in seeds that is described by the term "dormancy." Too often there

has been little success in breaking seed dormancy because its nature in various seed lots has not been understood. The failure of seeds to germinate in what would appear to be a suitable environment may be the result of (1) morphologically mature but physiologically dormant embryos, (2) rudimentary embryos, (3) immature embryos, (4) mechanically resistant seed coats, or (5) impermeable seed coats. Sometimes the failure of seeds to germinate is the result of two or even more of these. In *Rosa*, for example, seed germination is prevented by the mechanical restriction of a thick pericarp on embryo expansion as well as embryo dormancy caused by growth inhibitors in the achene (G. A. D. Jackson and Blundell, 1963). Impermeable seed coats and dormant embryos as well have been found in *Crataegus crusgalli*, *Juniperus*, *Taxus cuspidata*, and *Tilia americana* (Crocker and Barton, 1957). Double dormancy has also been reported in *Cornus*, *Machura*, *Cladraspis*, *Hamamelis*, *Pinus sabiniana*, *P. cembra*, and *P. albicaulis*. In *Ilex* both hard seed coats and immature embryos account for failure of seeds to germinate. *Fraxinus* seeds may have triple dormancy in which the pericarp of the indehiscent fruit is impermeable to oxygen, the embryo is immature, and there is a chilling requirement probably associated with presence of an inhibitor or formation of a germination promoter. *Fraxinus* seeds have a very deep dormancy which persists for at least two winters.

In some species, such as *Viburnum acerifolium*, *V. dentatum*, *V. dilatatum*, and *V. opulus*, the epicotyl is dormant whereas the roots are not. Subjecting such plants to low temperature will stimulate shoot elongation. Dormancy of seeds varies greatly in degree. Some seeds in a given lot may have a very deep-seated dormancy which is not easily broken, whereas others have only mild dormancy. According to the Woody Plant Seed Manual (Anonymous, 1948), 43% of the 444 species studied had internal seed dormancy, 17% had double dormancy, 7% had seed coat dormancy, and 33% had no obvious dormancy.

Embryo Dormancy

As mentioned previously, the most common type of dormancy is one in which morphologically mature embryos lapse into an incapacity to germinate. This type of seed dormancy is common in species of *Malus*, *Syringa*, *Quercus*, *Prunus*, *Castanea*, *Cornus*, *Carya*, *Ilex*, *Pyrus*, and *Platanus* among the angiosperms. Gymnosperm genera exhibiting internal seed dormancy include some pines, *Taxodium*, *Pseudotsuga*, *Tsuga*, *Juniperus*, *Larix*, *Picea*, and *Abies*. A relatively uncommon type of internal dormancy is one caused by immature embryos. When it occurs, however, an "afterripening" requirement must be met.

A state of physiological embryo dormancy, like bud dormancy, appears to develop in two stages in which mild and reversible dormancy passes

progressively into deep-seated dormancy which cannot be reversed by the same environmental conditions which induced it. Seeds of some species of *Fraxinus*, which normally become dormant, will germinate if they are harvested and planted before going through a drying phase. Villiers and Wareing (1965) showed that growth inhibitors of fruits and seeds of *Fraxinus excelsior* were metabolically produced but did not become detectable until after the fruits had dried and subsequently reimbibed water.

Growth Regulators and Seed Dormancy

There is a large body of evidence which shows that dormancy of embryos in seeds of many species is regulated by balances between hormonal growth inhibitors and promoters. The onset of seed dormancy appears to be associated with an accumulation of growth inhibitors and the breaking of seed dormancy with a shift in balance in favor of growth promoters which overcome the effects of inhibitors. The role of growth inhibitors and promoters in controlling seed dormancy appears to be somewhat analogous to their role in controlling bud dormancy. The connection between seed and bud dormancy is emphasized by the similarity in appearance of physiologically dwarfed seedlings produced from nonchilled embryos and the rosette growth of branches of fruit trees after a mild winter. Also, both seed dormancy and bud dormancy can be broken by chilling, gibberellic acid, and/or long days. Bud dormancy will be discussed further in Chapter 8 of this volume.

Inhibitors

Chemical substances which inhibit seed germination occur in many species of woody plants in all parts of seeds and fruits including the embryo, nucellus, testa, and pericarp (Villiers, 1961). Natural germination inhibitors include a wide variety of compounds such as ammonia, hydrogen cyanide, ethylene, essential oils, alkaloids, unsaturated lactones, and unsaturated acids (Evenari, 1949). The substance which appears to be the most inhibitory component of the "inhibitor" complex is abscisic acid (ABA) (also termed abscisin or dormin) (Cornforth *et al.*, 1965). The diversity of chemicals known to inhibit seed germination suggests that their mode of action varies among plants. Inhibitors have been detected in seeds of a number of species of angiosperms and gymnosperms and only a few examples will be given.

In *Quercus rubra* an inhibitor was found in the cotyledons (Cox, 1942). In the high bush cranberry (*Viburnum trilobum*) slow growth of the radicle and hypocotyl in some seeds, and lack of germination in others, were associated with a water-soluble inhibitor and need for an appropriate temperature treatment as well (Knowles and Zalic, 1958). Redmond and Robinson (1954) reported that in *Betula alleghaniensis* the seed coats contained a water-soluble

inhibitor which inhibited embryo growth. Whereas this substance lost its inhibiting properties on prolonged exposure to light, its injury to the embryo appeared to be permanent.

Lasheen and Blackhurst (1956) found concentrations of inhibitors of *Rubus* seeds to be highest in the endosperm, lower in the testa, and lowest in embryos. Exposure of seeds to low temperatures resulted in disappearance of the inhibitors and breaking of dormancy.

Inhibitors extracted from embryos of *Fraxinus excelsior* seeds blocked germination of excised embryos of the same species. The inhibition was overcome by thiourea and gibberellic acid, both of which are well known dormancy-breaking substances (Villiers and Wareing, 1965). Sondheimer *et al.* (1968) found abscisic acid present in both dormant seeds and pericarps of *Fraxinus americana*. The abscisic acid in the seed appeared to play a regulatory role in control of dormancy.

Evidence for the presence of inhibitors in the testa and pericarp of *Corylus avellana* nuts was obtained by Bradbeer (1968). Newly harvested seeds gave low germination and removal of the testa greatly accelerated germination. When the testa was stripped from the embryos, but allowed to remain in the dish with them during germination tests, the initial rate of germination was lowered but final germination percentage was not. A further significant decrease in the rate of germination and reduction in final germination percentage was found when both the removed testa and pericarp were placed together with the embryos. Additional support for the presence of germination inhibitors in the testa came from evidence of increased germination following leaching. Bradbeer (1968) also extracted an inhibitor from the testa and pericarp of imbibed seeds.

Seeds of *Pinus thunbergii*, *P. densiflora*, and *Sciadopitys verticillata* contain the inhibitor coumarin which might play a role in regulating germination (Hatano, 1967; Hatano and Nakamura, 1967).

Growth Promoters

The important role of increase in growth promoters in overcoming seed dormancy is emphasized by several lines of evidence. For example, during normal afterripening of seeds or following artificial chilling there often is no decrease in growth inhibitors, whereas growth promoters increase in amount. Furthermore leaching, which might be expected to stimulate germination by removing inhibitors, often causes development of dwarf seedlings. Finally, seed germination in many species with dormant seeds can be increased by exogenous applications of growth promoters. A few specific examples of such evidence will be cited.

The outer layers of freshly harvested apple seeds contained high concentrations of growth-inhibiting substances (Luckwill, 1952). These disappeared

when seeds were kept in moist storage for 68 days, the time required to break dormancy. However, little or no relationship was found between the inhibitor content of the embryo and its capacity for growth. During the first 40 days of afterripening, there was a large increase in the rate of germination of embryos, but no corresponding decrease in inhibitor content of embryo extracts. After 54 days in dry storage, inhibitors could not be detected in embryo extracts but embryos failed to germinate when placed under favorable conditions. The greatest difference between afterripened and non-afterripened seeds was appearance of growth promoting substances in afterripened seeds before germination. The data showed that formation of the growth promoting substances, rather than loss of inhibitors, was necessary to break dormancy.

In many species application of gibberellic acid (GA) overcame dormancy and stimulated seed germination. For example, in unchilled nuts of *Corylus avellana* and *Fagus sylvatica* only a few embryos germinated even after the pericarp and testa were removed. However, when treated with 100 mg/l GA the embryos and seeds germinated within three weeks (Frankland, 1961). Dormancy of *Rosa arvensis* seed appears to be associated with increase in inhibitors. However, seed dormancy can be largely broken by 6-benzylaminopurine or GA (G. A. D. Jackson and Blundell, 1963).

Chilling promoted the germination of embryos and seeds of *Fraxinus excelsior* but did not reduce the activity of growth inhibitors within the embryo or endosperm. Chilling also produced a highly active germination promoter some time before germination actually occurred (Villiers and Wareing, 1965). Hence, it appeared that seed dormancy of *F. excelsior* was controlled by a balance between a germination inhibitor and a promoter, with production of the latter in the embryo requiring low temperatures.

Several specific effects of gibberellin in promoting germination and various associated processes in *Corylus* seeds have been identified. For example, exogenous gibberellin induces embryonic axis growth (Bradbeer and Pinfield, 1967) and cotyledonary cell expansion (Bradbeer, 1968), promotes activity of enzymes which participate in conversion of fat to sucrose (Pinfield, 1968), increases labeling of glutamate at the expense of tricarboxylic acid cycle acids, and increases labeling of nucleotides (Bradbeer, 1968). Bradbeer and Pinfield (1967) suggested that the primary effect of gibberellin action on dormant *Corylus* seeds may occur in the cotyledons where its role in breaking seed dormancy may be in inducing increased levels of enzyme activity, especially those concerned with mobilization of cotyledonary oil reserves.

Seed Coat Dormancy

In some species the seed coats are relatively impermeable to water or oxygen or both, and thereby prevent seeds from germinating. This type of

dormancy is characteristic of seeds of *Diospyros*, and various species of Leguminosae, including *Acacia*, *Prosopis*, *Cladrastis*, *Robinia*, *Gleditsia*, *Gymnocladus*, and *Celtis*. In some species, as in *Rosa*, mechanically resistant structures which enclose the embryo prevent it from expanding.

BREAKING OF SEED DORMANCY

Dormancy of many seeds can be broken by various treatments directed toward overcoming the limitations of (1) inhibitors, (2) permeability of seed coats, and (3) resistance of seed coats to embryo enlargement. The efficiency of these treatments varies markedly with the degree and kind of seed dormancy. In some species seed dormancy is readily broken by any of several treatments, whereas in other species the seeds respond only to a single, specific treatment. Unusually deep dormancy of seeds of some species sometimes cannot be broken by any of the methods commonly used.

Various dormancy breaking treatments often operate by shifting the growth inhibitor-growth promoter balance in favor of the latter. This seems to be accomplished with some treatments by decreasing the levels of endogenous inhibitors and with other treatments by increasing growth promoters. For example, chilling of *Fraxinus americana* seeds decreased the inhibitor (abscisic acid) levels by 37% in the pericarp and 68% in the seed (Sondheimer *et al.*, 1968). Lipe and Crane (1966) also reported a decrease in the inhibitor concentration of peach seeds during chilling. However, other evidence shows that a decrease in inhibitor levels during cold-temperature afterripening is not a general control mechanism for breaking of dormancy of seeds which have a chilling requirement. Bradbeer (1968) reported that chilling, which breaks dormancy of *Corylus* seeds, induced gibberellin synthesis when the seeds were removed from the chilling temperature (5°C) to a temperature at which germination occurred (20°C). The dormancy of *Betula* seeds can be broken by a variety of treatments such as (1) leaching, (2) chilling, (3) exposure to light, (4) treatment with chemicals such as thiourea or gibberellic acid, or (5) increasing oxygen tensions. Whereas leaching of seeds and exposure to high oxygen tensions appear to remove inhibitors, the other treatments mentioned have been reported to excite the growth promoting systems (Wareing, 1965a).

Stratification

Embryo dormancy is most commonly broken by storing seeds at low temperatures, usually between 1° and 5°C, with abundant aeration and moisture, for periods varying from 30 to 120 days. Such "cold stratification" attempts to simulate outdoor conditions to which seeds are exposed when under natural conditions. The term "stratification" implies placing seeds

in layers of moisture-retaining media such as peat moss, sawdust, or sand. The layering, however, is not essential whereas moisture and low temperature are. Hence, seeds may be "stratified" in a moist condition in a plastic bag at low temperatures. After removal from cold stratification seeds can be planted without delay. If allowed to desiccate after stratification they may lapse into a very deep state of dormancy. The effect of low temperature stratification appears to be an increase in growth potential of the embryo.

Dormancy of seeds of some species is best broken by alternate exposure to warm and cold temperatures. Some species of *Viburnum*, for example, will produce roots but not shoots when exposed to normal germination temperatures. When exposed to high temperatures first and then to low temperatures both root and shoot growth follow.

Chemicals

Dormancy of seeds with embryo dormancy has been broken by various chemicals, for example, ethylene, thiourea, KNO_3 and hydrogen peroxide, and growth regulators such as gibberellic acid and kinetin.

In some species with relatively mild seed dormancy, including *Pinus taeda*, *P. caribaea*, *P. densiflora*, *Larix lyallii*, and *L. occidentalis* it has been possible to stimulate respiration and thereby induce germination by treating seeds with oxidizing agents such as hydrogen peroxide (Migita *et al.*, 1956; Shearer and Tackle, 1960; Shearer, 1961; Trappe, 1961; Carter and Jones, 1962). Ching (1959) noted, for example, that oxygen and water uptake were substantially higher in *Pseudotsuga menziesii* seeds that were treated with hydrogen peroxide than in water-soaked controls. This probably indicated that conversion of fats to reserve carbohydrates was stimulated in hydrogen peroxide-treated seeds, and more synthesis of cellular components took place in them than in untreated seeds. Trappe (1961) and Ching (1959) emphasized that for seeds of some species the use of a very strong hydrogen peroxide solution had a greater dormancy breaking effect than a weak solution. Kozlowski and Torrie (1964) observed that strong hydrogen peroxide solutions sometimes were effective in stimulating germination of *Pinus strobus* seeds, but only when treatment was of short duration. Exposure of seeds to strong hydrogen peroxide sometimes stimulated early germination but greatly reduced final germination percentages. Hence, some seeds within a lot were stimulated to germinate whereas others were killed. Significant seed source-treatment interactions were identified, which emphasized difficulty in establishing standardized hydrogen peroxide treatments for stimulating germination of all *Pinus strobus* seeds. Short-time treatment with strong hydrogen peroxide stimulated early germination of some seed sources, but not others. Treatment for long periods often inhibited total germination (Table 2.11).

TABLE 2.11

EFFECT OF SOAKING IN HYDROGEN PEROXIDE AND WATER ON EARLY AND FINAL GERMINATION OF THREE SEED SOURCES OF *Pinus strobus*^{a,b}

	Percent germination					
	Seed source A		Seed source B		Seed source C	
	18 days	40 days	18 days	40 days	18 days	40 days
Control—dry seeds	3.3	12.9	36.5	54.1	10.0	25.4
HP—0.5 hr	5.8	11.8	26.9	45.0	13.0	30.0
W—0.5 hr	4.0	14.5	40.0	54.8	9.6	26.9
HP—1 hr	2.3	3.3	15.4	28.3	10.5	17.8
W—1 hr	3.1	12.4	40.8	55.3	8.8	26.3
HP—2 hr	0.6	1.0	1.8	2.0	0.5	0.5
W—2 hr	4.0	14.9	39.3	54.6	8.4	28.4

^a Soaking from 0.5 to 2 hours in 30% hydrogen peroxide (HP) and Water (W).

^b From Kozlowski and Torrie (1964).

Scarification

Impermeable seeds coats in a number of species often can be rendered permeable by scratching seeds with abrasives. Such treatments usually greatly increase germination. Seed coat dormancy may also be broken by soaking seeds in concentrated H₂SO₄ for periods varying from 15 to 60 min. For further details on breaking dormancy of seeds of various species of trees the reader is referred to Crocker and Barton (1957) and the Woody Plant Seed Manual (Anonymous, 1948).

Patterns of Seed Germination and Seedling Development

As the embryo resumes growing during seed germination, the radicle grows and penetrates the soil. In some species the cotyledons are pushed out of the ground by the elongating hypocotyl (epigeous germination). In other species the cotyledons remain underground while the epicotyl grows upward and develops foliage leaves (hypogeous germination) (Figs. 2.12 and 2.13). Epigeous germination is characteristic of most gymnosperm seeds and those of *Fagus*, *Cornus*, *Robinia*, and most species of *Acer*. Examples of angiosperms with hypogeous seed germination are *Quercus*, *Juglans*, and *Aesculus*.

Various forms of abnormal germination may occur in seeds of low vitality because of seed aging, long-term storage, or unfavorable storage conditions. Examples of abnormal germination include: (1) reverse germination, with cotyledons emerging first and the radicle remaining in the seed, (2) albino

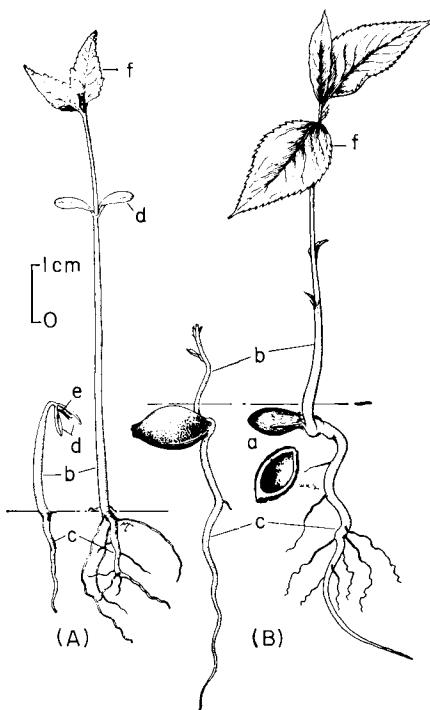


FIG. 2.12. Types of seed germination. (A) Epigeous germination of *Prunus pensylvanica* at 1 and 10 days; (B) Hypogeous germination of *Prunus alleghaniensis* at 1 and 9 days. *a*, seed; *b*, hypocotyl; *c*, primary root; *d*, cotyledons; *e*, plumule; *f*, primary leaves. [From Woody Plant Seed Manual (Anonymous, 1948).]

seedlings, (3) watery seedlings, (4) seeds which split open but with only short extension of endosperm and radicle, and (5) stunted and weak seedlings (Heit, 1961). Seeds which germinate abnormally often do not produce normal, vigorous seedlings.

Normal epigeous germination of a typical pine seed is shown in Fig. 2.14. As the seed coat imbibes water the expanding embryo splits the seed coat and the elongating radicle grows downward into the soil. The hypocotyl then elongates and arches to thrust the seedcoat into the air. By this time the cotyledons are exposed. Subsequently, primary and secondary needles are produced in order. During early growth of pine seedlings the roots at first often grow faster than the shoots.

Whereas all embryo cells divide during early germination, the division of cells in young seedlings is localized in shoot and root apices. Important events following seed germination include sequential formation of leaves,

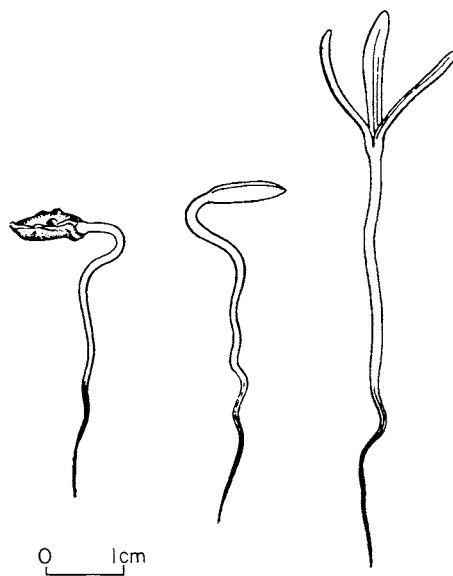
and internodes from apical meristems. Axillary shoots may originate from apical meristems in leaf axils. As such shoots may produce additional axillary shoots the young plant is provided with a system of branches. The root apical meristem forms a taproot or primary root. Often branch roots or secondary roots originate at new, deeply located apical meristems in the taproot (Esau, 1960).

Sequential developmental changes during seed germination and growth of young seedlings have been studied for a number of species and only a few examples will be given. Tepper (1964) described changes occurring in the shoot apex during germination of *Pinus ponderosa* seeds and growth of young seedlings. Cell divisions in germinating embryos first were noted on the flanks of the apex near the cotyledons. Reactivation of the other cells of the shoot apex was a rather orderly procedure. Cell division proceeded from the loci on the flanks, acropetally up the sides of the apex and inward toward cells of the rib meristem. Summital cells were the last to divide, and a rib meristem and several leaf primordia usually were present before this occurred. Within 12 days after planting, mitotic reactivation in seedlings was completed and cells in all regions of the apex were dividing.

Sasaki and Kozlowski (1969) studied developmental changes in *Pinus resinosa* embryos during seed germination. The embryos of dry seeds consisted of a hypocotyl-radicle axis, cotyledons, and an apex, but no primordia of primary needles were present. Procambial cells were present in the cotyledons and the hypocotyl-radicle axis but differentiation of a vascular system was not complete. Shortly after imbibition of water by the seed, a number of important events were noted (Fig. 2.15). These included in order: (1) enlargement of nuclei of embryonic cells, (2) differentiation of protophloem, (3) mitotic divisions in the peripheral zones of the apex, ground meristem, epidermal layers, cortical zone, and procambium of the hypocotyl, (4) xylem formation in the hypocotyl, (5) formation of primary needle primordia, (6) formation of stomata, and (7) formation of the vascular system in primary needles and its subsequent connection to that of the hypocotyl. Primary needles emerged later than cotyledons and required about twice as long to expand.

In *Pinus lambertiana* development of the hypocotyl-shoot axis was due almost wholly to intercalary growth (Berlyn, 1967). Incipient pith was the first tissue evident in the hypocotyl-shoot. Its pith initially differentiated in the upper part of the region between the epicotyl and root initials. Differentiation proceeded acropetally toward the epicotyl and basipetally toward the root initials. Procambium formed somewhat later than the pith and at a lower level. Cortical differentiation followed procambial formation. Long secretory cells differentiated early in the ground meristem before primordia of cotyledons appeared.

(A)



(B)

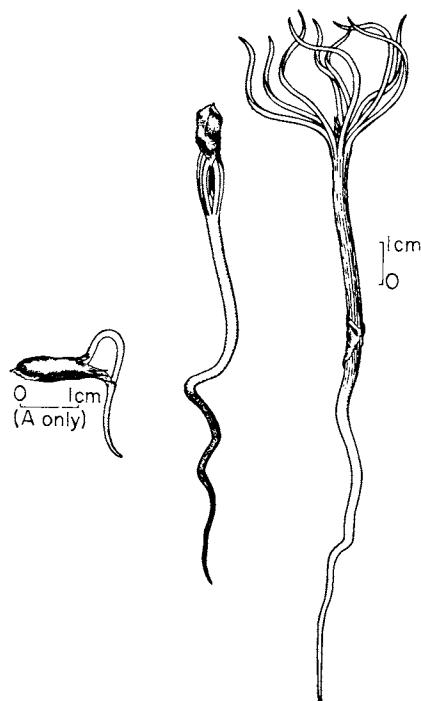


FIG. 2.13. Germination patterns. (A) *Tsuga canadensis* at 2, 4, and 7 days; (B) *Cedrus libani* at 1, 4, and 8 days; (C) *Quercus macrocarpa* at 1, 5, and 12 days; (D) *Fagus grandiflora* at 2, 5, and 7 days. [From Woody Plant Seed Manual (Anonymous, 1948).]

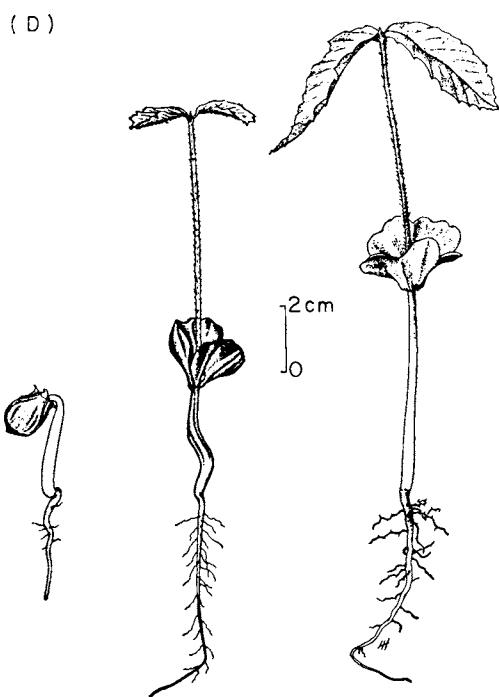
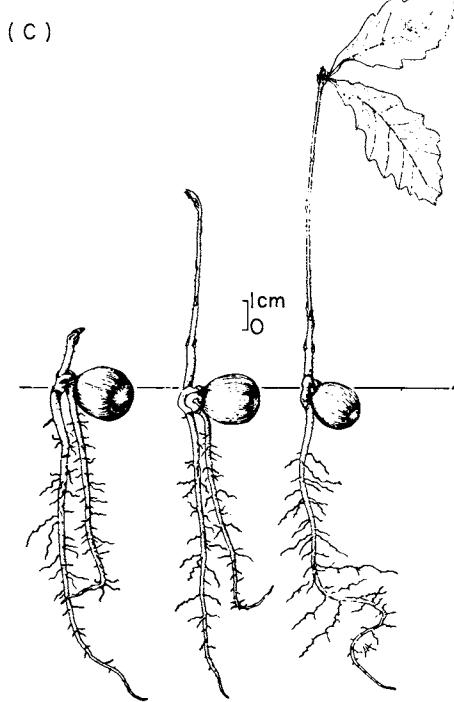




FIG. 2.14. Epigeous germination of pine seed. (Photo courtesy of St. Regis Paper Co.)

INITIATION OF THE VASCULAR SYSTEM

Following organization of an apical meristem in the bud, the primary vascular system is initiated as procambium which differentiates from derivatives of the apical meristem. Continuous acropetal differentiation of procambial strands has been reported to occur in a number of species of angiosperms and gymnosperms. Following differentiation of procambium, the general sequence of vascular differentiation involves acropetal differentiation of phloem from the axis toward the leaf, followed by initiation of xylem near the base of the leaf and its subsequent bidirectional differentiation. These general features of initiation of the vascular system have been reported in several species of angiosperms and gymnosperms, including *Ligustrum* (De Sloover, 1958), *Sambucus* (Esau, 1945), *Abies* (Parke, 1963), *Sequoia* (Sterling, 1946, 1947), and *Ginkgo* (Gunckel and Wetmore, 1946b).

LEAF DEVELOPMENT IN SEEDLINGS

The appearance of tree seedlings often contrasts greatly with that of older specimens of the same species. This is partly the result of differences between cotyledons or seed leaves and the leaves which follow. On the whole, cotyledons are much simpler than the final leaves. The generally entire cotyledons may be narrow as in *Platanus* or broad as in *Fagus*. Sometimes they are sessile as in *Acer* or *Laburnum*. Many cotyledons are thin and leafy but some are thick and fleshy as in *Rhus* and *Quercus* (Lubbock, 1892).

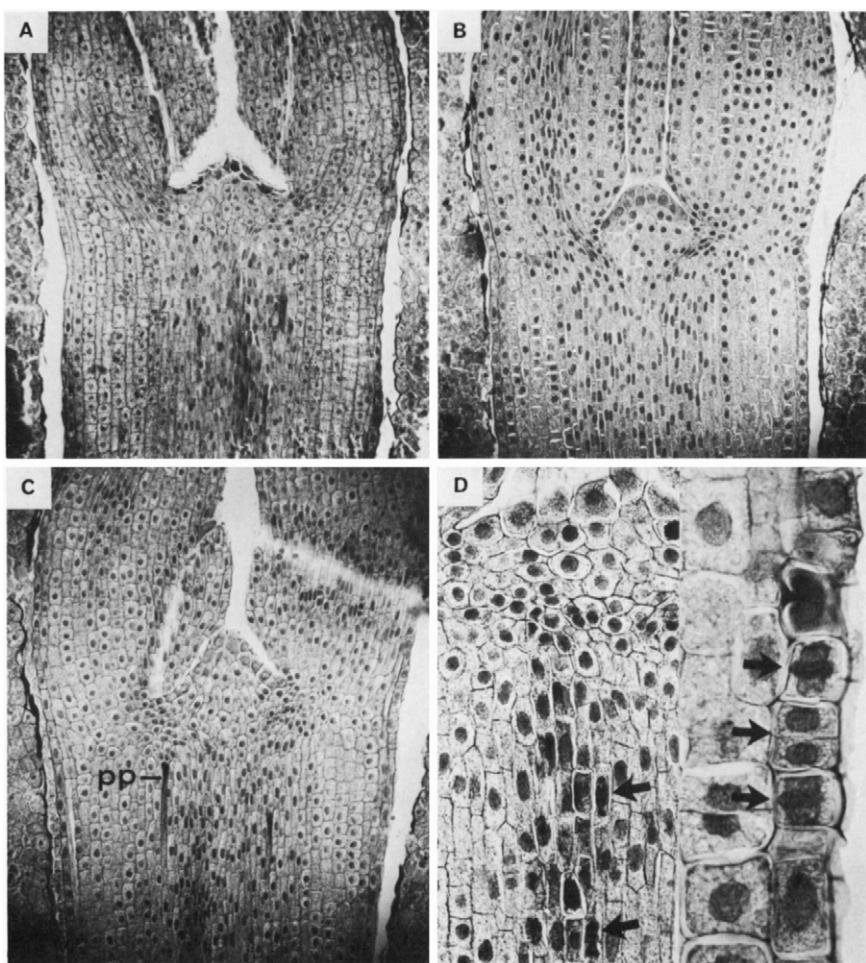
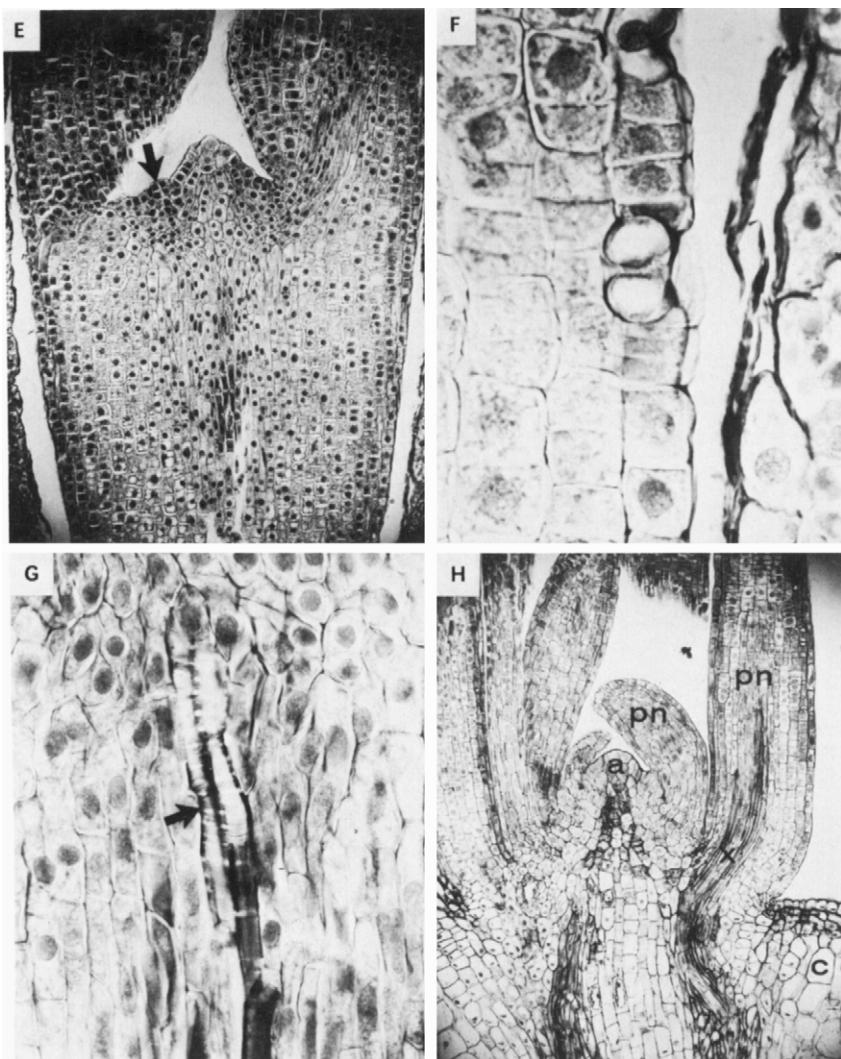


FIG. 2.15. Stages in development of *Pinus resinosa* seedlings after sowing seeds on wet filter paper. (A) Embryo in dry seed; (B) embryo at 1 day; (C) embryo at 2 days showing protophloem (pp); (D) embryo at 3 days showing mitotic divisions (arrows); (E) embryo at 5 days showing formation of primary needle primordia (arrow); (F) embryo at 5 days showing formation of stoma at epidermis of hypocotyl; (G) xylem formation (arrow) in cotyledon at 7 days after seeds were sown; (H) seedling apex at 20 days. Apex (a); primary needles (pn); xylem (x); cotyledon c. [From Sasaki and Kozlowski (1969).]

Seed germination in pines is followed by sequential development of three types of foliar appendages, including cotyledons, primary needles, and secondary needles. As the hypocotyl elongates and arches the cotyledons are exposed. Spirally arranged primary needles emerge sometime later.



Subsequently, secondary needles appear and primary needles are lost. The time of appearance of secondary needles varies considerably among species. In *Pinus banksiana* the seed coat of the young plant stays in contact with the cotyledons until they complete elongation and sometime thereafter the seed coat is shed (Riding, 1967). The primary needles emerge and form a rosette around the shoot apex. The first-formed primary needles elongate rapidly, usually in 1 to 2 weeks, and are shorter than late-formed primary

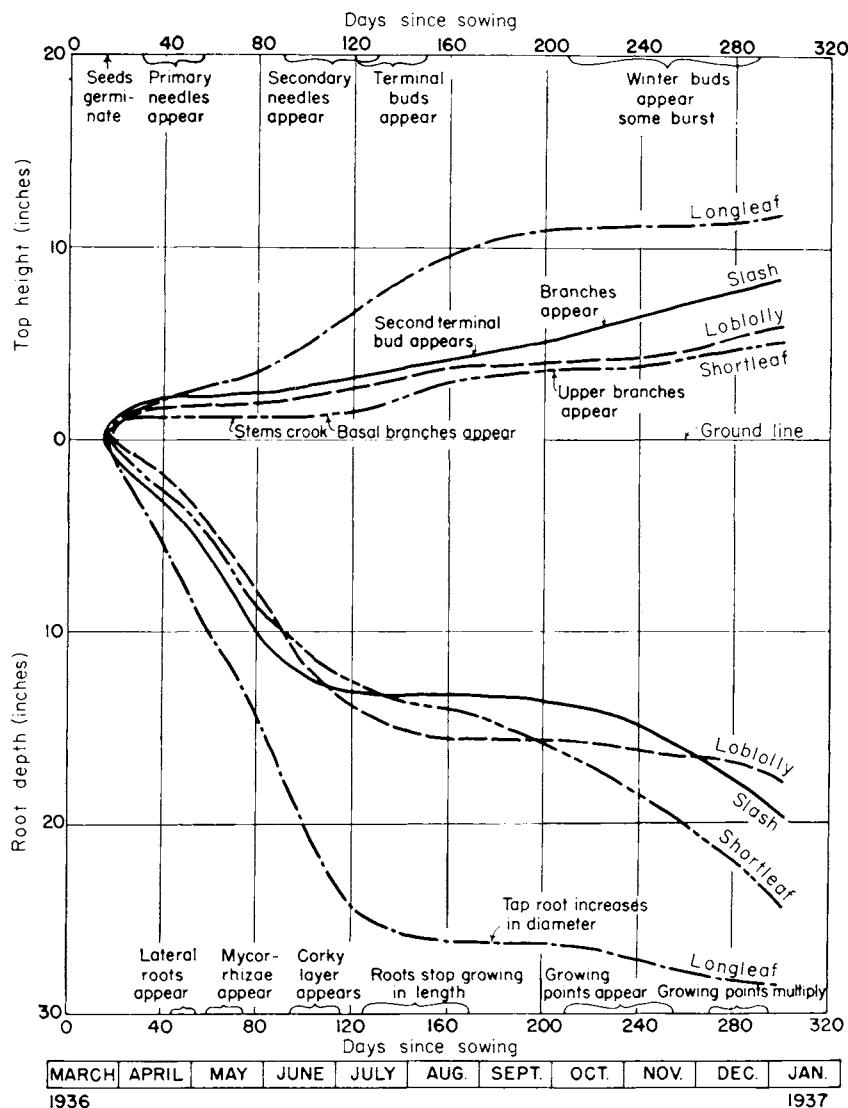


FIG. 2.16. Course of first-year development of four species of pines in Louisiana. [From Wakeley (1954).]

needles. Epicotyl elongation is arrested until the rosette of needles has formed. When the epicotyl elongates, axillary meristems are produced in the axils of some of the primary needles. In the terminal section of the stem these develop into dwarf shoots with prophylls, cataphylls, and secondary needles. Primary needles comprise the major type of leaf of the first growth cycle which ends with formation of a terminal bud. After the first growth cycle the shoots of *Pinus banksiana* are preformed in buds. Secondary needles predominate during the second growth cycle, with primary needles reduced to cataphylls.

Some pines, including *Pinus palustris* and *P. taeda*, produce secondary needles very early (Fig. 2.16). For example, in young *Pinus palustris* seedlings secondary needle fascicles formed in the axils of primary leaves within 10 to 12 weeks after seeds germinated. These secondary needles elongated considerably before the first terminal bud was formed. In *Pinus taeda* seedlings secondary needle fascicles formed within 14 to 16 weeks after seed germination (C. L. Brown, 1964).

Bormann (1958) studied the changing foliar composition of *Pinus taeda* plants over a 2-year period. Cotyledons comprised the entire foliage for a few weeks after seed germination. At 9 weeks all of the foliage was still composed of primary needles. By 16 weeks, however, 29% of total leaf weight was in secondary needles and by the end of the first growing season, at 23 weeks, the proportion of secondary needles was increased to 68%. During the winter the cotyledons and primary needles were lost. Throughout the second year essentially all of the needles were secondary.

The needle-shaped cotyledons of gymnosperms differ structurally from the needles formed later. In *Pinus resinosa* the cotyledons lack resin canals whereas both primary and secondary needles have them. Cotyledons of *P. resinosa* are triangular in cross sections. They lack a hypodermis and have more intercellular spaces than occur in later-formed needles. Usually they also have rounded mesophyll cells, one vascular bundle, and thin-walled epidermal cells. Primary needles of *P. resinosa* vary in shape but tend to have a flattened adaxial surface and a rounded abaxial one. The resin canals are adjacent to the abaxial epidermis. Secondary needles regularly have a semicircular shape in transection. They also usually have two vascular bundles, a thick-walled epidermis, and a hypodermis. The two resin canals are located near to the adaxial epidermis. Their mesophyll consists of strongly infolded (plicate) parenchyma cells.

In pines the physiological activity of cotyledons appears to have an important role in subsequent seedling development. In *Pinus resinosa*, for example, restriction of photosynthesis in cotyledons to varying degrees by reducing light intensity or applying herbicides was followed by proportional suppression of development of primary needles and decrease in dry weight

increment of seedlings (Sasaki and Kozlowski, 1968a, 1970). Complete elimination of cotyledon photosynthesis by germinating seedlings in the dark was followed by failure of primary needles to expand.

PRIMARY AND SECONDARY TISSUES

Both primary and secondary growth are involved in seedling development of woody angiosperms and gymnosperms. Growth is, at first, primary and involves development which terminates when direct derivatives of apical meristems become mature. Primary growth produces roots, stems, and leaves in the seedling and, in addition to these, also fruits and seeds in mature plants. Early in the development of the young seedling secondary growth, which results from activity of the vascular cambium, thickens both the stem and root.

The primary tissues are differentiated from three primary meristematic tissues, the protoderm, ground meristem, and procambium. The primary permanent tissues of the stem of a woody plant and the origin of each may be summarized as shown in the following tabulation. (Holman and Robbins, 1934).

	Meristems	Primary permanent tissues
Promeristem	Protoderm Ground Meristem Procambium	Epidermis Cortex Collenchyma Parenchyma Pericycle Pericyclic fibers Parenchyma Pith rays when present Parenchyma Pith Parenchyma Primary phloem Phloem parenchyma Sieve tubes Companion cells Phloem fibers Primary xylem Vessels Tracheids Wood parenchyma

The epidermis and cortex are continuous layers of cells whereas primary xylem and primary phloem are continuous in some species and separated into vascular bundles in others.

Before the end of the first year a vascular cambium forms in seedlings from one layer of procambial cells between the primary xylem and primary phloem. Species vary, however, with respect to details of cambial origin and activity. Esau (1965b) outlined the following three general patterns for woody plants: (1) primary vascular tissues form an almost continuous vascular cylinder in the internodes, as do the secondary vascular tissues; examples are *Syringa* and *Tilia*; (2) primary vascular tissues form a system of strands and secondary vascular tissues originate as a continuous cylinder; examples are gymnosperms, *Prunus*, *Salix*, and *Sambucus*; (3) primary vascular tissues form a system of strands, the interfascicular cambium produces only ray parenchyma, and secondary vascular tissues appear as strands; examples are stems of vines such as *Vitis*.

After the vascular cambium is formed the seedling begins to increase in diameter as a result of periclinal division of cambial cells to produce secondary xylem peripherally and secondary phloem centrifugally. The secondary xylem cells are added to the outside of the primary xylem, whereas secondary phloem cells are added to the inside of the primary phloem.

As a seedling increases in girth and accumulates secondary tissues, the primary phloem, epidermis, and cortex eventually are sloughed off from the plant. The seedling at this stage is protected from desiccation by periderms which form usually in the cortex. Periderms consist of three layers: a cork cambium or phellogen and its derivatives, dead phellem or cork which forms to the outside of the phellogen, and living phelloderm cells to the inside.

Before secondary growth is initiated, the weak and often succulent seedling lacks strengthening tissues and has only a rudimentary vascular system. However, the development of secondary xylem strengthens the seedling materially. The collapse of the cortex terminates a critical period in the life of the seedling during which it was especially vulnerable to direct heat injury, damping-off fungi, and attacks by birds and insects. The pattern of cortical collapse is variable. In *Pinus* the cortex collapses rather abruptly; in some species a development of cortical collenchyma causes the stem to become leathery; in *Taxodium* the seedling is strengthened by a hypodermis which develops beneath the epidermis (Baker, 1950).

Before the end of the first year most of the cambial growth increment of the young tree is made up of secondary xylem. In subsequent years, annual increments of secondary xylem and secondary phloem are added to Temperate Zone trees (Fig. 2.17). Eventually primary tissues in the main stem and large branches of a mature tree are obscured by the large accumulation of secondary tissues. Nevertheless, primary tissues are still produced at apices of old trees and can be located behind elongating root and shoot tips. The primary tissues at shoot tips of many mature trees are produced within a few weeks of the growing season and, after they are formed, growth in length of the fully differentiated axis ceases.

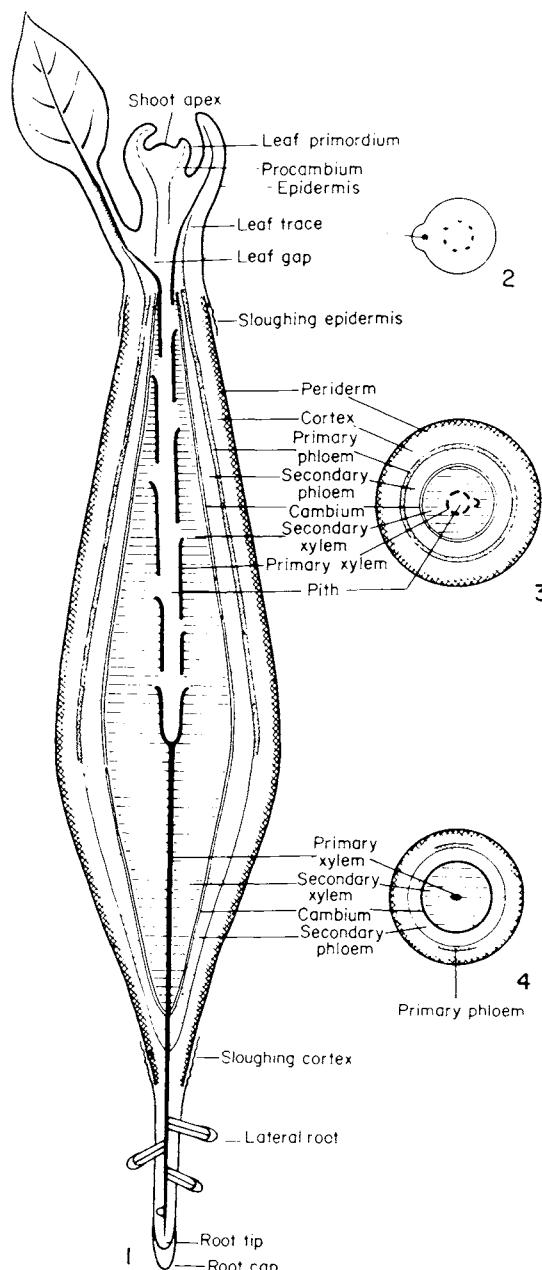


FIG. 2.17. Schematic diagram showing arrangement of tissues in seedlings after initiation of secondary growth. 1, Longitudinal section, 2, 3, and 4, cross sections at various heights. [From Fahn (1967) as adapted from Esau (1960).]

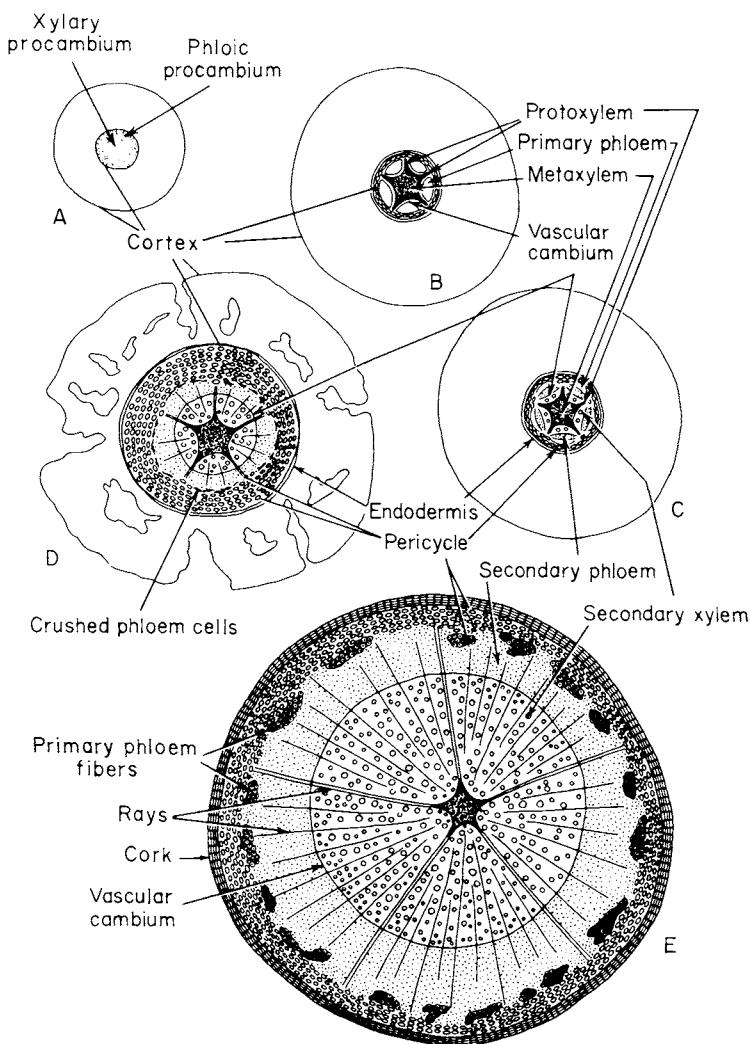


FIG. 2.18. Transections of *Pyrus* root in various stages of development. (A) Vascular cylinder in procambial state; (B) primary growth completed; (C) some secondary tissues have been formed by strips of vascular cambium between the xylem and phloem; (D) additional secondary tissues have been produced by the encircling vascular cambium. The endodermis is partly crushed and the cortex is breaking down; (E) secondary growth is more advanced. Periderm is present and cortex has been shed. [From Esau (1965b).]

Early in root development the first sieve tubes at each phloem pole are differentiated before the protoxylem elements form at the xylem poles. Primary differentiation of additional xylem and phloem cells then continues centripetally. As in the stem, primary growth is followed in many roots by secondary growth involving formation of secondary vascular tissues by the cambium and of periderm by a phellogen (cork cambium).

Various stages in the formation of the cambium and secondary growth of a woody root are shown in Fig. 2.18. At first some parenchyma cells and those of the pericycle become meristematic and form a wavy cambial band on the inner edges of the phloem strands and outside the xylem. Eventually the cambium produces xylem in a complete cylinder. Shortly after the vascular cambium appears, some of the pericycle cells divide to form the phellogen or cork cambium which cuts off phellogerm tissue to the inside and cork to the outside. After cork formation begins the cortex with its endodermis is sloughed off and the tissue arrangement thereafter resembles that of the stem.

Suggested Collateral Reading

- Amen, R. D. (1963). The concept of seed dormancy. *Amer. Sci.* **51**, 408–424.
- Amen, R. D. (1968). A model of seed dormancy. *Bot. Rev.* **34**, 1–31.
- Anonymous. (1948). Woody plant seed manual. *U.S. Dept. Agr., Misc. Publ.* **654**.
- Barton, L. V. (1961). "Seed Preservation and Longevity." Wiley (Interscience), New York.
- Berlyn, G. P. (1967). The structure of germination in *Pinus lambertiana* Dougl. *Yale Univ. Sch. Forest., Bull.* **71**.
- Crocker, W., and Barton, L. V., (1957). "Physiology of Seeds." *Chronica Botanica*, Waltham, Massachusetts.
- Esau, K. (1965). "Plant Anatomy," Chapter 20. Wiley, New York.
- Evenari, M. (1956). Seed germination. *Radiat. Biol.* pp. 518–549.
- Hatano, K., and Asakawa, S. (1964). Physiological processes in forest tree seeds during maturation, storage, and germination. *Int. Rev. Forest. Res.* **1**, 279–323.
- Koller, D., Mayer, A. M., Poljakoff-Mayber, A., and Klein, S. (1962). Seed germination. *Annu. Rev. Plant Physiol.* **13**, 437–464.
- Kramer, P. J., and Kozlowski, T. T. (1960). "Physiology of Trees," Chapter 14. McGraw-Hill, New York.
- Mayer, M., and Poljakoff-Mayber, A. (1963). "The Germination of Seeds." Pergamon Press, Oxford.
- Vegis, A. (1964). Dormancy in higher plants. *Annu. Rev. Plant Physiol.* **15**, 185–224.
- Wareing, P. F. (1963). The germination of seeds. *Vistas Bot.* **3**, 195–227.

Chapter 3

MATURATION OR PHASE CHANGE

Introduction

The growth of a young tree varies greatly in several respects from that of an old one. The distinction made by Wareing (1964a) between "maturation" or "phase change" and "aging" of trees will be retained in this volume. According to Wareing, maturation or phase change, which occurs during a restricted early period in the life of a tree, encompasses the relatively rapid and predictable changes characteristic of the transition from juvenility to adulthood. Aging involves reduction in vigor and associated changes which occur as trees gradually increase in size and complexity. Manifestations of aging include decrease in metabolism, reduced growth of vegetative and reproductive tissues, increase in dead branches, heartwood formation, slow wound healing, and changes in resistance to invasion by certain insects and fungus pathogens. The remainder of this chapter will discuss maturation or phase changes. Characteristics of aging will be discussed in Chapter 4 of this volume.

Juvenile and Adult Characteristics

During ontogenetic development woody plants progress from juvenile stages to maturity. Clearly defined juvenile phases have been described for several genera of gymnosperms and angiosperms including, for example, *Pinus*, *Thuja*, *Juniperus*, *Chamaecyparis*, *Fagus*, *Quercus*, *Carya*, *Ulmus*, *Acacia*, *Eucalyptus*, *Fraxinus*, *Hevea*, *Citrus*, and *Malus*. The juvenile stage of the young seedlings may differ from the adult form in one or more distinctive characteristics such as growth habit and vigor, flowering capacity, leaf shape and structure, phyllotaxy, ease of rooting of cuttings, internal stem anatomy, leaf retention, thorniness, and ability to produce anthocyanin pigments (Kramer and Kozlowski, 1960; Kozlowski, 1963a). When the

upper part of a tree reaches the adult phase the lower part often remains juvenile so that both phases may occur on the same plant simultaneously. For example, in adult *Robinia pseudoacacia* trees the basal branches are juvenile. They have thorns and do not flower. In contrast, the apical branches represent the adult phase inasmuch as they are thornless and produce flowers and fruits (Trippi, 1963a). The term "age" however, has no real meaning in reference to the difference between the kinds of growth that occur at the same time in the juvenile and adult parts of an old tree. The meristems involved in the two parts are equally young. This point is emphasized because of existing confusion in the literature on the relation between phase change and chronological age.

Although Schaffalitzky de Muckadell (1954) stated that juvenile stages occur quite commonly in woody plants, there is considerable variation among species in how well defined the growth phases are and how clearly they can be identified. Hence, the most obvious juvenile character in one species may be thorniness and in another species retention of dead, withered leaves.

Trees that show a small and gradual change from the juvenile to adult condition are described as "homoblastic" whereas those with an abrupt transition are called "heteroblastic." Plants grown from buds of the lower portions of seed-grown heteroblastic trees possess juvenile characters (thorniness, ease of rooting, etc.) whereas trees which develop from buds of peripheral portions show adult characters. Hence, budwood transmits the characters of the part of the plant from which it was derived. The resulting plant then usually sequentially completes the various subsequent changes that are part of its normal ontogenetic development.

DURATION OF JUVENILITY

The length of the juvenile period may vary greatly among species (Table 3.1). Some gymnosperms remain in the juvenile stage for less than a year and others may retain juvenility throughout their life. Outstanding examples of trees that remain juvenile permanently are the ornamental *Retinosporas* or juvenile forms of *Chamaecyparis* and *Thuja*. Because they differ so greatly in appearance from the adult forms these plants were erroneously classified in the genus *Retinospora*. In *Chamaecyparis pisifera*, in which needle leaves are typical of the juvenile phase, plants derived from needle-leaved cuttings retained juvenile foliage if the source tree did so. Otherwise imbricated leaves eventually developed (Langner, 1964). Hence, Langner concluded that stages of development in this species could not be fixed by vegetative propagation.

Sax (1962) emphasized that the age of first flowering, an indication of achieving the adult stage, shows great variability among different genera of

TABLE 3.1

VARIATION IN LENGTH OF JUVENILE PERIOD IN TREES AS DETERMINED BY TIME TO FIRST FLOWERING

Species	Juvenile period (years)	Reference
<i>Pinus sylvestris</i>	5-10	Wareing (1959)
<i>Larix decidua</i>	10-15	Wareing (1959)
<i>Pseudotsuga taxifolia</i>	15-20	Wareing (1959)
<i>Picea abies</i>	20-25	Wareing (1959)
<i>Abies alba</i>	25-30	Wareing (1959)
<i>Betula pubescens</i>	5-10	Wareing (1959)
<i>Fraxinus excelsior</i>	15-20	Wareing (1959)
<i>Acer pseudoplatanus</i>	15-20	Wareing (1959)
<i>Quercus robur</i>	25-30	Wareing (1959)
<i>Fagus sylvatica</i>	30-40	Wareing (1959)
Tea (<i>Camellia thea</i>)	5	Bubrjak (1961)
Apple (<i>Malus</i>)	7.5	Visser (1964)
Pear (<i>Pyrus</i>)	10	Visser (1964)
Tangerine (<i>Citrus reticulata</i>)	5-7	Furr <i>et al.</i> (1947)
Sweet orange (<i>Citrus sinensis</i>)	6-7	Furr <i>et al.</i> (1947)
Grapefruit	7-8	Furr <i>et al.</i> (1947)
Tangelo (<i>Citrus paradisi</i> × <i>C. reticulata</i>)	5-8	Furr <i>et al.</i> (1947)

plants. He found that some species bloomed in 3 years, whereas others required 10 years to produce flowers. Some varieties of apple, like Wealthy, may flower when 3 to 4 years old and others, like Northern Spy, often do not bloom until 15 to 20 years old (Kramer and Kozlowski, 1960). According to Righter (1939), *Pinus sinensis* required only 1 year to produce male cones but *Pinus resinosa* needed 9 years. Actually, the duration of the nonflowering juvenile stage is greatly modified by environmental factors which influence growth rate. Vigorous trees reach adulthood before suppressed ones of the same species. Occasional precocious flowering in some species does not necessarily mean that the adult stage has been reached. Citrus, for example, may flower as a very young seedling and then grow only vegetatively for several years until it completes its juvenile growth phase (Furr *et al.*, 1947).

Flowering

During the juvenile period, which varies greatly in length among species, woody plants do not flower. Once the capacity for flowering is achieved, it is usually retained. However, an important distinction should be made between the capacity for flowering and the annual initiation of flower primordia

(Wareing, 1964b). Many adult forest trees capable of flowering, do not do so every year. Environmental factors can control the initiation of flower primordia after the minimum size for flowering has been attained (Kramer and Kozlowski, 1960).

Internal Requirements for Flowering

Following a juvenile period of 5 to 7 years in *Pinus sylvestris* the female cones are produced first, usually on strong leading shoots, either leaders or lateral branches of the terminal leader (Wareing, 1958). Only female cones are formed at first, but when the trees are 10 to 15 years old, they begin to produce male cones in the basal region of lower branches on shoots of lower morphological categories. The more distal parts of branches retain a vegetative character or produce only female cones. As a branch increases in age, however, male cones are borne more distally in the branch on laterals of higher morphological category. Finally, male cones may be found near the female cones on leading shoots of a branch.

The reduction in vigor of a shoot often is associated with reduced formation of female cones and appearance of male cones. This suggests that a higher nutritional status is required for development of female cones than for male cones.

Floral primordia are differentiated by apical meristems apparently due to movement of a stimulus from a leaf to a bud. This was demonstrated in herbaceous plants by: (1) inducing flowering by exposing a single leaf to a factor such as appropriate daylength or, (2) grafting of an induced leaf to a receptor, noninduced plant, resulting in flowering of the latter (Zeevat, 1962).

Induction of flowering in plants which previously grew only vegetatively is thought to involve activation of previously inactive genes. Although a number of metabolic differences between the flowering and vegetative state have been identified, these often seem to be symptoms of flowering rather than its cause. Several types of growth regulators appear to be involved in reproductive growth including auxins, gibberellins, cytokinins, and growth inhibitors (Van Overbeek, 1962). Involvement of hormones is supported by the work of Longman and Wareing (1958) who found flowering in young *Larix leptolepis* trees to be influenced by the position of the branches relative to the gravitational field. As branch angle, measured from vertical upward, was increased, the amount of flowering increased. Since geotropic effects are related to differential hormone distribution, it appears likely that growth regulators were involved in the gravimorphic induction of flowering. There is considerable evidence that endogenous gibberellin may initiate flowering, but the mode of action has not been clarified. Pharis *et al.* (1965) postulated that exogenous gibberellin may supplement the endogenous supply sufficiently

to induce flowering in some species of gymnosperms, provided the plant is mature enough.

When 13-year-old olive trees were sprayed with 50 ppm solutions of uracil and xanthine, the plants flowered earlier than controls. Correlated with flowering, following uracil and xanthine applications, were increases in protein nitrogen and RNA/DNA ratios, suggesting that these may be related to floral induction (Kessler *et al.*, 1959). Control of flowering is discussed further in Volume II, Chapter 9.

CONTROL OF FLOWERING

There has been lively controversy over the years about whether or not flowering can be readily controlled in young trees. Girdling of apple trees of different ages was followed by fruiting only in mature or nearly mature plants and grafting failed to accelerate flowering unless seedlings were several years old when grafted (Fritzsche, 1948). Kemmer (1962) also showed that girdling of apple seedlings in an early stage did not promote flowering on their own roots or on Malling IX rootstocks. These findings suggest that in apple, at least, the juvenile stage cannot be readily shortened. In contrast to this view are those of Passeecker (1952) who believed that the juvenile stage could be reduced by stimulation of vegetative growth, and of Wareing and Robinson (1963) who successfully grew seedlings of several species of woody plants continuously under long days in a warm greenhouse to attain the minimum size for flowering as rapidly as possible. By this technique they induced flowering in *Larix leptolepis* within 4 years, whereas normally this species remains juvenile for 10 to 15 years. For promotion of flowering, they advocated that seedlings be grown to a critical minimum size as rapidly as possible and then subjected to additional treatments favorable to flowering. These additional treatments varied with species. For example, long days were required for *Betula*, short days for *Ribes rubrum*, and horizontal training for *Larix leptolepis*. When Doorenbos (1955) exposed *Rhododendron* plants to very long photoperiods they grew approximately twice as fast as in normal daylengths. Under long days azalea seedlings flowered in less than 2 years, and azalea-rhododendron hybrids flowered in less than 3 years, or about twice as fast as without the long-day treatment.

Wareing (1964b) reemphasized that normally the critical factor in readiness for first flowering was attainment of a certain minimum size, rather than the accomplishment of a given number of periods of growth and dormancy. This conclusion was based on experiments in which plants grown continuously under long days flowered when they reached a critical size. However, the minimum plant size at which first flowering usually occurs does not provide insight into the physiological mechanism which triggers the change from

juvenile to adulthood. This was demonstrated by Robinson and Wareing (1969) who carried out further experiments to determine if the attainment of a critical minimum size was always necessary for achievement of adulthood and the flowering state. Shoot tips of *Ribes nigrum* seedlings were removed when they had reached a size at which flowering does not occur and were rooted as cuttings. The latter plants were treated similarly and the process was repeated twice. The final series of plants so derived produced flowers in response to short days and thus they had achieved adulthood, even though the successive rooted cuttings had not attained the minimum size at which phase change normally occurred in the species. Thus, the critical size at which flowering normally occurs evidently is correlated with internal changes which are more directly responsible for causing phase change.

TABLE 3.2
INFLUENCE OF ROOTSTOCK ON FLOWERING OF APPLE SEEDLINGS^a

Length of juvenile phase (years)	Number of trees that flowered	
	On Malling IX	On their own roots
4	15(25) ^b	0(0)
5	11(43)	6(10)
6	15(67)	11(28)
7	9(82)	20(61)
8	8(95)	11(79)

^a From Visser (1964).

^b Numbers in parenthesis indicate cumulative percent of seedlings that produced flowers.

The rootstock may have some effect on the length of the juvenile stage. Visser (1964) shortened the juvenile phase of apple seedlings by budding them on Malling IX rootstocks and found that the average length of the juvenile period for the seedlings that flowered was 5.7 years on Malling IX rootstocks, as against 7.0 years on their own roots (Table 3.2). When Campbell (1961) worked apple seedlings on apomictic seedling rootstocks from *Malus sikkimensis* they had a shorter juvenile phase than when worked on Malling IX rootstocks. In further experiments 25 seedlings were raised from three crosses. These were multiplied the first year by budding onto 1-year-old seedlings of *M. sikkimensis*. Fifteen percent of the trees flowered within 3 years after budding and 53% flowered after 4 years. None of the adjacent original 25 seedlings flowered over the 4-year period.

Despite the evidence that "weak" rootstocks accelerate flowering the bulk of the literature supports Wareing's contention (1959) that a certain

minimal size normally is associated with attainment of the flowering condition. The time to reach the critical size can be modified considerably by manipulating the environment. Visser (1964), for example, showed that the amount of sunshine, soil cultivation, and spacing among plants influenced the time of first flowering of apple seedlings.

Much evidence suggests that gibberellins may be helpful in promoting flowering and studying the mechanism of flower induction. Gibberellins were the first chemicals to promote flower formation in a really reproducible way (Van Overbeek, 1962). In concentrations of 50 to 500 ppm gibberellic acid induced flowering in a wide variety of gymnosperm genera including *Cryptomeria*, *Metasequoia*, *Taxodium*, *Chamaecyparis*, *Cupressus*, *Glyptostrobus*, *Libocedrus*, *Thuja*, and *Juniperus* (Sato, 1963).

Extremely early production of staminate strobili was promoted by gibberellic acid in *Cupressus arizonica* (Pharis *et al.*, 1965). This species, which normally does not produce flowers until 4 to 5 years old was induced to flower in 55 days after seed germination by spraying with gibberellic acid. Within 18 to 20 days after the first hormone application the meristem changed from a vegetative to a reproductive condition. The earliest age that the plant produced strobili depended on the concentration of gibberellic acid. Pharis and Morf (1967) induced formation of staminate and ovulate strobili of *Thuja plicata* at an age of 4 months with foliar applications of gibberellin A₃. Also foliar application of gibberellin A₃ and mixtures of gibberellin A₄/A₇ to *Cupressus pygmaea*, *C. lusitanica*, and *C. arizonica* at age 7 to 9 months resulted in induction of staminate strobili. By comparison, *Cupressus funebris*, in a juvenile needle stage at an age of 9 months was not responsive to foliar application of gibberellin A₃ for at least 100 days.

The application of gibberellic acid to new shoots causes changes in several constituents. In summarizing these Sato (1963) stated that indoleacetic acid (IAA) decreased from immediately before to the time of flower initiation and thereafter it increased gradually with flower development. Another but unknown promoting substance also increased rapidly at the time of flower initiation. Water and total nitrogen decreased after gibberellic acid treatment, while soluble and insoluble carbohydrates increased. Hence, gibberellic acid treatment of shoots was followed by an increased C/N ratio. It is not clear whether these changes were the cause or the result of the flowering process.

J. Bonner (1962) suggested that gibberellin itself is not the actual flowering hormone but rather something produced by the plant under the influence of the flowering regulator. Bonner gave two reasons for this conclusion: (1) applied gibberellin does not induce flower formation permanently; and (2) applied gibberellin does not affect flowering of short-day plants. On the other hand, Pharis and Morf (1968) emphasized that gibberellins played an important role in some plants such as members of the *Cupressaceae* and

Taxodiaceae. They supported the hypothesis of Lang (1965) that juvenile plants could not generate the induced state and produce flowering hormones. Experiments by Pharis and Morf (1968) in which the flowering state was induced in *Thuja* and *Cupressus* by gibberellins suggested that the juvenile, nonflowering state was one in which gibberellins in these genera had not yet reached the critical condition for floral induction. Discontinuing gibberellin application to young *Cupressus* plants caused abortion of many induced strobili as well as reduction in the rate of formation of new strobili. This suggested that gibberellin did not end the juvenile phase, but rather had increased to a sufficiently high concentration to induce flowering after a natural termination of juvenility.

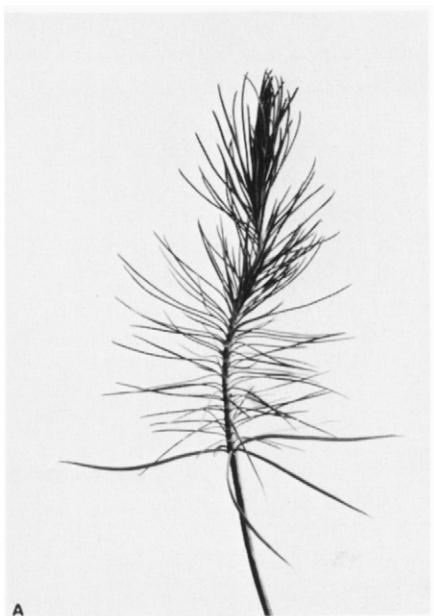
Growth Habit

Ivy plants in the genus *Hedera* often are cited as classical examples of phase change. The juvenile form is a nonflowering prostrate or climbing vine with lobed leaves and a stem which produces aerial roots. The adult, fruiting phase is a shrub with entire leaves, which rarely produces aerial roots (Robbins, 1960). Brink (1962) described a striking case of phase change in which *Hedera* vines ascended tree stems to a height of 7 m or more. At a height of less than 2 m, the plants changed from a juvenile to adult form which bore inflorescences. Certain *Hedera* plants which ascended trees for less than 2 m had juvenile leaves only. In some trees transition from the juvenile to the adult stage is identified by a change in growth habit from a shrub to a tree with a single stem (Philipson, 1964). Robbins (1957) stated that *Ficus repens* has both juvenile and adult forms. Cuttings from the fruiting stage produce small shrubs.

Extension growth of juvenile and adult shoots often varies appreciably, but the differences among species are not consistent. For example, Trippi (1963a) found that shoots of the juvenile zone grew significantly more than those of the adult zone in *Tilia parviflora*, *Robinia pseudoacacia*, and *Castanea vulgaris*. Growth of branches of the juvenile zone in adult *Tilia parviflora* trees was similar to that of branches of juvenile plants grown from seed (Table 3.3). In adult *Ilex aquifolium* and *Aesculus hippocastanum* trees, however, branches of the adult zone grew more than those from the juvenile zone.

Form and Structure of Leaves

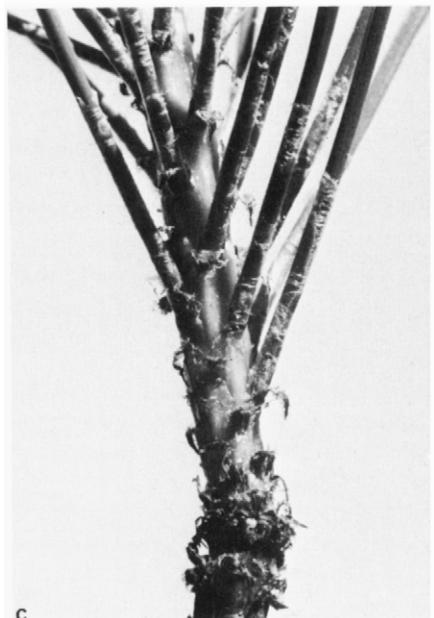
There are many illustrations of changes during ontogeny in form and structure of foliage of both angiosperms and gymnosperms, and only a few examples will be given.



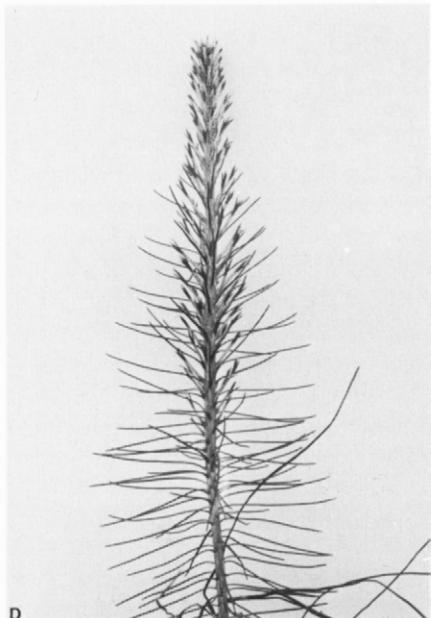
A



B



C



D



FIG. 3.1. Juvenile and adult leaves of *Pinus* (A) cotyledons and needlelike primary leaves of *P. taeda* during the first growing season; (B) adult form of primary leaves on stem of 2-year-old *P. taeda*; (C) adult form of primary leaf on lower branch of 18-year-old *P. taeda*; (D) *P. taeda* seedling after 4 weeks growth during second growing season. New primary leaves show progressive size reduction, with terminal ones scale-like. Spur shoots are breaking through the fascicle sheath; (E) long shoot of 7-year-old *P. echinata* showing variations of primary leaves from a scalelike form to an intermediate form between scalelike and needlelike leaves. [From Bormann (1963).]

Morphological expression of primary leaves in *Pinus* varies in juvenile and adult forms (Bormann, 1963). The primary leaves borne on long shoots of first-year seedlings are flat, glaucous, needlelike structures somewhat similar to secondary leaves. In contrast, adult primary leaves, which appear

TABLE 3.3

VARIATION IN SHOOT GROWTH OF JUVENILE AND ADULT PLANTS OF *Tilia parviflora*^a

	Juvenile plant		Adult plant	
	5 years old	Juvenile zone	Adult zone	
Average length (cm)	10.19	11.95		6.38
Growth (%)	100	117		62

^a From Trippi (1963a).

several years after germination, are scale- or bractlike structures. These function as bud scales in the bud and as sterile and fertile bracts on the long shoots (Fig. 3.1). In most species of *Pinus* the needlelike primaries are not produced after 2 or 3 years. After the transition occurs from a juvenile to adult form of the primary leaf, a shoot may occasionally revert to production of needlelike primaries because of injury or changes in environment (Doak, 1935).

Marked differences in form occur between the juvenile and adult leaves of certain species of the *Cupressaceae*. In *Juniperus virginiana*, for example, the juvenile form has acicular leaves while those of the adult form are imbricated (Fig. 3.2). In contrast, *Juniperus communis* bears acicular leaves throughout its life cycle (Brink, 1962).

Among the angiosperms which show phase change clearly is the classical *Hedera* with lobed juvenile leaves and entire adult leaves (Fig. 3.3). According to Penfold and Willis (1961), most species of *Eucalyptus* develop several distinct leaf types during ontogeny including cotyledons, seedling leaves, juvenile leaves, and adult leaves. The juvenile leaves, which are oriented horizontally, usually have structurally different upper and lower surfaces, with most stomata on the lower surface. The pendant adult leaves, in contrast, have stomates on both surfaces. In many species of *Eucalyptus* the juvenile leaves are more glaucous than adult leaves. Often the changeover of leaf types is slow and gradual with relatively large and coarse transitional leaves preceding the adult forms. The transitional leaves comprise a graded series, and because of the high degree of variability among them, they are difficult to describe (Fig. 3.4). *Eucalyptus globulus* shows striking differences between its juvenile and adult leaves. The relatively thin juvenile leaves, which normally are borne horizontally, are sessile and cordate (E. D. Johnson, 1926). They have a pointed apex, are approximately twice as long as wide, and are arranged in pairs at right angles to each other. The thick, spirally-borne adult leaves are sickle shaped. Their petioles are twisted so they hang vertically. Adult leaves lack the heavy wax coating found on juvenile leaves. In *Acacia* juvenile leaves are pinnately compound, whereas adult foliage consists of flattened phyllodes. In *Ilex aquifolium* trees the leaves varied from dentate in the juvenile zone to entire in the adult zone (Fig. 3.5).

According to Schaffalitzky de Muckadell (1959) the leaves of adult grafts of *Fraxinus excelsior* were narrower than juvenile ones. Ratios of length to width in leaflets of two clones of *Fraxinus excelsior* were consistently higher over a 2-year period (Table 3.4). Schaffalitzky de Muckadell (1959) noted that young *Ulmus carpinifolia* plants produced scabrous and nonoblique leaves whereas old trees had smooth and markedly oblique leaves. These characters were stable when grafts were made from juvenile and adult parts of trees.

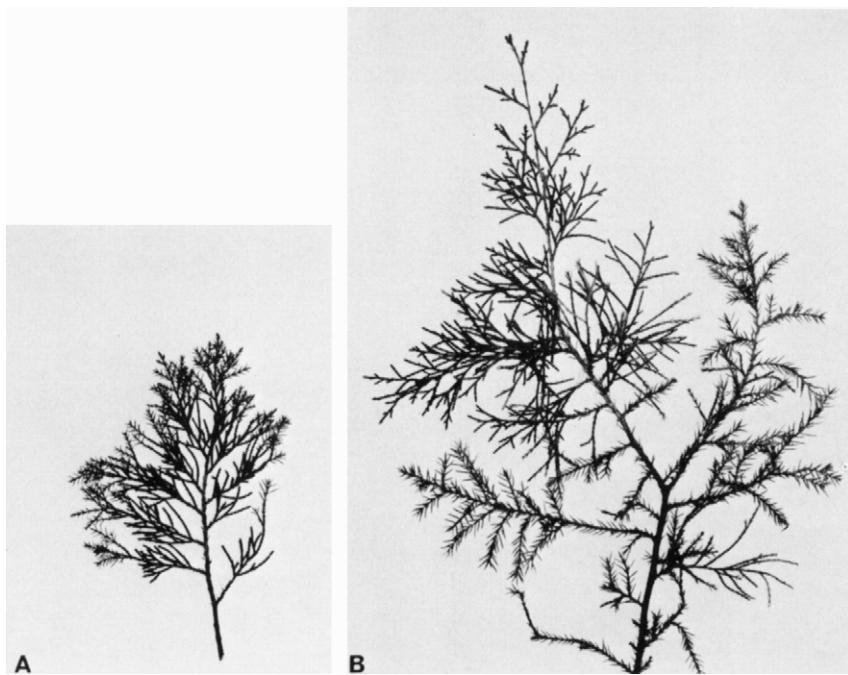


FIG. 3.2. Juvenile and adult foliage of *Juniperus virginiana*: (A) Needlelike juvenile leaves on proximal parts of the branch and scalelike, adult leaves on distal portions; (B) phase reversal in a single branch. Adult leaves on proximal parts are scalelike and appressed. Leaves most recently produced at tips are needlelike and represent a reversion to the juvenile condition. [From Brink (1962).]

TABLE 3.4

RATIO OF LENGTH TO WIDTH IN LEAFLETS OF TWO CLONES OF *Fraxinus excelsior*^a

Clone No.	Age of parent tree (years)	Graft year	Origin of scion wood	Length/width ratio of leaflets	
				1956	1957
1	40	1954	Top branches	3.4	4.0
			Low epicormic branches	2.6	2.9
2	70	1956	Top branches	4.5	3.5
			Low epicormic branches	2.6	2.7

^a Grafts from juvenile low epicormic branches are compared with those from adult top branches.

^b From Schaffalitzky de Muckadell (1959).

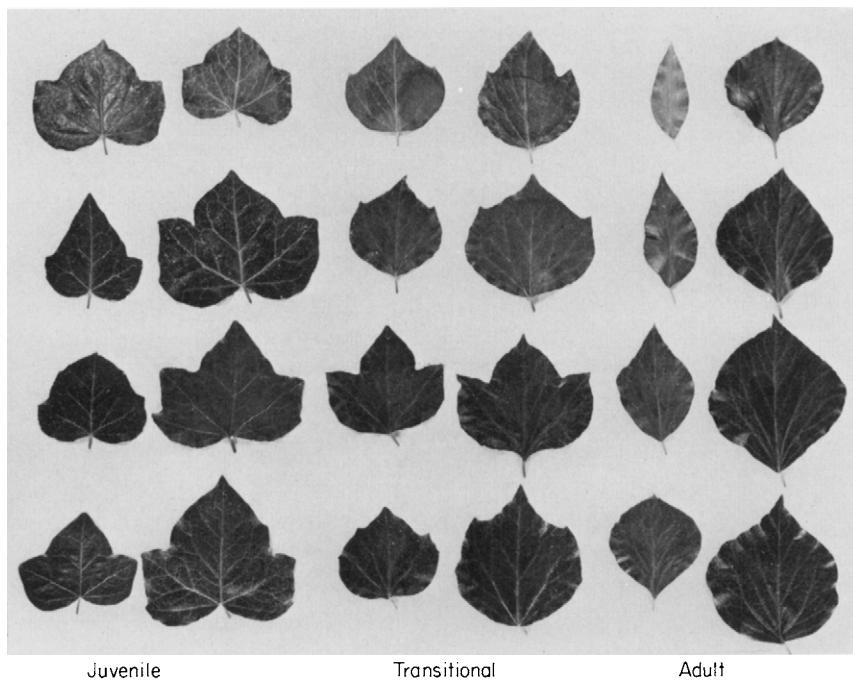


FIG. 3.3. Variations in leaf form of juvenile, transitional, and adult leaves of *Hedera*. (Photo courtesy of V. T. Stoutemyer.)

Leaf Retention

In deciduous trees the leaves of adult plants usually abscise earlier in the year than leaves of juvenile plants (Fig. 3.6). For example, near Paris by mid-November no leaf abscission had occurred in 1-2 or 10-year-old *Robinia pseudoacacia* trees but leaves were falling in 50-year-old trees (Trippi, 1963b).

Often the base of a tree remains juvenile while the top shows adult characteristics as demonstrated by Schaffalitzky de Muckadell (1959). He collected scions from basal leafy epicormic branches as well as from top branches of the same *Fagus* tree. When these were grafted to uniform seedling stocks, the scions from the basal branches produced leafy grafts whereas leafless grafts arose from the top branches. In another experiment leaf-retaining scions did not shed leaves when grafted to leaf-shedding branches of old *Fagus* trees. The ability of *F. sylvatica* to retain its withered leaves during winter was shown to be a juvenile character (Schaffalitzky de Muckadell, 1962). The juvenile leaf-retaining part of young *F. grandifolia* trees could be outlined as a cone. In *Quercus* there is considerable variation among trees of certain species in the capacity of their juvenile parts to retain

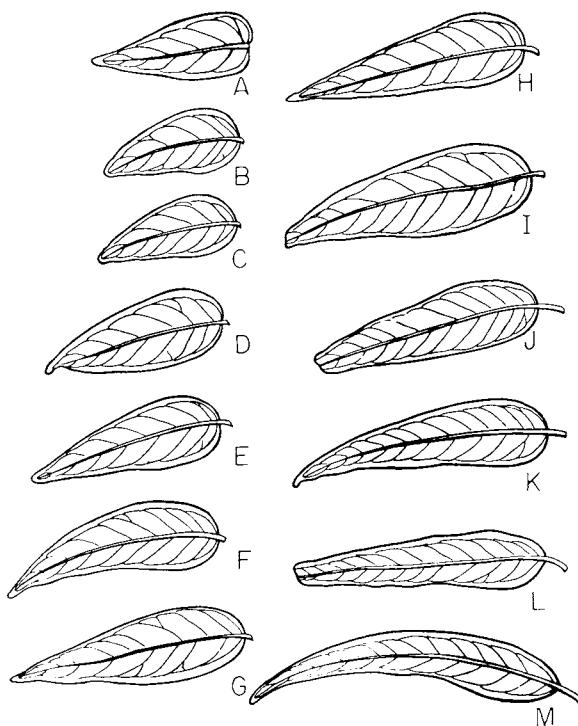


FIG. 3.4. Series of leaves from a single tree of *Eucalyptus macarthuri*, showing the transition from juvenile (A) to adult (M) foliage. [From Penfold and Willis (1961).]

leaves (Fig. 3.7). For example, many specimens of *Quercus robur* and *Quercus petrea* never kept their withered leaves, while others retained leaves at the base up to a very old age. A juvenile, leaf-retaining stage also existed in *Carpinus betulus*.

Thorniness

It is well known that thorniness is a juvenile characteristic of many woody plants, including orchard and forest trees (Fig. 3.8). For example, juvenile citrus trees have an abundance of thorns (Furr *et al.*, 1947). Whereas young shoots of *Malus robusta* were rough, twiggy and thorny, old shoots lacked a spiny and twiggy character (Blair *et al.*, 1956). Furthermore, when buds were removed from the old shoots and budded in the nursery the shoots which developed from them were smooth and spineless. This was in contrast to the juvenile, thorny shoots which developed from adventitious buds of cut-back *Malus robusta*.



FIG. 3.5. Variations in leaf form of *Ilex aquifolium* (A) Branch from juvenile zone (B) branch from adult zone. [From Trippi (1963a).]

Formation of Anthocyanin Pigments

Coloration in young leaves due to anthocyanin pigments and their disappearance with maturity have been widely reported. For example, in *Malus*, *Hedera*, and *Acer rubrum*, cuttings from juvenile material contain more anthocyanin than those from the adult phase (Bachelard and Stowe, 1963). The decrease with aging in ability to form anthocyanin pigments was also shown by Schaffalitzky de Muckadell (1959) who grafted scions from adult top branches and low juvenile epicormic branches of *Fraxinus excelsior*. Whereas grafts from top branches remained green, those from the low epicormic branches were purplish. This character was persistent for at least three growing seasons.

Stem Anatomy

Transformation from a juvenile to adult stage often is accompanied by changes in wood anatomy. The physiologically young wood near the center

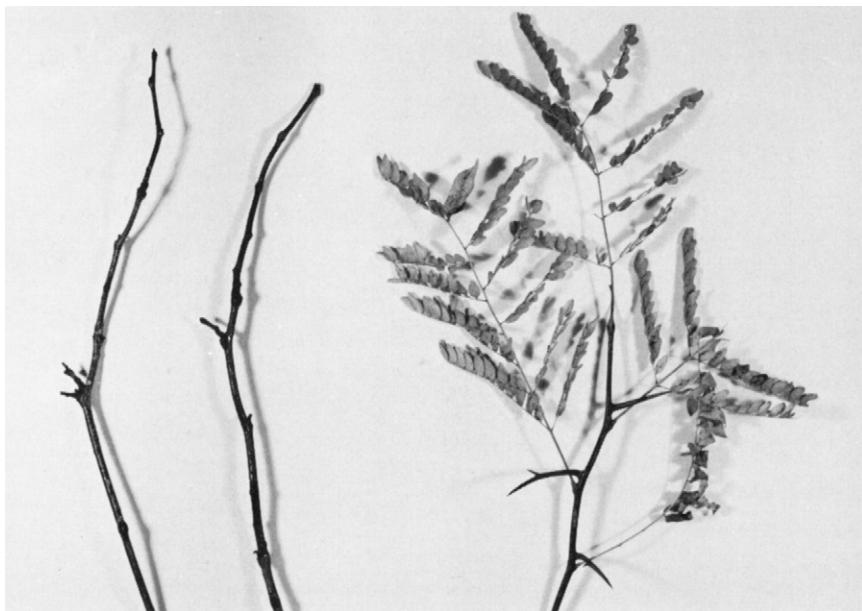


FIG. 3.6. Branches from the juvenile zone (*right*) and the adult zone (*left*) of a senile *Robinia pseudoacacia* plant. [From Trippi (1963b).]

of a stem exhibits gradual changes in the structure of components of successive annual rings. Usually from the center outward progressively older rings show an increase in cell dimensions as well as changes in structure and proportions of various tissues. For example, the ring-porous character of xylem, which often is not obvious in seedlings of typically ring-porous angiosperm species, develops gradually in a series of adjacent rings. In gymnosperms, the first formed rings show a less abrupt transition from early-wood to latewood than older rings, and they often have less dense latewood (Rendle, 1960). Because of such differences, the wood in the region of the pith, which is formed early and under the influence of apical meristems in the crown, is termed juvenile (sometimes called core or pith) wood. The wood of the outer layers is considered to be adult (sometimes called outer or mature) wood. Rendle (1960), considered adult wood to have cells which generally had achieved maximum dimensions and with a more or less stabilized structural pattern except as influenced by environment.

Rumball (1963), studied wood structure of twigs of heteroblastic trees which carried the juvenile habit at the stem base and the adult habit at the top. Wood structure of twigs at two stem heights of homoblastic trees also was studied. In *Podocarpus dacrydioides*, a heteroblastic species, the mean tracheid length of adult twigs was much greater than in juvenile twigs. However, in *Podocarpus totara*, a homoblastic species, differences in wood



FIG. 3.7. Leaf-retaining juvenile characteristic of the lower stem of *Quercus alba*. [From Brink (1962).]

structure of juvenile and adult twigs were few. It was suggested that the change in growth habit may subsequently cause change in wood structure.

De Bruyne (1952) has shown that the structure of wood rays is altered considerably in ontogenetic development. In stem cross sections of *Pterospermum diversifolium* most of the high rays near the center were composed of alternating uniseriate parts, one cell high, and uni- or biserrate parts of procumbent cells. In the old wood (at 30 cm from the center) the very high rays had disappeared. Practically all the rays at this distance were multi-seriate, and newly formed uniseriate rays were infrequent. Rays of *Pterospermum* had not reached maturity until at a distance of 30 cm from the inner core where the 68th growth ring was counted. Studies with eccentric stems showed that ray structure altered with physiological tree age rather than with distance from the core (De Bruyne, 1952). According to Chalk (1934), the

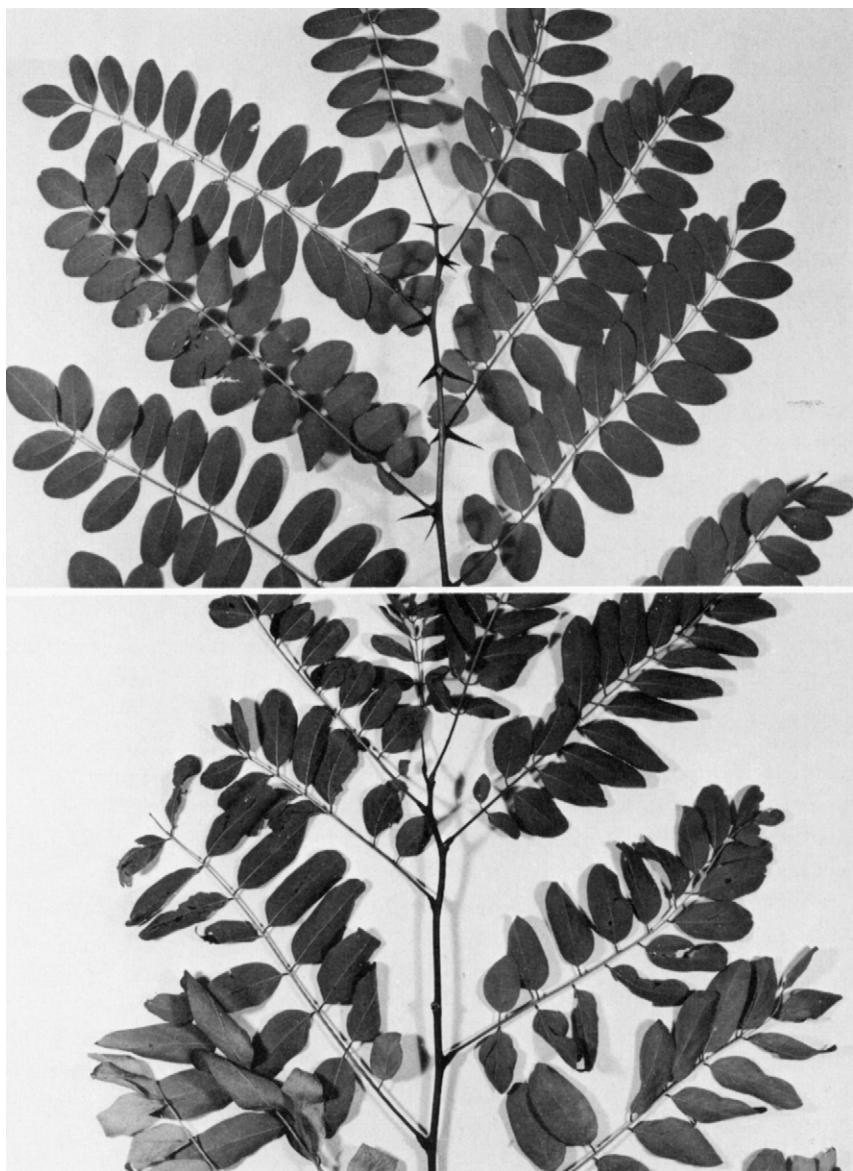


FIG. 3.8. Thorniness in 1-year-old plants (upper photo) and absence of thorns in 10-year-old plants (lower photo) of *Robinia pseudoacacia*. [From Trippi (1963a).]

wide rays which are characteristic of mature wood of *Quercus* are absent in seedlings and develop later. In *Fagus*, however, some wide rays do occur in young seedlings. Other rays, which are only one cell wide at the pith, increase in size rapidly to form broad rays within a season or two.

Gooding (1965) examined *Hedera helix* for characters which might be associated with a change in growth phase. No marked anatomical differences were found in leaves, roots, or buds of juvenile and mature tissues. However, there was greater lignification of tissues in the mature stem, with a discontinuous ring of fibers encircling the phloem. Phloem fibers were very rare in juvenile stems. Transitional-phase plants had a few fibers which became more numerous as these plants progressed in age.

Rooting of Cuttings

One of the most consistent characteristics of juvenile trees is the relative ease of rooting of their cuttings when compared with cuttings from old trees of the same species. Voluminous data are available to demonstrate this and only a few examples will be cited. Patton and Riker (1958), for example, found higher rooting ability for the first few years of cuttings from *Pinus strobus* trees grown from previously rooted cuttings over that of cuttings from seedling origin. As the trees which developed from rooted cuttings grew older, the cuttings from them declined steadily in rooting ability. Delisle (1954) also clearly showed the influence of age on rooting ability. Rooted cuttings of *Pinus strobus* that were planted in 1938 were grown to 4-year plants, and then cuttings from these were rooted and planted. This process was repeated every 4 years through 1954, and rootability was found to decrease with each successive generation of cuttings.

When Schaffalitzky de Muckadell (1959) rooted cuttings of *Populus × canadensis serotina* from adult top branches, intermediate branches, and juvenile epicormic branches from a height of 2 m he found good correlation between the degree of juvenility and success in propagating cuttings (Table 3.5). Stoutemyer *et al.* (1961) set buds of adult *Hedera canariensis* on juvenile understocks. Later the budded shoots were cut back to the bud union and the top growth was classified as adult, transitional, or juvenile. Shoots from these buds also were cut into top, middle, and basal portions. Cuttings made from shoots with juvenile or transitional characters rooted easily (Table 3.6). In addition when shoots showed juvenility the wood near the tips rooted more easily than that near the base.

Bark inversion by D. L. Smith (1959) induced the development of juvenile shoots from the base of seedling ornamental apple trees. Cuttings taken from these shoots in June rooted much more readily than cuttings from the fruiting branches. Root suckers of a mature ornamental apple tree rooted

TABLE 3.5

VARIATIONS IN ROOTABILITY OF CUTTINGS OF 2 CLONES OF *Populus*
× canadensis serotina OBTAINED FROM DIFFERENT PARTS OF THE TREE^a

Origin of Cuttings	Percent of living cuttings	
	Clone 1	Clone 2
Top branches with flower buds	0	20
Intermediate branches	35	33
Epicormic branches 2 m above ground	80	80

^a From Schaffalitzky de Muckadell (1959).

well, even when they had developed 6 to 7 ft from the base of the tree, whereas cuttings taken from the fruiting branches produced no roots even with hormone treatment. Garner and Hatcher (1958) compared for three seasons the behavior of root cuttings of the apple clone Crab C taken from source plants of five ages. Rooting and growth of root cuttings both declined with increasing age of establishment of the parent plant. The decline in rooting with age in the clone had close resemblance to that found in seedlings. In juvenile cuttings of *Hevea*, rooting decreased as the age of the parent plant increased, and cuttings taken from the base of the stem retained their rooting capacity longer than those from other parts (Wiersum, 1955). Many juvenile cuttings could be obtained from a single parent plant by stumping a young seedling at regular intervals, and by using the stems of young established

TABLE 3.6

ROOTING CHARACTERISTICS OF ADULT, TRANSITIONAL, AND JUVENILE SHOOTS OF *Hedera canariensis*^a

Type of growth	Percent rooted		
	6 Weeks	12 Weeks	
Adult	Tip	37	64
Adult	Mid	31	29.3 ^b
Adult	Basal	20	38
Transitional	Tip	86	96
Transitional	Mid	52	56.3
Transitional	Basal	31	54
Juvenile	Tip	90	97
Juvenile	Mid	67	71.0
Juvenile	Basal	56	77

^a From Stoutemyer *et al.* (1961).

^b Average.

cuttings of the first and even the second generation. With mature cuttings or with cuttings from material "rejuvenated" by budding on or below the collar of the young seedlings, no rooting was obtained. Morphological and physiological controls of rooting of cuttings in juvenile and adult phases are discussed in Volume II, Chapter 5.

Control of Phase Change

The fact that several investigators have been successful in causing phase change is of considerable practical importance as it may lead to control of flowering and fruiting and rooting of cuttings. Acceleration of maturation by controlling photoperiod and exogenous application of gibberellin to promote flowering was discussed in an earlier section of this chapter. Another example of promoting maturation was cited by Scurfield and Moore (1958). They observed that *Eucalyptus melliodora* plants treated with gibberellic acid developed the alternate arrangement and falcate-lanceolate shape of adult leaves earlier than control plants.

REVERSION TO JUVENILITY

Reversion of adult to juvenile forms has been accomplished by several techniques including heavy pruning, grafting adult scions on juvenile stages, and treating adult material with gibberellin.

Doorenbos (1954) produced many reversions of *Hedera helix* to the juvenile form by grafting the mature fruiting form on two- and three-year-old seedlings or on plants grown from cuttings. Reversion to juvenility of adult *Hedera canariensis* tissues grafted on juvenile forms was influenced both by temperature and amount of mature tissue initially present in the graft combinations. Whereas 80°F promoted reversion, 60°F did not. Also, the greater the amount of mature type of wood on the scion in grafting, the less the tendency for reversion to juvenility.

Frank and Renner (1956) noted that new shoots on adult *Hedera helix* cuttings reverted to a juvenile form when they were grown in a nutrient solution together with juvenile cuttings that rooted readily. They also showed that when adult ivy cuttings were exposed to a temperature of -10°C for a few hours the new branches that formed a few weeks later had juvenile characteristics.

Robbins (1960) induced reversion to a juvenile condition by spraying adult *Hedera canariensis variegata* plants with gibberellic acid 13 times over a period of 19 weeks. In another experiment, 11 out of 24 *Hedera helix arborescens* plants treated with gibberellic acid developed juvenile branches, but not all new shoots on these branches were juvenile (Table 3.7). Robbins

TABLE 3.7

INFLUENCE OF GIBBERELIC ACID (GA) ON DEVELOPMENT OF JUVENILE CHARACTERS BY
Hedera helix^{a,b}

Number of plants	First treatment	Second treatment	Number of plants with	
			Fully juvenile shoots ^c	Aerial roots
13	None	None	0 ^f	4(1) ^e
14	None	GA ^d	3(2)	7(6)
5	GA ^c	None	4(2)	5(6)
5	GA ^c	GA ^d	4(5)	5(8)

^a The figures in parenthesis represent average number of branches per plant showing full juvenility or aerial roots.

^b From Robbins (1960).

^c Sprayed nine times in 11 weeks beginning May 7, 1958. No juvenile shoots October 27, 1958.

^d Sprayed ten times in 15 weeks beginning October 27, 1958.

^e Data taken 47 weeks after first treatment began and 24 weeks after second treatment began.

^f One plant with 1 branch with juvenile leaves.

also caused production of juvenile shoots by heavy pruning of arborescent *Hedera helix* plants. Stoutemyer *et al.* (1961) treated adult *Hedera canariensis* plants with potassium gibberellate injected into the stem of the decapitated shoot. After 120 days all gibberellin-treated plants reverted to a juvenile or transitional growth stage. Juvenile characteristics were observed in only 30% of the control plants. Cuttings were taken from all plants to ascertain if ease of rooting typical of juvenile plants could be obtained with reverted plants. Juvenile or transitional cuttings from all treatments showed greater than 90% rooting. Adult cuttings from gibberellin-treated plants rooted better than 70%, whereas those from controls rooted 30% (Table 3.8). The increased rooting after gibberellin treatment was related to change in phase.

As emphasized by Brink (1962), the mechanism of phase change, whereby certain characteristics are maintained and perpetuated in somatic cells, remains an exceedingly important unsolved problem. When Wareing (1964b) cut up whole *Hedera helix* plants into sections and rooted them independently he found that in the transition region between the juvenile base and adult upper part of the vine there were shoots that were intermediate in character. This suggested that the transition from a juvenile to adult state first existed in individual cells and that the adult condition was later transmitted by cell lineage.

TABLE 3.8

ROOTING OF CUTTINGS OBTAINED FROM ADULT, TRANSITIONAL AND JUVENILE GROWTH TYPES TREATED WITH POTASSIUM GIBBERELLATE^a

Type of growth	Percentage rooted			
	GA 0.18mg	GA 0.91mg	GA 1.8mg	Control
Adult	70.0	77.5	82.5	30.0
Transitional	92.5	96.6	100.0	95.0
Juvenile	90.0	95.0	97.5	100.0
Weighted mean	82.22	87.75	93.33	63.75

^a From Stoutemyer *et al.* (1961).

Suggested Collateral Reading

- Brink, R. A. (1962). Phase change in higher plants and somatic cell heredity. *Quart. J. Biol.* **37**, 1-22.
- Langner, W. (1964). The origins of so-called juvenile forms in *Chamaecyparis*. *Silvae Genet.* **12**, 57-63.
- Robbins, W. J. (1954). Physiological aspects of aging in plants. *Amer. J. Bot.* **44**, 289-294.
- Robbins, W. J. (1960). Further observations on juvenile and adult *Hedera*. *Amer. J. Bot.* **47**, 485-491.
- Sax, K. (1962). Aspects of aging in plants. *Annu. Rev. Plant Physiol.* **13**, 489-506.
- Schaffalitzky de Muckadell, J. (1954). Juvenile stages in woody plants. *Physiol. Plant.* **7**, 782-796.
- Schaffalitzky de Muckadell, J. (1962). Environmental factors in development stages of trees. In "Tree Growth" (T. T. Kozlowski, ed.). Chapter 18, Ronald Press, New York.
- Stoutemyer, V. T., Britt, O. K., and Goodin, J. R. (1961). The influence of chemical treatments, understocks, and environment on growth phase changes and propagation of *Hedera canariensis*. *Proc. Amer. Soc. Hort. Sci.* **77**, 552-557.
- Trippi, V. S. (1963a). Studies on ontogeny and senility in plants. I. Changes of growth vigor during the juvenile and adult phase of ontogeny in *Tilia parviflora* and growth in juvenile and adult zones of *Tilia*, *Ilex aquifolium* and *Robinia pseudoacacia*. *Phyton (Buenos Aires)* **20**, 137-145.
- Trippi, V. S. (1963b). Studies on ontogeny and senility in plants. V. Leaf-fall in plants of different age and the effect of gibberellic acid on *R. pseudoacacia* and *Morus nigra*. *Phyton (Buenos Aires)*, **20**, 167-171.
- Trippi, V. S. (1963c). Studies on ontogeny and senility in plants. VI. Reversion in *Acacia melanoxylon* and morphogenetic changes in *Gaillardia pulchella*. *Phyton (Buenos Aires)* **20**, 172-174.
- Wareing, P. F. (1959). Problems of juvenility and flowering in trees. *J. Linn. Soc. London, Bot.* **56**, 282-289.

Chapter 4

AGING

Introduction

As a tree ages its growth changes markedly. Among the major manifestations of aging are decrease in metabolism, reduced growth of vegetative and reproductive tissues, increase in dead branches, heartwood formation, slow wound healing, and changes in resistance to invasion by certain insects and fungus pathogens.

Vegative Growth

The effects of aging on shoot growth, cambial growth, root growth, and distribution of dry matter in trees will be discussed separately.

SHOOT GROWTH

In young trees the amount of annual shoot growth increases for a number of years but it attains a maximum relatively early in the life of the tree and declines thereafter. The effects of aging on shoot growth vary with species, environmental fluctuations, and site conditions.

Forward and Nolan (1964) analyzed the effect of age of *Pinus resinosa* trees on shoot growth in the upper, middle, and lower crown. As may be seen in Fig. 4.1, in the three age classes studied the amount of annual shoot elongation in the upper crown was greatest in 20-year-old trees, somewhat lower in 27-year-old trees, and by far the lowest in 50-year-old trees, illustrating a strong aging effect on shoot growth. The differences in shoot growth with age became less pronounced as the amount of shoot expansion decreased toward the tree base. Thus, in the mid-crown, shoots of 50-year-old trees grew less than those of younger trees, whereas in the lower crown the amount of shoot growth was low, with no differences in shoot expansion among age

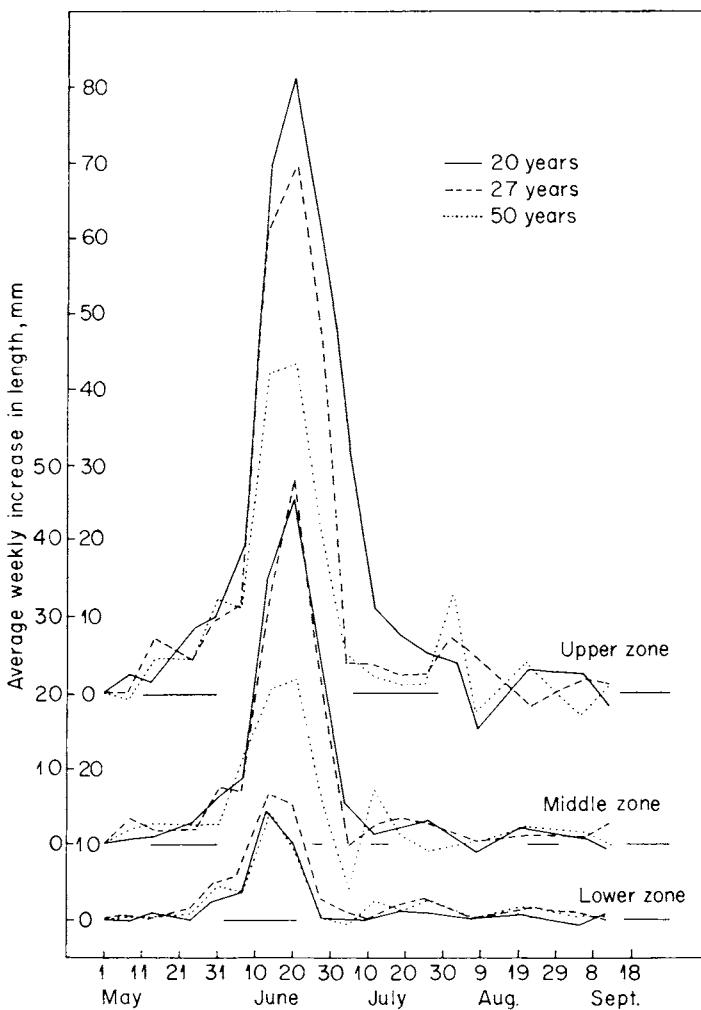


FIG. 4.1. Variations in shoot growth for *Pinus resinosa* trees of different ages. Data are given for different locations on the tree. [From Forward and Nolan (1964).]

classes. The low amount of shoot elongation in the upper and middle crown of old trees, when compared with young trees, was due mainly to a slower rate of growth, since the upper shoots of the 50-year-old trees ceased elongating only slightly earlier than those of the young trees. Other data are available, however, which indicate that the seasonal duration of shoot growth often varies appreciably among trees of different age. For example, Wareing

(1956) reported that shoots of *Robinia pseudoacacia* seedlings grew into autumn in England, whereas, those of mature trees stopped growing by the end of July. In the 2- and 3-year-old seedlings of *Pinus taeda* studied by Kramer (1943) in North Carolina, shoot elongation began at about the same time as in the 13-year-old trees of Young and Kramer (1952), but stopped later. Shoot elongation of mature, bearing apple or pear trees (except for "water sprouts") often requires about 6 to 8 weeks. By comparison, shoots of young trees may continue to elongate for 10 to 12 weeks. Shoot expansion of mature tung (*Aleurites fordii*) trees in the United States often is completed before July but young orchard trees may continue shoot growth until August, and vigorous seedlings in the nursery until September or October. Hence, results vary among species, and the greater amounts of shoot growth of

TABLE 4.1

TOTAL ANNUAL ELONGATION DURING TWO SUCCESSIVE YEARS OF LATERAL SHOOTS OF YOUNG AND OLD *Pinus ponderosa* TREES GROWING ON TWO DIFFERENT SITES^a

Site and year	Shoot elongation (mm)	
	young trees	old trees
1952		
Thatuna	28.5 ± 3.5	26.5 ± 11.5
Clearwater	89.5 ± 17.0	43.5 ± 12.0
1953		
Thatuna	41.0 ± 13.0	23.0 ± 7.0
Clearwater	67.0 ± 10.5	50.0 ± 11.0

^a From Turner (1956).

young, relative to old, trees appear to be traceable to differences in both rate and duration of growth.

According to Turner (1956), 22- to 30-year-old *Pinus ponderosa* trees differed markedly from 63- to 78-year-old trees in shoot growth characteristics. Lateral shoots of the young trees grew more than those of old trees on two sites during 1952 and 1953 (Table 4.1). There also was considerable variation in seasonal patterns of growth. Lateral shoots in both young and old trees began elongating at about the same time, but the younger trees grew more slowly at first. However, shoots of the young trees maintained a fast growth rate for a long period of time and completed 95% of their total growth earlier.

In many tropical species young trees exhibit far less intermittency of shoot growth than do old ones. In mango (*Mangifera indica*), for example, terminal

buds characteristically resume growth several times a year. Flushing in young trees is more or less continuous. In contrast, shoots of old trees often are inactive for several weeks at a time and then tend to produce leaves simultaneously (Holdsworth, 1963). *Albizia falcata* seedlings are considered "evergrowing" whereas old trees show periodicity in shoot growth (Simon, 1914). Njoku (1963, 1964) showed marked differences in duration of leaf production of young and old tropical trees in Nigeria. Seedlings of *Bombax buonopozense* produced leaves during 8 months of the year, but leaf production of old trees was restricted to a period of 1 to 3 months. These differences did not occur in all species, however. For example, seedlings of *Millettia thonningii* and *Cola millenii* had periods of dormancy that were almost as long as those of mature trees. In *Sterculia tragacantha* and *Holarhena wulffbergii* the period of dormancy increased from 1 or 2 months in the first year, to 3 or 4 months by the fourth year. Njoku (1964) concluded that the variation in age at which periodicity of leaf production became established in various species was correlated with dryness of their natural habitats. Under experimental conditions in which seedlings were well watered, the onset of dormancy occurred late in species adapted to wet sites and early in those of dry sites. For example, young trees of *Musanga cecropioides*, a wet site species, showed no dormancy; those of *Triplochiton scleroxylon*, found on dry sites, showed marked dormancy by the third year, and *Hildebrandia barteri*, characteristic of dry sites and rocky hills, exhibited pronounced dormancy for as much as 3 or 4 months, even in the first year of growth.

Shoot Growth and Apical Dominance

Overall loss of apical dominance accompanies reduction of shoot growth in aging trees. Wareing (1958) and Moorby and Wareing (1963) showed that as a branch of *Pinus sylvestris* or *Larix leptolepis* aged the leader of the branch continued to grow rapidly for several years, but growth of many-branched laterals arising from proximal parts of the branch was impeded. The senescent condition gradually spread up the tree until finally the terminal leader lost its dominance and the tree formed a flat-topped crown. Also, as the branches became older, they changed their angle of growth to a more nearly horizontal and finally a drooping one. Second-order laterals often grew vertically downwards. This change of growth pattern due to aging can be reversed by vegetatively propagating the old part. Hence, rooting or grafting of part of an old shoot on a seedling stock results in a revitalized shoot showing increased growth and strong apical dominance.

The above experiments with *Pinus sylvestris* and *Larix leptolepis* suggest that aging involves increased competition among shoots for nutrients as a branch system increases in complexity. In intact plants the leading shoots obtained larger quantities of mineral nutrients than did higher order laterals.

When distal parts of a branch were removed by pruning, increased growth of the remaining laterals followed. After addition of P³² to soil, this element was more abundant in laterals of distally-pruned branches than in those of intact branches. These observations emphasized the disadvantages of the laterals when competing for nutrients with leading shoots in intact branches.

Formation of Short Shoots

Several species of gymnosperms and a few angiosperms produce more short shoots (shoots with negligible or short internodes) when adult than when they are young. Table 4.2 shows this tendency for both terminal and

TABLE 4.2

A. DEVELOPMENT OF LONG AND SHORT SHOOTS FROM TERMINAL AND LATERAL BUDS OF *Ginkgo* SEEDLINGS GROWN FROM SEED GERMINATED IN 1934^a

	Development of terminal buds				
	1942	1943	1944	1945	1946
Number of short shoots	0	0	3	2	8
Number of long shoots	30	30	27	28	22
Percent long shoots	100	100	90	93.5	73.5

B. DEVELOPMENT OF LONG SHOOT LATERALS FROM SHORT SHOOT LATERALS OF THE PREVIOUS YEAR ON 8-YEAR-OLD PLANTS^a

	1942	1943	1944	1945
Number of short shoot laterals	399	316	290	385
Number of long shoots from short shoot laterals	77	24	36	20
Percent long shoots	19.3	7.6	12.4	5.2

^a From Gunckel *et al.* (1949).

lateral buds of *Ginkgo biloba*. Gunckel *et al.* (1949) found that practically all the terminal buds on a 15-year-old *Ginkgo* tree produced long shoots whereas a 100-year-old tree had approximately equal numbers of long- and short-shoot terminals. Young trees of this species have an excurrent form due to predominance of long shoots. Old trees become globose in form as the terminal buds begin producing short shoots and lateral buds produce long ones. This change takes place when trees become reproductive at an age of 35 to 40 years. As may be seen in Table 4.3 the removal of a terminal long shoot in young plants caused one or more laterals to become

TABLE 4.3

INFLUENCE OF TREE AGE ON DEVELOPMENT OF LATERAL LONG SHOOTS BEFORE AND AFTER REMOVAL OF TERMINAL SHOOT^a

	Age of plants (years)						
	3	4 ^b	13 ^b	14 ^b	15	35	100
Percent of long shoot laterals on previous year's growth (intact plants)	27	0	0	0	—	—	— ^c
Percent of removals of terminals which cause one or more laterals to become long							
Same season	100	93	87	10	Rarely	Rarely	0
Following season	0	—	—	—	90	35	10

^a From Gunckel *et al.* (1949).^b Greenhouse plants in pots.^c Five percent of all laterals on the tree, irrespective of age.

long. With increasing age and decreasing vigor, however, the ability of laterals to form long shoots disappeared.

In young plants of *Cercidiphyllum japonicum* long shoots predominate. When plants are 15 to 20 years old and adult as indicated by flowering, the production of short shoots begins. Thereafter, proportionally more short shoots are produced as the tree ages until 90% or more of the buds of mature trees expand into short shoots (Titman and Wetmore, 1955).

Larix decidua seedlings produce mostly long shoots. In trees 4 to 5 years old the main axis grows vertically by monopodial growth and its axillary buds grow vigorously as long shoots. With increasing age, the growth of lower branches becomes suppressed and their terminal buds tend to develop into weak twigs which may wither at the tip. Most axillary buds of all branches then begin to form spur shoots. In old trees small terminal buds of low branches also often produce short shoots. As trees age, vertical elongation continues whereas laterally shoot growth is progressively decreased (Frampton, 1960).

CAMBIAL GROWTH

As trees age the rate of cambial growth follows a definite trend which varies with species and environment (Fig. 4.2 and 4.3). As may be seen in Fig. 4.3 cambial growth accelerated annually for a number of years, attained a maximum, and then declined, at first rapidly and then more gradually. The declining part of the curve resembled a hyperbola which approached zero (Mikola, 1950, 1951), with each successive xylem ring narrower than the

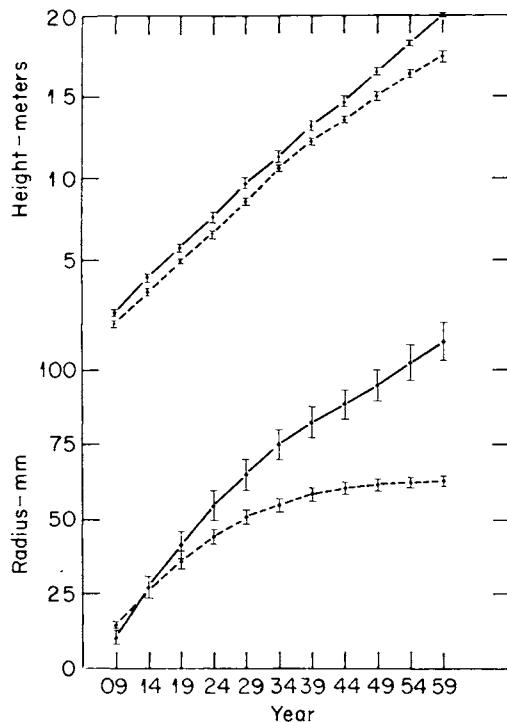


FIG. 4.2. Effects of aging on height growth (upper graph) and diameter growth (lower graph) of dominant (solid lines) and suppressed (dashed lines) *Pinus strobus* trees. [From Bormann (1965).]

previous one, unless the pattern was altered materially by environmental influences. After maximum ring width is attained, the narrowing of annual rings as an aging phenomenon often amounts to less than 1% annually, but is sometimes much greater. For example, on good forest soils in South Finland xylem rings narrowed annually by 4–5% as trees aged (Mikola, 1950). The curve of basal area change with tree age differs from that of ring width, with each successive ring having a greater radius than the preceding one. As trees senesce there is an increasing tendency toward production of discontinuous and missing rings. This is discussed further in Volume II, Chapter 2.

ROOT GROWTH

Many investigators have reported variations in root growth of trees during aging. In North Carolina the number of roots of loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) up to 0.10 in. in diameter increased rapidly

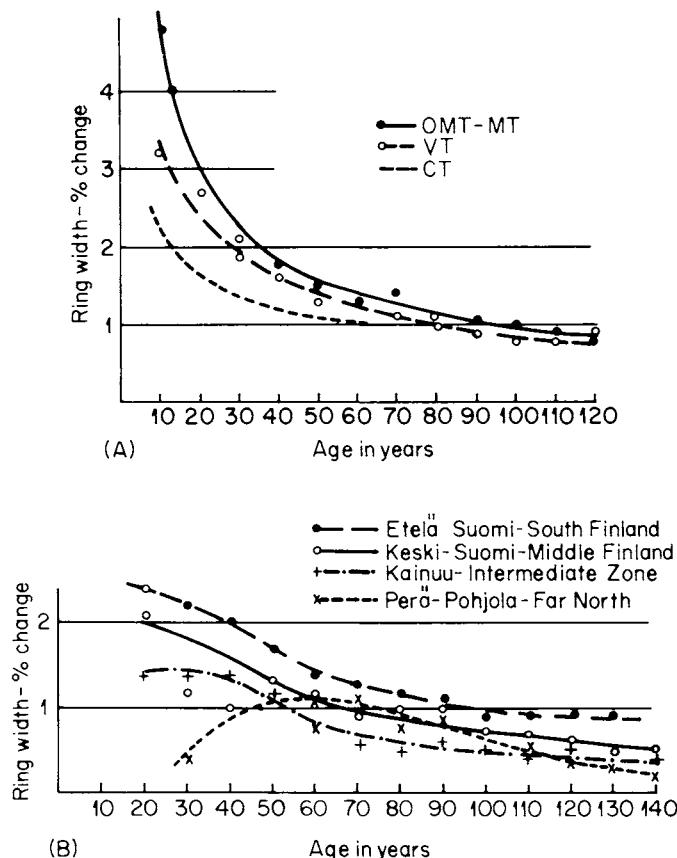


FIG. 4.3. Effect of aging on cambial growth of: (A) *Pinus sylvestris* in three locations in south Finland; (B) *Picea excelsa* from 4 locations in Finland. [From Mikola (1950).]

until stands reached 20 years of age after which increase was slower. By the time the stands were 30 years old the amount of absorbing roots had reached a near constant value (Scholtes, 1953). Kalela (1950) showed differences in rate of root growth of *Pinus* and *Picea* at various ages. Young *Pinus* trees had larger root systems than *Picea* trees but they both had about the same amount of root system when diameters were 16 cm. Thereafter, *Picea* had the more extensive root system.

In the northern hemisphere roots of first-year apple seedlings differed in growth pattern from roots of older seedlings (Bosse, 1960). After the seeds germinated in April the roots showed positive geotropism. By the end of July they grew to a depth of 50 cm and by the end of September to 100 cm.

From June to August root growth of young seedlings was at its highest rate of 16.5 cm per day. From September to October the daily rate decreased to 6.9 mm. In the second and subsequent years root growth was much slower.

Adventitious Rooting and Tree Age

The capacity of both intact trees and cuttings for producing adventitious roots is correlated with their age. After some critical tree age is reached, rooting capacity declines rapidly (Chapter 3). For example, in intact *Picea*, *Betula*, and *Populus* trees the maximum capacity for adventitious rooting was demonstrated by trees varying in age from 25 to 30 years (Kosceev, 1953). *Picea abies* formed adventitious roots up to an age of 45 years, and inability of older trees to produce such roots probably accounted for their dieback on waterlogged soils (Kosceev, 1952). According to Krasilnikov (1960), *Pinus sibirica* formed profuse adventitious roots until the trees were 20 years old, after which formation of new adventitious roots decreased sharply.

Every plant propagator is familiar with difficulty in rooting cuttings from old trees. Hence, to retain desirable characteristics of a tree cuttings should be rooted as soon as desired characteristics appear (Kramer and Kozlowski, 1960). When Delisle (1954) grew rooted cuttings of *Pinus strobus* to an age of 4 years and then successively grew cuttings from these trees for several generations he found rootability to decrease with each older generation of plant material.

DRY WEIGHT INCREMENT

Changes with tree age in activity of apical and lateral meristems are reflected in dry weight accretion. Total dry matter increment of communities of trees and of individual trees, as well as distribution of increment within trees, are altered predictably as trees mature. When a plantation is first established, annual dry weight increment per unit area of land is small. After tree crowns close and roots extend throughout the soil a maximum level of productivity is attained. Thereafter, annual increment decreases as a stand approaches maturity (Ovington, 1958). In *Betula verrucosa* and *Pinus sylvestris* dry weight increase at first was logarithmic, but when the trees were sufficiently large to provide a complete leaf cover so the maximum amount of light was absorbed under prevailing conditions, the annual increase in dry weight reached a maximum value (Ovington and Pearsall, 1956). As may be seen in Table 4.4 dry weight production of 8-year-old stands of *Fagus sylvatica* was low. It was higher and relatively constant in stands 25 to 46 years of age. Thereafter, a decline associated with aging ultimately occurred until 85-year-old trees produced dry matter at about 80% of the maximum

TABLE 4.4

EFFECT OF AGING ON PHOTOSYNTHETIC EFFICIENCY OF EVEN-AGED STANDS OF *Fagus sylvatica* AND *Pinus sylvestris*^a

Species and age (years)	Current annual dry weight production		Photosynthetic efficiency (%)
	(gm/acre)	(cal/acre)	
<i>Fagus sylvatica</i>			
8	3.0×10^6	12.1×10^6	1.4
25	5.4×10^6	21.8×10^6	2.5
46	5.4×10^6	21.8×10^6	2.5
85	4.6×10^6	18.5×10^6	2.1
<i>Pinus sylvestris</i>			
12	4.0×10^6	16.0×10^6	1.0
22	8.1×10^6	32.4×10^6	2.0
28	8.8×10^6	35.2×10^6	2.2
33	8.1×10^6	32.4×10^6	2.0
41	6.1×10^6	24.4×10^6	1.5
50	4.0×10^6	16.0×10^6	1.0

^a From Hellmers and Bonner (1960). Data are based on yield data of Möller *et al.* (1954), and Ovington (1957).

value. In *Pinus sylvestris* dry weight production of young stands increased with age to a maximum at about 20 years. At approximately age 30 a slow decline in dry weight increment was evident. The decrease was accelerated after age 40, with 50-year-old trees producing only half as much dry matter as 33-year-old trees.

In individual aging trees the progressively decreasing crown size in relation to the stem results in a diminished ratio of food produced to that used in respiration (Kramer and Kozlowski, 1960). According to Möller *et al.* (1954), 40% of the total photosynthate was used in respiration in 25-year-old *Fagus* trees, but the amount increased to 50% in 85-year-old trees (Fig. 4.4). Gross annual production reached a climax in stands 40- to 60-years-old. In very general terms, approximately 60% of the gross photosynthate was lost by respiration and shedding of plant parts, and only 40% remained. The decrease in old stands was attributed to a decline in total photosynthesis and slight increase of loss of dry matter.

Although it sometimes is assumed that dry matter is lost from trees, primarily through leaf abscission, appreciable losses from shedding of other tissues such as fruits also occur. In addition significant losses in dry matter also result from death of many fine roots each year (Vol. II, Chapter 5) and from sloughing of dead outer bark tissues. Furthermore, branches of

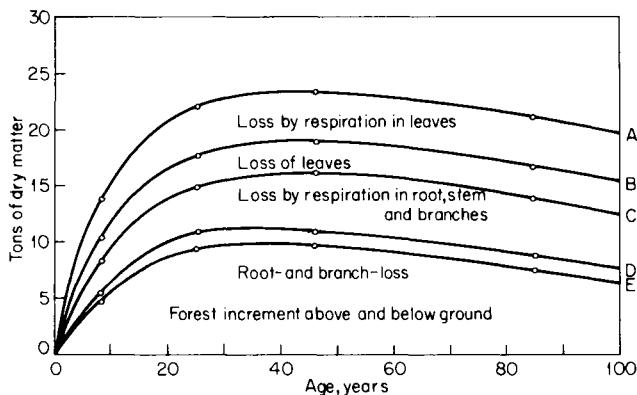


FIG. 4.4. Dry matter losses due to various causes in *Fagus sylvatica* trees of varying age. The ordinate gives dry matter increment per hectare per year. [From Möller, *et al.* (1954).]

many species are shed by natural pruning, especially from mature trees in dense stands. According to Van der Pijl (1952), branch abscission occurs in virtually all families of gymnosperms. Abscission of branches also occurs commonly in many families of angiosperms including Salicaceae, Casuarinaceae, Juglandaceae, Fagaceae, Ulmaceae, Leguminosae, Sonneratiaceae, Euphorbiaceae, Lauraceae, Aceraceae, and Vitaceae. Loss of branches by abscission occurs very commonly in the tropical genera *Albizzia*, *Casuarina*, *Xylopia*, *Sonneratia*, and *Persea*. Van der Pijl (1952) described a specimen of *Casuarina sumatrana* from which 99% of the small twigs on the main axis had abscised.

Distribution of Dry Matter in Individual Trees

The relative proportions of crown, stem, and root system vary with age of trees (Fig. 4.5). In old trees more of the dry weight is in the main stem and proportionally less in the crown and root system. Whereas roots of young *Pinus sylvestris* trees accounted for almost half the total weight of the plant, in old trees the proportion was much lower (Ovington, 1957). Throughout the life of trees loss of dry weight due to mortality and abscission varied greatly for different tissues. In trees 20 years old or older, more dry matter was in the stem than in the crown, but this was not true in terms of gross production. In fact, at no stage was total production of the stem greater than that of the crown. Most of the total dry matter produced actually went into the crown and least into the root system. Ovington and Madgwick (1959) found striking changes in proportions of leaf, branch, and bole material of *Betula verrucosa* trees as they became older (Fig. 4.6). As the trees became

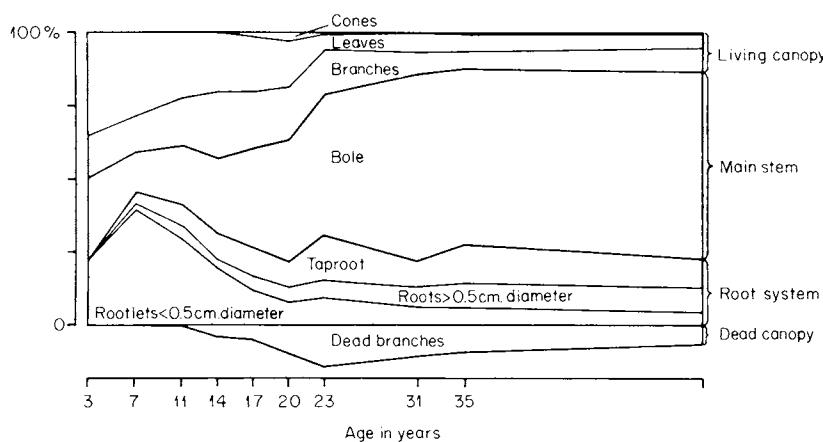


FIG. 4.5. Changes in proportion of various plant parts as *Pinus sylvestris* trees age.
[From Ovington (1957).]

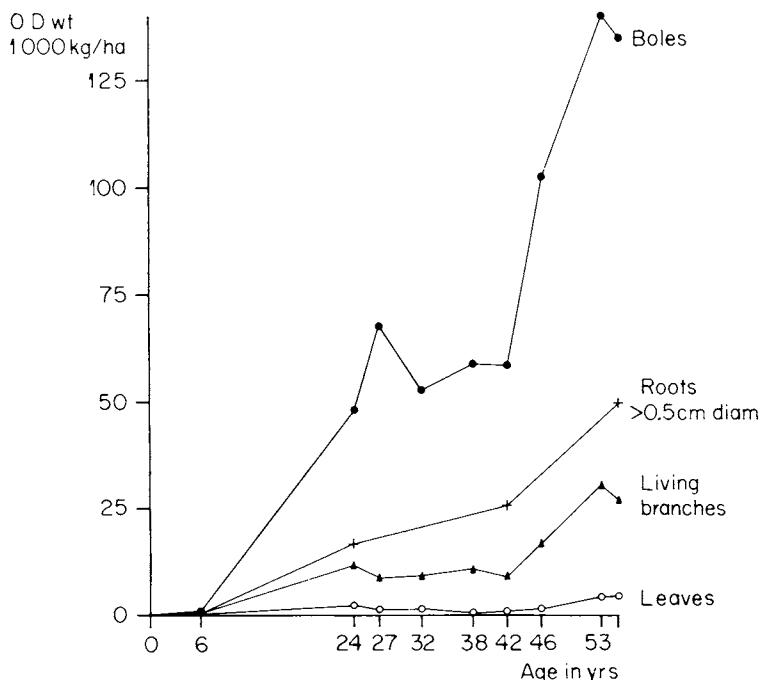


FIG. 4.6. Variation with age in dry weight production of natural stands of *Betula verrucosa*. [From Ovington and Madgwick (1959).]

larger, however, the canopy and particularly the leaves formed a smaller percentage of total shoot weight. Compared with branch material the weight of leaves per tree was relatively small but it increased as the trees aged. In mature trees the leaves represented only 1 or 2% of the total shoot weight, and the living branches accounted for about 18%. The weight of leaves, unlike that of boles or branches, did not continue to increase with age in older stands.

Reproductive Growth

The capacity for reproductive growth changes remarkably during the life-span of a tree. There is first of all a juvenile period of several years during which only vegetative tissues are produced. Eventually adulthood is attained as indicated by initial capacity for flowering (Chapter 3). Spurs of apple trees often produce their first fruit when they are 4 years old. They may then intermittently produce fruit for 10 or more years and gradually lose their capacity for fruiting as they are left behind in shaded portions of the tree.

The quantity and quality of seed produced by adult forest trees vary greatly with their age. Most trees produce greatest amounts of seed during middle age. Hence, reproductive capacity is correlated with longevity. Eventually trees reach an age at which reproductive capacity declines. However, it is somewhat difficult to establish precise ages of first and optimal flowering capacity for any species because these are greatly modified by plant competition and tree vigor. For example, middle-aged dominant trees are prolific seeders whereas suppressed trees of the same age often produce no seed or only negligible amounts (Kramer and Kozlowski, 1960). In *Pinus monticola* cone production continued to increase until trees were about 20 in. in diameter. Thereafter seed production was highly correlated with tree vigor and poorly correlated with age (Haig *et al.*, 1941).

Even-aged *Pinus sibirica* forests showed a rapid increase in seed production when they were 120 to 150 years old. By the time they were 180 years old the rate of increase decreased but the plantation gave maximum seed yield when trees were 180 to 220 years old. During the next 80 to 100 years seed production was reduced slightly, and in plantations over 300 to 350 years old it was greatly reduced. In uneven-aged plantations, characterized by continuous seed production, maximum seed production usually began from 50 to 130 years later than in even-aged stands. *Pinus sibirica* regularly produced reproductive tissues. Complete failure of seed production in certain years resulted only from shedding of current and previous year's female cones. From 70 to 130% more female primordia were produced in years of low seed yield than in years of high yield (Ironshnikov *et al.*, 1966).

TABLE 4.5

EFFECTS OF AGE ON REPRODUCTIVE CAPACITY OF VARIOUS SPECIES OF FOREST TREES^a

Species	Commercial seed bearing age (years)	Optimum seed bearing age (years)
Angiosperms		
<i>Carya ovata</i>	40	60–200
<i>Carya laciniosa</i>	40	75–200
<i>Celtis laevigata</i>	15	30–70
<i>Diospyros virginiana</i>	10	25–50
<i>Fagus grandifolia</i>	40	
<i>Gleditsia triacanthos</i>	10	25–75
<i>Juglans nigra</i>	12	30–130
<i>Juglans cinerea</i>	20	30–60
<i>Liquidambar styraciflua</i>	20–30	150
<i>Liriodendron tulipifera</i>	15–20	200 +
Gymnosperms		
<i>Juniperus virginiana</i>	10	25–75
<i>Larix occidentalis</i>	25	40–400
<i>Picea engelmannii</i>	16–25	200–250
<i>Picea glauca</i>	30	60 +
<i>Pinus resinosa</i> (open grown)	20–25	50–150
<i>Pinus resinosa</i> (closed stand)	50–60	
<i>Sequoia gigantea</i>	150	

^a From Fowells (1965).

As may be seen in Table 4.5 both the intial age and duration of production of large amounts of seed vary greatly among species. Whereas *Gleditsia triacanthos* begins to produce large amounts of seed at approximately 25 years of age, *Sequoia gigantea* does not do so until trees are at least 150 years old. *Picea glauca* produces large amounts of seeds for only about 10 years, but *Carya ovata* does so for well over 100 years, further emphasizing marked differences among species in effects of age on reproductive growth. Viability of seeds also varies greatly with tree age. In *Abies balsamea*, for example, seeds from 40-year-old trees showed highest germinative capacity, 68 %. Seed viability decreased in older trees and averaged 10 % from 155-year-old trees (Benzie, 1960). In *Sequoia sempervirens* seeds from trees less than 20 years old showed less than 1 % viability and those from trees more than 1200 years old were either sterile or not more than 3 % viable (Metcalf, 1924).

Anatomical Changes During Ontogeny

Several important anatomical changes occur during ontogenetic development of trees. During the first year of development there is a changeover from primary to secondary tissues. The early change from cotyledons to foliage leaves is conspicuous (Chapter 2) as are changes in wood anatomy and leaf structure as trees pass from the juvenile to adult conditions. These early changes associated with phase change are discussed in Chapter 3.

After the adult stage is reached, external alterations of aging trees are characterized by various internal structural changes in tree stems which influence wood quality (Dadswell, 1957). For example, the average length of xylem elements at any stem height in both angiosperms and gymnosperms increases from the pith outward for a number of years and then becomes more or less constant (Volume II, Chapter 2). Such changes in length of xylem elements parallel those in size of cambial initials. The fibril angle is large in short cells and small in long cells. Hence, the increase in cell length from the pith outward is accompanied by a decrease in fibril (micellar) angle. Correlated with these changes is a decrease in longitudinal shrinkage and an increase in tangential shrinkage from the pith outward. Also with increasing age the percentage of latewood increases for a number of years and this change is accompanied by increase in specific gravity and strength. Also with increasing age the durability of heartwood increases. In over-mature trees, however, the specific gravity of wood often declines and little or no latewood is produced. This was illustrated by Hale and Clermont (1963) who compared wood formed by a *Pseudotsuga menziesii* tree when it was 50 years old and when it was 300 years old. When 50 years old the tree was vigorous and producing about 20 rings of xylem per radial inch, with each annual xylem increment showing the normal progressive transition from large-diameter, earlywood cells to small-diameter, latewood cells with thick walls. However, by the time the tree was 300 years old the narrow xylem rings were made up primarily of thin-walled cells, with negligible latewood and very low specific gravity. This over-mature wood had a higher lignin and lower α -cellulose content than wood formed when the tree was 50 years old.

HEARTWOOD FORMATION

The wood of young trees consists entirely of sapwood. Although sapwood is made up mostly of dead cells an average of about 10% of its cells are alive and physiologically active. This percentage is variable, however, since sapwood of some species may contain as low as 5% of living cells and in other

species up to 40%. The living cells of sapwood consist mostly of longitudinal parenchyma and transversely oriented ray cells. Sapwood is physiologically important because it serves as an avenue for translocation of water and minerals. Its living cells also carry on metabolic processes and store foods. In contrast, the dead heartwood is considered physiologically inactive.

After a certain age, which varies greatly among tree species and with environment, all the living cells in the central core of the main stem and large branches die, usually darken, and lose their physiological role. Hence, stems and branches of fairly mature trees contain an approximately conical shaped, central core of dead heartwood cells, surrounded by an external layer of sapwood. The outline of the heartwood core often undulates and usually cuts across parts of annual rings (Chapter 1). The boundary zone between sapwood and heartwood may be either diffuse or distinct. Once normal heartwood formation begins the process is continuous so that usually the innermost sapwood rings are converted to heartwood annually and in many species the number of sapwood rings remains more or less constant.

The amount and rate of heartwood formation vary greatly with species, tree age, rate of growth, environment, and silvicultural practice. As may be seen in Table 4.6, crown class often influences the width of the sapwood band

TABLE 4.6

VARIATIONS AMONG CROWN CLASSES IN WIDTH OF SAPWOOD AT DIFFERENT STEM HEIGHTS
OF *Pseudotsuga menziesii*^a

Crown class	Average diameter at breast height (in.)	Mean width of sapwood (in.)		
		Top	Middle	Base
Dominant	11.4	1.50	1.23	1.73
Codominant	8.0	0.99	0.86	1.06
Intermediate	7.2	0.73	0.69	0.85

^a From Wellwood (1955).

with dominant trees having wider sapwood than lower crown classes (Wellwood, 1955). The age at which heartwood formation begins varies greatly among species. For example, *Eucalyptus* heartwood usually begins to form relatively early in the life of the tree (about 5 years), later in several *Pinus* species (15 to 20 years), still later in *Fraxinus excelsior* (60 to 70 years) and even later in *Fagus sylvatica* (80 to 100 years) (Dadswell and Hillis, 1962).

Changes Occurring During Heartwood Formation

The most critical change in transformation of sapwood into heartwood is death of ray and longitudinal parenchyma cells. Other changes accompanying heartwood formation include altered metabolic rates, changes in enzymatic activity, starch depletion, darkening of xylem associated with deposition of extractives, changes in wood density, anatomical changes such as increased pit aspiration in gymnosperms and formation of tyloses in angiosperms, and changes in moisture content. Some of these changes will be discussed separately.

Death of parenchyma cells

It is widely acknowledged that living cells die during the transformation of sapwood to heartwood. Frey-Wyssling and Bosshard (1959) demonstrated that nuclei of living ray parenchyma cells in sapwood of several species of gymnosperms and angiosperms changed shape, lost their vitality, decreased in chromatin content and size, and gradually disappeared toward the heartwood boundary. As may be seen in Fig. 4.7 the nucleus in ray cells of *Pinus sylvestris* was oblong-elliptical near the cambium. Deeper in the wood, from the 9th to the 16th xylem ring, the nucleus was more rounded. Still deeper in the wood and near the heartwood boundary (after the 16th ring) the integrity of the nucleus was lost from the ray cells of a given ring. Fahn and Arnon (1963) found that nuclei of fibers and ray or wood parenchyma cells of *Tamarix aphylla* changed in shape and disintegrated in one annual ring. The surface of the nucleus first became wrinkled and irregular in form. Thereafter, the nucleus lost its staining properties, and in late stages of degeneration chromatin bodies were seen dispersed in the cell lumens. The first structures to disappear from fiber and ray cells were starch grains (7 to 13th growth rings). In the final step before heartwood formed (16 to 21st growth rings) the nuclei disintegrated. These changes occurred simultaneously in fibers and in ray or wood parenchyma cells.

Metabolic Changes

Restriction of metabolic activity to the sapwood was emphasized by Frey-Wyssling and Bosshard (1959). They found mitochondria only in outermost annual rings. A gradient of diminishing metabolic activity was shown along a ray through the sapwood toward the heartwood. Reductive capacity of mitochondria ceased well before the heartwood boundary was reached. Some of the physiological changes in trees which lead to the formation of heartwood as postulated by Frey-Wyssling and Bosshard are shown in Fig. 4.20.

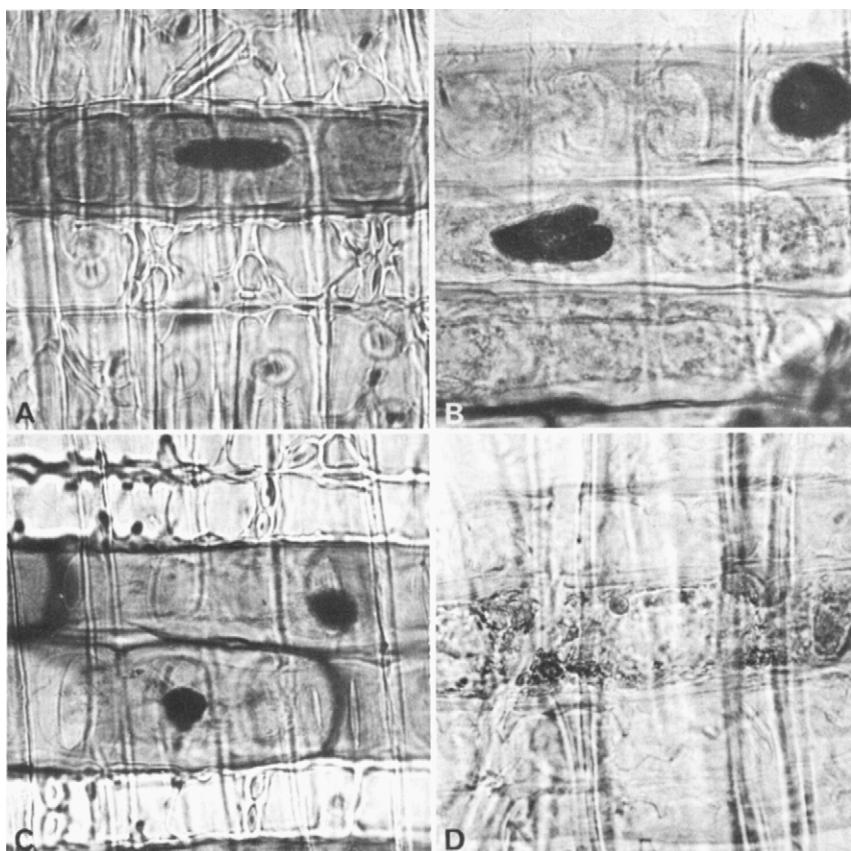


FIG. 4.7. Disappearance of nuclei in ray parenchyma of *Pinus sylvestris*. (A) Upper left: Normal nucleus, 4th ring ($\times 260$); (B) upper right: Nucleus rounding off, 9th ring ($\times 800$); (C) lower left: Rounded-off nucleus, 16th ring ($\times 760$); (D) lower right: Nucleus has disappeared, 36th ring ($\times 1180$). [From Frey-Wyssling and Bosshard (1959).]

Enzymatic Activity

The activity of various enzymes changes from the cambial zone inward, apparently in an inconsistent way. Some enzymes show increased activity in the intermediate zone between sapwood and heartwood, whereas others show progressively decreased activity from the outside of the stem inward. In *Pinus* and *Larix* peroxidase activity increased markedly in the stem area adjacent to the heartwood (Lairand, 1963). Similarly the activity of enzymes which hydrolyzed sucrose and oxidized catechol was greatest in the intermediate zone and decreased progressively in the sapwood, heartwood, and controls of sterilized wood (T. Kondo, 1964). In contrast, phenylalanine

deaminase which might be concerned with biosynthesis of heartwood phenols, showed highest activity in the cambial region of *Cryptomeria* and *Chamaecyparis*, but activity decreased progressively inward until none was found in the heartwood (Higuchi and Fukazawa, 1966). The high activity in the cambial region was related primarily to production of a lignin precursor. However, in the sapwood and intermediate zone where cells were completely differentiated and lignified, the pheynylalanine deaminase was mostly responsible for synthesis of heartwood phenols.

Deposition of Extractives

Heartwood contains a wide variety of extractive substances, including tannins, assorted dyestuffs, oils, gums, resins, salts of organic acids, etc. During heartwood formation these extractives accumulate in cell lumens and walls resulting in a dark colored wood (Figs. 4.8 and 4.9). Some of these substances also occur in sapwood, but usually in relatively low amounts (Kramer and Kozlowski, 1960). Chattaway (1952) suggested, for example, that as metabolism of ray and parenchyma cells was altered preceding their death, the production of tannin increased. When the cells died the tannins escaped and filled the lumens of wood cells.

Among the most important of the heartwood extractives are the polyphenols. These are aromatic compounds, with one or more phenolic hydroxyl groups. Usually most phenolic substances, obtained from tissues with living cells occur as glycosides or esters, while polyphenols obtained from heartwood are almost exclusively found as aglycones. The important chemical pathways leading to formation of extractives were summarized by Hillis (1968). Extractives are synthesized from intermediates of breakdown of sugar in primary metabolism, with shikimic acid and pyruvate, which leads to acetyl coenzyme A as important precursors. From acetyl-CoA the tricarboxylic acid cycle is entered as are two pathways which lead to formation of two important classes of extractives. One path leads to malonyl-CoA and thence to fatty acids, and the other to acetoacetyl-CoA and isoprenoid substances (e.g., terpenoids, steroids, etc.). Some woods contain extractives that are largely formed from pyruvate. The shikimic acid-prephenic acid pathway leads to formation of the C₆, C₆C₁, C₆C₂, C₆C₃ phenolic compounds. Several groups of heartwood extractives (e.g., flavonoids, stilbenes, isoflavonoids) are produced from a combination of the acetate and shikimic acid pathways. A wide range of enzymatic reactions is involved. For a more detailed description of biosynthetic processes leading to formation of various extractives the reader is referred to the volume by Hillis (1962).

In certain species crystals of characteristic form are found in heartwood. Chattaway (1953) found yellowish-brown crystals in heartwood ray cells where a ray adjoined a vessel. Crystals also appeared in adjacent cells to form

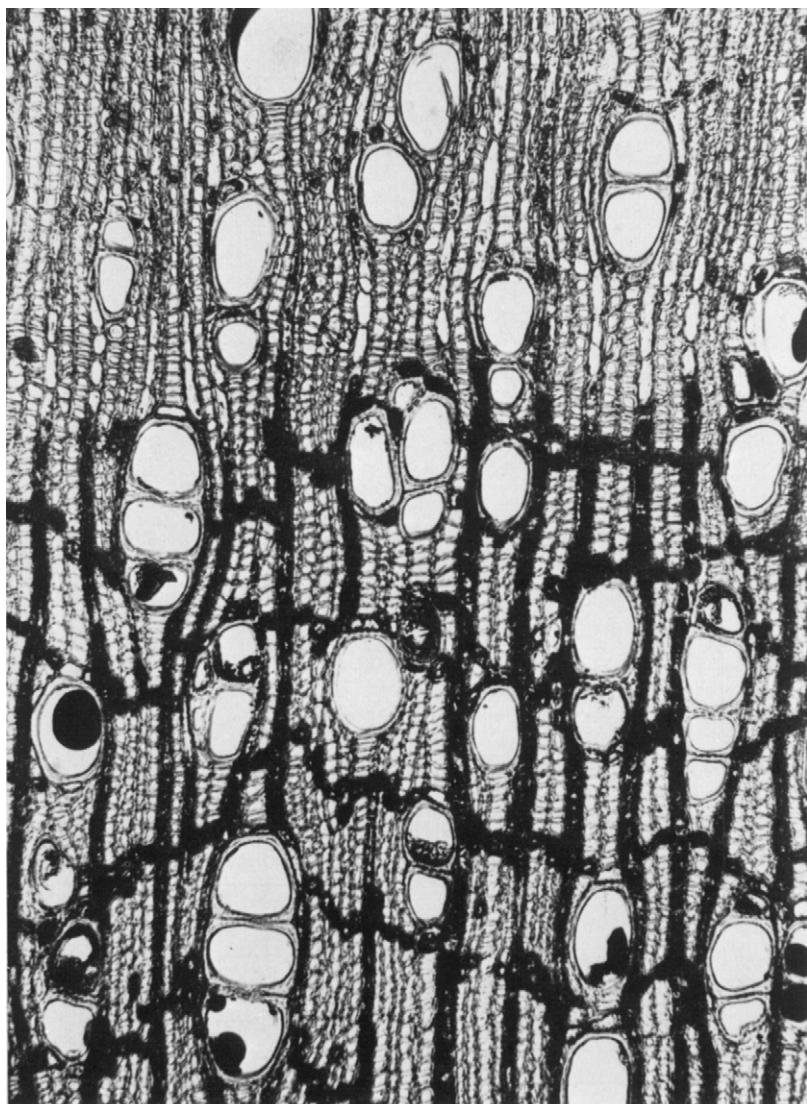


FIG. 4.8. Transection of stem of *Excoecaria parvifolia* showing formation of polyphenols at sapwood-heartwood boundary. (Photo courtesy R. K. Bamber).

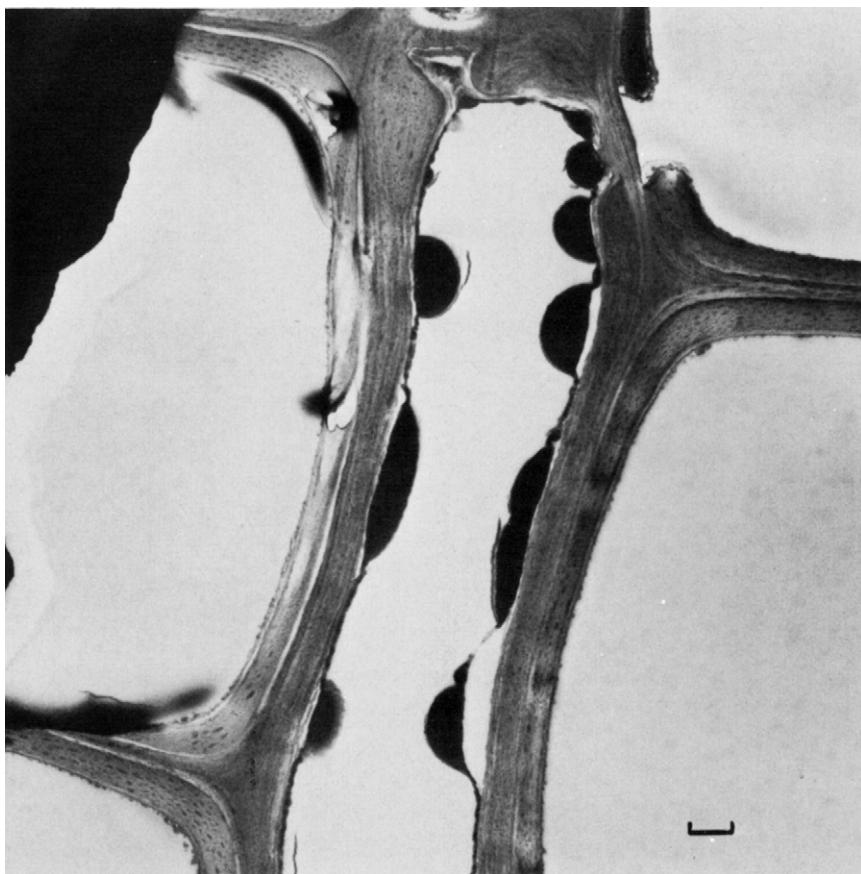


FIG. 4.9. Cross section of ray cell in *Tsuga canadensis* heartwood. Cell contents line the lumen on the ray cell and also occlude the half-bordered pit pair between the ray cell and longitudinal tracheid. [From Krahmer and Coté (1963).]

large patches in the wood. In every species examined the crystals were present in the proximity of the sapwood-heartwood boundary at various heights in the stem.

Pit Aspiration

Pits apparently aspirate where a tracheid wall is between a tracheid containing water and another tracheid containing gas (Fig. 4.10). Harris (1954) studied the numbers of aspirated pits from near the cambium to the heartwood in stems of dominant, codominant, and suppressed *Pinus radiata* trees (Fig. 4.11). The "dry wood" zone is that which surrounds colored

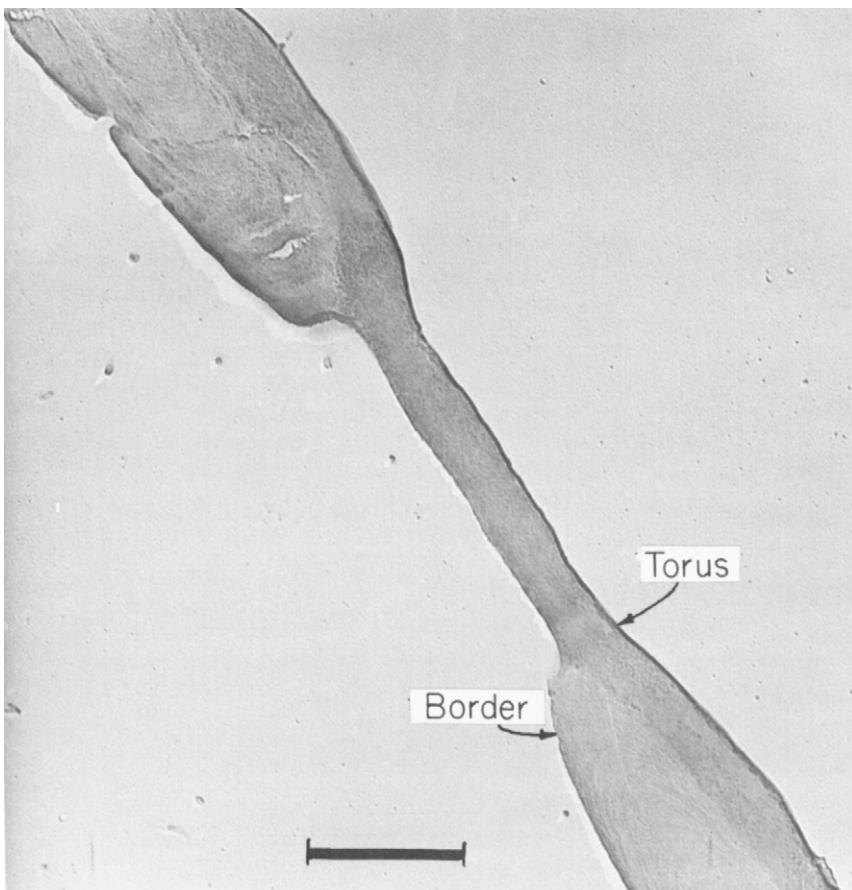


FIG. 4.10. Tangential section of a torus aspirated over the pit aperture in *Pseudotsuga menziesii*, forming a tight seal between the pit border and torus. [From Krahmer and Coté (1963).]

heartwood and has a much lower water content than sapwood but has not yet become deeply colored as has the true heartwood. The percentage of pits aspirated increased rather gradually from a low value in the outermost annual ring to the border of the dry wood zone where approximately 50% of the pits were aspirated. There was an increase in aspirated pits within the dry wood zone to over 90%, and this increased slightly through the heartwood. Dominant trees had a lower percentage of pits aspirated in the outermost annual rings than did suppressed trees. Since codominant trees were intermediate to these crown classes it was concluded that a faster growth rate

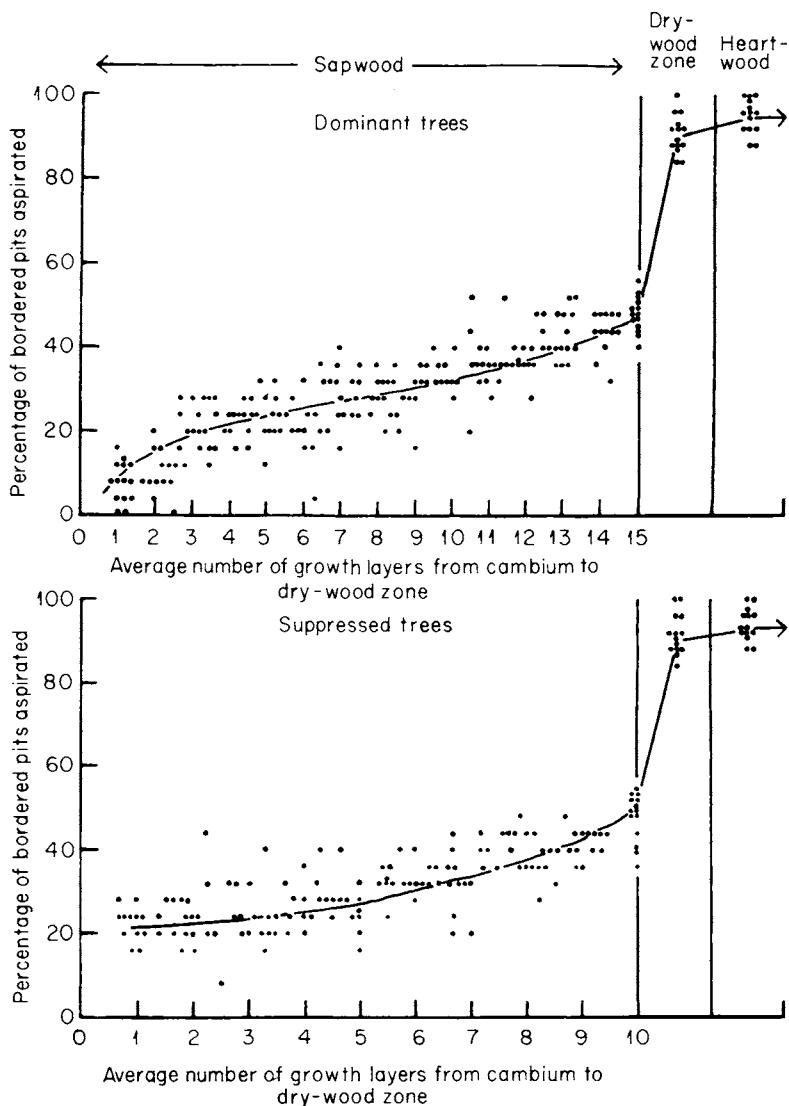


FIG. 4.11. Variation in aspiration of bordered pits in different zones of sapwood and heartwood of *Pinus radiata*. Data are given for dominant (upper photo) and suppressed trees (lower photo). [From Harris (1954).]

was correlated with a lower percentage of aspirated pits in the outermost growth increments. Harris (1954) concluded that when more than 50% of the bordered pits of *Pinus radiata* were aspirated, water transport through the system could not occur. Hence, tracheids of the dry wood zone no longer had direct connections to those of the outer sapwood.

Formation of Tyloses

Saclike structures called tyloses develop when parts of parenchyma cells project through pit pairs into adjoining cell lumens (Figs. 4.12 and 4.13). They form when pressure in the living parenchyma cell causes ballooning of the protoplast into an adjacent air-filled cell. They may also form as a result

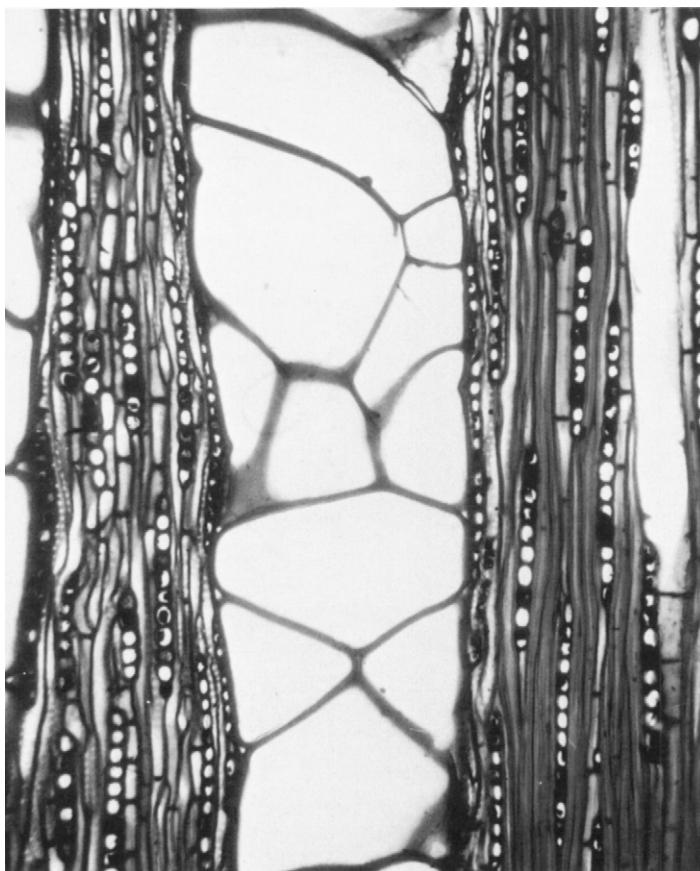


FIG. 4.12. Tyloses in large vessel of *Quercus alba* as shown in longitudinal section, $\times 160$. [From Coté (1967).]

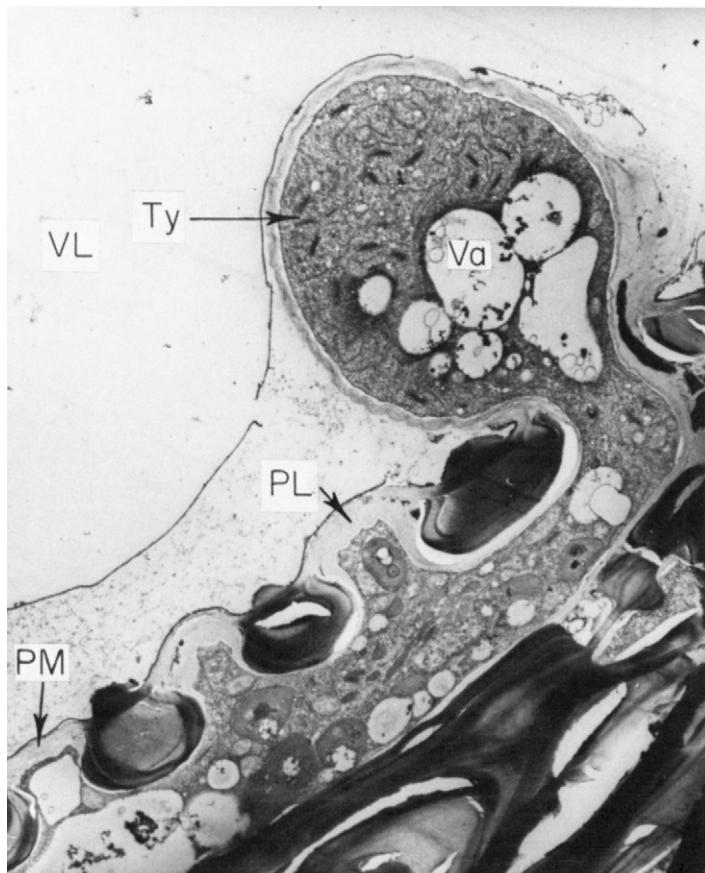


FIG. 4.13. Fine structure of tylosis (TY) of vessel of *Quercus alba*, $\times 9000$. PL-protective layer; PM-pit membrane; Va-vacuole; VL-vessel lumen. [From Coté (1967).]

of growth of pit membranes. Jurasek (1960) has shown that osmotic pressure of ray cells influences growth of tyloses after they once start to form. Formation of tyloses also is influenced by temperature and moisture content of wood. In *Fagus sylvatica* tyloses stopped forming when wood dried to a moisture content of 50% (Jurasek, 1958). Tyloses commonly occur in xylem vessels of many species of angiosperms and sometimes in lumens of gymnosperm tracheids. According to Strelis and Green (1962), they are characteristic of such genera as *Populus*, *Rhus*, *Robinia*, *Morus*, *Sassafras*, *Catalpa*, *Juglans*, and *Quercus*, and they never occur in many other genera.

Tyloses vary greatly in structure and may have a thin wall or a thick,

lignified secondary wall. They often proliferate greatly. In *Fraxinus americana* tyloses vary in size and shape and often are collapsed and wrinkled. In *Fagus grandifolia* they are very simple in structure. In *Quercus alba* tyloses are characteristically balloon-shaped at first but later become irregular in shape and size as they become crowded and occlude vessels. Sometimes analogous structures called tylosoids develop because of growth of walls of living cells into adjacent space. For example, tylosoids sometimes form in gymnosperms through growth of epithelial cells which tend to fill resin canals. For a good discussion of the structure of tyloses the reader is referred to Koran and Coté (1965).

Tyloses may be found in normal sapwood or in response to wounding, invasion by fungus pathogens, or virus infection. Beckmann *et al.* (1953), for example, showed that formation of tyloses in vessels of *Quercus ellipsoidalis* was a response to invasion of the fungus which caused oak wilt disease. Tyloses formed extensively in large vessels and less commonly in small ones and were especially abundant in the outer two rings of sapwood where the bulk of water transport took place.

In many angiosperm genera the formation of tyloses is an important feature of changeover of sapwood to heartwood. Hence, those species which normally produce tyloses in the sapwood have a greater abundance of them in the heartwood. Gerry (1914) found tyloses in the sapwood of all species that had them in the heartwood. An important feature determining whether tyloses will form appears to be a critical minimum size of the pit aperture between vessels and ray cells. Chattaway (1949) concluded that when the pit aperture exceeded approximately $10\ \mu$ tyloses developed in the heartwood of a variety of species of angiosperms. When pit apertures were less than 10μ in diameter a gumlike material was secreted into the vessels. These conclusions were essentially confirmed by Jurasek (1956) who noted that tyloses in *Fagus sylvatica* were formed only by cells with pit pairs in the diameter range of 10 to $15\ \mu$.

During heartwood formation both tyloses and gums originate almost exclusively in the ray cells rather than in axial parenchyma cells. As Chattaway (1949) emphasized, the ray cells play the predominant role in heartwood formation while axial parenchyma appears to be only a storage tissue. As Chattaway found, complete blocking of vessels resulted from growth and proliferation of tyloses which emerged from the ray cells only, even when vessels were surrounded by a parenchymatous sheath.

Changes in Moisture Content

The water content, and therefore the weight of the sapwood, usually is considerably higher than that of heartwood in most species in which the latter is well differentiated (Kramer and Kozlowski, 1960; Kozlowski,

1964b). The basic density of sapwood is lower, however, because heartwood is impregnated with various extractives, as mentioned earlier. Some idea of the variations in moisture contents of sapwood and heartwood of gymnosperms is given in Table 4.7. There often is a rather steep moisture gradient

TABLE 4.7

VARIATIONS IN MOISTURE CONTENTS OF SAPWOOD AND HEARTWOOD IN VARIOUS SPECIES

Species	Moisture content (% dry weight)		Reference
	Sapwood	Heartwood	
<i>Pinus contorta</i>	85-165	30-40	Reid (1961)
<i>Pinus ponderosa</i>	124	110	Parker (1954)
<i>Thuja plicata</i>	194	30	Parker (1954)
<i>Pseudotsuga menziesii</i>	118	38	Parker (1954)
<i>Pinus radiata</i>	92-111	38-44	Fielding (1952)
<i>Thuja occidentalis</i>	236-262	31-38	Clark and Gibbs (1957)
<i>Picea glauca</i>	136-162	47-48	Clark and Gibbs (1957)
<i>Picea rubens</i>	93-142	33-42	Clark and Gibbs (1957)
<i>Abies balsamea</i>	138-186	57-75	Clark and Gibbs (1957)

even within the sapwood. In *Pinus contorta* moisture content decreased from 160% in the outer sapwood to 30% in the inner sapwood and was low throughout the heartwood (Reid, 1961). According to Dadswell and Hillis (1962) the sharp decrease in moisture content along a radius may occur very abruptly, as over one or two annual rings.

Many deviations from the patterns cited above have been noted. It should be remembered that the moisture content of sapwood of a species varies greatly with site and environmental conditions. It is not surprising, therefore, that many investigators have recorded higher moisture contents in heartwood than in sapwood (e.g., in *Carya*, *Fraxinus*, *Ulmus*, *Quercus*, *Nyssa*, *Juglans*, *Populus*, *Morus*, and *Eucalyptus* (Hillis, 1965). In some species (e.g., *Fraxinus mandshurica* and *Ulmus davidiana*) the heartwood is wetter than the sapwood at all seasons of the year (Yazawa and Ishida, 1965).

It is well known that heartwood does not play a role in upward transport of water in living trees (Kozlowski, 1961, 1964b). Krahmer and Côté (1963) related low permeability of heartwood to sealing of pit pairs through pit aspiration, occlusion of pits with extractives, incrustation of ligno-complex substances in the bordered pit pairs, and combinations of these. In *Pseudotsuga menziesii* pit aspiration effectively sealed bordered pit pairs of heartwood, although the pit membranes did not become as heavily

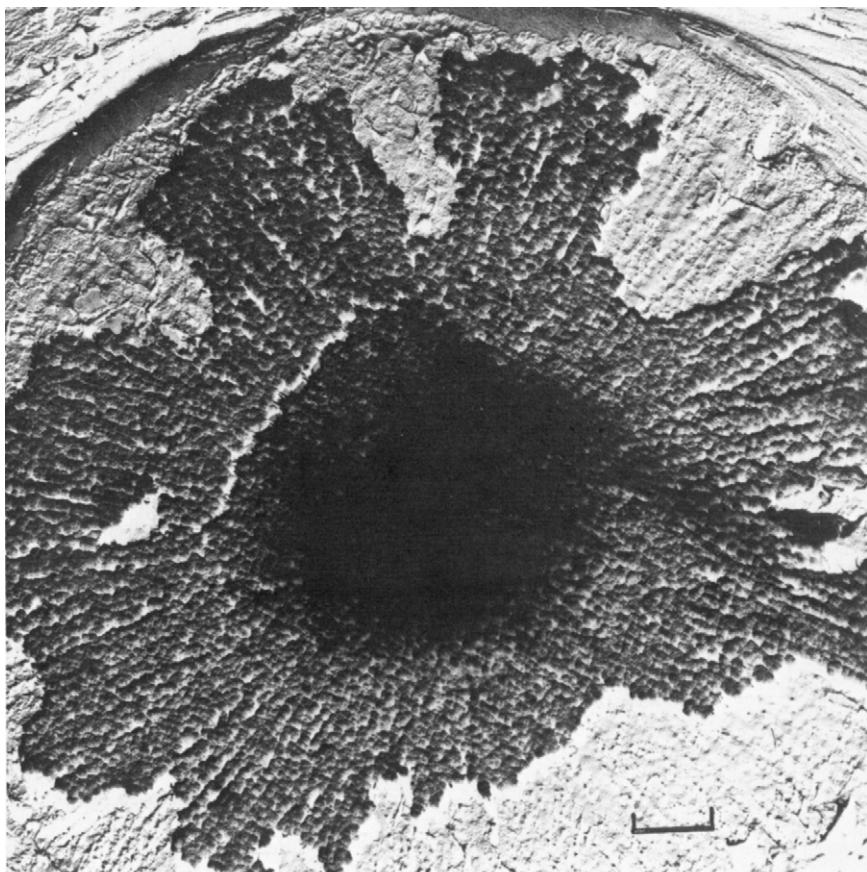


FIG. 4.14. Replica of the incrusted pit membrane of *Thuja plicata* heartwood. [From Krahmer and Coté (1963).]

incrusted in this species as they did in *Thuja plicata* (Fig. 4.14). Slight incrustations also were noted on pit membranes of *Thuja* sapwood only several rings from the cambium, but at the sapwood-heartwood boundary all the pits showed heavy incrustations. Many pits in *Thuja plicata* were not aspirated and it appeared that the heavy pit incrustations greatly reduced permeability of the pit. In *Tsuga heterophylla* both pit aspiration and membrane incrustation were observed.

Krahmer and Coté (1963) presented evidence that cell contents in the rays also contributed to pit blocking. Air permeability of sapwood of gymnosperms greatly exceeded that of heartwood. In the colored heartwood of

Thuja plicata and *Pseudotsuga menziesii* the permeability dropped rapidly from that in the sapwood. In *Tsuga heterophylla*, which does not have very dark heartwood, the permeability transition was gradual from sapwood to heartwood. Permeability also was higher in the late sapwood over early sapwood.

Heartwood extractives also decreased air permeability. Increase in heartwood permeability occurred after extraction with water, ethanol, or ethanol-benzene solvents, but it was increased least by extraction with hot water (Table 4.8). Hence, it appeared that the extraction process enlarged some of

TABLE 4.8

AIR PERMEABILITY OF UNEXTRACTED AND EXTRACTED HEARTWOOD OF THREE SPECIES OF GYMNOSPERMS^a

Species	Extraction solvent	Heartwood permeability ^b		
		Before extraction (K_1)	After extraction (K_2)	Ratio (K_2/K_1)
<i>Pseudotsuga menziesii</i>	Hot water	58.1	64.6	1.1
	Ethanol	34.4	54.7	1.6
	Ethanol-benzene	36.9	63.3	1.7
<i>Tsuga heterophylla</i>	Hot water	39.1	45.6	1.2
	Ethanol	34.4	71.8	2.1
	Ethanol-benzene	36.7	139.9	3.8
<i>Thuja plicata</i>	Hot water	17.1	27.0	1.6
	Ethanol	17.5	51.0	2.9
	Ethanol-benzene	21.4	54.4	2.5

^a From Krahmer and Coté (1963).

^b $K \times 10^7 \text{ cm}^4 \text{ sec-dyne}$.

the fine capillaries in the pit pairs but did not remove incrustations from pit membranes.

Mechanism of Heartwood Formation.

Although many of the changes occurring when sapwood turns into heartwood have been described, the important question of why trees form heartwood is not completely understood. A few of the major theories of the triggering mechanism of heartwood formation will be discussed briefly and more details can be found in the review by Hillis (1968).

1. *Air Accumulation in Closed Vessels.* Air can accumulate gradually in closed xylem elements. J. H. Priestley (1932) postulated that heartwood formed because of an accumulation of air in closed vessel systems, with

consequent effects on permanent water content of the wood, which in turn caused changes in secretion from living parenchyma cells. This theory is consistent with the relatively constant thickness of sapwood within species.

2. *Wounding.* Many investigators have observed development of a central core of discoloration in tree stems following wounding by dying of branches, insects, squirrels, logging, increment borings, etc. Such discolorations, which may be superimposed on normal heartwood, have been variously classified as heartwood, "false heartwood," "wound heartwood," "redheart," and "blackheart." Wound-induced cores of discoloration occur in various species of *Fagus*, *Betula*, *Acer*, *Populus*, and *Pinus* (Panshin *et al.*, 1964).

Some investigators considered that because of similarity in color, wound-induced discolorations were an extension of normal heartwood into the sapwood. Büsgen and Münch (1931), for example, stated that wound-induced discoloration of sapwood was identical to that of normal heartwood. Jorgensen (1962) concluded that pathological heartwood differed from normal heartwood only in location in the stem. He suggested that both normal heartwood and pathological heartwood be termed "protective wood" as both were protective in nature. Despite the similarity in color there appear to be some important differences between normal heartwood formed from internal stimuli associated with aging and the discoloration of sapwood which is induced by wounding. These will be discussed briefly.

As mentioned, once normal heartwood is initiated it continues to increase in diameter throughout the life of the tree (Kramer and Kozlowski, 1960). In contrast, wound-initiated discoloration of wood of several species does not continue to increase in diameter but its limited to the diameter of the tree when it was wounded or its branches died (Figs. 4.15 to 4.19). Shigo (1965a,b, 1967a,b), characterized the development of wound-initiated discoloration in stems of *Acer*, *Fagus*, and *Betula* trees. When several branches at the same whorl died at about the same time a single column of discoloration and decay developed. However, when wounds occurred at different stem positions, discoloration and decay developed as separate columns. Logging wounds also caused internal discolorations, with the appearance of the wound face indicating the amount of internal defect (Shigo, 1966). Internal discoloration and defects usually were confined to the wounded side of the tree. Xylem tissues which formed after wounds were inflicted did not become discolored. Thus, the girth of discolored cores in tree stems was limited by the diameter of the tree when its branches died or when it was wounded. Unwounded trees, which had no large branch stubs and were not otherwise wounded, lacked the discolored cores found in wounded trees or those with large branch stubs. Mature trees with small side branches that had self-pruned early in the life of the tree had very small central columns of discoloration.



FIG. 4.15. Variations in wound-initiated discoloration in *Acer saccharum*. Although both trees had 8-year-old basal wounds of about the same size, the wound of the tree on the right had a hard protective zone and the wound did not initiate discoloration. In contrast, the marked discoloration in the tree on the left was associated with large, dead upper branches and the basal wound. (U.S. Forest Service Photo.)



FIG. 4.16. Branch stub of *Acer rubrum* infected with *Polyporus glomeratus*. The central column shows the diameter of the tree when the branch died. The decay fungus later affected the tissues. A band of sound discoloration surrounds the decay column. (U.S. Forest Service photo.)

When branches died or wounds occurred at approximately the same time, the discolored core which subsequently formed, was contained within tissues bordered by the same growth ring. However, when dying of branches and wounding of stems by logging occurred at different times, the areas of discoloration caused by these wounds coalesced to form columns with rather uneven margins.

J. H. Hart (1965) compared sapwood, heartwood, and discolored sapwood (induced by wounding with an increment borer) of *Quercus alba*, *Acer saccharinum*, and *Juglans nigra*. Although no living cells were found in either the heartwood or discolored sapwood these were not identical morphologically. The discolored sapwood of *Quercus alba* was dark brown in color, whereas the heartwood was a lighter shade of brown. The discolored sapwood of *Acer saccharinum* was dark brown and the heartwood a cinnamon or almond color. In this species plugs of gum were common in heartwood but seldom occurred in discolored sapwood. Moreover, from a chemical viewpoint, discolored sapwood was very different from normal heartwood (Table 4.9). In *Maclura pomifera* and *Robinia pseudoacacia* J. H. Hart (1968)



FIG. 4.17. Wood discoloration initiated at a branch stub of red oak (*Quercus rubra*) advancing downward through true heartwood. The very dark central column is discoloration initiated at the branch stub and is superimposed on the lighter, true heartwood. Tissues from the bark inward are sapwood, heartwood, discolored heartwood (these tissues were sapwood when the branch died), heartwood, and the central column of discolored heartwood. (U.S. Forest Service Photo.)

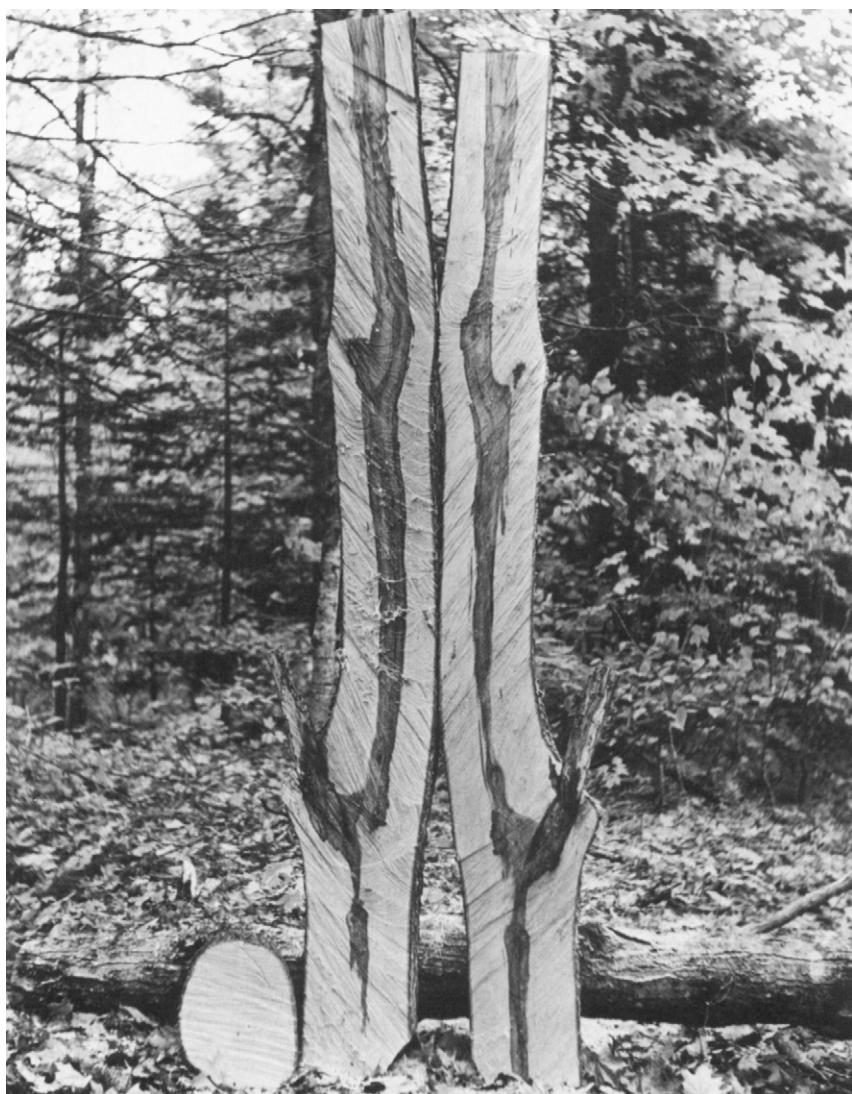


FIG. 4.18. Wound-initiated discoloration in *Acer saccharum*. The base of the stem was uniformly light in color from the bark to the pith. The discoloration above was initiated by death of branches. (U.S. Forest Service photo.)

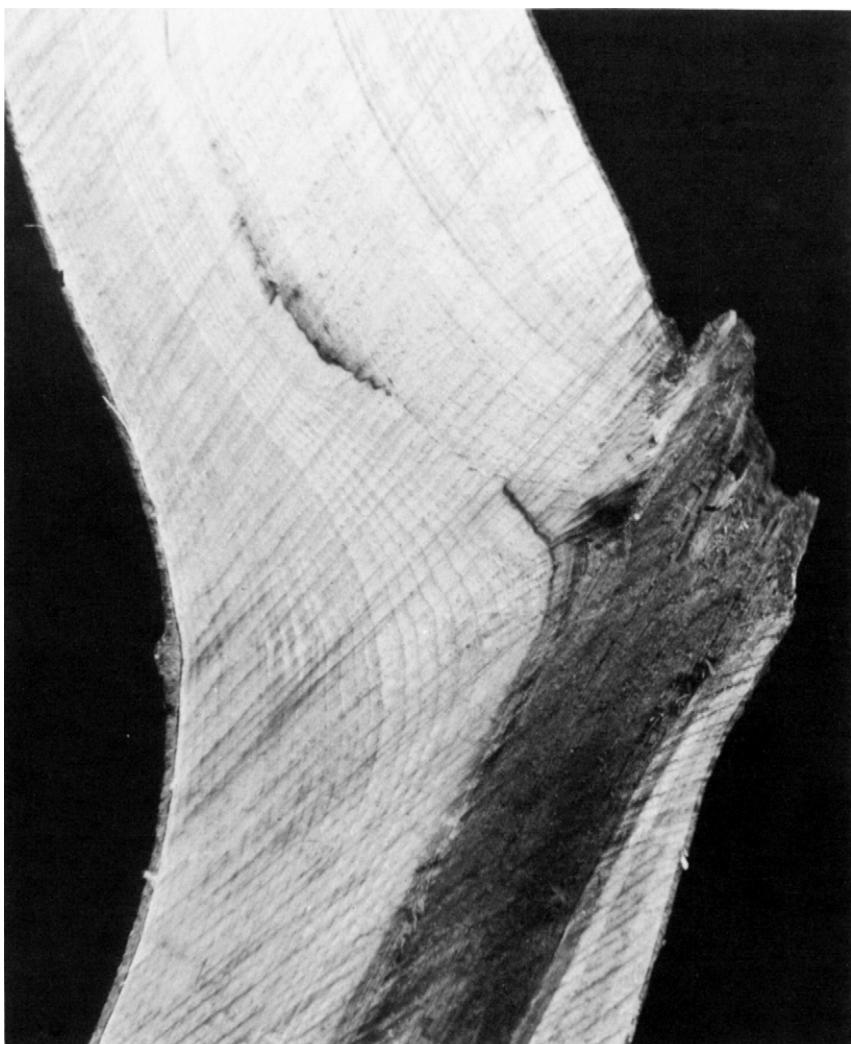


FIG. 4.19. Discoloration of wood of *Fagus grandifolia* initiated at a stem stub. The diameter of the stub is the same as the diameter of the column of discoloration and defect that developed downward into tissues present when the leader died. (U.S. Forest Service photo.)

TABLE 4.9

CHEMICAL CHARACTERISTICS OF SAPWOOD, HEARTWOOD, AND DISCOLORED SAPWOOD OF
Quercus alba AND *Acer saccharinum*^a

		Sapwood	Heartwood	Discolored sapwood
Moisture content (% dry wt.)	<i>Q. alba</i>	63.3	55.4	76.8
	<i>A. saccharinum</i>	80.5	52.9	86.4
Ash content (% dry wt.)	<i>Q. alba</i>	0.65	0.39	1.25
	<i>A. saccharinum</i>	0.40	0.53	0.90
Cold water solubility (% dry wt.)	<i>Q. alba</i>	4.3	5.3	3.2
	<i>A. saccharinum</i>	2.3	1.3	1.5
Hot water solubility (% dry wt.)	<i>Q. alba</i>	5.6	7.7	4.2
	<i>A. saccharinum</i>	3.5	1.9	2.7
Solubility in 1% caustic soda (% dry wt.)	<i>Q. alba</i>	18.9	21.1	17.7
	<i>A. saccharinum</i>	19.3	17.6	18.4
pH of cold and hot water filtrates	<i>Q. alba</i>			
	Cold	6.5	4.8	6.8
	Hot	5.3	4.2	5.9
	<i>A. saccharinum</i>			
	Cold	6.4	6.8	7.0
	Hot	5.7	6.1	6.4

^a From J. H. Hart (1965).

found that normal heartwood and discolored sapwood in the vicinity of wounds differed significantly in color, water content, frequency of amorphous deposits, percent of material soluble in water or 1% NaOH, ash content, and pH. These differences emphasize that when living cells die as a result of injury of a type which results in discolored tissue, this tissue should not be considered an example of precocious development of normal heartwood.

Wound-initiated discolorations result from cellular changes and may or may not be associated with organisms. In most of the angiosperm trees he examined, Shigo (1965b) found organisms associated with the discolored columns. Fungi causing discoloration invaded the tree first and were followed by decay fungi. Bacteria were also associated with these fungi. In some *Fagus* and *Betula* trees, however, no organisms were found and it appeared that discolorations often developed in advance of invasion by organisms. The discolorations may be caused by deposits formed during death of cells or by soluble pigments formed by invading organisms (Jorgensen, 1961).

3. *Variations in Respiration of Inner and Outer Stem Tissues.* Frey-Wyssling and Bosshard (1959) advanced a theory of heartwood formation which involved semi-aerobic respiration in inner parts of stems. The theory proposed that starch hydrolysis occurred in the transition zone, and when starch

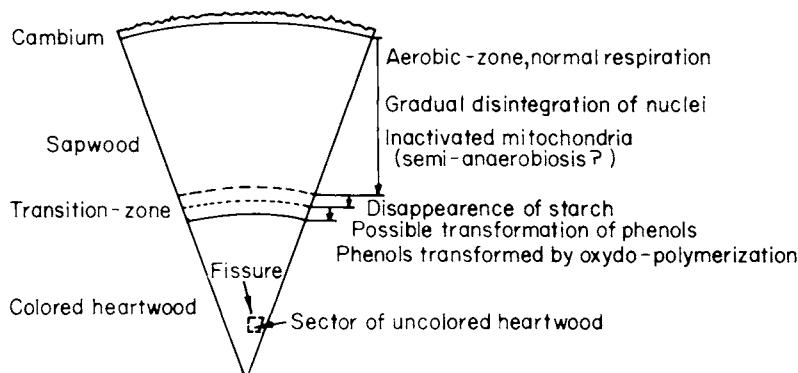


FIG. 4.20. Part of transection of a tree stem showing cytological and physiological characteristics of different zones between the cambium and pith. [From Frey-Wyssling and Bosshard (1959).]

disappeared, the enzymes of sapwood-parenchyma no longer controlled the ray cells. At the boundary of the colored heartwood the phenols absorbed in cell walls might be oxidopolymerized (Fig. 4.20).

4. Accumulation of Extractives. When heartwood is formed from sapwood the amount of extractives increases sharply, sometimes within a few rows of cells. Erdtman (1955) considered that the secondary constituents formed in the cambium are disposed of by transportation via the vascular rays to the dead portions of the tree, heartwood and bark, where they accumulate and sometimes exert a useful though generally unspecific protective function. Stewart (1966) extended this proposal and considered these materials to be the "excretory substances" formed during differentiation, respiration, and biosynthesis and degradation of starch. He believed these materials were translocated in nontoxic concentrations along the rays toward the pith where they accumulated to lethal levels. As a result, the innermost parenchyma cells died to form the outer heartwood cylinder. The earlier formed heartwood impeded further inward translocation and the continued accumulation of toxic components at the sapwood-heartwood boundary caused death of cells and resulted in a gradual outward movement of the heartwood core.

The above proposals exemplify the theories that heartwood extractives are translocated inward from the cambium along the rays. These ideas are challenged by an impressive body of evidence which indicates that heartwood extractives arise *in situ* from translocated or stored carbohydrates. As Hillis and Carle (1962) emphasized, if translocation of polyphenols occurred readily there should be marked biochemical relationships of polyphenols of various tissues along the translocation path. However, sapwood polyphenols can be

absent from the heartwood or the heartwood may have components which do not occur in the sapwood. For example, *Pinus radiata* sapwood contained small amounts of vanillin, substituted benzoic acids, and traces of pinosylvin monomethyl ether. By comparison, the heartwood contained pinosylvin and its methyl ether, and the flavonoids, pinobanksin and pinocembrin (Hillis, 1968). In *Eucalyptus astringens* sapwood ellagittannins are present. In the heartwood, stilbenes and chlorogenic acid occur in appreciable quantities with smaller amounts of other monomeric substances (Hillis and Carle, 1962). Furthermore, the composition of polyphenols is different in heartwood, damaged sapwood, sapwood affected by the wood boring insect *Sirex*, and knotwood of *Pinus radiata*, indicating that polyphenols are formed *in situ*. This view has also been supported by tracer studies. After administering labeled glucose-¹⁴C to a kino vein in *Eucalyptus*, Hillis and Hasegawa (1963) identified labeled polyphenols in the kino. The labeled glucose moved from the phloem through the sapwood to the sapwood-heartwood boundary in 19 days. Hasegawa and Shiroya (1967) administered labeled sucrose to the cambial region of *Prunus yedoensis*. If polyphenolic compounds were translocated via the ray cells the specific activity of the labeled polyphenols should have decreased gradually from the sapwood to the transition zone. However, specific activities of flavonoids in the transition zone were higher than those in the inner sapwood. The data indicated that the flavonoid compounds were not translocated from the inner sapwood to the transition zone. In another study Hillis *et al.* (1962) showed that the inner sapwood of *Angophora costata* trees had a starch content that was too low to account for the quantity of polyphenols present in the heartwood, indicating that a major part of the heartwood polyphenols was formed at the sapwood-heartwood boundary from translocated carbohydrates which had not been utilized in growth. This conclusion is consistent with the observation that rapid growth and efficient utilization of available carbohydrates often are associated with a low amount of heartwood phenols (Hillis, 1968).

Wardrop and Cronshaw (1962) also provided evidence of origin of phenolic substances within cells. A relationship was found between loss of reserve starch and processes leading to the formation of phenolic substances. Cells rich in phenolic substances had few or no starch grains.

5. Water Deficit and Low Carbohydrate Utilization in Growth. Hillis (1962) considered the effect of vegetative growth, temperature, oxygen, and moisture stress on the hydrolysis of starch in sapwood. Although moisture stress could be one of the factors responsible for disappearance of starch, it was noted that starch content decreases some distance from the heartwood periphery and before a marked fall in moisture content occurs. Rudman (1966) postulated that a combination of water stress, leading to hydrolysis of starch to sugar, and centripetal movement of unused carbohydrates, which

were transformed to extractives, was involved in heartwood formation. According to this theory, young trees do not form heartwood because they utilize carbohydrates rapidly in growth. In old trees, however, reserve foods and by-products of increased respiration are not completely reutilized and are available for inward transport and sequential conversion to an ultimate extractive, with low solubility in sap, which is precipitated.

Rudman (1966) explained the formation of concentric rings of included sapwood as the result of variations in amounts of reserve foods available for centripetal flow. When the amount available was low, heartwood was produced which was sufficiently low in extractives to resemble sapwood.

The above theories are summarized to indicate the unsettled state of knowledge and disagreement on the mechanism of heartwood formation. Obviously much more research is needed on this important topic.

Insect Resistance

Once beyond the sapling stage trees apparently acquire some resistance to insect attack. However, as trees become mature to overmature they enter a natural state of reduced physiological activity and become subject to widespread attack by certain insects (Kramer and Kozlowski, 1960; Kozlowski, 1969). For example, in the Rocky Mountains of the United States, outbreaks of the Mountain pine beetle (*Dendroctonus monticolae*) usually did not develop in *Pinus contorta* stands less than 80 years old, and the hazard of attack increased greatly after the trees were 100 years old (Hopping, 1951). Outbreaks of the hemlock looper (*Lambdina fiscellaria*) usually occur in slow-growing, mature, or overmature trees (Carroll, 1956).

The age at which trees are most likely to be invaded by insects often reflects some specific physiological condition which predisposes a tree to attack. Such predisposing characteristics vary greatly and may include threshold levels of flowering, cambial activity, resin flow, critical sapwood moisture content, etc. (Kozlowski, 1969). Production and copious exudation of oleoresin in gymnosperms and flow of sap or gum in angiosperms are known to provide resistance to attack of bark beetles. Vité (1961) demonstrated that success of bark beetle attack was closely correlated with low oleoresin exudation pressure. Initial insect attack occurred at random, but only beetles in trees with low oleoresin exudation pressure made successful invasions that led to mass attacks later. Vité and Wood (1960) noted that of 40 trees attacked successfully, 33 had oleoresin exudation pressures of less than 4 atm. Differences in susceptibility due to site and stand conditions were correlated with rates of oleoresin flow and these, in turn, with stem hydration. Oleoresin exudation pressures decrease under conditions of internal water

stress, emphasizing that drought is an important factor which predisposes trees to bark beetle attack. These observations indicate that age alone is not always the most critical factor in predisposing trees to insect attack. Beal (1943) stressed this point in stating that decreased growth rates of trees, whether associated with age, drought, or stagnation of stands through over-crowding, provided favorable conditions for a change from an endemic to epidemic status of the Black Hills beetle (*Dendroctonus ponderosae*).

There are many examples in the literature of increasing susceptibility of trees as they age to attacks by certain insects and only a few examples will be cited. For a fuller discussion of this subject the reader is referred to the book by K. Graham (1963).

Most bark beetles favor mature or overmature trees. Hopping and Mather (1945) cited a number of examples of *Pinus contorta* stands in which the Mountain pine beetle (*Dendroctonus monticolae*), although continually present in small numbers, did not cause extensive damage until the stands were 160 to 170 years old. Thereafter, the insect completely destroyed the stands within a decade. In general the *Pinus ponderosa* trees most susceptible to attack by the Western pine beetle (*Dendroctonus brevicomis*) are weak or old trees. Using tree age and vigor (Keen, 1936, 1943) classified *Pinus ponderosa* trees into four age groups (young, immature, mature, and overmature) and, within each of these groups, into four degrees of crown vigor. There was a gradual increase in susceptibility to attack with advancing tree age. In each age group susceptibility also increased with decreased crown vigor. In fact differences in crown vigor within a class often were more important in predisposing trees to attack than was the age difference between one class and the next.

Different species of bark beetles may show individual preferences for trees of particular age classes. Whereas *Dendroctonus brevicomis* attacks old trees of low vigor, *Dendroctonus monticolae* attacks much younger trees, and *Ips confusus* prefers relatively young trees or tops of old ones (Rudinsky, 1962). *Dendroctonus monticolae* did not attack *Pinus contorta* trees that were less than 5 or 6 in. in diameter. For each inch of diameter above this there was an increase of infestation of about 5% (Hopping and Beal, 1948).

Normally the bronze birch borer (*Agrilus anxius*) shows preference for mature or overmature *Betula alleghaniensis*, *B. papyrifera*, and *B. populifolia* trees, or those in a very low state of vigor. Severe damage occurs primarily in mature stands (Balch and Prebble, 1940). R. F. Anderson (1944) found very decadent trees to be the most suitable for attack. Cessation of cambial growth created conditions especially conducive to larval development. Even in suppressed trees in which cambial tissues were proliferating very slowly, conditions were unfavorable for development of larvae. Epidemics of spruce budworm (*Choristoneura fumiferana*) usually are associated with

mature stands of *Abies balsamea*. In this species frequent and abundant production of staminate flowers, a characteristic of old age, appears to be the critical factor in providing conditions favorable to population increases of the spruce budworm. In western Ontario *Abies balsamea* trees growing in full light attain maturity at between 50 and 65 years of age (Blais, 1952). According to K. Graham (1963) mature trees were more susceptible to heavy attack than immature trees because the male strobili provided food early in the year when opening of vegetative buds lagged behind the emergence of larvae. Blais (1958) showed that after attack by spruce budworm *Abies balsamea* trees which flowered heavily tended to die earlier than intermediate or nonflowering trees. As the amount of defoliation necessary to kill flowering or nonflowering trees within a stand was similar, the greater vulnerability of flowering trees resulted from presence of more insects and greater amounts of defoliation of the flowering trees.

Disease Resistance

Resistance of trees to several fungus diseases varies with age of the tree. Some disease fungi attack only very young trees while others favor those advanced in age and lacking in vigor. However, the relations of fungal pathogens to host susceptibility often are rather complex and, as Patton (1962) emphasized, many diseases such as rusts are even favored by vigorous growth of the host.

"Damping-off" disease is, for the most part, confined to very young trees. Susceptibility to this disease complex rapidly decreases with increasing plant age as tissues harden over a period of days to weeks. Most damping-off is caused by a variety of species of *Pythium* and *Rhizoctonia*. These fungi attack a wide variety of young woody angiosperms and gymnosperms, probably reflecting their wide nutritional tolerances (Zak, 1964). The radicle of the germinating seed of the root system of the new seedling may be destroyed in pre- or post-emergence damping off. The period from the time of radicle emergence until the root system expands and matures is a dangerous one indeed for the young plant. As Zak (1964) emphasized, during the early stages the susceptibility of root tissues to fungal attack is high and capacity for root replacement low. Seedling survival is assured only after the root system has grown appreciably and accumulated enough reserve foods to insure rapid root replacement. Prior to that time fungal attack usually kills the plant.

Needle rusts of conifers, which are most damaging to seedlings and lower crowns of saplings, only rarely cause damage to old trees under forest conditions. The pine stem rusts of the genus *Cronartium* do most damage to

trees in seedling, sapling, and small pole size classes when they cause reduced growth, malformations, and death of trees. Patton (1961), testing resistance of grafts of *Pinus strobus* selections and their progeny to white pine blister rust caused by *Cronartium ribicola*, found a decrease in susceptibility with increasing age of scion source. The percentage of infections varied from 81 in 4-year-old grafts to 22 in grafts of 80-year-old shoots (Table 4.10).

TABLE 4.10

INFECTION BY *Cronartium ribicola* AFTER ARTIFICIAL INOCULATION OF 4-YEAR-OLD *Pinus strobus* SEEDLINGS AND OF GRAFTS IN VARIOUS AGE CLASSES^a

	Age (years)	Total No.	No. infected	Percent infected
Control Seedlings	4	141	139	99
Grafts	4	21	17	81
Grafts	10	17	13	76
Grafts	20	16	8	50
Grafts	40	12	5	42
Grafts	80	11	3	27

^a From Patton (1961).

Soegaard (1956) showed differences due to tree age in resistance of *Thuja plicata* to leaf blight caused by *Didymascella thujina*. Whereas plants in the juvenile stage were severely attacked by the disease the cuttings representing the adult stage were highly resistant. By the time trees were 25 years old they had outgrown the susceptible stage characteristic of young trees. Root fungi attack trees of all ages but the critical infection period, which varies with species, occurs when trees are 20 to 40 years old (Boyce, 1954; Patton, 1962).

Although cankers are most obvious on old trees, infection usually occurs when trees are young, usually before they are 20 years old. Butt heart rots are most prevalent in the trunks of old and large trees. A vertical and horizontal gradient occur in trees, with decay resistance of heartwood decreasing from the base to the top of a tree and from inner to outer layers. Such variable resistance appears to be associated with the balance of extractives which show fungicidal properties. A. B. Anderson *et al.* (1962) indicated that as a tree aged and extractives formed, certain phenols were converted by enzyme systems or time to quinones and phenol ethers which reduced the decay resistance of heartwood.

Longevity and Senescence

Trees are by far the oldest living things on earth. There is wide variation, however, in the life-span of various species. Many species of trees survive

less than a hundred years, but a few grow for several thousand years. A number of woody species stand out for their unusual longevity. The oldest living plants appear to be *Pinus aristata* trees growing in California. Some of these were confirmed by Schulman (1958) to be well in excess of 4000 years old. *Sequoia sempervirens* achieves an age greater than 3000 years. Other species noted for their unique longevity include *Pseudotsuga menziesii*, *Cedrus libana*, *Fitzroya cupressoides*, *Taxodium mucronatum*, *Pinus flexilis*, *Ginkgo biloba*, *Taxus* spp., *Pistacia atlantica*, and several species of *Quercus*. Some examples of very old trees are shown in Figs. 4.21 and 4.22. For additional data on longevity of trees the reader is referred to Tables 7.1 and 7.2 of this volume.

THEORIES OF SENESCENCE

The question of what causes senescence in trees and controls variations in longevity among species has intrigued plant physiologists for a long time. Many investigators have assigned a causative role to reproductive growth in effecting a senescent state. It is well known, for example, that removal of flowers and fruits will delay senescence. A classic example of the effect of flowering on senescence is that of bamboo which flowers once and then promptly dies. Resende (1964) showed that leaves of several species aged and fell when flower buds appeared, emphasizing the role of reproduction in accelerating senescence. Molisch (1938) suggested that developing fruits monopolized nutrients to such an extent that senescence of vegetative tissues inevitably resulted. Although it is clear that flowering and fruiting cause movement of various compounds away from vegetative tissues, the relationship of such mobilization to the actual senescence-inducing mechanism is not fully understood (Leopold, 1964).

As trees age, several changes in food, water, and hormone relations occur which may contribute variously to an increasingly unfavorable balance of anabolism to catabolism leading to a deteriorative condition. Jacobs (1955) pointed out that in the life of a tree the proportion of crown to stem gradually decreases with age and size, and the sheath of new xylem becomes progressively thinner. These changes alone, which create physiological stresses resulting from reduced food supply and difficulties of translocation, would limit longevity. At the same time there is increasing susceptibility to pathogenic agents and the possibility of infection increases as a function of age. For example, pathogenic virus populations may build up and weaken the host tree. Fungal attacks occurring from the pith outward eventually may weaken the stem sufficiently to subject the tree to windthrow. Long-lived trees have characteristically durable woods and they resist fungal attacks in the heartwood. As Westing (1964) emphasized, an important factor in the long life-span of *Sequoia* and *Pinus aristata* is resistance to decay and fire. Decay



FIG. 4.21. Very old, multiple-stemmed and branched *Pinus aristata* tree in California. Only one side of the tree is alive. (U.S. Forest Service photo.)



FIG. 4.22. Gnarled old cedar tree in California. (U.S. Forest Service photo.)

resistance often is increased by high contents of resin or phenolic compounds.

The progressively decreasing crown size in relation to the stem of aging trees results in a diminished ratio of food produced to that used in respiration (Kramer and Kozlowski, 1960). As Möller *et al.* (1954) demonstrated, the leaf area of aging trees remains fairly constant but its total photosynthetic output declines slightly while respiratory consumption of food increases appreciably. As may be seen in Fig. 4.4 about 40% of the photosynthate was used in respiration by 25-year-old *Fagus* trees, but about 50% was used by 85-year-old trees. Hence, the leaves appear to be unable to supply adequate food for the requirements of the old tree.

Increasing difficulty in translocation of food, water, minerals, and hormones as distance from root to shoot increases appears to be very important in promoting senescence. Went (1942) strongly emphasized that translocation of water to the crown became progressively difficult in aging trees and caused sufficiently severe water deficits in some leaves and branches to cause their death. Hence, tissue senescence is promoted by gradually decreasing availability of essential compounds. Enzymatic activity decreases as shown by an overall diminished metabolic rate. Hormone supplies tend to become limiting as the leaf mass becomes inadequate to supply the tree. Furthermore, as growth regulators are translocated in the assimilate stream, a decreased flow of carbohydrate from the leaves is correlated with decreased movement of hormones. The diminishing tendency for aging *Ginkgo* trees to produce long shoots was associated with decreased hormone supply. The importance of hormones in senescence is shown by extensive literature on aging of leaves. This is discussed in more detail in Chapter 8.

At the cellular level senescence may be considered an expression of deteriorative changes involving the breakdown of structural integrity of aging tissues. According to Sacher (1957) and Varner (1961) deterioration of cell membranes may be responsible for cellular decline. This is consistent with observations that as leaves age there is increase in leakage of substances from them (Leopold, 1964).

LONGEVITY OF ORGANS AND TISSUES

It is important to distinguish between longevity of the plant as a whole and of its relatively short-lived organs and tissues. During tree development there is continuous death of cells and formation of new living ones, with the proportion of dead to living tissues increasing as a tree ages. For example as may be seen in Fig. 4.21 very old trees often are composed of a small number of living cells in contrast to a tremendous accumulation of dead cells.

Various organs of trees vary greatly in their longevity. Apical and lateral

meristematic tissues remain alive throughout the life of a tree, but even meristematic cells are continually replaced. Protoplasts of xylem cells are lost early. Therefore, most wood cells, including the majority of those in the sapwood, are dead. Sieve tubes usually function for one season and then die. In some species, however, they may live for 2 years, and in others for several years. Pith cells and longitudinal parenchyma cells are relatively long lived. Ray parenchyma cells of *Carnegia* may stay alive in excess of 100 years. Longevity of flowers usually varies from only a few hours to several months. Fruits are somewhat longer lived, but usually survive on the tree for less than a year. Some roots are perennial and have a long span, but many die each year and some remain alive for only a few weeks. This is discussed in more detail in Volume II, Chapter 5. Leaves of most angiosperm trees have a life span of less than a year, but in some species the leaves may live up to 5 years. Usually leaves are shed prior to or after death, but in some trees (for example, certain species of *Fagus* and *Quercus*) dead leaves may persist on the tree throughout the winter. Leaves of gymnosperms are relatively long-lived and in certain species remain physiologically active for many years. This is discussed in more detail in Chapter 6 of this volume.

Suggested Collateral Reading

- Bosshard, H. H. (1965). Aspects of the aging process in cambium and xylem. *Holzforschung* **19**, No. 3, 65–69.
- Chattaway, M. M. (1952). The sapwood-heartwood transition. *Aust. Forest.* **16**, 25–34.
- Frey-Wyssling, A., and Bosshard, H. H. (1959). Cytology of the ray cells in sapwood and heartwood. *Holzforschung* **13**, 129–137.
- Hart, J. H. (1968). Morphological and chemical differences between sapwood, discolored sapwood, and heartwood in black locust and osage orange. *Forest Sci.* **14**, 334–338.
- Hillis, W. E., ed. (1962). "Wood Extractives and their Significance to the Pulp and Paper Industries." Academic Press, New York.
- Hillis, W. E. (1968). Chemical aspects of heartwood formation. *Wood Sci. Technol.* **2**, 241–259.
- Kozlowski, T. T. (1969). Tree physiology and forest pests. *J. Forest.* **69**, 118–122.
- Krahmer, R. L., and Coté, W. A., Jr. (1963). Changes in coniferous wood cells associated with heartwood formation. *Tappi* **46**, 42–49.
- Kramer, P. J., and Kozlowski, T. T. (1960). "Physiology of Trees," Chapter 15. McGraw-Hill, New York.
- Moorby, J., and Wareing, P. F. (1963). Aging in woody plants. *Ann. Bot. (London)* [N.S.] **27**, 291–308.
- Rudman, P. R. (1966). Heartwood formation in trees. *Nature (London)* **210**, 608–610.
- Wareing, P. F., and Seth, A. K. (1967). Aging and senescence in the whole plant. *Symp. Soc. Exp. Biol.* **21**, 543–558.
- Went, F. W. (1942). Some physiological factors in the aging of a tree. *Proc. 18th Nat. Shade Tree Conf.* (1942) pp. 330–334.
- Westing, A. H. (1964). The longevity and aging of trees. *Gerontologist* **4**, 10–15.

Chapter 5

BUD DEVELOPMENT AND SHOOT EXPANSION

Introduction

Shoots, which may be considered to be collections of leaves joined into a stem, typically are divided into nodes and internodes. The term node is used to designate the part of the stem at which one or more leaves are attached. The term node is also often used in relation to “uninodal” (e.g., *Pinus resinosa*) and “multinodal” (e.g., *Pinus taeda*) species and refers to the place (or region) where long shoots or branch whorls are attached to the stem. Internodes are lengths of stem between two successive nodes.

Shoots elongate only at their terminal portions and typically as the result of bud expansion through the activity of many growing points or apical meristems which are distributed over the tree stem, branches, and twigs. As emphasized by Wardlaw (1965), the apex of a shoot is a harmoniously developing continuum consisting of an apical meristem as well as subapical and maturing regions. The overall growth of a shoot axis consists of several sequential phases including division of cells of the apical meristem as well as their elongation, differentiation, and maturation. These phases, which are not sharply delimited, occur at increasing distances from tips of stems or branches (Kramer and Kozlowski, 1960). The region of cell elongation extends for an appreciable distance behind the apex and includes several internodes. Almost all of shoot extension results from internodal elongation which projects the shoot tip upward.

Opening of buds is the result of activity of one or more meristematic tissues. Bud opening may involve leaf enlargement, meristem activity in the internodes between leaves, or faster growth of bud scales on inner than on outer surfaces (Fig. 5.1). In *Picea sitchensis* the first visible signs of bud opening were swelling of the bud and loss of the dark resinous color of the scales. Bud swelling and needle elongation continued, but adhesion of



FIG. 5.1. Buds of *Carya* in various stages of opening (U.S. Forest Service photo).

bud scales to the tips of elongating needles caused them to curve outwards. Scales separated about a week after the first stage of growth began (Burley, 1966a).

Expansion of a bud to produce a shoot involves both increase in size of preexisting cells as well as cell division. In some species, shoot growth involves both expansion of internodes and enlargement of those preformed leaves or leaf primordia which were contained in the unopened bud. In other species additional leaf primordia form and expand during the current growing season. The lengthening of internodes and leaves may or may not be correlated. In

many recurrently flushing species each wave of shoot elongation is highly correlated with leaf expansion. In contrast, in some species such as *Pinus resinosa*, which contains fully preformed shoots in its unopened buds, internode elongation occurs for a shorter time than does leaf elongation. In many pines the opening of buds is followed by rapid early elongation of internodes with very little early expansion of needles, resulting in the "candle" stage of shoot growth. In short shoots of some gymnosperms (*Larix*, *Ginkgo*, and *Cercidiphyllum*) and angiosperms (*Populus*, *Betula*) bud opening is followed by expansion of leaves and no appreciable internodal growth. By comparison, growth of long shoots of the same species involves both leaf and internode expansion.

APICAL MERISTEMS IN SHOOTS

Apical meristems, which consist of several integrated regions, vary in size and shape among species (Fig. 5.2), differently located shoots in the same

TABLE 5.1
WIDTH OF SHOOT APICES AT LEVEL OF INSERTION OF
THE YOUNGEST LEAF PRIMORDIUM^a

Species	Apex width (μ)
<i>Pinus mugo</i> (long shoot)	280
<i>Taxus baccata</i>	140
<i>Ginkgo biloba</i> (long shoot)	400
<i>Ginkgo biloba</i> (short shoot)	400
<i>Syringa vulgaris</i>	40–100

^a From Clowes (1961).

tree (Tepper, 1963b), and with stage of development. The apical meristems of gymnosperms generally are larger than those of angiosperms. Shoot apices of most gymnosperms are narrow and conical but *Ginkgo* and cycads are exceptions as they have broad and flat shoot apices. Some variations in width of shoot apices are given in Table 5.1.

Sacher (1955) showed that in *Pinus lambertiana* the apices of short shoots differed from those of long shoots in their smaller size, absence of clear cytohistological zonation, and higher rate of mitotic activity. Tepper (1963b) compared dimensional and zonational variation in shoot apices of the dormant terminal leader and terminal branches of *Pinus ponderosa* trees. Although there was considerable variation in size of apices within an individual tree, two dimensional trends were present. The diameter of the apex generally decreased and the height-diameter ratio of the apex increased in progressively lower positions in the tree crown (Table 5.2). The

TABLE 5.2

AVERAGE DIMENSIONS OF SHOOT APICES ON A 32-YEAR-OLD *Pinus ponderosa* TREE^a

Location on tree	Diameter (μ)	Height (μ)	Height-Diameter ratio
Terminal leader	474	94	0.20
5-year-old branch	482	130	0.27
10-year-old branch	471	144	0.29
15-year-old branch	388	124	0.33
20-year-old branch	288	118	0.41

^a From Tepper (1963b).

cytohistological zonation of apices in all common positions was similar, but apices of large diameter had a more extensive distal zone, rib meristem zone, and peripheral zone than those of small diameter.

In a given species the size of the shoot meristem is small in the embryo and enlarges during plant development. For example, Ball (1941) reported the width of the apical meristem of *Phoenix canariensis* to be 80 μ in the embryo, 140 μ in the seedlings, and 528 μ in the mature plant. Several investigators have described seasonal changes in the size of apical meristems, with the height of the apical dome generally larger in an active shoot tip than in a dormant one. For example, the apices of *Pinus lambertiana* became more conical in form when they were undergoing active division prior to formation of a new bud (Sacher, 1954). Some idea of actual variations in the size of apices during the seasonal growth cycle may be gained from the following measurements of height and diameter of *Abies concolor* apices obtained by Korody (1937): 45 μ by 160 μ at the end of bud expansion; 80 μ by 240 μ at the end of bud scale formation; 180 μ by 310 μ immediately before leaf formation; and 70 μ by 210 μ at the end of the period of leaf formation. Seasonal variations in the size of the apex of *Abies concolor* shoots are also shown in Fig. 5.16.

Changes in the size and shape of the shoot apex often can be seen as leaf primordia form below the apical dome (Sinnott, 1960). For example, in opposite-leaved species the apical dome often flattens as the two leaf primordia form. With further development, but before another pair of leaf primordia appears, the dome bulges upward again. Thus the shoot meristem may be considered to be a dome which expands, cuts off another leaf primordium, etc. (Clowes, 1961).

ORGANIZATION OF APICAL MERISTEMS

Much interest has been shown in the zonation of cells of apical meristems. The surface cells of many angiosperm apices form a distinct mantle because they divide only anticlinally (perpendicular to the surface). The cells below

the surface divide in several planes, periclinally (parallel to the surface) as well as anticlinally and obliquely. This arrangement of cells in apical meristems fits the tunica-corpus concept of Schmidt (1924) who termed the surface, anticlinally dividing cells the tunica and the deeper cells which divide in several planes, the corpus. The number of tunica layers varies, but many species have a two-layered tunica.

Apical meristems of some angiosperms do not easily fit a rigid tunica-corpus pattern, leading to some disagreement about nomenclature. Some investigators consider the tunica to fluctuate in number of layers, with some cells of the inner layers dividing periclinally and becoming part of the corpus (Clowes, 1961).

Apical meristems of most gymnosperms, including *Ginkgo*, *Cycas*, *Zamia*, *Torreya*, *Pinus*, *Picea*, *Abies*, *Sequoia*, and *Pseudotsuga* do not show a tunica-corpus organization (they do not possess surface layers which divide only anticlinally). Cells of the outermost layer of apices of many gymnosperms divide periclinally at the summit and on the flanks. Korody (1937) considered the apex of most gymnosperms to be a naked corpus. Examples of gymnosperm genera which are exceptions and have been fitted into the tunica-corpus concept include *Araucaria*, *Agathis*, *Cupressus*, *Ephedra*, and *Gnetum* (Clowes, 1961).

Tepper (1966) examined apical meristems of dormant, terminal branch buds of a large number of species of adult pine trees growing in an arboretum at Placerville, California. Apices of all species showed the same type of cytohistological zonation. In some, zonation was more distinct than in others (Fig. 5.2). A group of large cells with large nuclei which stained less intensely than in other apical cells was present in the distal part of the apex. This zone, called the distal zone, was flanked laterally by a peripheral zone consisting of small cells with small nuclei. Cells of the peripheral zone generally stained more intensely than those in the distal zone. Subjacent to the distal zone was a rib meristem zone with cells arranged in longitudinal chains. Many cells in the rib meristem zone contained tannin vacuoles (these appear black in Fig. 5.2). Superimposed on the cytohistological zonation described was a cell net pattern. In all species examined, except *Pinus pinea*, the cells in the apex appeared to converge on a cell or small group of cells at the most apical, axial portion of the apex (Fig. 5.2, A-C). In *Pinus pinea* proceeding up from the rib meristem zone, the cell files continued in straight lines or diverged on an initial group of cells. Each of these cell files appeared to originate from its own initial (Fig. 5.2, D).

There often is considerable variation in cytological zonation of apical meristems in different branches of the same tree. In *Pinus strobus*, for example, cytological zonation was present in apices of shoots located in upper parts of the live crown but not in shoots lower down in the crown

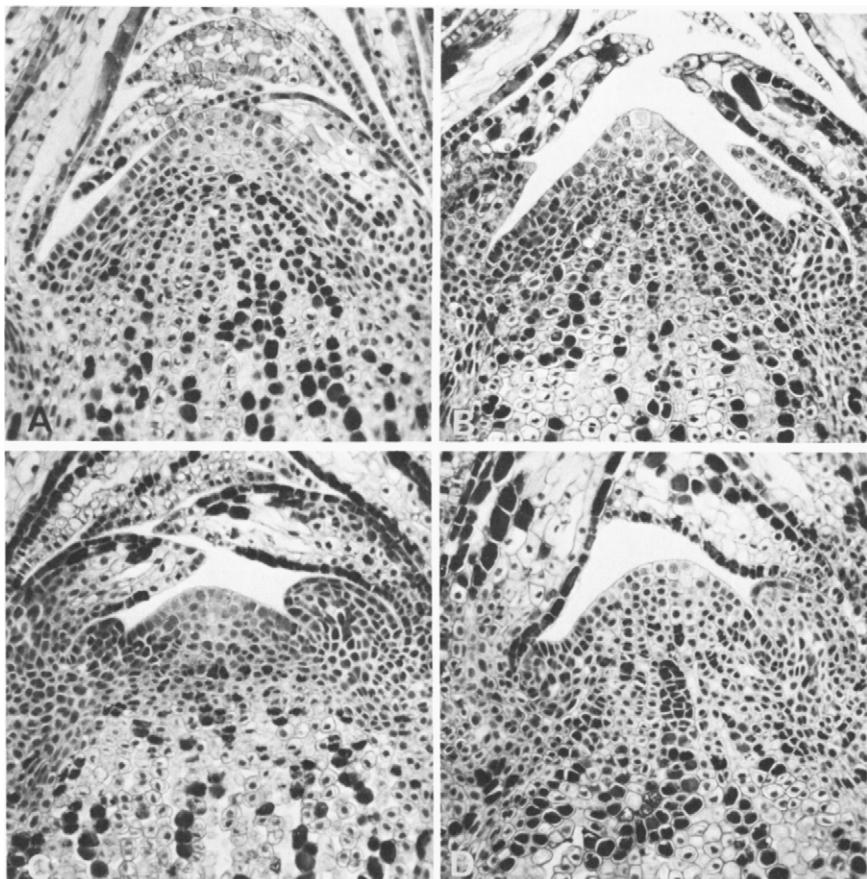


FIG. 5.2. Variations in shapes and cell net patterns in shoot apices among four species of pines: (A) *Pinus taiwanensis*; (B) *P. radiata*; (C) *P. rigida*; (D) *P. pinea*. [From Tepper (1966).]

(Owston, 1969). Zonation of apical meristems may also change during ontogeny of the shoot apex. In *Pinus ponderosa*, for example, the apex of the embryo was initially zonate, changed during its first 12 days of development into one that was not zonate, and thereafter gradually returned to a zonate condition (Tepper, 1964). In *P. ponderosa* seedlings a zonal pattern similar to that of mature trees was first observed 64 days after germination. For additional details of structure and zonation of apical meristems of angiosperms and gymnosperms the reader is referred to Foster (1941), Popham (1951, 1960), M. A. Johnson (1951), Gifford (1954), Clowes (1961), Newman (1961), Romberger (1963), and Tepper (1963b, 1964, 1966).

Growth of Buds

A mature bud is a telescoped shoot, or part of a shoot, bearing at the tip the apical meristem from which it originated. For convenience the initiation of buds will be considered the initial phase of shoot growth.

Most buds are initiated in leaf axils. Axillary buds arise in relatively superficial tissues. Some axillary buds remain dormant and others develop into shoots. In pines, foliage primordia are initiated by axillary buds which develop into dwarf shoots, rather than by the apical meristem of the main axis (Romberger, 1963).

Bud initiation commonly involves anticlinal divisions in surface layers of a young axis, as well as divisions, which often are primarily periclinal, in deeper layers. As a result of such growth in surface area and volume, a bud protrusion forms. The apical meristem of the bud, which is organized during early cell division produces leaf primordia before internodes develop (Esau, 1960).

ORIGIN OF LEAVES AND INTERNODES

Leaf primordia appear in acropetal succession at the base of the apical dome (Fig. 5.3). The leaves begin to form as a result of periclinal divisions in

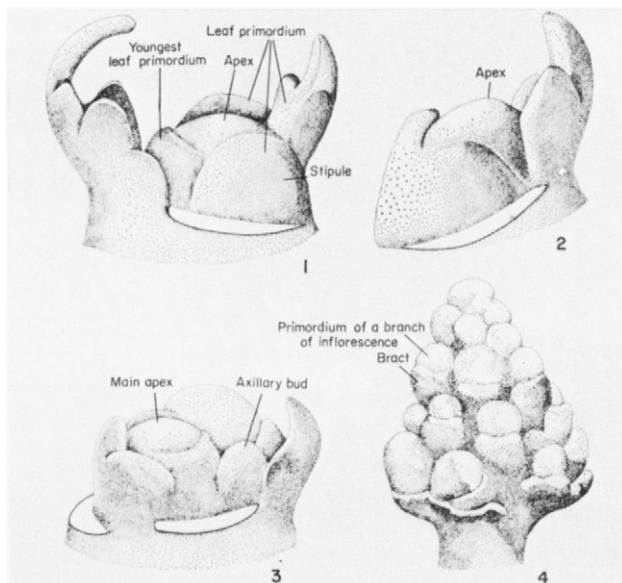


FIG. 5.3. Shoot apices of *Vitis vinifera*. 1. Vegetative shoot apex. 2. Asymmetrical vegetative shoot apex. 3. Apex in which the main apex and an axillary bud are present. 4. Primordial inflorescence. [From Fahn (1967).]

subsurface cells of the apical meristems. Such divisions cause the formation of a prominence, the leaf base or buttress, on the side of the shoot apex. The leaf subsequently grows upward from the buttress. As the bulge forms, the cells of the surface layer undergo anticlinal divisions. Both the tunica and corpus variously participate in forming leaf primordia in angiosperms. The extent to which each is involved depends on the depth at which the initiating cell divisions occur.

When leaves are first formed they occur close together and nodes and internodes are absent. Subsequently, as meristematic activity occurs between the leaf insertions, internodes become recognizable (Esau, 1960). The growth of an internode includes both cell division and cell enlargement. Internodal elongation, an example of intercalary growth, often varies in degree and timing within the internode. For example, during the earliest phases of elongation of *Syringa vulgaris* shoots, growth took place throughout the very short internode, but subsequently it became localized in the upper part as a wave of maturation spread upward from the base (Wetmore and Garrison, 1959).

In pines the winter bud is a compound structure with unextended internodes that contain all the primordia of the subsequent season's shoot. Such a bud is formed by activity of the shoot apex to produce, in order, sterile bracts which do not subtend buds (Fig. 5.4 A), cataphylls bearing dwarf shoots or needle primordia (Fig. 5.4 B), lateral buds (Fig. 5.4 C), and finally, the terminal bud scales which enclose the bud (Sacher, 1954).

Inside the bud procambial strands develop acropetally to each leaf primordium. These strands become vascular traces as primary phloem and primary xylem are added to the procambial surfaces. Phloem elements usually differentiate acropetally from connections with phloem of older leaf traces. Xylem differentiation then follows, beginning near the base of the needle primordium and moving acropetally into the needle as well as basipetally to join with primary xylem of older traces (Larson, 1969).

Morphogenetic development of axillary buds of angiosperms often requires a long time. In *Magnolia stellata*, for example, 12 to 17 months elapsed from the time an axillary bud originated until it was mature (Garrison, 1955). In some plants axillary buds are initiated near the apical meristem of the parent shoot, whereas in others they form much later and at a considerable distance from the apical meristem.

The sequential patterns of tissue development in vegetative buds appear to be very similar in many species. For example, Garrison (1955) found some quantitative but no real qualitative differences in bud development in ten structurally different angiosperm species from widely separated families. Nevertheless, the timing of development of axillary buds during the first season was extremely variable among species.

In some species all the leaves of buds which open in the spring are formed

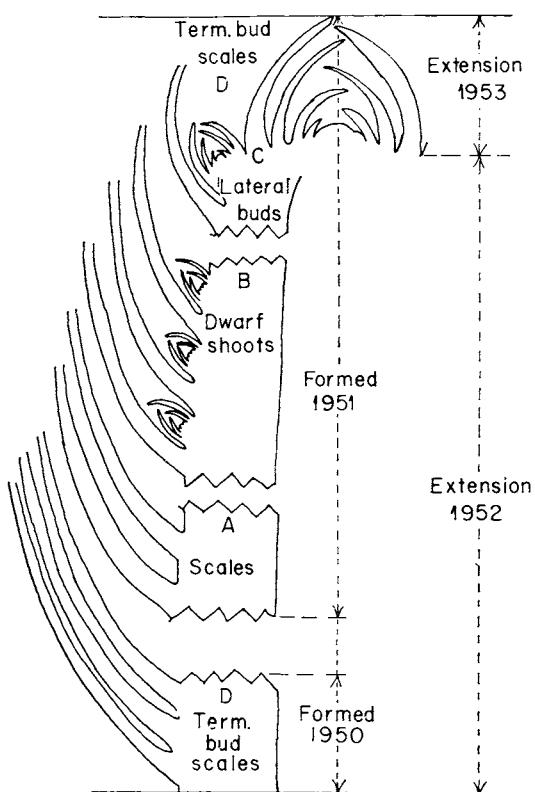


FIG. 5.4. Diagram of winter bud of pine showing structures present and the order of their formation. [From Sacher (1954).]

by the middle of the summer of the previous year. In others, leaves do not develop until shortly before bud opening. In still others, some leaves develop after bud opening. For example, after the first growing season, secondary buds of *Liriodendron*, *Juglans*, *Syringa*, *Betula*, and *Euptelia* were only bud primordia or buds with one to three leaves. Those of *Akebia* and *Schisandra* varied considerably in size and ranged from bud primordia to buds with many leaves (Garrison, 1949a,b, 1955). In *Acer pseudoplatanus* and *Sambucus nigra*, the bud primordia and leaves were formed during the same growing season (White, 1955). In *Pinus lambertiana* all foliar organs of axillary short shoots developed during the first season (Sacher, 1955). Similarly the over-wintering bud of *Pinus strobus* contained all of the primordia for the next season's growth (Owston, 1969). This developmental pattern differed considerably from that in *Pinus resinosa* grown in Ontario. In the latter species new terminal buds began forming in July. As cataphylls developed, small

mounds of tissue formed above them to become axillary dwarf shoot primordia. Their growth was slow during late summer and autumn, and no leaf primordia were initiated until spring (Duff and Nolan, 1958). The number of leaves and primordia in dormant buds also may vary greatly among species. In *Betula papyrifera* and *Juglans cinerea* mature buds consisted of a short axis bearing three cataphylls and six or seven young leaves (Garrison, 1949b). In *Akebia quinata*, however, a mature axillary bud had 18 to 25 leaves, of which six to eight of the youngest were foliage primordia and the others were variously modified cataphylls (Garrison, 1955).

The general features of development of axillary buds are shown in Fig. 5.5 a-g for *Syringa vulgaris* growing in Massachusetts. In this species some 13 to 14 months elapsed from the time axillary buds were initiated until they matured. A bud primordium was formed in one season whereas cataphylls and foliage leaves were produced in the next season (Garrison, 1949a). After the bud primordium was formed in late spring or early summer, there was little activity for several months. By October the bud primordia were small mounds of meristematic cells and leaf primordia were not yet



FIG. 5.5a. Development of axillary buds in *Syringa vulgaris*. Terminal bud in October. [From Garrison (1949a).]

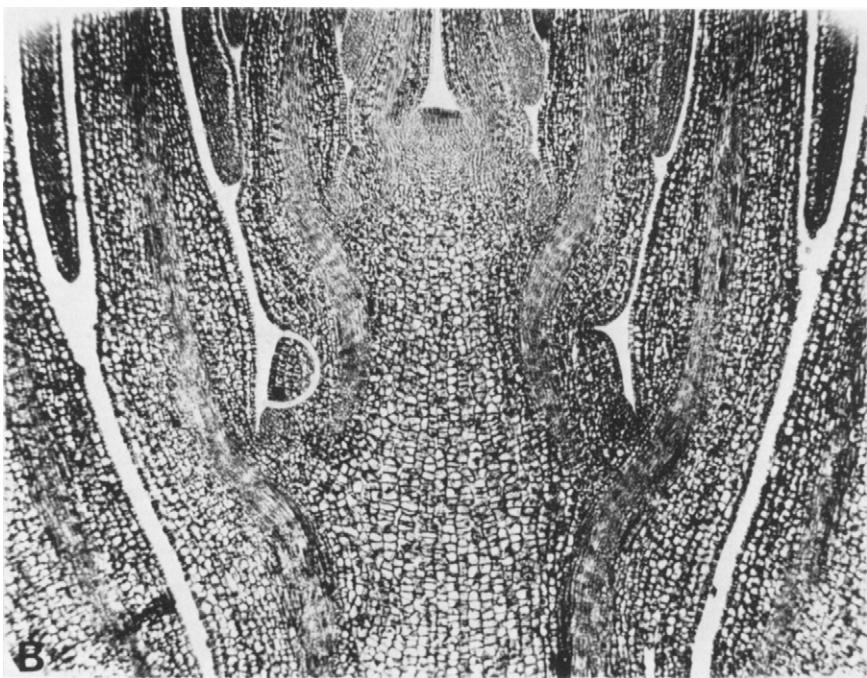


FIG. 5.5b. Development of axillary buds in *Syringa vulgaris*. Enlarged bud apex to show bud primordia in the axils of leaf primordia. Bud primordium at left encircled. [From Garrison (1949a).]

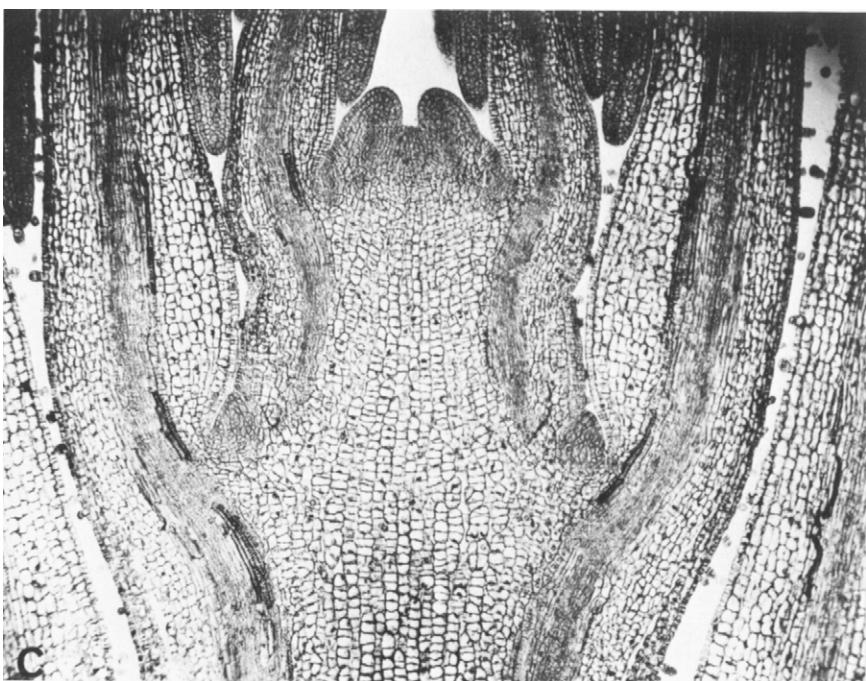


FIG. 5.5c. Development of axillary buds in *Syringa vulgaris*. Axillary bud primordia in mid-March. [From Garrison (1949a).]

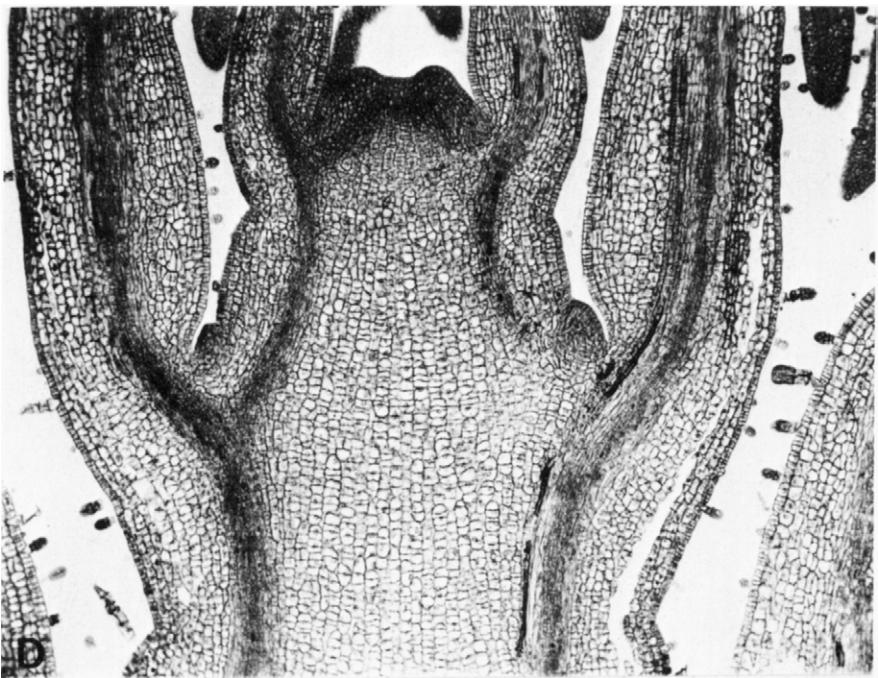


FIG. 5.5d. Development of axillary buds in *Syringa vulgaris*. Axillary bud primordia in mid-April. [From Garrison (1949a).]

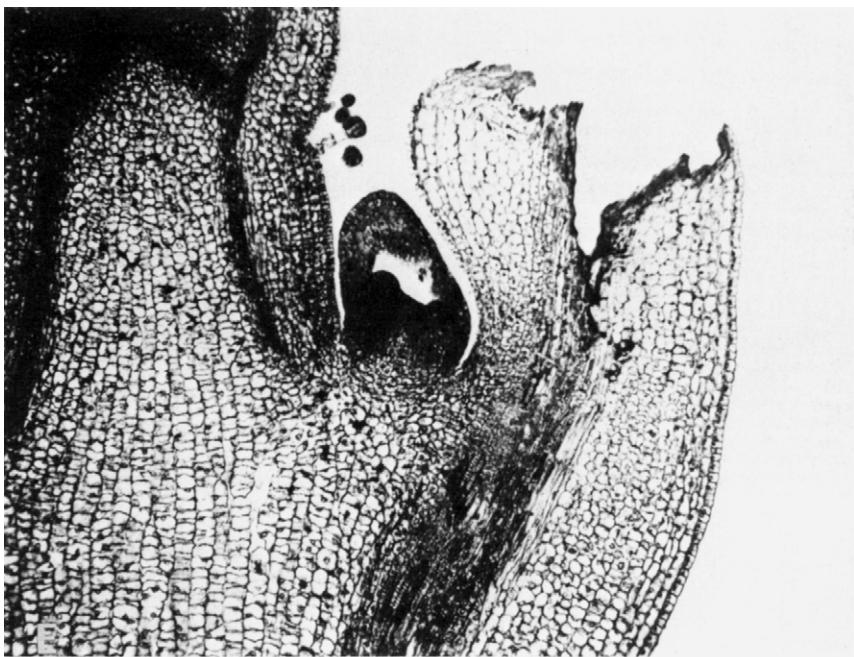


FIG. 5.5e. Development of axillary buds in *Syringa vulgaris*. Axillary bud showing the second pair of leaf primordia in late April. [From Garrison (1949a).]

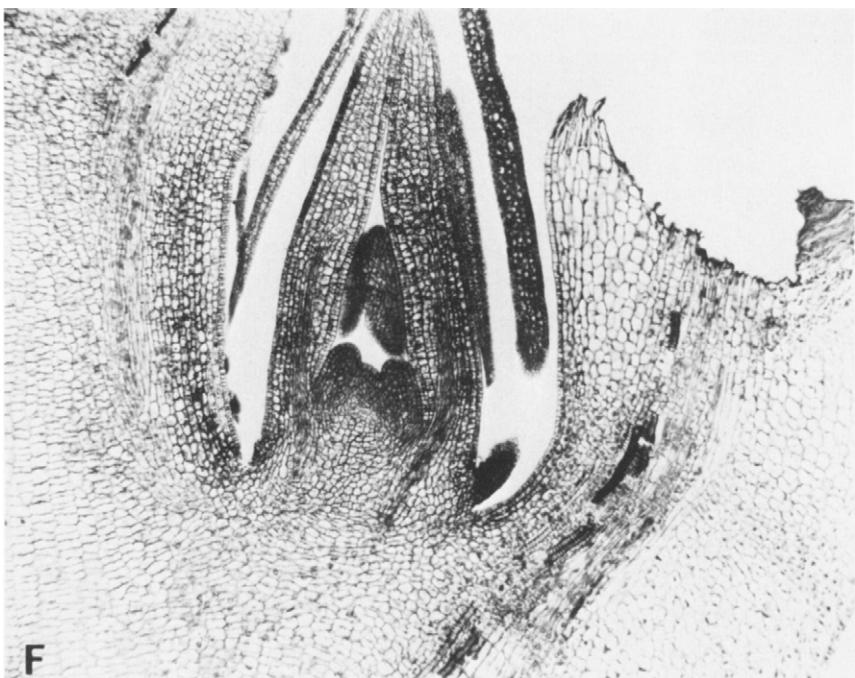


FIG. 5.5f. Development of axillary buds in *Syringa vulgaris*. Axillary bud showing the second and fourth pair of leaf primordia in mid-May. [From Garrison (1949a).]

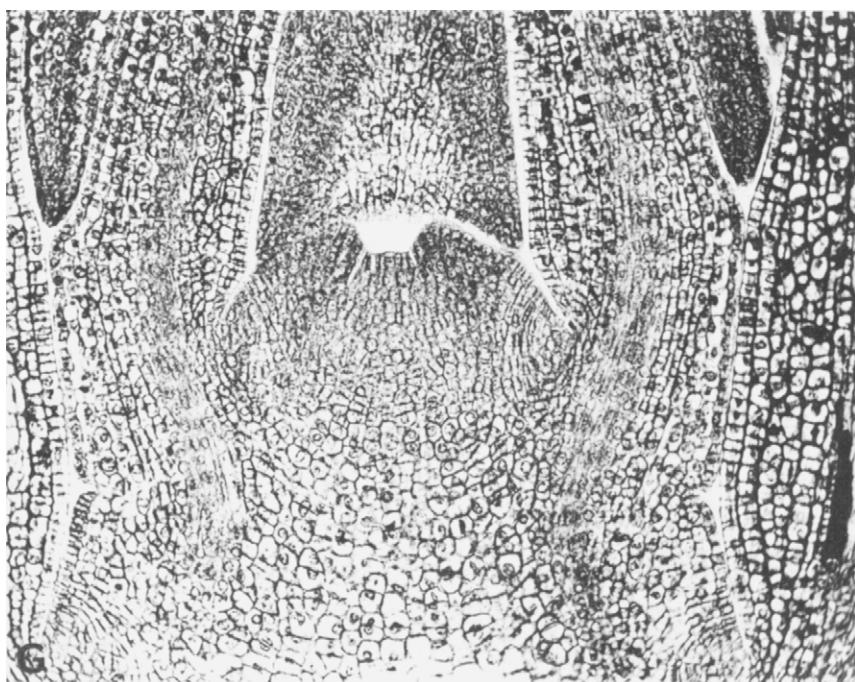


FIG. 5.5g. Development of axillary buds in *Syringa vulgaris*. Apical region of a bud showing a nest of meristematic cells located in the axil of a leaf primordium. [From Garrison (1949a).]

formed. The bud stayed dormant through the winter but by mid- or late-March scattered cell divisions could be seen in it. Within the next 2 weeks it grew considerably, and by early April the first pair of leaf primordia were apparent. During April the main axis of the primary bud elongated and the secondary bud with one pair of leaf primordia enlarged. Additional leaf primordia were produced during the next few months, with the first five to nine pairs destined to become cataphylls or bud scales, and those subsequently produced developing into foliage leaves. By August or September the formation of leaf primordia ceased. The mature bud had five to nine pairs of cataphylls and six to eight pairs of leaf primordia.

Characteristics and Classification of Buds

Usually buds are classified as to location, contents, or activity. They may be called terminal, lateral, axillary, collateral, superposed adventitious, vegetative, flower, or mixed buds. Any of these types may be further classified as active or dormant. A vegetative bud contains a small mass of meristematic tissue, nodes, internodes, and small rudimentary leaves with buds in their axils, all usually enclosed in bud scales. The largest and oldest leaf primordia are located at the bud base and the smaller rudimentary leaves occur toward the growing point. Flower buds contain embryonic flowers and most also contain rudimentary leaves. Mixed buds contain both flowers and leaves. One type which terminates in a flower cluster is typical of *Malus*, *Pyrus*, *Rubus*, and *Vitis*. Another type of mixed bud which bears flowers or flower clusters in leaf axils is found in *Diospyros*, *Persea*, *Quercus*, and *Fagus*.

TERMINAL BUDS

Many woody plants are monopodial and have buds at the ends of shoots which limit their seasonal elongation. During the dormant season terminal buds may or may not contain all the leaf primordia and unextended internodes of the following season's shoot. This will be discussed later.

In sympodial species, which do not form true terminal buds at the ends of shoots, the succulent leading shoot abscises and the uppermost lateral bud becomes a false terminal bud from which further shoot elongation occurs. In *Citrus*, for example, shoot expansion occurs in recurrent flushes from false terminal buds. The ends of shoots of most gymnosperms with scale leaves have buds which are not considered to be true terminal buds (de Laubenfels, 1953). Such gymnosperm buds do not have morphologically distinct scales and they do not contain a fully preformed shoot. Growth nevertheless is arrested during the winter.

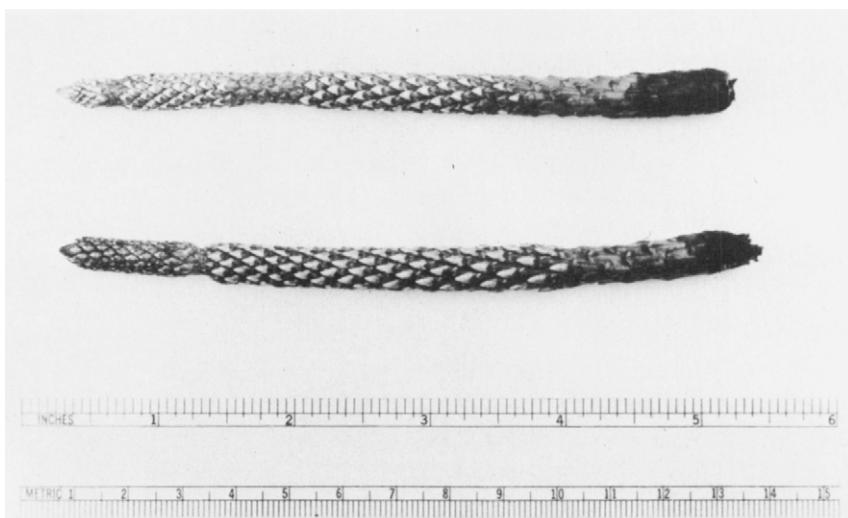


FIG. 5.6. Elongating winter buds of *Pinus rigida*. The bud scales were removed to show multinodal character and dwarf shoot primordia. [From Tepper (1963a).]

UNINODAL AND MULTINODAL BUDS

A distinction should be made between vegetative buds which contain only one expandable node and those which contain more than one. Buds of many pines (e.g., *Pinus resinosa*) are uninodal and contain only one series each of sterile and fertile scales. In contrast, winter buds of a number of other pines (e.g., *Pinus rigida*) are multinodal and contain, in addition to basal sterile scales, one or more series of sterile scales alternating with series of fertile scales along the bud axis (Fig. 5.6). The multinodal character of a simple bud often is not evident until the bud expands. Some multinodal buds, however, can be recognized by their externally visible whorls of branch buds (Fig. 5.7).

When a multinodal bud expands into a shoot the coordinated elongation of its internodes varies in time and rate as shown by Tepper (1963a) for terminal leaders of *Pinus rigida* (Fig. 5.8). The basal internode generally was the first to expand, and accounted for most of the increase in shoot length during the first few weeks of growth. In early stages of shoot growth, the second internode of a multinodal bud grew more slowly than the basal internode. Later in the growing season, however, expansion of the second internode contributed increasingly more to total leader elongation. The third internode did not begin to expand until the second one had expanded appreciably. Growth of the third internode was slow at first and increased gradually. Maximum growth rate of the basal internode was achieved on May 7, the second internode on May 21, and the third internode on May 28. The



FIG. 5.7. Variations in winter buds of *Pinus rigida*. From left to right a simple, a binodal, and a trinodal bud. [From Tepper (1963a).]

growth curve of each internode was sigmoid and the growth of the separate internodes synchronized so that the curve of total shoot elongation also was sigmoid.

DORMANT BUDS

Only some of the winter buds of a tree produce shoots whereas the rest remain dormant, sometimes throughout the life of the tree. Dormant buds often persist in large numbers. For example, about two-thirds of the lateral buds which formed on apical shoots of young *Quercus rubra* trees remained dormant and failed to produce branches in the subsequent year (Ward, 1964). MacDaniels (1953) found an abundance of persistent dormant buds on young and mature apple trees.

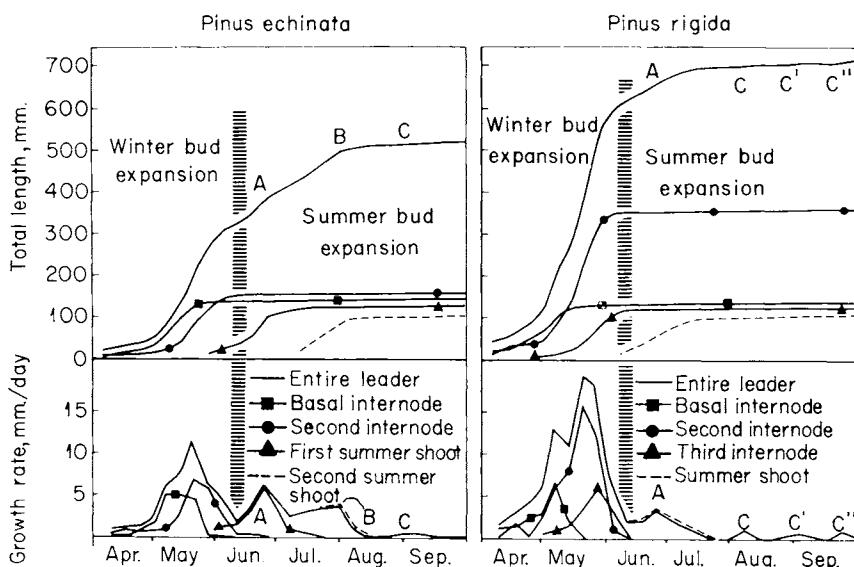


FIG. 5.8. Total length and growth rate of the terminal leader and internodes which comprise the leaders of *Pinus echinata* and *P. rigida* seedlings. The letters represent growth peaks of the first summer shoot (A), second summer shoot (B), and winter bud formation (C, C', C''). [From Tepper (1963a).]

Old dormant buds may eventually develop into shoots, or they may finally die. Often they enable a tree to survive as they are stimulated to grow by fire, injury, or removal of actively growing buds above them. If young tender leaves of new shoots are killed by early spring frosts, new ones often develop from dormant buds. However, whether dormant buds become active depends on the degree of defoliation. In *Populus tremuloides*, for example, refoliation occurred only in trees in which defoliation was essentially complete (Rose, 1958).

There has not been complete agreement about the morphology of dormant buds. Most investigators agree that dormant buds, originally located in leaf axils of twigs, are thereafter connected to the pith by a bud trace. They remain undeveloped under the bark and grow only enough each year for the tip to keep pace with cambial growth. Hence, a dormant bud really consists of an encased, modified branch which may later be stimulated to sprout. Questions have sometimes been raised about whether survival of dormant buds requires their connection to the pith by a bud strand or stele. For example, Strasburger *et al.* (1912) stated that dormant buds sometimes continued to grow after they lost their connection with the woody parts of the parent stem. Nevertheless, most modern workers identify dormant buds by their bud trace to the pith.

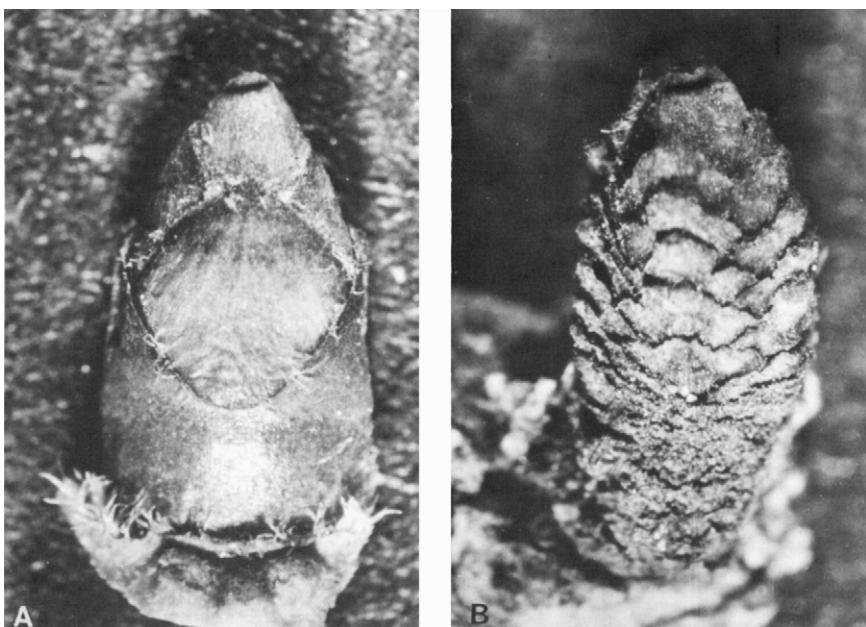


FIG. 5.9. Variations in structure of 1-year-old axillary bud (A) and 15-year-old dormant bud (B) of *Acer saccharum*. (U.S. Forest Service photo.)

Dormant buds often differ appreciably in appearance from buds destined to produce shoots if no injury occurs (Fig. 5.9). In *Acer saccharum* new dormant buds were nearly spherical in shape and only a tenth to a fifth as large as the conical axillary buds which formed on the same shoot (Church and Godman, 1966). As dormant buds aged, they became more nearly conical and developed concentric rings of presumably annual bud scales (Fig. 5.10).

Dormant bud traces sometimes cause defects in sawn lumber (Jane, 1956). On a radial surface dormant buds are cut longitudinally and appear as "spike knots," whereas in a tangential surface they show as small "pin knots." Surfaces of boards of *Taxus* and *Ulmus* often show numerous small knots close together. Here the saw probably passed through a burl which had numerous dormant buds, or small shoots developed from them, on the surface (Jane, 1956).

Branching of dormant buds occurs rather commonly (Hahne, 1926; Kormanik and Brown, 1964). Chandler (1947) presented evidence that secondary dormant trace buds originated in the axils of bud scales. A primary dormant bud can become the ancestor of numerous secondary buds, with its trace branching and extending to them (Aaron, 1956). In many cases dormant buds at the stem base of certain pines not only keep pace with



FIG. 5.10. Old, dormant bud of *Acer saccharum* showing concentric rings of scales. (U.S. Forest Service photo.)

diameter growth of the parent axis bud, but they form laterals which again branch, just keeping up with diameter growth. This produces the effect of a tree within a tree (Fig. 5.11).

In *Liquidambar styraciflua* dormant buds showed patterns of both multiple and dichotomous branching. In the latter case, forking resulted in abortion of the apical meristem of the dormant bud trace. This may have been due to insect or frost damage to the bud in the periderm, stimulating release of 2 scale buds (Kormanik and Brown, 1964). Liashenko (1958) found branching of dormant buds in several species of shrubs including *Syringa vulgaris*,

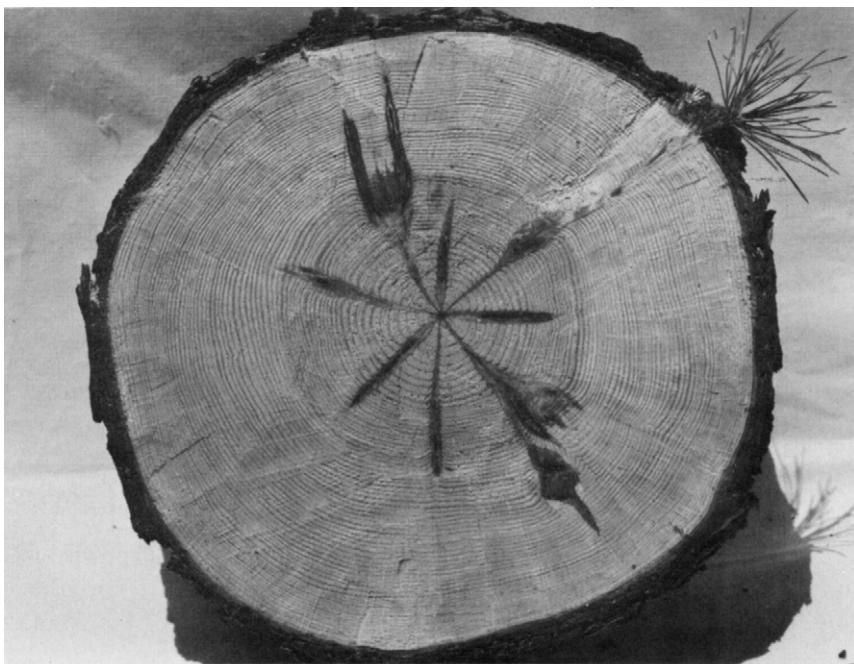


FIG. 5.11. Transection of stem of *Pinus echinata* showing short shoots and branching dormant buds. [From S. Little and Somes (1956).]

Lonicera tartarica, *Philadelphus coronarius*, and *Crataegus rotundifolia*. The primary buds often had daughter buds in axils of outer scale leaves. If the primary bud expanded annually while growth of secondary buds was inhibited for several years, both types were served by a single bud trace. However, if secondary buds grew in the second year, they became independent, moved away from the primary bud, and had traces which branched from the trace of the mother bud.

ADVENTITIOUS BUDS

Buds which form rather irregularly on older portions of a plant and not at the stem tip or in the leaf axil are called adventitious buds. These form on parts of the root or stem which have no connection to apical meristems. They vary as to origin and may spring from deep-seated tissues or peripheral ones. For example, adventitious buds may arise from callus tissue around wounds, in the cambium, or from mature tissues in the endodermis or pericyclic region (MacDaniels, 1953). As mentioned earlier, the important distinction

between adventitious and dormant buds is the lack of a bud trace all the way to the pith in the former.

Many adventitious buds arise from mature tissues near or adjacent to a wound. They usually produce a shoot without going through a dormant period, with their activity apparently regulated by hormone balance (Eliasson, 1961). The cambium of stumps of *Populus*, *Aesculus*, *Fagus*, and *Juglans*, often proliferates to produce callus in which bud primordia originate and develop into adventitious shoots. Adventitious buds also occur commonly on roots of many species including *Robinia pseudoacacia*, *Ailanthus altissima*, and *Rhus* (Romberger, 1963), but not on their boles or branches. R. T. Ward (1961) described regeneration of *Fagus grandifolia* trees by root sprouts originating from adventitious buds. Vasilevskaya and Kondratjeva (1955) studied adventitious buds in 34 species of woody plants which are reported to sucker. Adventitious buds were found on all but eight of these species, and they were always located in areas where dieback of lateral roots occurred. Buds originated variously from the cambium plus phloem parenchyma, from phloem parenchyma alone, or from the phellogen. In the dioecious species, *Populus pruinosa* and *Diospyros virginiana*, roots of staminate trees formed more buds than those of pistillate trees.

ORIGIN OF SHOOTS FROM DORMANT OR ADVENTITIOUS BUDS

Whether sprouts originate from dormant or adventitious buds is a point of confusion. E. L. Stone and Stone (1943a) emphasized that the term "adventitious" has been imprecisely used in regard to the origin of sprouts. Some of the difficulty in terminology occurs because, when once formed, true adventitious buds may also remain dormant. Furthermore, adventitious buds may be mistaken for dormant buds when the bud traces begin near but not at the pith. Recognizing such difficulties, Aaron (1956) referred to true dormant buds as "trace buds." Unfortunately, this useful term, which specifically refers to the trace to the pith which identifies a true dormant bud, has not received wide acceptance. A few examples of the origin of common types of sprouts will be given.

Many of the new branches following pruning arise from dormant rather than adventitious buds. Stump sprouts originating from root collars and the lower part of the stem usually arise from previously existing dormant buds rather than adventitious ones. In contrast, root sprouts ("root suckers") arise from adventitious buds. MacDaniels (1953) found that true adventitious buds occurred freely on 1-year-old apple seedlings, but only rarely on stems. True adventitious buds were not observed on nursery trees and older trees. When apple trees were heavily pruned, sucker shoots developed first from dormant buds, most of which were not related to other buds or scars. Later

sucker shoots grew from dormant buds adjacent to scars of shoots which had been removed in pruning.

Stem sprouts of multinodal pines such as *Pinus rigida* and *P. palustris* arise from small buds at the intermediate nodes of stems, as well as from small lateral buds at the winter nodes which may remain dormant for a few years. Usually these buds become very short branches with few leaf fascicles but they can form normal long branches following injury to the tree. Stem sprouts of other multinodal pines including *Pinus rigida* var. *serotina*, *P. echinata*, *P. leiophylla*, *P. pungens*, and *P. sabiniana*, probably have a similar origin (E. L. Stone and Stone, 1943b). In *Abies balsamea* and *A. concolor* meristems in the axils of many needles persist as very small dormant buds. Some elongate within a few years whereas others remain dormant for several years after leaf fall. Nevertheless, they may elongate thereafter when stimulated by environmental changes (E. L. Stone, 1953b).

Sprouting of a few species of gymnosperms following fire or mutilation of seedlings often has been attributed to adventitious buds (Mattoon, 1908). However, E. L. Stone, Jr. and Stone (1954) concluded that several such reports were erroneous. They found that a variety of species of *Pinus* had small buds in the axils of primary needles just above the cotyledons. At that location the needles were closely spaced, and the buds often appeared clustered after the stem thickened. These buds often produced basal or root collar sprouts. When a stem was sectioned the bud steles were traced back to an origin in the first-year stem. Hence, the sprouts did not arise from true adventitious buds. Distortion of the lower stem may result in occurrence of buds near or below lateral shoots and lead to the assumption that the buds originated in root tissues. Phares and Crosby (1962) found the reaction of basal buds of *Pinus echinata* following a fire to be related to tree size, with more basal sprouts produced on the taller trees. They stated that the larger trees had a greater basal diameter and more basal buds, hence more sprouts. Furthermore, the tallest sprouts occurred on the largest trees, possibly because their extensive root systems could supply large amounts of water and minerals to the developing sprouts. According to Little and Somes (1960), *Pinus taeda* trees do not sprout after fire because their buds are situated above ground and are easily killed. However, *Pinus taeda* trees up to 7 or 8 years of age often sprout after cutting. The sprouts originate from buds or meristems in axils of primary needles, needle fascicles, small branches which originate at the axillary sites, and occasionally, nodal buds (Little and Somes, 1960).

Shoot Growth Characteristics

Seasonal patterns of shoot growth vary greatly among species. Whereas many species of woody plants of the Temperate Zone show only a single

period of annual shoot elongation, which is completed rather early in the frost-free season, other species continue to expand their shoots for a longer time. When only one short period of seasonal shoot growth occurs it usually involves expansion of both leaves and internodes contained in the winter bud, or in the case of short shoots, of leaf expansion and virtually no inter-nodal extension.

Shoots of some species elongate for a long time as a result of continuous production and expansion of new leaf primordia during the growing season. Other species show recurrent flushing of shoots. This involves formation and expansion of current-year buds after the initial growth flush from the winter bud has been completed. Some species produce occasional and more-or-less irregular late-season flushes of growth from opening of current year buds in response to unusually favorable environmental conditions. Such late-season growth flushes are considered abnormal because they occur less frequently than single flushes.

Shoots and branches may be variously classified on the basis of their location in the plant body, development, or the type of bud from which they are derived. On the basis of location alone, shoots often are classed as terminal leaders, laterals, or basal shoots. Coppice shoots are sprouts which arise near the base of a tree from dormant buds. Short shoots of limited growth with very short internodes are called spur shoots. Root suckers are shoots which arise from the roots. Among other important shoot types are determinate and indeterminate shoots, preformed and heterophyllous shoots, recurrently-flushing shoots, long and short shoots, epicormic shoots and various abnormal late-season shoots such as lammas shoots, proleptic shoots, sylleptic shoots, and long buds. Some of the more important types of shoots will be discussed briefly.

DETERMINATE AND INDETERMINATE SHOOTS

As mentioned earlier, shoot growth in many species such as some pines, spruces, oaks, and hickories results from opening and expansion of the contents of terminal buds on the main axis and branches. After the terminal shoot is fully developed, a period of inactivity ensues and further shoot elongation depends on the formation of a new terminal bud and its subsequent expansion. In these monopodial, determinate species, only one bud may form on an axis and open per year, or there may be two or more periods of elongation from opening of the winter bud, and from subsequent opening of additional buds formed on the same axis during the current year. When several annual flushes of shoot growth occur on the same axis, as in multi-nodal pines, each flush of shoot growth is followed by an intervening period of development of a new bud. Occasionally late-season shoots, which develop

from opening of current-year buds, may not have sufficient time to harden and are killed by frost. When this occurs further axial extension is continued from expansion of a lateral bud.

In many sympodial or indeterminate broadleaved trees, such as *Ulmus* and *Tilia*, the stem does not develop from opening and expansion of true terminal buds but rather is made up of successive secondary axes. Indeterminate or sympodial growth may result when a reproductive structure terminates a branch or when a shoot tip aborts. Shoots of indeterminate species usually continue to expand during the summer without the obvious period of rest which characterizes determinate species. In indeterminate species the crown usually is unsymmetrical, and the main stem often is lost in the many large branches of the crown.

Abortion of Shoot Tips The shoot tips of indeterminate species usually abort. The subtending bud, which sometimes is mistaken for a true terminal bud, can be identified as a lateral bud by the scar resulting from abortion of the shoot tip. Shoot tip abortion is a natural characteristic of a wide variety of Temperate Zone woody plants and some tropical ones. According to Romberger (1963) and Millington (1963), abortion of shoot tips has been reported in *Ailanthus*, *Betula*, *Carpinus*, *Castanea*, *Catalpa*, *Celtis*, *Cercidiphyllum*, *Corylus*, *Diospyros*, *Gleditsia*, *Gymnocladus*, *Platanus*, *Rhamnus*, *Robinia*, *Salix*, *Staphylea*, *Syringa*, *Tilia*, and *Ulmus*, among other genera.

Loss of shoot tips occurs in a rather well-defined pattern. First the young leaves stop growing and new primordia fail to form. The shoot then yellows and abscises at the base of an internode. After the shoot drops off, a protective layer forms over the area of severance. When a shoot tip aborts the immediately subjacent tissues including leaves, axillary buds, and internodes are growing normally. Stages in abortion of shoot tips are shown in Figs. 5.12 to 5.15.

The physiology of apical abortion is complicated and not well understood. The time of abortion varies with age and among shoots in the same plant, with the most vigorous shoots aborting last. Plant vigor delays abortion as shown by inverse correlation between growth rate and time of abortion, by accelerated abortion in plants with pot-bound roots, and by delay of abortion in plants which have been heavily fertilized. Garrison and Wetmore (1961) concluded, however, that mineral deficiency was not a critical factor in shoot abortion since shoot tips of *Syringa* that were cultured on a medium which sustained growth for long periods eventually aborted. The evidence does not point to water stress as causal because shoot tips often abscise when they are highly hydrated (Romberger, 1963). Millington (1963) could find no evidence of vascular blocking prior to tip abortion and observed no acceleration of abortion in flaccid shoots. These observations were

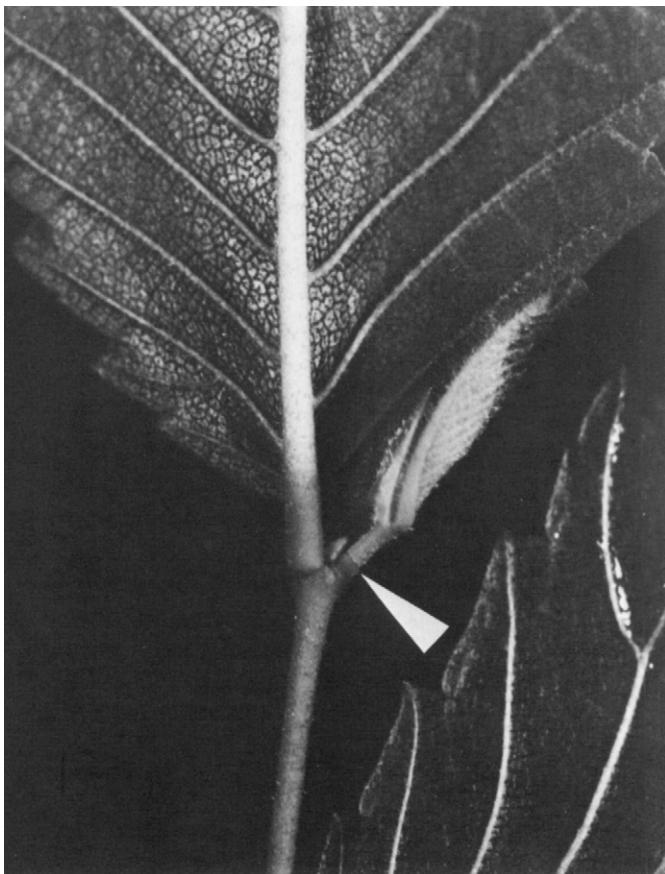


FIG. 5.12. Aborting shoot tip of *Ulmus americana* showing abscission site (arrow). [From Millington (1963).]

substantiated by Garrison and Wetmore (1961) who noted that loss of shoot tips of *Syringa* occurred in a saturated atmosphere.

Photoperiod affects abortion of shoot tips (Nitsch, 1957a,b), with short days accelerating abortion and long days often delaying but not necessarily preventing it. Under 61 short days, 90% of the shoots of young *Ulmus americana* trees aborted, as against 40 to 50% under long days (Millington, 1963). The effect of photoperiod on loss of shoots often is modified by plant age. Abortion of shoots of young trees growing in the same photoperiodic regime with those of older trees may be delayed for several weeks. In *Ulmus americana* shoot tip abortion occurs at the time of fruit drop. This relationship apparently is not a causal one, however, because flowering and

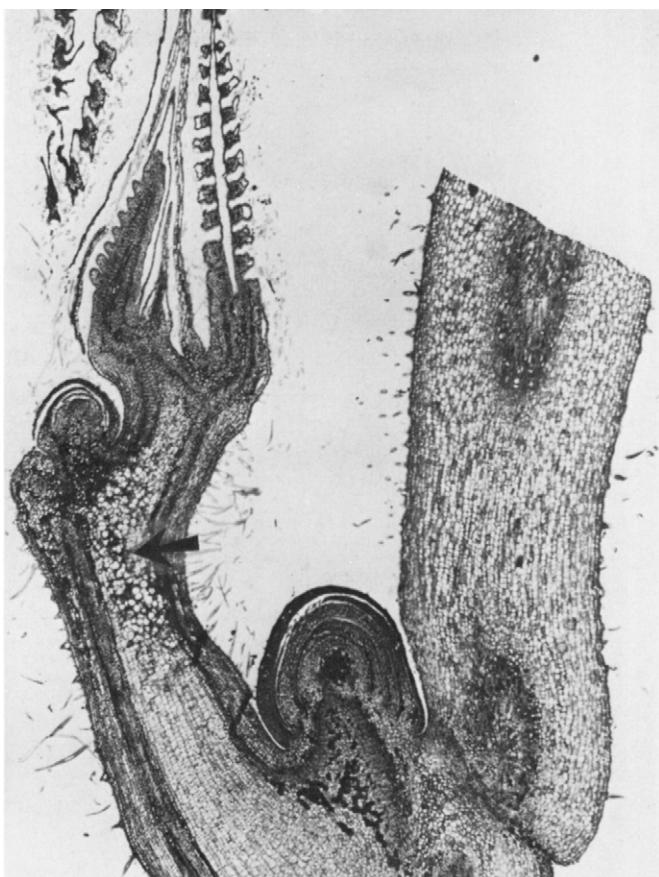


FIG. 5.13. Section through tip of aborting shoot of *Ulmus americana*. There is acropetal progress of necrosis in leaves, necrotic areas in pith and cortex (arrow), and absence of an abscission zone at the future abscission area below the necrotic region. [From Millington (1963).]

nonflowering trees often lose their shoots concurrently. In *Syringa* diffusible auxin was found in opening buds and shoots, but it was absent in tips after abortion started (Garrison and Wetmore, 1961). Despite the correlation between observations of auxin deficiency and loss of shoot tips it was not demonstrated that auxin initiated the aborting process. In vigorous shoots the removal of uppermost axillary buds or of young leaves delays abortion, possibly by reducing competition for growth regulators. Possibly the continued growth of shoot tips depends on a balance of growth factors rather than a threshold level of a single internal growth regulator. More research is needed on the physiology of shoot tip abortion.

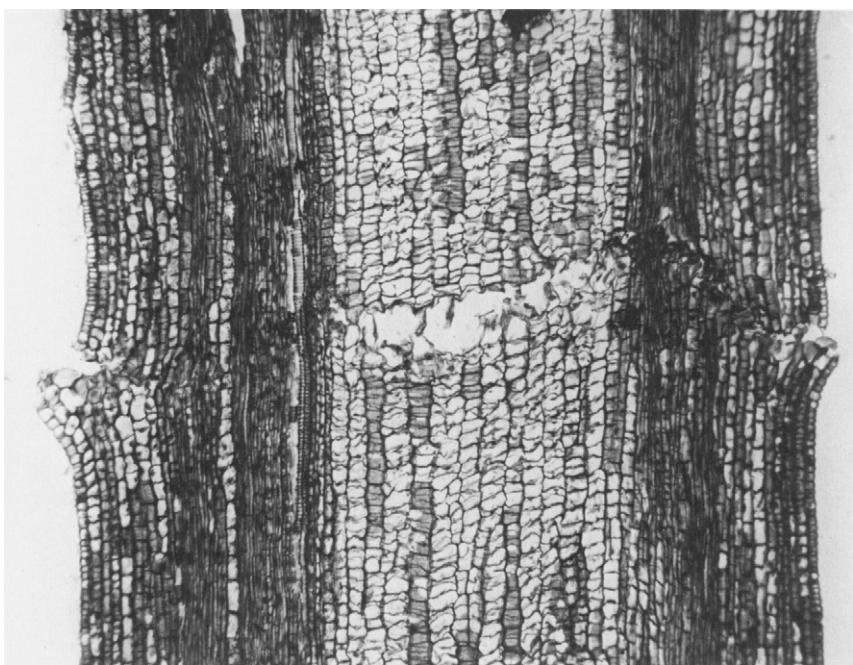


FIG. 5.14. Longitudinal section through abscission zone of aborting shoot tip of *Ulmus americana*. From Millington (1963).

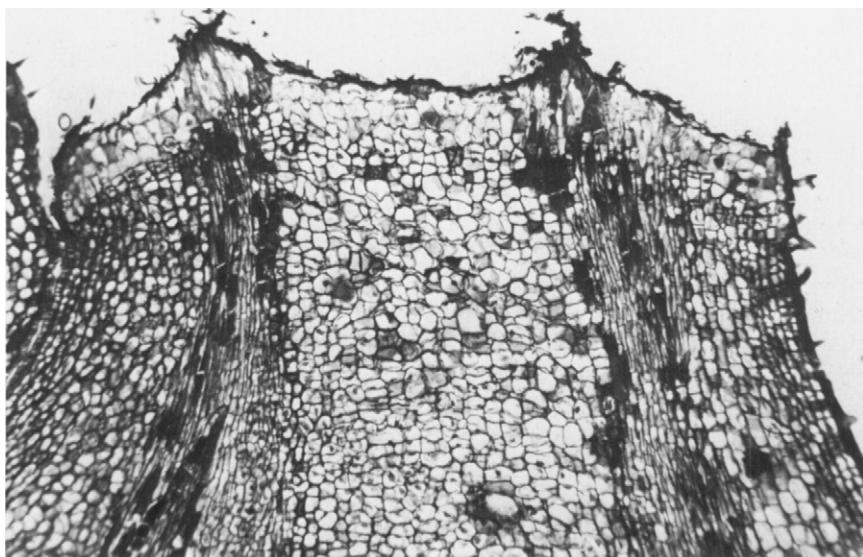


FIG. 5.15. Longitudinal section of stem after abscission of shoot tip of *Ulmus americana* showing early stage in formation of protective layer. [From Millington (1963).]

PREFORMED AND HETEROPHYLLOUS SHOOTS

It is important to distinguish between species whose winter buds contain a telescoped, fully preformed shoot and those which do not. Winter buds of many species contain primordia of all the leaves that will expand during the following growing season. In such species shoot formation involves differentiation in the bud during the first year and extension of the preformed parts into a shoot the second year (Sacher, 1954; Kozlowski, 1964a). Only one type of leaf occurs. Examples are some species of *Pinus*, *Picea*, and *Fagus*. In such species the growth of their predetermined shoots is completed in a relatively short part of the frost-free season. Various stages in the growth of the predetermined shoots of *Abies concolor* in the Sierra Nevada of California are shown in Fig. 5.16. The dormant buds contained fully formed, telescoped, or unextended shoots. These buds, containing 50 to 60 needle primordia, were surrounded by 20 to 30 cataphylls. With the advent of warm weather in April, the shoots expanded vertically as a result of rib meristem activity in the future pith and cortex. The bud scales were soon torn loose as shoots expanded. During early phases of shoot elongation the apical meristem was inactive. After the shoots elongated 2 to 3 cm, however, the apical meristems began to form new scale primordia. Shoot elongation and formation of scale primordia continued until mid-June. Thereafter, and continuing to September, new unelongated axes bearing many needle primordia were formed (Parke, 1959).

In a second group of species, some shoots are not fully preformed or predetermined in the dormant bud and both early and late leaves are produced. For example, several species of *Betula* and *Populus* show heterophyly or leaf dimorphism (Kozlowski and Clausen, 1966; Critchfield, 1960). Leaves at the base of the shoot are typical of the species and frequently differ from distal leaves in venation, size, toothing, thickness, stomatal development, and other characteristics. The basal, or early, leaves emerge at or shortly after bud break. The distal, or late, leaves appear later in the growing season after the first leaves are well expanded. Early leaves sometimes are called spring, vernal, crown, or normal leaves, whereas late leaves may also be called summer, sprout, aestival, or juvenile leaves. Early leaves also occur on short shoots whose internodes fail to elongate appreciably and which lack late leaves. Heterophylloous shoots usually grow for a much longer time than fully preformed shoots. Although heterophyly has very important implications in leaf sampling, it often has been overlooked by proponents of foliar diagnosis.

Shoot development is rather complicated in heterophylloous genera. The late leaves often appear one after another and their continuous development resembles that of leaves of many herbaceous plants (see Chapter 6 of this volume). *Populus* may actually have three types of shoots, (1) those with early leaves only, (2) heterophylloous shoots with both early and late leaves,

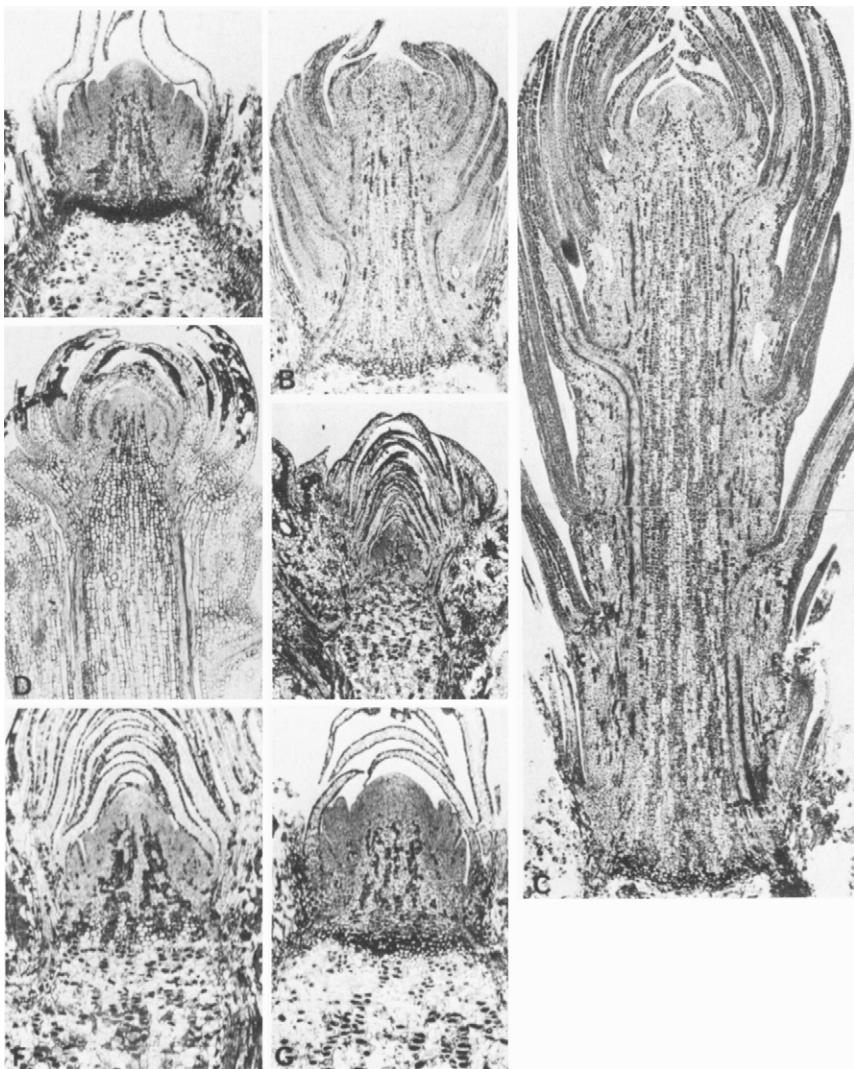


FIG. 5.16. Shoot expansion in *Abies concolor*: (A) Longitudinal section of dormant bud showing numerous needle primordia, $\times 35$; (B) Longitudinal section of bud during early stage of growth phase I. Some internodal elongation has occurred. Vascular differentiation is evident in the basal region of the shoot $\times 40$; (C) Longitudinal section of entire shoot during the middle of growth phase I. Leaf traces and developing vascular tissues are evident $\times 35$; (D) Longitudinal section of upper portion of a shoot during middle of growth phase I. Scale primordia are on flanks of the shoot tip, $\times 35$; (E) Median longitudinal section of developing winter bud during the middle of growth phase II. Shoot tip flanks bear several needle primordia; (F) Longitudinal section of developing winter bud near end of growth phase II. Note the almost differentiated crown and needle primordia on flanks of the compressed shoots. [From Parke (1959).]

and (3) shoots with only late leaves. The ratio of heterophyllous shoots to short shoots determines the branching habit of a tree. In young *Populus trichocarpa* trees the bole and main branches are comprised primarily of heterophyllous shoots but as trees age they tend to produce more short shoots. In old trees the short shoots outnumber heterophyllous shoots and most of the leaves in the crown are early leaves of short shoots (Fig. 5.17).

RECURRENTLY FLUSHING SHOOTS

Shoot growth of some species occurs in several recurrent waves or "flushes" of growth within the same growing season. In many tropical and subtropical pines (e.g., *Pinus caribaea*, *P. merkusii*, *P. insularis*, *P. oocarpa*), and some Temperate Zone pines (e.g., *P. taeda*, *P. elliottii*, *P. palustris*), shoot growth involves the elongation of more than one terminal bud per shoot each year. In these species, while the internodes of the first bud are expanding early in the season, the apical meristem becomes active and initiates primordia which become the leaves and axis of a new terminal bud. The bud forms rapidly and commonly expands to produce a second shoot the same season and often shortly after it was formed. Furthermore, on any one shoot additional buds may subsequently form and expand, all within the same season. The number of successive current-year buds which form and open on the same shoot is variable. As many as seven buds have been observed to elongate in one season on the terminal leader of multinodal pines of the southern United States (Wakeley and Marrero, 1958). Nevertheless most individual shoots do not show more than two or three separate flushes of growth in a year (Fig. 5.18).

In addition to the gymnosperms mentioned, recurrent flushing of shoots is especially common in many tropical and subtropical angiosperms such as *Citrus*, *Theobroma*, *Olea*, *Hevea*, and *Camellia*. Citrus usually produces two major flushes and from one to three lesser ones. Jaffa orange trees in Palestine, for example, produced four flushes. The major one occurred in late winter, others in midsummer and early autumn, and a very minor one in the early winter period during warm years (Cossmann, 1939). Orange shoots in the Mildura (Victoria) area of Australia grow in three rather distinct phases. The early flush begins in late July and the second and third usually in early December and early February. However, the second two flushes are neither as regular nor as pronounced as the first one (Sauer, 1951). The pattern resembles that for orange in California (Webber and Batchelor, 1943). In the Punjab, however, citrus may flush from two to five times in a single growing season (Rhandawa and Dinsa, 1947). Patterns of recurrent flushing of shoots are discussed further in Chapter 6.

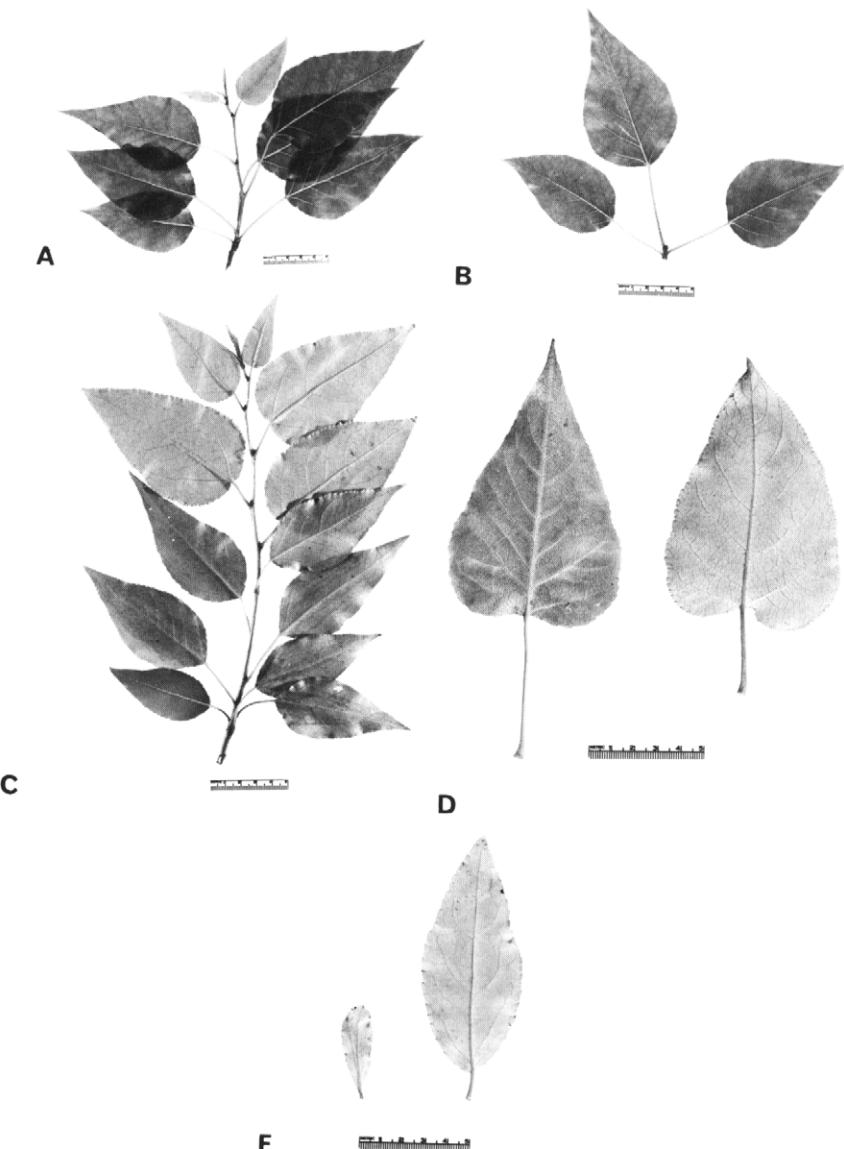


FIG. 5.17. Leaf dimorphism in *Populus trichocarpa*. (A) Early stage (5 weeks after bud opening) in development of heterophyllous shoot. The six early leaves have almost completed expanding and the first late leaf is beginning rapid growth. (B) A short shoot collected on same date as A. Three early leaves are mature and the terminal bud is beginning to form. (C) Later stage in development of a heterophyllous shoot. The six early leaves are fully expanded and the first one or two late leaves nearly so. (D) Early and late leaves. (E) Leaves 1 and 7 of an adventitious shoot. [From Critchfield (1960).]



FIG. 5.18. One year's stem elongation of *Pinus echinata*. The two upper nodes of the year's growth represent summer shoots. [From Tepper (1963a).]

LONG AND SHORT SHOOTS

In several species of woody plants the failure of a shoot axis to elongate appreciably results in forming short or dwarf shoots as opposed to the more characteristic long shoots (Figs. 5.19, 5.20). Long shoots have leaves separated by internodal intervals, whereas short shoots are devoid of appreciable internodes and have leaves crowded at the stem tip. Although short shoots are a characteristic feature of such genera as *Ginkgo*, *Larix*, and *Cercidiphyllum* (Gunckel and Wetmore, 1946a) they also occur in some angiosperms.

In some species such as *Ginkgo* and *Cercidiphyllum* there are no obvious morphological differences between buds destined to form long or short shoots. In other species, such as *Larix decidua* the putative long and short shoot buds are structurally different (Frampton, 1960).

In *Ginkgo biloba* all terminal and lateral buds initiate short shoots as they open in the spring. This involves enlargement of leaves and little or no internodal elongation. Several weeks later the internodes of some of the shoots elongate to produce long shoots. This changeover is rather gradual and can occur on any shoot at any time during the growing season, even on short shoots of many seasons. Furthermore, a long shoot of previous seasons may suddenly assume the short-shoot habit. Gunckel *et al.* (1949) considered bud



FIG. 5.19. Seasonal changes in development of short shoots (above) and long shoots (below) of *Larix laricina*.

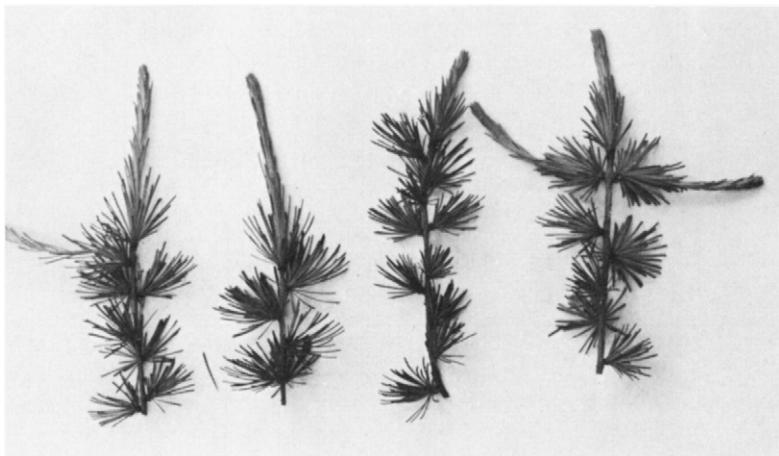


FIG. 5.20. Branches of *Larix laricina* bearing both long and short shoots.

development of *Ginkgo* to occur in two distinct stages and viewed lateral short shoots as a special case of bud inhibition.

Long shoots develop in *Larix decidua* from terminal buds and a few upper axillary buds located on long shoots of the previous year. All other axillary buds characteristically produce short shoots (Frampton, 1960).

EPICORMIC SHOOTS

Sudden and excessive exposure of trees often results in stimulation of dormant buds on the main stem or branches to produce epicormic (literally, "on the bole") shoots or "water sprouts." Epicormic shoots, which occur much more commonly in angiosperms than in gymnosperms, are of serious concern to foresters because they produce knots which seriously degrade lumber. For example, epicormic branching of Louisiana hardwoods caused a reduction of grade in 40% of the logs sampled, with 23% of the logs lowered by two or more grades (Hedlund, 1964).

Most epicormic shoots develop in the upper part of the stem and only few within the crown. W. W. Ward (1966) demonstrated a correlation between the distribution of live branches at various stem heights and subsequent development of epicormic shoots in *Quercus alba* and *Q. velutina*. Species vary markedly in their capacity to produce epicormic shoots. For example, exposed *Betula alleghaniensis* trees produced 66 epicormic shoots; *Acer saccharum* had 29, and *Fagus sylvatica* only 5 epicormic shoots per tree (Blum, 1963). Species differences also were noted by W. W. Ward (1966), with *Quercus alba* trees in heavily thinned stands producing almost twice as many epicormic shoots as *Q. velutina* under comparable conditions.

As previously mentioned, formation of epicormic shoots has been shown to be strongly related to the degree of opening of forest stands. For example, average *Quercus alba* trees in heavily thinned stands produced over 35 epicormic shoots within 2 years, as against 21 shoots for trees of moderately thinned stands, and only about 7 per tree of unthinned stands (Table 5.3).

TABLE 5.3

EFFECT OF THINNING ON PRODUCTION WITHIN TWO GROWING SEASONS OF EPICORMIC SHOOTS IN *Quercus alba* AND *Q. velutina* STANDS^a

	Residual basal area per acre (ft ²)					
	<i>Quercus alba</i>			<i>Quercus velutina</i>		
	115	70	30	115	70	30
Tree size and vigor						
Diameter (inches)	11.7	12.5	11.7	14.1	13.6	13.8
Height (feet)	75.7	79.2	76.4	83.4	85.4	80.4
New epicormic shoots						
North	1.1	4.9	10.7	0.7	1.8	6.3
South	2.0	5.3	6.4	1.3	4.5	3.5
East	1.8	5.1	9.4	2.1	5.2	5.8
West	1.7	6.1	8.0	1.3	5.0	4.2
	6.6	21.4	34.5	5.4	16.5	19.8

^a From W. W. Ward (1966).

In Louisiana epicormic branching of angiosperm trees was most frequent in stands with basal areas less than 75 ft.² per acre (Hedlund, 1964). Blum (1963) found that more epicormic branches were produced by border trees of hardwood stands than by those growing just inside the border.

As dormant buds are discernible in many species, and species vary greatly in abundance of such buds, the likelihood of epicormic sprouting is, to a degree, predictable. For example, the capacity for epicormic sprouts tends to be high in *Quercus*, moderate in *Prunus*, and slight in *Fraxinus*. Within the same species, young and small trees usually show a greater tendency than old and large trees to produce epicormic shoots. Krajicek (1959) noted that development of epicormic branches on *Quercus alba* trees was related to crown class, with dominant trees producing fewer branches than those of lower crown class. The number of epicormic branches in the lower 17 ft of 95-year-old trees in uncut stands varied from less than three on dominant trees to nearly ten on suppressed trees. Bachelard (1969b) also observed that

trees most likely to form epicormic shoots were those showing restricted cambial activity, i.e., suppressed trees. He suggested that a competitive relationship may exist between cambial activity and production of epicormic shoots.

ABNORMAL LATE-SEASON SHOOTS

The abnormal late-season flushes of growth from bursting of a current-year bud have been variously named. Many late shoots are commonly called "lammas shoots" because they presumably appear around Lammas day on August 1. In Germany they are called "Johannestriebe" in honor of the midsummer festival of St. John, and in France St. Martin's shoots. The present chapter will distinguish between four types of abnormal late-season shoots. These include (1) lammas shoots, (2) proleptic shoots, (3) sylleptic shoots, and (4) long buds (Fig. 5.21). Lammas shoots result from bursting and elongation of a current-year, terminal bud on the main shoot or a branch, whereas proleptic shoots emerge from current-year lateral buds at the base of the terminal bud. Less well known are sylleptic shoots which form when axillary buds of an elongating shoot develop into branches before they are fully formed. Sylleptic shoots may be unnoticed because they may form earlier than lammas or proleptic shoots, i.e., when normal early shoots are still growing. Long buds are terminal buds which have elongated but have not opened. When they occur in pines, they do not have externally visible needles on the elongated axis, and they can be easily distinguished from the needle-bearing lammas and proleptic shoots. Leaves of late-season shoots often differ from those of early shoots.

Some species of pine, such as *Pinus strobus*, are considered to be essentially uninodal as they usually produce only one whorl of lateral branches per year from expansion of preformed primordia. Sometimes, however, *Pinus strobus* produces late-season lammas shoots from opening of buds formed during the current year. This species also has been reported on occasion to produce very weak, mid-season second flushes of shoot growth from expansion of preformed primordia. Owston (1968) observed such second flushes in mid-June on terminal leaders and upper lateral branches. These shoots averaged only about an inch in length. Since these weak second flushes appeared before apical meristems began current-year production of dwarf shoot primordia, the primordia for the second mid-June growth flushes apparently were already present in the overwintering buds.

Abnormal late-season shoots develop widely in both angiosperms and gymnosperms. Anic (1956) found them on 23 species of angiosperms and many species of gymnosperms. Among the former group *Quercus*, *Fagus*, *Carya*, *Alnus*, and *Ulmus* have a tendency to form lammas shoots (Kramer

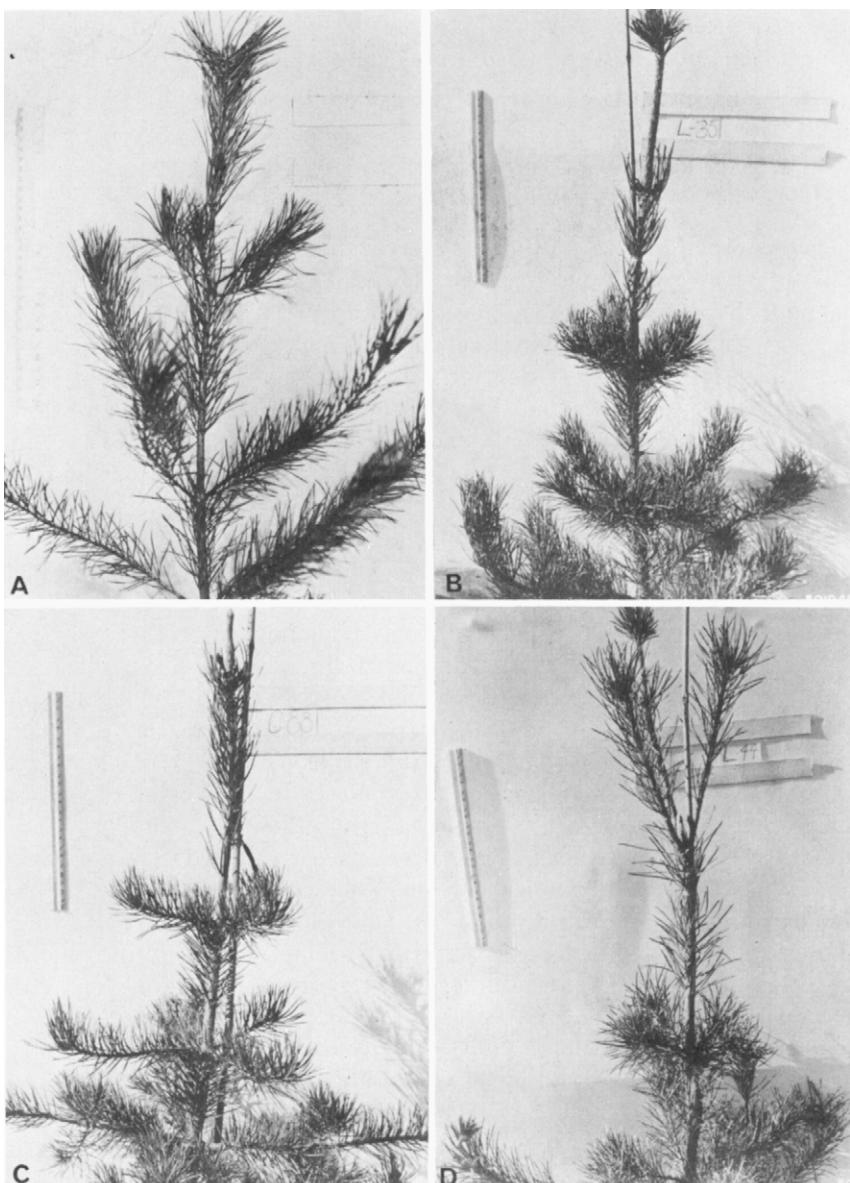
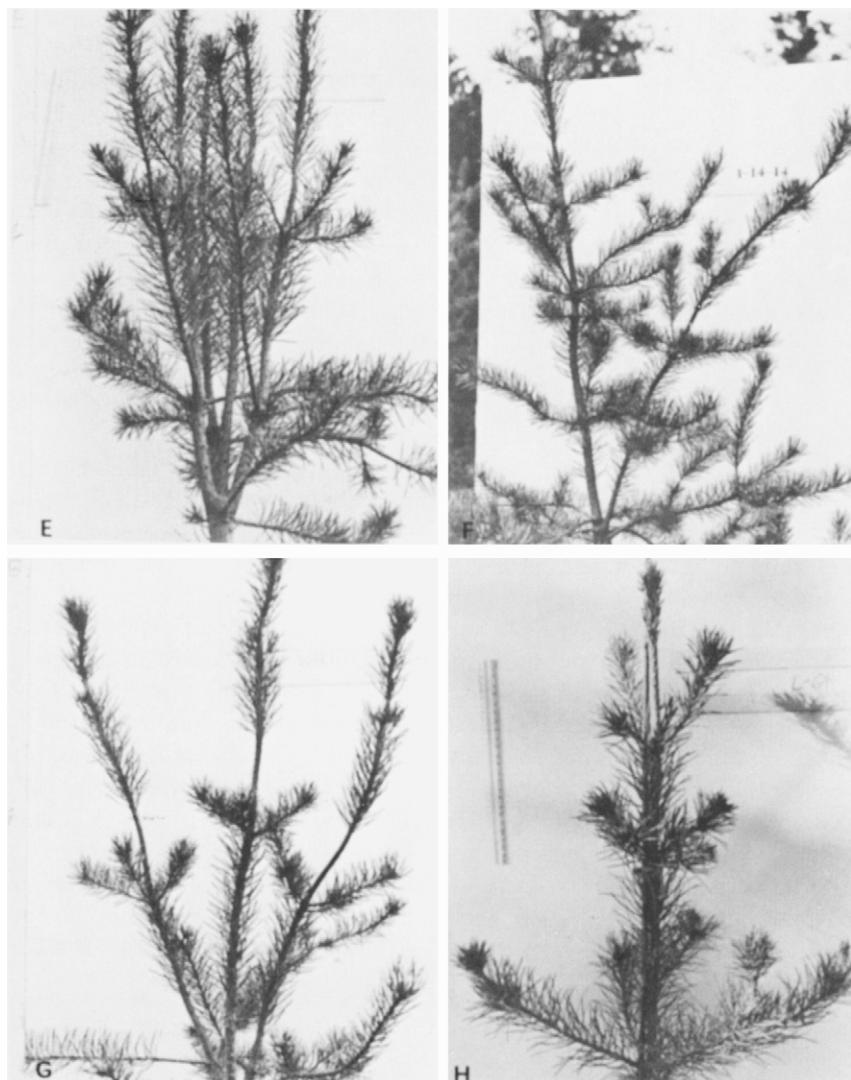


FIG. 5.21. Normal shoots (A) and abnormal late-season shoots (B to H) of *Pinus banksiana*. (A) Normal shoot and winter bud; (B) Typical lammas shoot. All but the upper part of the lammas shoot is bare of shoot needles, indicating that elongation occurred primarily in the lowermost sterile bract portion of the preformed shoot; (C) Typical "long bud". Unlike the lammas shoot, no secondary needles appear on the long bud; (D) Prolepsis.



Three lateral buds at the base of the terminal bud cluster lost dormancy and grew after completion of normal seasonal growth. The terminal buds, however, remained dormant; (E) Prolepsis, resulting in competition for dominance among shoots; (F) Proleptic lateral shoot which has become the leading terminal shoot. The original terminal leader is the long acute-angled branch at the right; (G) Typical "basket whorl" resulting from unsuccessful competition for dominance by 2 or more proleptic shoots and the terminal shoot; (H) Lammas growth and prolepsis occurring simultaneously. These shoots had greener color, more succulent appearance, and shorter needles than normal shoots. [From Rudolph (1964).]

and Kozlowski, 1960). Among gymnosperms with a tendency to produce late season shoots are *Pinus resinosa* (Carvell, 1956; Littlefield, 1956), *P. strobus* (McCabe and Labisky, 1959), *P. sylvestris* (Sokolev and Artyushenko, 1957; J. B. Thomas, 1958; Rudolph, 1962), *P. banksiana* (Rudolph, 1964), *P. nigra* (Wright and Bull, 1962), *P. radiata* (Fielding, 1960), *Abies sachalinensis* (Tamari, 1962), *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Abies grandis*, *A. amabilis*, *A. concolor*, *Pinus monticola*, *Picea sitchensis*, *P. abies*, and *P. omorika* (Walters and Soos, 1961). In some tropical areas prolepsis is a serious source of difficulty with exotic pines.

Late-season lammas or proleptic shoots may be longer or shorter than the early shoots of the first flush. For example, lammas shoots in *Quercus* were longer than the early shoots (Wight, 1930). In contrast, in pines of the northern United States lammas and proleptic shoots generally are shorter than the typical early shoots (Rudolph, 1964).

Lammas shoots often form in response to abundance of available water. Kovalenko (1960) found abundant lammas shoots on one- to five-year-old *Pinus palustris* and *P. pallasiana* trees but none on 10- to 20-year-old trees. According to Walters and Soos (1961), the tendency for forming lammas shoots in *Pseudotsuga menziesii* declined with increasing tree age and with decreasing site quality. Walters and Soos emphasized that formation of lammas shoots may depend more on environmental factors than on genetic ones. Nevertheless, there is considerable evidence of strong genetic control of late-season shoots. For example, work with various seed sources of *Pinus banksiana* showed that the frequency of late-season shoots increased with more southerly latitude of origin, with increase in degree days over 50°F of origin, and with higher average July temperature of the origin. Variation in late-shoot formation between sources exhibited a clinal or continuous pattern (Rudolph, 1964). Wright and Bull (1962) found strong genetic control of lammas growth in *Pinus nigra* and Fielding (1960) reported that multiple shoots in *Pinus radiata* were most likely to occur on genotypes of weak apical dominance.

Structure of Late-Season Shoots

Several investigators have observed variations between structure of late-season lammas shoots and normal shoots of both angiosperms and gymnosperms. In *Quercus*, leaves of lammas shoots were more deeply incised than those on normal, early-season shoots and sometimes were variegated rather than typically green (Späth, 1912; Stout, 1916).

An increase in needle number per fascicle has often been noted on lammas and proleptic shoots. For example, in *Pinus banksiana*, three-needed fascicles were more common on lammas shoots than on normal shoots. Whereas 42% of the fascicles were three-needed on lammas shoots, only 22% of the normal shoot tips had such fascicles. Three-needed fascicles also were more common

close to the tip of normal shoots than they were a short distance from the apex. The occurrence of supernumerary needles appeared to be governed by gradients of apically produced growth regulators (Ghent and Thomas, 1960).

Needles of lammas shoots in gymnosperms quite often are shorter than normal. The lammas shoots of *Pinus banksiana*, which typically had needles that were less than half as long as those of normal shoots, gave a tufted appearance to the shoot because of the reduced elongation of the stem in that region (Rudolph, 1964). Kienholz (1934) reported a mean length of 33 mm for needles on late-season shoots in *Pinus resinosa* compared to 140 mm for those on normal shoots. Jump (1938) observed very short needles on proleptic shoots of *P. resinosa* and noted also that they did not elongate further the following season. Thornlike, green, and apparently photosynthetically active primary needles on proleptic shoots of *Pinus radiata* were described by Jacobs (1938).

Effects of Late-Season Shoots on Growth and Form of Trees

Abnormal late-season shoots often have important influences on various aspects of apical and cambial growth and on tree form. Some studies show that total annual height growth of trees forming lammas shoots is greater than in those which do not produce late-season shoots. Other studies show opposite conclusions. The effects of late-season shoots on cambial growth are more definite, with both false rings and frost rings (Volume II, Chapter 2) associated with trees having late shoots. However, lammas shoots may not cause false rings to form if the pause between termination of growth of early shoots and the beginning of growth of late shoots is brief. Furthermore, late shoots do not always produce a false ring (Volume II, Chapter 2) for extended lengths in branches. Hence, sampling the base of a main stem or even of a large branch in which late shoots formed may not show a false ring. Nevertheless, false rings may have formed in the terminal portions of the branch.

Both lammas and proleptic shoots often render trees susceptible to winter injury because late shoots do not always harden adequately. Hence, frost rings with distorted xylem elements often occur in trees with abnormal late-season shoots. The degree of frost injury often varies with the stage of lignification of the new tissues at the time of occurrence of frost and with the severity of the frost. Frost rings are discussed further in Volume II, Chapter 2.

Whereas the tendency for prolepsis often is associated with forking of the main stem of gymnosperms, the production of lammas shoots generally has little effect. Prolepsis sometimes also causes forking in angiosperms but the most drastic effects on stem form occur in gymnosperms. The most serious forking occurs when prolepsis is not accompanied by formation of lammas shoots.

Prolepsis, especially in the absence of lammas growth often influences the

size of branches and their angle of juncture with the main stem. The abundant, large-diameter proleptic shoots contribute food and growth regulators for cambial growth below the node from which the shoots emerge. Hence, stem diameter above a whorl of proleptic shoots often is appreciably less than below the whorl. The formation of lamas shoots, which often are very short, may result in a false whorl of branches arising from the same node as a normal whorl. Hence, lamas growth often causes profuse branching and knotty lumber. Proleptic shoots also promote branchiness because of their numerous secondary lateral branch buds. The shortened proleptic shoots characteristically produce many second-order lateral branches near the main stem. These branches eventually become buried in the main stem where they appear as numerous knots.

ROOT SUCKERS

Following disturbances of forest stands by heavy cutting or fire, some species of trees regenerate largely by root suckers or shoots which originate from buds on the horizontal roots of the residual and cut trees. Reproduction by root suckers probably is best known in *Populus tremuloides* and *P. grandidentata* but it also occurs in other species such as *Liquidambar styraciflua*, *Fagus americana*, and *Robinia pseudoacacia* (Brown and Kormanik, 1967). The importance of opening of *Populus tremuloides* stands to production of root suckers was shown by data of Stoeckeler and Mason (1956). They observed over 2800 aspen sprouts per acre on open sites following heavy cutting and as few as 377 sprouts per acre in undisturbed stands. Annual height growth of sprouts varied from 1.37 ft in the open to 0.40 ft in heavy shade. According to M. W. Day (1944), the root systems of an aspen seedling can initiate suckers during its second year.

S. A. Graham *et al.* (1963) cited the following lines of evidence for regeneration of *Populus tremuloides* stands by root suckers:

(1) Composition of a forest stand consisting primarily of one age class of trees but with scattered individual trees older than the stand as a whole.

(2) Attachment of a tree stem to a horizontal root which has more annual xylem rings than the tree itself.

(3) Clonal arrangement of trees, with the stand consisting of groups of trees, each of the same sex and with similar leaves, bark, and growth habit.

As previously mentioned, root suckers arise from adventitious buds. A. B. Brown (1935) described the origin of root suckers in the phellogen of *Populus* roots. Buds differentiated from meristematic cells just beneath the phellem. Kormanik and Brown (1964) found that root suckers in *Liquidambar styraciflua* developed commonly from previously suppressed buds, which were found imbedded in the phloem of roots. The bud traces of some of these buds extended to the primary xylem of the stele, and of other buds only back to a



FIG. 5.22. A stand of root sprouts from a 40-year-old *Liquidambar styraciflua* tree [From Kormanik and Brown (1967).]

point of apparent bark injury several years earlier. These suppressed buds, like many of those on stems, grew only enough annually to keep pace with the radially increasing cambium. Occasionally they produced short shoots underground and produced leaf primordia annually for several years. Finally, they developed into long shoots above ground (Fig. 5.22).

Suggested Collateral Reading

- Clausen, J. J., and Kozlowski, T. T. (1967). Seasonal growth characteristics of long and short shoots of tamarack. *Can. J. Bot.* **45**, 1643-1651.
- Clowes, F. A. L. (1961). "Apical Meristems." Blackwell, Oxford.
- Critchfield, W. B. (1960). Leaf dimorphism in *Populus trichocarpa*. *Amer. J. Bot.* **47**, 699-711.
- Doak, C. C. (1935). Evolution of foliar types, dwarf shoots, and cone scales of *Pinus*. *Ill. Biol. Monogr.* **13**, No. 3.
- Garrison, R. (1949). Origin and development of axillary buds: *Syringa vulgaris* L. *Amer. J. Bot.* **36**, 205-213.
- Gifford, E. M., Jr. (1954). The shoot apex in gymnosperms. *Bot. Rev.* **20**, 477-529.
- Johnson, M. A. (1951). The shoot apex in gymnosperms. *Phytomorphology* **1**, 188-204.
- Kozlowski, T. T. (1963). Growth characteristics of forest trees. *J. Forest.* **61**, 655-662.

- Kozlowski, T. T. (1964). Shoot growth in woody plants. *Bot. Rev.* **30**, 335–392.
- Kozlowski, T. T., and Clausen, J. J. (1966). Shoot growth characteristics of heterophyllous woody plants. *Can. J. Bot.* **44**, 827–843.
- MacDaniels, L. H. (1953). Anatomical basis of so-called adventitious buds in apple. *N.Y. Agr. Exp. Sta., Mem.* **325**.
- Newman, I. V. (1961). Pattern in the meristems of vascular plants. II. A review of shoot apical meristems of gymnosperms, with comments on apical biology and taxonomy, and a statement of some fundamental concepts. *Proc. Linn. Soc. N.S.W.* **86**, 9–59.
- Popham, R. A. (1951). Principal types of vegetative shoot apex organization in vascular plants. *Ohio J. Sci.* **51**, 249–270.
- Romberger, J. A. (1963). Meristems, growth, and development in woody plants. *U.S. Dep. Agr., Tech. Bull.* **1293**.
- Rudolph, T. D. (1964). Lammas growth and prolepsis in jack pine in the Lake States. *Forest Sci. Monogr.* **6**.
- Sacher, J. A. (1955). Dwarf shoot ontogeny in *Pinus lambertiana*. *Amer. J. Bot.* **42**, 784–792.
- Stone, E. L., and Stone, M. H. (1943a). "Dormant" versus "adventitious buds." *Science* **98**, 62.
- Stone, E. L., and Stone, M. H. (1943b). Dormant buds in certain species of *Pinus*. *Amer. J. Bot.* **30**, 346–351.

Chapter 6

LEAF GROWTH AND DEVELOPMENT

Introduction

Trees bear several types of leaves including cotyledons, foliage leaves, and cataphylls. Cotyledons or “seed leaves” are developed in the seed and contain or have access to stored foods. Although cotyledons of some species are active in photosynthesis, the foliage leaves, which develop later, are the primary food and hormone producing structures of woody plants.

Some specialized and modified leaves do not function primarily in photosynthesis. For example, the spines of some plants such as *Berberis*, are specialized leaves because they have buds in their axils. However not all spines are modified leaf blades. Some are stem modifications because they arise from the cortical tissues beneath the epidermis. In *Robinia* and various *Euphorbia* species the paired spines at the base of leaves are modified stipules.

Cataphylls or “lower leaves,” which usually are involved in storage, protection, or both, are represented by bud scales. In early developmental stages a cataphyll primordium generally is indistinguishable from one which ultimately becomes a foliage leaf. Cataphyll tissues usually develop rapidly and show less differentiation than those of foliage leaves. The vascular system and mesophyll of cataphylls usually are weakly developed and stomates are infrequent or lacking. Romberger (1963), however, emphasized that cataphylls and foliage leaves often differ only in degree, as shown by various intermediate stages between scales and leaves and by gradual transition in development of cataphylls to leaves in many species. He further suggested that primordia were not predestined to form scales or leaves and were inherently capable of becoming either of these. Morphogenic determination was imposed at an early developmental stage by existing environmental conditions. The remainder of this chapter will be devoted to foliage leaves.

Origin and Differentiation of Leaves

Following initiation of leaf primordia, a leaf achieves final shape and size by cell division and expansion. Ultimate leaf size depends on the number of cells in the primordia, the rate and duration of cell division, and sizes of mature cells, but cell number appears to be the most important (Humphries and Wheeler, 1963). According to E. Ashby (1948) final leaf shape depends on distribution of cell division and expansion, on planes of cell division, and direction of cell expansion.

ANGIOSPERMS

Leaves of angiosperms form only on apices of shoots. The apex swells to form a leaf primordium consisting at first of uniform meristematic cells. Shortly thereafter, cell division stops in the area of attachment and the leaf base is differentiated. The upper part of the primordium continues to divide and forms the blade. The petiole forms later from an intermediate meristematic zone. The various leaf parts, such as petiole, blade, sheath, and stipules are initiated very soon after the primordium has formed.

Growth of the leaf at first is localized at the tip but this is of short duration and is followed by generalized intercalary and marginal growth of the primordia. Hence, overall leaf development is the result of combined apical, marginal, and intercalary growth, with apical growth becoming of negligible importance after bud opening. Marginal growth often occurs simultaneously with apical and intercalary growth (Clowes, 1961). However, marginal growth often stops while leaves are small and thereafter the leaf reaches full size by intercalary growth, cell expansion, and maturation.

The leaf blade or lamina is formed from marginal and intercalary meristematic activity which gives rise to the upper and lower epidermis and submarginal initials (Fig. 6.1) from which the interior tissue of the blade originates. The mesophyll differentiates after derivatives of marginal meristems undergo intercalary growth. Cell division occurs mostly in a plane perpendicular to the leaf surface (anticlinal). Cell division in the mesophyll takes place only in very young stages and is not uniform throughout the leaf. It usually occurs in patches between the major veins, and cells stop dividing first near the vascular bundles. Differences in cell division and expansion account for variations between palisade and spongy parenchyma tissues (Esau, 1965b). Cell division usually stops first in the upper epidermis and continues for a longer time in palisade cells (MacDaniels and Cowart, 1944). At first cell division and growth of palisade and upper epidermal cells are closely correlated and palisade tissue consists of closely packed cells. Later, differential enlargement of epidermal and palisade layers results in

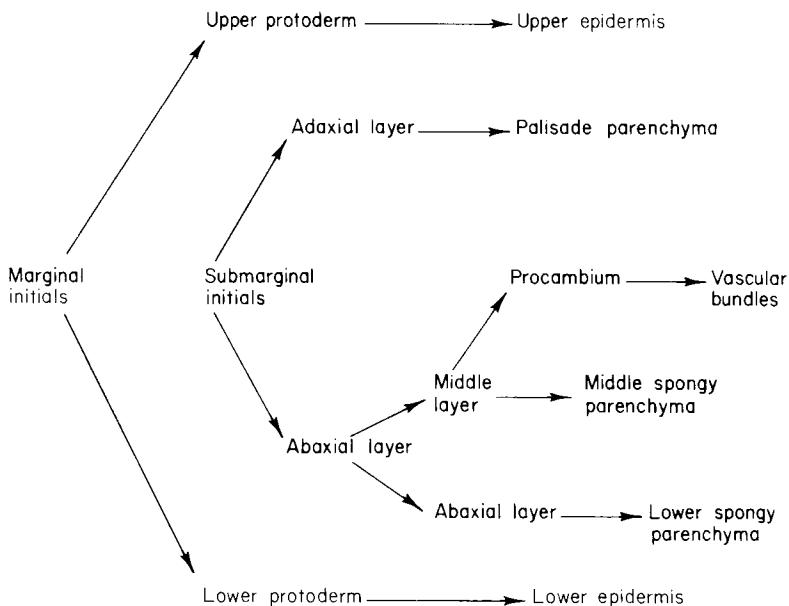


FIG. 6.1. Diagram of tissue differentiation in the leaf blade of *Carya buckleyi* var. *arkansana*. [From Foster (1936).]

formation of intercellular spaces in the latter tissues. When cells of the upper epidermis of *Vitis vulpina* stopped dividing both they and the palisade cells averaged about 7μ in diameter. At that time there were no intercellular spaces in the palisade tissue. Thereafter, cell enlargement in the epidermis varied greatly from that of palisade cells. By the time the leaf was mature, the surface area of epidermal cells had increased some 20 times. Meanwhile the cross-sectional area of palisade cells had increased about eight times and there were about five palisade cells to one epidermal cell (Mounts, 1932). In mature apple leaves there were eight to ten palisade cells to each cell of the upper epidermis (MacDaniels and Cowart, 1944). The strains resulting from much greater expansion of epidermal cells than palisade cells causes the latter to separate, especially at their lower end. After cell division ceases in spongy mesophyll the cells expand and become separated to form many intercellular spaces. Cells of the spongy mesophyll remain attached to each other and form irregular filaments which connect the lower epidermis with palisade tissues and vascular bundles.

The epidermal tissue from which stomates originate is differentiated early. Young apple leaves were green by the time they were a few millimeters wide (MacDaniels and Cowart, 1944). Hence, most stomates are found in young

buds but differentiation may also occur late in leaf development. Some epidermal tissues contain both mature stomates and undifferentiated stomatal mother cells. The stomatal mother cells develop from embryonic epidermal cells by asymmetric, differential division. The stomatal pore is formed shortly after separation of guard cells at a median position.

Formation of the vascular system of an angiosperm leaf begins early during blade formation. As a primordium elongates, differentiation of the procambium of the midvein progresses upward. The differentiation of procambium occurs as a continuous process, giving rise to large lateral veins and then progressively smaller ones. Lateral, first-order veins develop from the midrib toward the margins. The small veins mature basipetally so the procambial system is completed first near the leaf apex. Maturation of vascular elements of the leaf occurs before differentiation of the procambial system is complete (Esau, 1965a).

Stages in the differentiation of the leaf blade of *Salix alba* are shown in Fig. 6.2. The cells of principal leaf tissues underwent more or less similar stages of differentiation before they matured. In early meristematic stages the cells were thin-walled, had large nuclei, and were filled with dense cytoplasm. After cells divided they increased in size and vacuoles gradually appeared, cell walls expanded and ultimately became rigid as they were thickened by deposition of cellulose suberin, cutin, etc.

Some differences occur among species in the rate and extent of development of leaf tissues (Tetley, 1936). In net-veined dorsiventral leaves, cells of the upper epidermis are differentiated before those of the lower epidermis. In some ericoid species the upper epidermal cells enlarge very early in leaf ontogeny while cells of other leaf tissues remain small and meristematic, causing leaves to roll on each side of a vascular bundle.

Leaf shapes vary because of differences in activity of marginal meristems. Compound leaves also form from such variable activity, with individual marginal meristems forming each leaflet in a manner similar to development of a simple leaf. The order of leaflet formation is variable, with apical ones forming first in some species and basal ones in others. In some species such as palm and banana the compounding of leaves is the result of late splitting of a single, relatively mature leaf blade (Esau, 1960). Lobing of leaves occurs when growth rates vary within marginal meristems. For a more detailed description of anatomical and physiological aspects of leaf growth the reader is referred to Esau (1960, 1965b), Milthorpe (1956), and Clowes (1961).

GYMNOSPERMS

As previously mentioned (Chapter 2) many gymnosperm seedlings sequentially form three distinct types of foliar appendages including

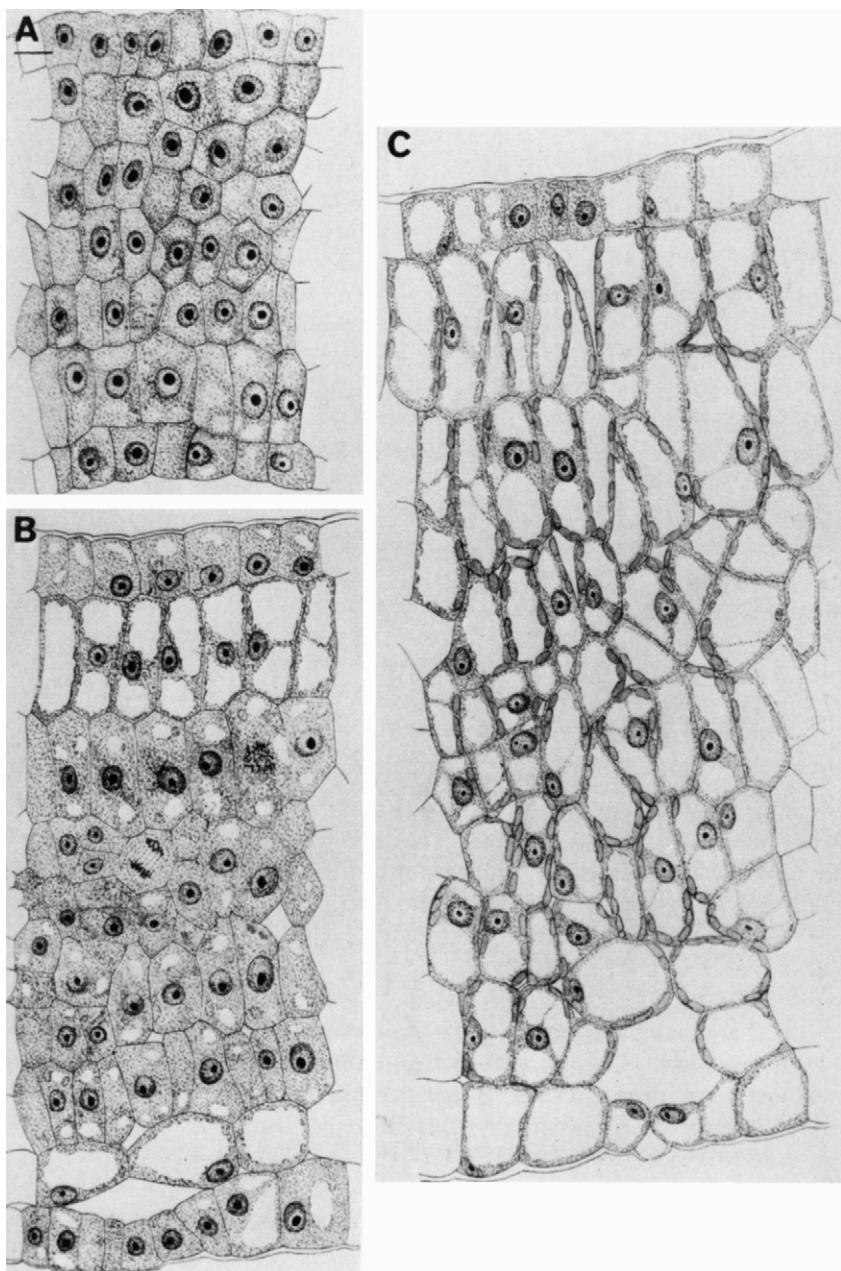


FIG. 6.2. Stages in development of leaf blade of *Salix alba*. [From Tetley (1936).]

cotyledons, primary needles, and secondary needles. In adult gymnosperm trees the time of formation of primordia of secondary needles in buds varies among species. A few examples will be given. After annual shoot extension of *Abies concolor* slowed down numerous needle primordia formed. This occurred when the new telescoped shoot was forming and continued into late September (Parke, 1959). In *Pseudotsuga menziesii* growing in Victoria, British Columbia, initiation of leaf primordia began early in July. The rate of leaf initiation then was rapid for the next 6 weeks. Thereafter, the rate of leaf initiation slowed down but did not end until mid-November (Owens, 1968). In *Pinus resinosa*, however, new terminal buds began to form in July after most shoot elongation was completed, but no needle primordia formed on the dwarf shoots until the following spring (Duff and Nolan, 1958). By comparison, all the foliar organs in short shoots of *Pinus lambertiana* were produced during the first season (Sacher, 1955).

Leaf growth in gymnosperms starts with foliar primordia located on the flanks of apical meristems. Both apical growth and intercalary rib meristem activity form the leaf axis, but apical growth is of short duration. The narrow leaf blade is initiated by marginal growth (Esau, 1960). The leaves of *Taxodium distichum* increased in length by apical and intercalary growth until they were 2 to 3 mm long. Cells at the tip then matured and subsequent growth was intercalary (Cross, 1940). The origin and early development of foliage leaves of *Cryptomeria* and *Cunninghamia* were essentially the same as for *Taxodium* (Cross, 1940, 1942). Most of the internal tissue of gymnosperm leaves is produced by derivatives of the rib meristems.

Various stages in the initiation and development of leaves of *Pseudotsuga menziesii*, as described by Owens (1968), are presented in Figs. 6.3 and 6.4. Developmental processes of *Pseudotsuga* leaves were similar to those of other gymnosperms. The first indication of leaf initiation was differentiation of a procambial strand in the apex toward the site of the presumptive primordium. The procambium differentiated outward by oblique divisions of procambial cells and tangential elongation. Early increase in size of the primordium resulted from cell division in all planes in deep layers and anticlinal and periclinal divisions in overlying protoderm cells (Fig. 6.3B). Growth in length of leaves resulted from combined activities of apical and subapical initials and intercalary cells. Apical and subapical initials matured early, as in most angiosperms. After dormancy, the growth of leaves occurred primarily by cell elongation although cell division occurred also throughout a large part of the leaf, most frequently in the basal intercalary meristem. Apical and subapical initials were inactive after dormancy.

As in angiosperms, the development of air spaces in gymnosperm leaves usually results from continued elongation of epidermal cells after growth stops in the mesophyll (Cross, 1940). In leaves of *Pseudotsuga menziesii*,

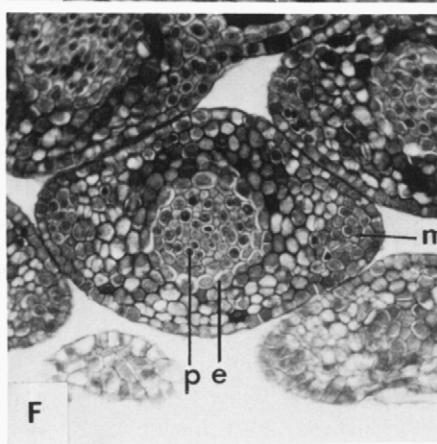
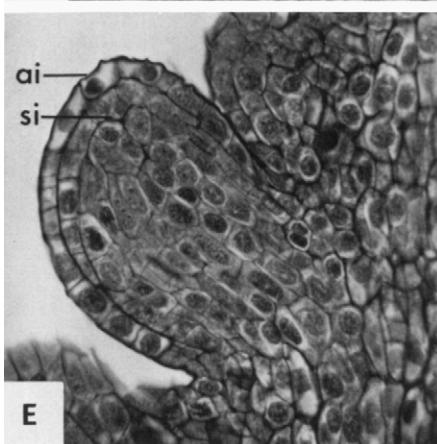
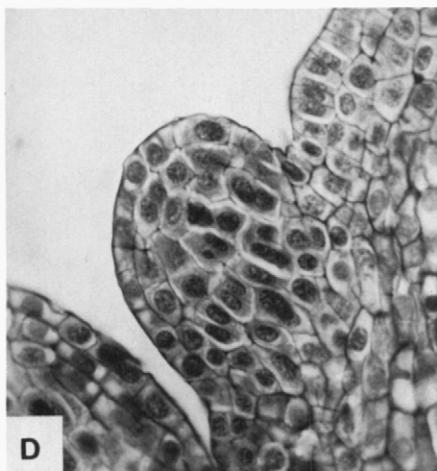
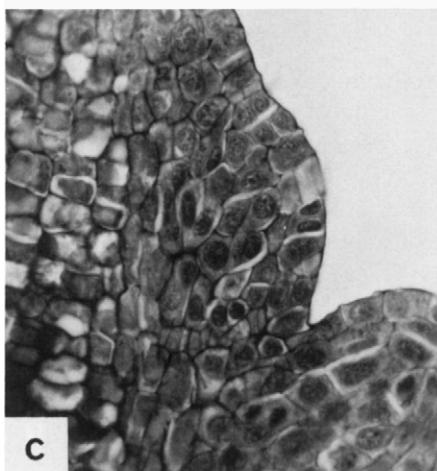
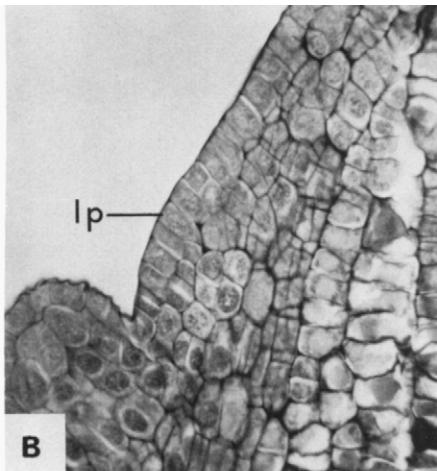
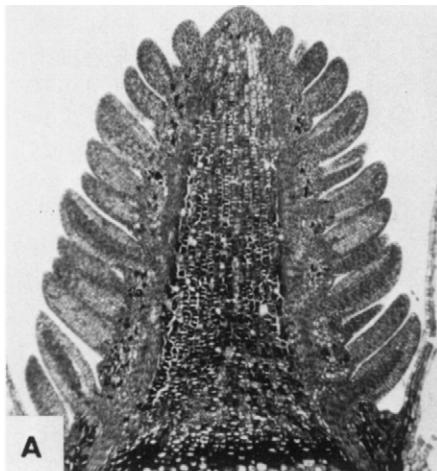
growth stresses were primarily on the abaxial mesophyll cells since the future palisade cells continued dividing. The abaxial mesophyll cells were pulled from each other and transverse air spaces were formed. The final expansion of air spaces resulted from elongation of epidermal cells (Owens, 1968).

There was no maturation of tissues in *Pseudotsuga menziesii* leaves before or during dormancy. After dormancy, the maturation of tissues was initiated before leaves achieved full length and occurred during the rest of the growing season. The rate of maturation of some tissues varied considerably. For example, resin ducts matured long before the growing season ended, whereas most other leaf tissues began to mature when leaf elongation was initiated and they continued to mature throughout the growing season.

Seasonal Leaf Growth Characteristics

Many different patterns of seasonal production of foliage leaves have been demonstrated. Trees of some species achieve maximum leaf area early in the season and produce no more new leaves during the year, whereas others continue to add new leaves, either by continued production of new leaf primordia in expanding shoots or by recurrent formation and opening of buds during the growing season and expansion of their contents.

Leaf production in a number of species (e.g., *Fagus*) usually is confined to a single period of relatively rapid expansion of leaf primordia contained in the resting bud. When the preformed complement of leaves in such species is expanded, no others normally are formed and expanded during the same growing season. However, sometimes species with preformed shoots, such as oaks, produce a second crop of leaves when they are stimulated to produce late-season lamas or proleptic shoots from bursting of current-year buds. It should be remembered also that species usually designated as heterophyllous, such as *Populus* and *Betula*, often contain some shoots which are fully preformed in the winter bud and which expand rapidly while other shoots on the same tree expand slowly as a result of forming and expanding new leaves during the growing season. The shoot system of *Acer rubrum* is comprised of a framework of long shoots, each bearing leaves, flower buds, and short shoots. The short shoots bear leaves and flower buds, but no lateral shoots. Wilson (1966) found that 85–95% of all *Acer rubrum* branches were short shoots. Shoots which produced only early leaves were short shoots or partially suppressed long shoots. Shoots which produced both late and early leaves were typically long shoots. In *Malus* the development of young leaves varies with the kind of the shoot on which it is borne, the kind of bud within which it develops, and its position in the bud (MacDaniels and Cowart, 1944). Leaf buds on spurs and short terminal shoots of *Malus*



apparently have the number of leaves determined for the following year's shoot. In some vigorous shoots, such as those that develop into suckers, shoot growth is indeterminate. The terminal meristem in such shoots continues to form new primordia, during the growing season, with the number formed controlled by current environment.

Although some pines have fully preformed shoots which expand by a single growth flush, their leaf area may increase for much of the growing season because the leaves continue to grow by basal intercalary meristems long after internode expansion has ceased. In some angiosperms the leaf area decreases seasonally, after a period of increase, as a result of leaf abscission coupled with lack of new leaf primordia. For example, in Japan the weight and area of leaves of 3-year-old *Ulmus parvifolia* trees varied throughout the growing season. At the beginning of the growing season leaf area increased rapidly and reached a maximum in about 50 days. Thereafter it decreased gradually to a constant value which was only a half to a third of the maximum value. The decrease was traceable largely to abscission of leaves in the lower parts of stems (Tadaki and Shidei, 1960).

RATES OF LEAF GROWTH

The seasonal duration of leaf expansion varies greatly among species, the type of shoot, and environmental conditions, especially temperature. The individual leaves of deciduous angiosperms as a group develop rather rapidly, usually requiring from a few days to a few weeks. According to Büsgen and Münch (1931), major expansion of *Quercus* leaves occurred in 10 to 14 days. Individual *Vitis* leaves expanded and matured in 40 days (Mounts, 1932). The early leaves of *Betula* and *Populus*, which were contained in the winter bud, expanded within 2 to 3 weeks after buds opened (Kozlowski and Clausen, 1966). In *Malus* the time required for expansion of leaves from dormant spur buds varied from 2 days for basal spur leaves to 15 days for other leaves. The basal spur leaves which were the first to mature, attained full size in about 5 days (MacDaniels and Cowart, 1944). In Wisconsin spring temperatures usually are rather high and vegetative spurs of *Malus*, which are less than one-half inch long, frequently open in 8 to 10 days after

FIG. 6.3. Stages of leaf development of *Pseudotsuga menziesii* (A) Longitudinal section through a dormant vegetative bud; (B) Earliest stage of leaf initiation showing recent oblique divisions of peripheral cells; (C) Enlargement of leaf primordium by cell division in all planes; (D) Leaf primordium showing origin of darkly staining procambial cells; (E) Primordium showing early upward growth and apical initials (*ai*) and subapical initials (*si*); (F) Transection of leaf primordium in dormant bud showing procambium (*p*), future endodermis (*e*), and marginal meristem (*m*). [From Owens (1968).]

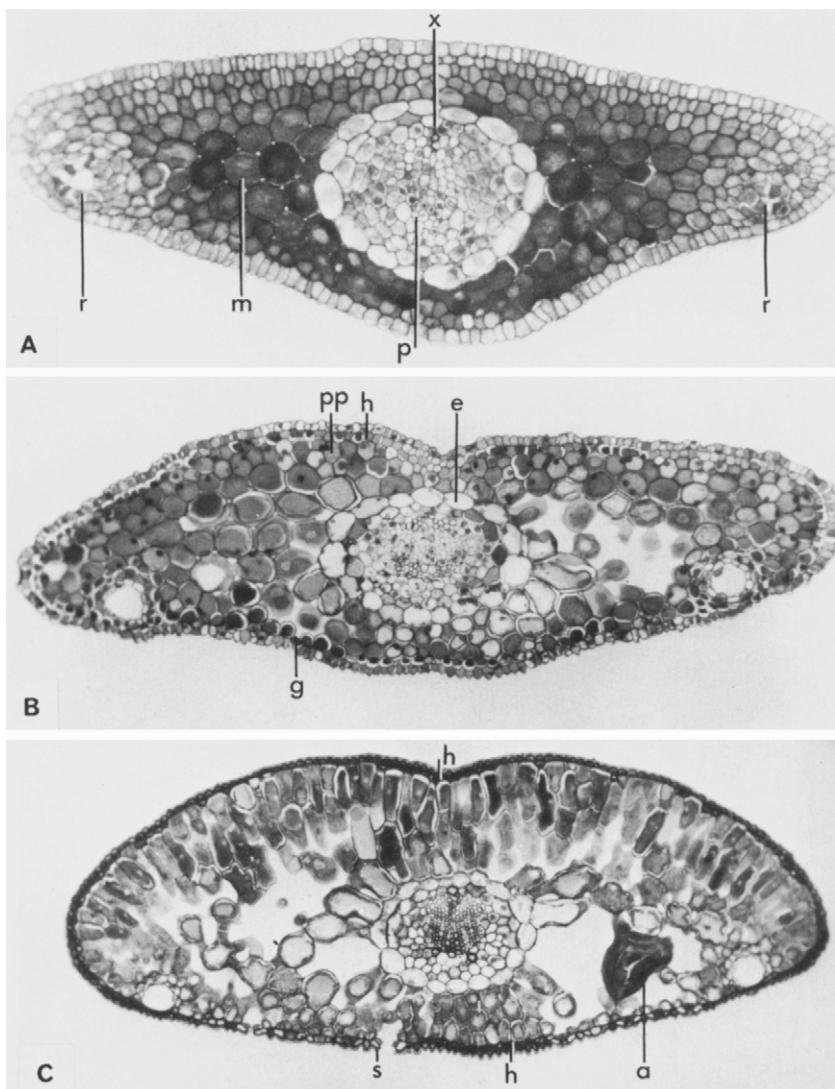


FIG. 6.4. Transections of *Pseudotsuga menziesii* leaf at various stages of development (A) Leaf 2 mm in length at first stages of differentiation of phloem (*p*), xylem (*x*), mesophyll (*m*), and resin ducts (*r*); (B) Leaf which is nearly fully elongated, showing later stages of differentiation of spongy mesophyll, resin ducts, vascular tissue endodermis (*e*) and hypodermis (*h*). Note undifferentiated isodiametric palisade parenchyma (*pp*), differentiating guard cells (*g*), and large air space in the lamina; (C) Mature leaf with fully differentiated tissues. Note thick cuticle, scattered hypodermis (*h*), subsidiary cells (*s*), definite palisade parenchyma, and large air spaces in spongy mesophyll with the large astrosclereid (*a*). [From Owens (1968).]

bud break. However, the duration of leaf expansion is very responsive to temperature. For example, during the cool spring of 1919 it took 25 days for *Malus* spurs to expand or twice as long as in the warmer year of 1917 (R. H. Roberts, 1920). Because of the rapid expansion of leaves contained in winter buds a deciduous forest in the Temperate Zone attains a high leaf area index very early in the growing season (Wareing, 1966). In Minnesota, for example, maximum leaf area in a deciduous forest was achieved by mid-June (Ovington *et al.*, 1963).

Despite the rapid development of individual leaves of many deciduous angiosperms, the total amount of foliage per tree may nevertheless continue to increase over the growing season in certain species. Whereas a number of species usually expand their total complement of foliage in one early-season growth flush, others such as *Quercus*, tend to produce an additional late seasonal growth flush to produce lammas shoots from opening of bud formed earlier in the current growing season. Heterophyllous species such as *Liriodendron*, *Eucalyptus*, *Populus*, and *Malus* continue to produce leaves and increase the total amount of foliage per tree over much of the growing season.

The rather rapid expansion of individual leaves of many deciduous angiosperms is in marked contrast to the relatively slow growth of gymnosperm leaves. In some gymnosperms such as *Abies lasiocarpa* individual needles often increase in length for more than 2 years (Stover, 1944). Internode extension of *Pinus sylvestris* in England was virtually completed by mid-June (Rutter, 1957) but needle elongation continued until at least the end of July or early August. In the United States, internode elongation of *Pinus strobus*, *P. resinosa*, and *P. rigida* shoots was completed early in the growing season. By comparison, the needles on the new shoots elongated at an increasing rate to a maximum in early July, and thereafter at a gradually decreasing rate until late August (Table 6.1). All of the late extension of needles was the result of intercalary growth localized at the extreme base within the fascicle sheath (Kienholz, 1934).

The amounts and seasonal patterns of needle elongation vary considerably in different parts of shoots (Kienholz, 1934). Needles at the base of the terminal leader of *Pinus resinosa* were 9.4 mm long on June 1, reached maximum growth rate on June 24. Thereafter, needle growth slowed down gradually to August 17. Needles at the tip of the leader had a different growth pattern. They were not yet visible above the bract base on June 1, and appreciable growth did not begin until June 12. Such needles achieved maximum rates of growth two weeks later than basal needles. Subsequently, growth rate of needles decreased until it ceased early in September (Fig. 6.5).

There also appear to be variations among gymnosperm species in growth of 2-year-old needles. According to Haasis (1931), needles of *Pinus radiata* elongated during the second year and Lodewick (1931) also found this to be

TABLE 6.1
MEAN DAILY ELONGATION OF NEEDLES OF THREE SPECIES OF GYMNOSPERMS DURING THE GROWING SEASON^a

No. of needles	Length (mm)						
	June 2	June 12	June 18	June 24	July 1	July 8	July 15
<i>Pinus</i> <i>resinosa</i>	268	3.4	1.03	1.63	1.86	1.74	1.96
<i>Pinus</i> <i>strobus</i>	144	4.2	0.55	0.90	0.98	1.08	1.32
<i>Pinus</i> <i>rigida</i>	72	4.2	0.80	1.12	1.42	1.24	—
					1.34	0.94	0.70
						0.53	0.34
						0.30	0.04
						13	19
						2	

^a From Kienholz (1934).

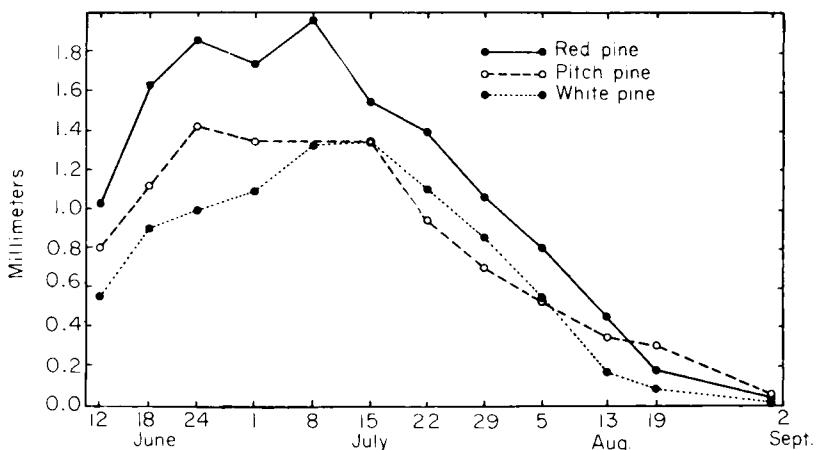


FIG. 6.5. Seasonal course of elongation of needles of three species of pine. Daily increment is given by weekly periods in mm. [From Kienholz (1934).]

true for *Pinus palustris*. Kienholz (1934) did not find any elongation of *Pinus strobus* needles during the second year.

Leaves of evergreen angiosperms expand much more slowly than those of deciduous angiosperms. For example, *Citrus* leaves grew in length and width for about 130 days (Scott *et al.*, 1948). The rate of leaf expansion was uneven. Two periods of rapid expansion occurred and these coincided with the time of spring and fall growth flushes. Leaf growth of evergreen angiosperms usually is completed during the first growing season. However, lamas shoots of *Rhododendron panticum* were an exception. They ceased growing at the end of the first year when they were only about one-third normal size, and they resumed growing during the following growing season, but failed to achieve normal size (Elliot, 1937).

LEAF GROWTH IN HETEROPHYLLOUS SPECIES

Leaf development is rather complicated in genera such as *Populus* and *Betula* which produce both early and late leaves on the same tree. The late leaves often appear one after another and their continuous development resembles that of leaves of many herbaceous plants. Critchfield (1960) found that the early leaves of *Populus trichocarpa* were preformed in the winter bud. The first late leaves also overwintered in the bud but as arrested primordia. Additional late leaves formed at the tip of the shoot later in the growing season.

As mentioned in Chapter 5, *Populus* may actually have three types of shoots: (1) those with early leaves only, (2) heterophyllous shoots with both

early and late leaves, and (3) shoots with only late leaves (usually sprout shoots). Short shoots of *Populus* which have only early leaves do not elongate much and they complete their growth very early. In contrast, growth of heterophyllous shoots occurs in two phases and lasts much longer (Figs. 6.6 and 6.7). During the first growth phase, which is very short, all of the early leaves of *Populus trichocarpa* expand quite rapidly and growth rate begins to decline when the leaves achieve about nine-tenths of their full length (Table 6.2). Growth rates usually begin to decline about 4 to 6 weeks after buds open. Very little stem elongation takes place during this first growth phase. The second growth phase involves development of the late leaves and the bulk of shoot elongation. Late leaf development includes growth of two or three leaf primordia which were present in the winter bud and the initiation and expansion of new late leaves during the current growing season. Most rapid stem elongation begins only after rapid expansion of the first one or two late leaves. A long internode separates the two sets of leaves. Shoot elongation tapers off before the last late leaves achieve maximum size and the upper internodes are very short in comparison to those further down the shoot.

Structure of Early and Late Leaves

As mentioned in Chapter 5, the structure of early and late leaves of heterophyllous species often varies appreciably. Critchfield (1960) pointed

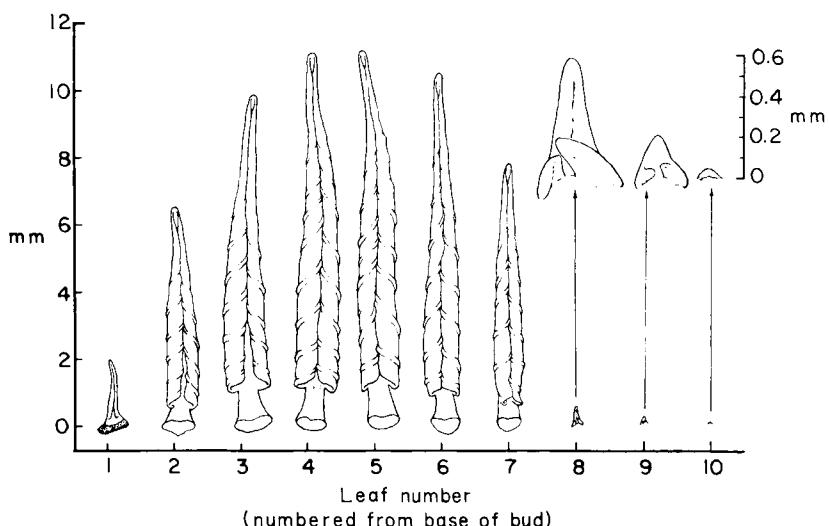


FIG. 6.6. Contents of a winter bud of *Populus trichocarpa*. The first leaf has aborted. The three leaf primordia (8 to 10) are shown in an enlarged scale at the upper right [From Critchfield (1960).]

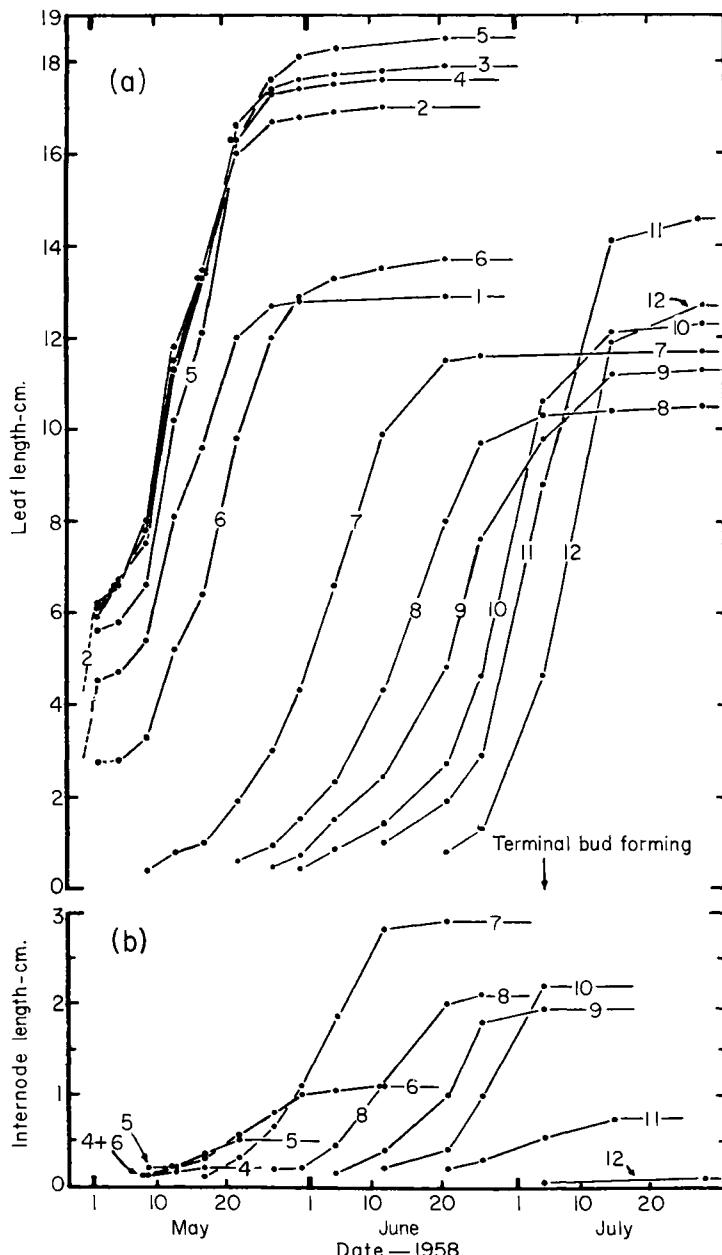


FIG. 6.7. Development of a heterophyllous shoot of *Populus trichocarpa*. Growth in length of early leaves (1 to 6) and late leaves (7 to 12) is shown in upper graph. Growth of internodes (4 to 12) is shown in the lower graph. The numbers of the various internodes are the same as the leaf numbers at the upper end. [From Critchfield (1960).]

TABLE 6.2
VARIATIONS IN TIME OF EARLY- AND LATE-LEAF MATURATION IN 4 CLONES OF *Populus trichocarpa* DURING 1957 AND 1958. THE TABLE GIVES DATES ON WHICH LEAVES ACHIEVED 90%^a OF FINAL LENGTH^b

Clone No.	Early leaves						Late leaves					
	1	2	3	4	5	6	1	2	3	4	5	6
1957												
897	May 9	May 8	May 9	May 10	May 12		May 29		June 14	June 21	June 28	
919	May 6	May 7	May 8	May 10	May 14		June 12	June 17	June 21	June 26	July 2	July 9
1958												
1456	May 21	May 21	May 21	May 21	May 23	May 23	May 28	June 14	June 25	July 1	July 6	July 14
1460	May 21	May 21	May 21	May 27	May 23	May 26	June 25	July 4	July 9	July 16	July 26	

^a From Critchfield (1960).

^b Leaf damaged by insects during expansion.

out a number of structural differences between leaves of *Populus trichocarpa* which expanded early in the growing season and those produced in late summer. Early leaves were larger and had longer petioles than late leaves. Although both types had serrulate margins the late leaves were more conspicuously toothed. Early leaves were tipped by a large, resin-secreting gland, whereas late leaves either had small glands or none at all. Early leaves had a fine network of veins and the late leaves had a coarse one. Air spaces of the spongy parenchyma of the late leaves were much larger than those of early leaves. Whereas stomates in the upper epidermis of early leaves were confined to the blade tip and midrib, the numerous stomates of late leaves were widely distributed in the upper epidermis. R. F. Smith (1967) described leaf dimorphism in mature *Liquidambar styraciflua* trees. The species produced both early leaves from primordia which were present in the overwintering bud and late leaves which were produced directly from the apical meristem without overwintering as leaf primordia. The early leaves were relatively shallow-lobed. By comparison, the late leaves were more deeply lobed and generally had shorter petioles. Seedlings did not have two forms of leaves.

Kozlowski and Clausen (1966) observed that spring buds of heterophyllous shoots of *Betula papyrifera* contained both embryonic leaves and leaf primordia. The former were leaflike with well-defined teeth, petiole, and veins. The latter were small-lobed structures. The two large, early leaves began to unfold around the middle of May in north central Wisconsin and grew very rapidly in the next 2 weeks. Their growth then slowed in the third week. The third leaf became apparent when the first two were more than half grown, usually not later than the end of May. Succeeding late leaves appeared at intervals of about 5 to 10 days. Late leaves elongated more slowly than early ones. The number of leaves produced during the summer was greater than the number of small embryonic leaves in the winter bud. Hence, some of the late leaves probably developed from small embryonic leaves and also from primordia present in the spring (Kozlowski and Clausen, 1966).

LEAF GROWTH IN RECURRENTLY FLUSHING SPECIES

As mentioned earlier, it is difficult to characterize in general terms the leaf development of recurrently flushing species because the number of growth flushes for a species may vary considerably in different areas. Some features of leaf growth in a few recurrently flushing species will be described briefly.

Pinus taeda of the southern United States resumes shoot growth in late March or early April in the northerly parts of its range and about a month earlier in the southerly part. In North Carolina about one-fifth of its annual shoot growth occurs during each month from April to August (Kramer,

1943). Young trees usually produce three flushes of height growth with the first one the longest and the last the shortest. However, as many as seven annual flushes of growth have been reported. The number of annual growth flushes often is lower in the northern part of the range than in the southern part. The number of growth flushes of recurrently flushing pines often is positively correlated with tree vigor. Some races of pines can be made to flush throughout the year by favorable environmental conditions (R. M. Allen and McGregor, 1962).

In recurrently flushing pines there may or may not be distinct periods of inactivity between growth flushes. The shoots of recurrently flushing *Pinus echinata* and *P. rigida* trees in New Jersey had definite periods of bud inactivity between growth flushes. A peak in growth rate of each recurrent growth flush produced a new maximum in the seasonal growth curve (Tepper, 1963a). Kramer (1957) also emphasized the intermittent character of shoot elongation of some recurrently flushing species. He found, for example, that even when *Pinus taeda* seedlings were grown in a controlled environment under apparently near optimum environmental conditions, they grew intermittently rather than continuously. Other studies show, however, that in some areas recurrently flushing species may grow more or less continuously during much of the growing season. For example, in Louisiana, Eggler (1961) observed that when seasonal shoot elongation of young *Pinus taeda* trees resulted from two or more buds on the same shoot, the buds elongated more or less consecutively. As soon as one terminal bud on a shoot stopped elongating, the next one began to produce a shoot and there was no period of inactivity between growth flushes. The resulting seasonal elongation curve for a shoot generally was smooth. R. M. Allen and Scarbrough (1969) also found rather continuous seasonal shoot elongation among sequential flushes of shoot growth in 10-year-old *Pinus palustris* trees in Mississippi. Annual shoot expansion occurred mostly between March 1 and October 1. The winter bud contained all the nodes of the first growth flush. In the spring, internodal elongation occurred and essentially all activity was below the apical meristem. The apical meristem was inactive until sometime during the grand period of growth in the first flush and then it started forming the next bud. The first growth flush, in which the maximum rate of shoot elongation occurred in April, attained the greatest length followed by the second flush (Fig. 6.8). Each of the subsequent flushes produced about the same shoot length. The second flush of elongation began in mid-April, when the first flush was making its most rapid elongation. The third flush of elongation began shortly before the first flush stopped. The fourth flush started elongating before the second stopped, and the fifth started elongating before the third stopped. Thus, at least two flushes were elongating concurrently from the middle of April until late July, further emphasizing seasonal continuity of shoot

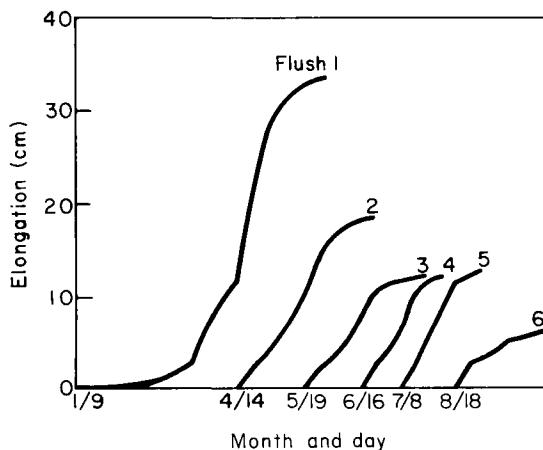


FIG. 6.8. Average cumulative seasonal elongation of successive growth flushes and formation of the winter bud of *Pinus palustris* saplings. [From R. M. Allen and Scarbrough (1969).]

expansion in this species. Similarly in the Mediterranean species, *Pinus halepensis* and *P. laricio*, recurrent flushes of growth often occur with negligible lapses of inactivity between periods of growth. In tropical and sub-tropical areas the terminal leaders of some pines, which usually are considered to grow in recurrent flushes, expand continuously throughout the year from activity of a single bud which does not go into dormancy. Such "foxtail" pines, which produce extremely long terminal internodes, are discussed further in Chapter 7 of this volume.

Because many gymnosperms produce only one internode and one whorl of branches per year their age can be easily determined by internode counts. This is not always easily accomplished in recurrently flushing species which annually produce variable numbers of internodes and branch whorls. The beginning of any one year's height growth in such multinodal species often can be recognized by a long internode. In some trees, however, the second internode of the year may be long also, adding to the difficulty of identifying the beginning of a previous year's growth. Wakeley and Marrero (1958) noted, however, that the last internode of multinodal pines in the southern United States invariably was short. This was true no matter how many internodes formed and whether the second internode was short or long. In addition, the whorl of branches which originated from overwintering lateral buds and identified the beginning of a year's shoot growth, usually had thicker branches than whorls which identified the beginning of branches formed later.

In *Citrus* increase in shoot length is the result of recurrent growth flushes from false terminal buds. These start to elongate, slowly at first, and then more rapidly. Thereafter, shoot elongation decelerates and finally ceases. This is followed by desiccation and abscission of the apical bud of the new shoot. Next there is a dormant period of approximately a week to several months during which new leaves and buds mature. Elongation of the shoot may begin again when one or more lateral buds near the terminal bud become active and produce new shoots in another growth flush (Schroeder, 1951).

Shoots of trees of the genus *Oreopanax* (Araliaceae), which grow in non-seasonal tropical climates, elongate in successive flushes and form "resting" buds between flushes (Borchert, 1969). The rhythm of flushing shows almost no correlation with major climatic factors. The first expanding leaves have a long petiole and a large, lobed, palmate leaf. In successive leaves both petiole length and blade size are reduced. Because of progressive reduction in leaf size and decrease in internode elongation, leaves of an increment are arranged in a terminal rosette. A conspicuous bud is absent when a leaf rosette enters a period of arrested growth. Following growth resumption, a bud emerges from the leaf rosette. As the bud emerges the bud scales grow to final size, and internodes between the scales elongate. The last bud scale is followed by the first of several new foliage leaves. As these expand and mature the bud scales are shed. At least 6 weeks go by from the time of emergence of the terminal bud from the leaf rosette to bud opening. During the rest period the small young bud contains only embryonic bud scales and primordia of some foliage leaves. The foliage leaves grow and develop only during the growth of the bud. Hence, bud development of *Oreopanax* is different than in many other recurrently flushing species whose buds contain a preformed shoot including well-developed but unexpanded leaves.

Periodicity of shoot growth in tea (*Camellia thea*) is a marked species characteristic. A vegetative shoot goes through recurrent cycles of growth alternation, involving periods of unfolding of cataphylls and normal foliage leaves, and of dormant "banjhi" periods during which growth in length is completed and lignification occurs, but no leaves unfold (T. E. T. Bond, 1942). Following dormancy the "banjhi" bud swells and finally produces an oval-shaped, unserrated cataphyll. Then a second cataphyll unfolds and the first one drops off. When the second cataphyll breaks off, a new small, blunt and partially serrated "fish-leaf" develops. In Assam the first cataphyll is called the "janam" and the fish-leaf is called the "gol-plat." With further bud opening, several normal flush leaves are produced and, having completed one cycle, the shoot goes into dormancy. In Ceylon a growth cycle involves two cataphylls, a fish-leaf and four flush leaves (T. E. T. Bond, 1942). About four full growth flushes are completed each year in Ceylon and they appear to be generally independent of seasonal climatic changes. Although five

annual flushes have been reported, they occur only rarely and apparently are confined to certain genotypes (Wight and Barua, 1955). The growth pattern varies slightly in Assam where tea usually has five growth flushes and a flush usually produces five normal leaves (Harler, 1964). The cyclic flushing pattern of tea sometimes is modified to the extent that strong "leader" shoots may grow more or less continually. Although the banjhi period appears to be one of inactivity, the apical bud in tea has no period of complete physiological dormancy. New leaf primordia for the ensuing growth flush are produced continuously but with a regular change of growth rate. The most intense activity is at the time of active flushing, after the first scale leaf of the current cycle has expanded. Thereafter, activity decreases to a minimum and later slowly increases again to the maximum. The rate of leaf growth is highly correlated with the rate of internode growth (T. E. T. Bond, 1945). During shoot expansion growth flushes on branches of two orders, such as the second and third order, may be occurring at the same time on different shoots of the same plant. However, when a new flush appears the initiation of additional flushes of a lower order ceases. Therefore, the beginning of the third flush prevents some shoots which are lacking in vigor from having more than one growth flush. In Assam, shoot growth of tea begins in February and ends in December, with the growth interval decreasing between each successive growth flush (Harler, 1964).

Cacao (*Theobroma cacao*) exhibits very intermittent shoot growth, with the exact pattern varying with the climatic regime. According to Alvim (1964) each recurrent cycle of shoot growth of cacao in the tropical lowlands of Costa Rica took about 8 weeks from bud opening to leaf hardening. The most intensive flushing took place in early spring (March) and the beginning of autumn (September to October). Alvim measured several climatic variables concurrently with shoot growth and found good correlation between diurnal temperature fluctuations and bud opening. In the Gold Coast area of Tafo, cacao shoot growth occurred in a series of periodic flushes which were similar from year to year (Greenwood and Posnette, 1950). Usually two flushes occurred in the dry season (December to March), a third early in the rainy season in May, a fourth during October when precipitation was plentiful, and a fifth at the end of the rainy season in November or early December. Consistently there was a long dormant period from June to September. Vidal Suarez (1955) noted that leaf flushes of cacao occurred irregularly except in clonal material derived from cuttings. The intervals between the periods of leaf flushes were different for all the trees observed. The total time required from beginning to ending of a leaf flush was about 30 days.

In young *Herea* trees the first growth flush produces a long internode which may exceed a foot in length. The internode of the second growth

flush may be less than an inch long and successive ones even shorter. The young, pendant red leaves are at first small, but they increase in size, change to a green color, and became horizontal after internode elongation ceases (Polhamus, 1962).

LEAF GROWTH IN LONG AND SHORT SHOOTS OF GYMNOSPERMS

As mentioned in Chapter 5, the presence of both long and short shoots in the same tree is characteristic of such genera as *Larix*, *Ginkgo*, and *Cercidiphyllum*. The structure of buds of putative long shoots of *Larix decidua* differs morphologically from short shoot buds (Frampton, 1960). The large terminal buds destined to become long shoots are borne on strong twigs and contain both "axial" and "fascicular" regions. The axial part rises vertically in the center of the bud and ends in the apical cone. The earlier formed fascicular part surrounds the axial portion. No internodes are discernible in either part. In England there are indications that dormancy comes to an end by February. In late March or early April the fascicular leaves elongate and push off the tips of the bud scales. Until early in May the development of the expanding long shoot resembles that of a short shoot. By the third week in May, however, the fascicular leaves achieve their maximum length of 1 to 2 cm and the young shoot axis then emerges. Thereafter, the shoot lengthens rapidly and after the middle of August elongation essentially ceases. Sequential development involves shoot lengthening, maturation of leaves, organization of a new terminal bud, and emergence of lateral buds.

The short shoot buds, which are borne on weak twigs lack the leaf bearing region of the axial part. When such a bud expands, the fascicular leaves push off the bud scales, as in long shoots, but as there is no axial portion to continue growth, the development of the short shoot is restricted and rapid. The needles elongate and development of new bud scales is well advanced in May (Frampton, 1960).

J. J. Clausen and Kozlowski (1967b) studied seasonal development of long and short shoots of *Larix laricina* in north central Wisconsin (Fig. 6.9). On short shoots all early needles appeared at bud break. These increased in length rapidly and when fully expanded were slightly longer than early needles of long shoots. Internode elongation on short shoots was negligible. On long shoots both early and late needles were produced. The full complement of 25 to 30 early needles appeared at bud break on long shoots of lateral branches. At first the outer early needles were the longest ones present, but they were eventually surpassed in length by early needles near the center of the cluster and slightly higher on the stem. Early needles increased in length from 1.5 mm just before bud break to 11 to 13 mm by late June. In contrast

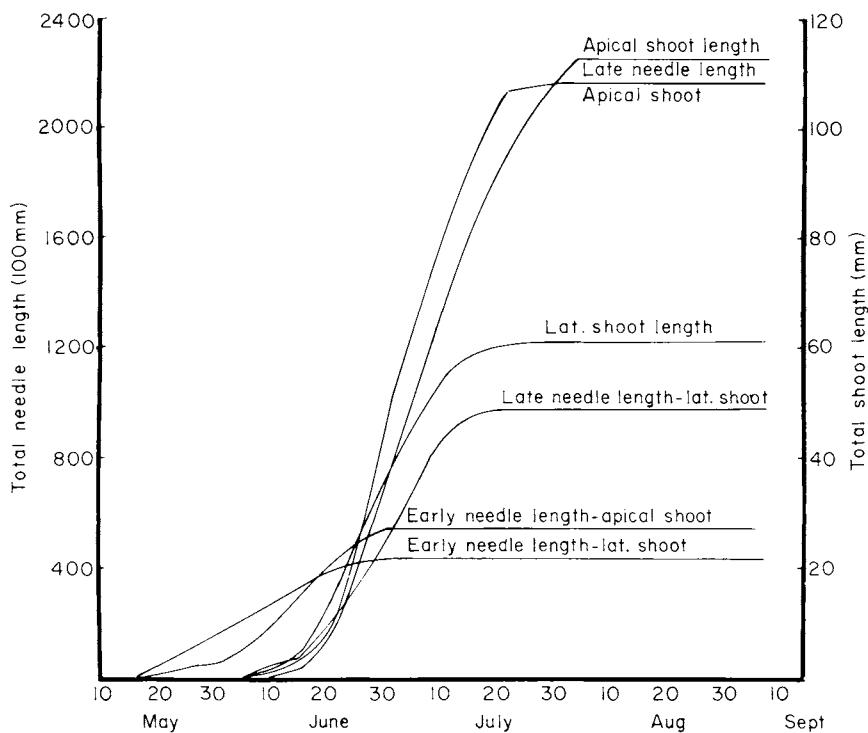


FIG. 6.9. Seasonal patterns of elongation of shoots and early and late needles of *Larix laricina*. [From J. J. Clausen and Kozlowski (1967b).]

to early needles, late needles were produced continuously during much of the growing season. Externally visible late needles averaged only 13 in number at bud break and increased to approximately 40 by late July, by which time they also attained their maximum length of approximately 7 mm. The number of early needles was about the same on apical long shoots as on lateral long shoots. However, at the end of the season there were almost twice as many late needles on apical long shoots as on laterals. On both apical and lateral long shoots, total elongation of all late leaves was highly correlated with internode growth. However, as some late leaves completed elongation much earlier than others, the timing of internode expansion was not correlated with growth of individual late leaves.

About 75% of stem elongation, more than 70% of stem weight increment, and 65–70% of late-needle elongation occurred after early needles of long shoots were full sized. After late needles achieved maximum length and weight, the weight of needles began to decline and stem weight increased,

probably largely because of translocation of carbohydrates from needles to stems. Early needles on long shoots probably utilized large amounts of food reserves while they were growing and later contributed current photosynthate to growth of the stem and late needles.

In *Larix laricina* the long shoot bears a cluster of needles at the base as well as needles inserted along the stem. J. J. Clausen and Kozlowski (1970) examined these two types of needles for dimorphism but did not find any obvious external morphological differences between them. All the basal needles and about half the stem needles were preformed in the unexpanded bud. As about half the stem needles were not preformed, it was postulated that they might show distinct late-leaf characteristics. However, there was an overlap in appearance and length between basal and stem needles and no discontinuity was found between needle length of preformed and nonpreformed stem needles. The older stem needles were morphologically indistinguishable from adjacent basal needles. Thus, it was not possible to determine by external examination of the needles which portion of the shoot was preformed.

Both long and short shoots of *Cercidiphyllum japonicum* are characterized by a single, precociously expanding leaf. Such a leaf matures in the short shoot and other leaves remain primordia. Growth of long shoots involves elongation of internodes and maturation of four to six pairs of leaves. After a month or two of growth the apex and terminal internode of the long shoot abscise. In the following year sympodial growth occurs from the uppermost axillary buds. Short shoots also grow sympodially from lateral axillary buds (Titman and Wetmore, 1955).

Leaf Senescence

For most of their existence leaves are either growing or senescent. For example, during a life-span of about 200 days leaf expansion in *Acer* and *Parthenocissus* occupied about 80 days and senescence another 80 days. The time during which leaves were neither growing nor senescent was only about 40 days (Moore, 1965).

Everyone is familiar with the relatively rapid synchronous aging of leaves of common deciduous trees. The most obvious sign of leaf senescence is abscission, but before this occurs the aging leaves undergo a series of internal changes. During leaf senescence there is a general trend from anabolism to catabolism. Both photosynthetic and respiratory capacity decline. Other signs of leaf senescence include changes in pigments, decreases in dry weight, proteins, and in minerals, as well as changes in enzymatic activity. Some of these changes will be described briefly.

PHOTOSYNTHESIS

In very young leaves total CO₂ uptake is low, reflecting the small amounts of mesophyll and chlorophyll. Photosynthesis then increases progressively in the growing leaf until maximum photosynthetic capacity usually is attained near the time of completion of most rapid growth. With further aging, photosynthesis generally decreases until abscission occurs. Typical patterns of changes in photosynthesis with aging of leaves of deciduous species were shown by Richardson (1957). In *Acer saccharinum*, for example, photosynthesis in very young leaves was low, somewhat higher in half-expanded leaves, and highest when the leaves were fully expanded. The rate then declined until in old leaves it was only one-half to one-third that of fully expanded leaves. Photosynthesis of date leaves declined progressively after the first year (Fig. 6.10). Four-year-old leaves were only about 65% as efficient in CO₂ uptake as were 1-year-old leaves (Nixon and Wedding, 1956). Similar patterns were shown for *Citrus* with youngest leaves having low rates of photosynthesis which increased to leaf maturity and then slowly decreased (Rhoads and Wedding, 1953).

Several investigators have shown decreasing photosynthesis in gymnosperm leaves beginning approximately when maturity was attained. According to Freeland (1952), leaves of five species of gymnosperms attained maximum

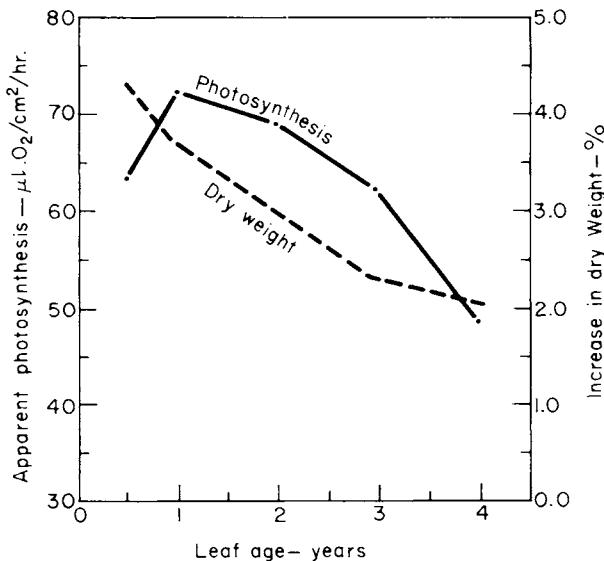


FIG. 6.10. Rate of apparent photosynthesis in date leaves compared with dry weight increase over a 10.5-hour period during the day. [From Nixon and Wedding (1956).]

photosynthesis near the time of leaf maturity during the first season of growth. Beginning during the second year the rate of photosynthesis decreased slowly with increasing age of needles. Clark (1961) also demonstrated that, with the exception of new needles, CO₂ uptake during the growing season of *Picea glauca* and *Abies balsamea* was fairly constant with each age of needle, but it decreased progressively with increasing needle age from 1 to 6 years. Reduction in photosynthesis in old over young needles in *Picea* was greater than in *Abies*. In new needles apparent photosynthesis was negative early in the season but increased steadily to reach positive values by mid-June. Maximum photosynthesis of the new needles was achieved in September and October. By that time photosynthesis of the new needles exceeded that of all older needles. These observations were consistent with those of Kuroiwa (1960) who found that needle thickness increased but photosynthesis decreased with aging of needles of *Abies veitchii* and *A. mariesii*.

RESPIRATION

Young leaves have high rates of respiration. As they age respiration per unit of dry weight decreases, to a large extent because of an increase in dry weight largely due to thickening of cell walls (Kramer and Kozlowski, 1960). Richardson (1957), for example, related the higher respiration of young leaves over old ones to the greater proportion of protoplasm to cell wall material in the former. At some advanced stages of leaf senescence respiration may suddenly increase. Such a late burst of respiratory activity resembles the climacteric of senescent fruits and often is characteristic of detached leaves. Respiratory measurements on leaf discs of *Prunus serrulata* showed a continuing increase in oxygen uptake as soon as leaves were detached from the tree, with a peak reached in 10 days. During this 10-day period both protein level and chlorophyll declined. After this initial phase there was a continuous decrease in respiration which corresponded to a slow decrease in protein level (Osborne and Hallaway, 1960a).

PIGMENTS

In many species aging leaves gradually lose their green color and yellowing, the result of unmasking of carotenoid pigments, eventually is followed by internal disintegration of cellular structure. In other species the development of anthocyanin pigments which produce the characteristic pink, red, and purple autumn colors takes place during senescence. Hence, arrested chlorophyll synthesis and breakdown of chlorophyll already present in senescent leaves often are obscured by formation of bright anthocyanin pigments. The anthocyanins form during cool weather in trees having hereditary potentiality for producing these pigments.

Moore (1965) studied changes in chlorophylls, carotene, sugar, shikimic acid, and anthocyanin pigments in leaves of *Acer pseudoplatanus* and *Parthenocissus tricuspidata*. In *Parthenocissus* losses of chlorophylls, carotene, sugar, and shikimic acid during senescence were closely correlated, and were inversely related to anthocyanin accumulation. In *Acer* leaves losses of chlorophylls, carotene, and sugar were also closely correlated. Significant differences were found in shikimic acid content between *Acer* leaves, which did not form anthocyanins, and *Parthenocissus*, which did.

Different species of woody plants vary greatly in autumn color. In *Acer saccharum*, *A. rubrum*, *Sassafras*, and *Amelanchier* magnificent displays of colors ranging from yellow to orange, scarlet, crimson, and purple may be seen, sometimes on the same tree. *Quercus alba*, *Q. coccinea*, *Rhus*, and *Viburnum* often show deep red autumn colors, but they may vary from scarlet to crimson. In marked contrast, *Gleditsia*, *Morus*, *Populus*, *Ginkgo*, and most species of *Betula* assume various shades of yellow. Leaves of still another group including *Juglans*, *Catalpa*, *Ulmus*, *Carya*, *Tilia*, *Aesculus*, and *Castanea* tend to become yellow-green to yellow. In *Alnus*, *Robinia*, *Sambucus*, and *Salix* the senescent leaves exhibit little or no color change. The yellow-brown colors of *Fagus* and some species of *Quercus* have been traced to the presence of tannins as well as carotenoid pigments.

The extent and rate of chlorophyll disintegration in aging leaves vary among species. Whereas rapid chlorophyll breakdown (35 days) occurred in leaves of *Magnolia kobus* var. *borealis*, slow disintegration (more than 60 days) took place in *Morus alba*. Before they abscised the leaves of *Acer platanoides* and *Fagus* lost practically all their chlorophyll whereas *Syringa* lost only 40%. In some species, such as *Morus alba*, chlorophyll breakdown stopped rather suddenly before leaf fall (Wieckowski, 1958). Wolf (1956) demonstrated very large decreases in chlorophyll content during autumnal leaf aging (Table 6.3). The extent of chlorophyll destruction in yellow leaves of the species examined averaged 84.4% with a range of 69.7–96.2%. In green leaves chlorophyll *a* averaged 69.4% of the chlorophyll present but in yellow leaves it comprised only 56.2% of the total. Chlorophyll *a* was destroyed more rapidly than chlorophyll *b* in many species.

Goodwin (1958) followed changes in both chlorophyll and carotenoids from June to November in *Prunus nigra*, *Quercus robur*, and *Acer pseudoplatanus* (Figs. 6.11 and 6.12). In *Quercus* and *Acer* both chlorophylls and carotenoids decreased almost to zero. In *Quercus* these were depleted simultaneously, whereas in *Acer* the decline in chlorophyll preceded that in carotenoids. In *Prunus* the carotenoids tended to disappear first, but carotenoids and chlorophylls decreased only by about half. In *Acer platanoides* the number and kind of carotenoids present in leaves in summer and autumn remained constant while the leaves were green. When the leaves began to change color, however, a carotenoid pigment formed which was different

TABLE 6.3
CHLOROPHYLL CONTENT OF GREEN AND YELLOW AUTUMN LEAVES OF FOREST TREES^a

Species	Total chlorophyll (mg/gm)		Chlorophyll A (%)		Reduction in total chlorophyll Percent
	Green leaves	Yellow leaves	Green leaves	Yellow leaves	
<i>Liriodendron tulipifera</i>	2.19	0.29	67.5	40.1	86.8
<i>Populus nigra</i> var. <i>italica</i>	1.79	0.27	73.6	63.4	85.2
<i>Magnolia grandiflora</i>	1.74	0.14	75.4	47.9	91.9
<i>Cercis canadensis</i>	1.55	0.12	71.8	43.0	92.2
<i>Acer saccharum</i>	1.38	0.19	69.4	56.5	86.5
<i>Liquidambar styraciflua</i>	1.23	0.05	70.1	57.4	96.2
<i>Acer saccharinum</i>	1.19	0.26	62.5	42.7	78.1
<i>Juglans nigra</i>	1.10	0.26	65.4	49.4	76.4
<i>Celtis occidentalis</i>	1.06	0.32	71.5	65.1	69.7
<i>Cornus florida</i>	0.97	0.18	64.9	53.6	81.4
<i>Ulmus americana</i>	0.93	0.15	70.4	57.9	83.6
<i>Quercus macrocarpa</i>	0.92	0.11	68.0	47.4	87.6
<i>Fagus grandifolia</i>	0.90	0.22	64.4	57.4	75.3
<i>Quercus palustris</i>	0.87	0.17	71.3	54.2	80.6
<i>Carya</i> sp.	0.76	0.16	70.7	67.1	78.9

^a From Wolf (1956).

from those present in the summer and the total amounts of carotenoids decreased (Eichenberger and Grob, 1962).

Leaf senescence does not occur simultaneously throughout the leaf blade. In *Acer* and *Parthenocissus* leaves, for example, senescence typically occurred first in tissues most remote from leaf veins, i.e., at leaf edges. The area of senescent tissue subsequently enlarged toward the center of the leaf between the major and minor veins. Each area of tissue senesced first in the center of vein islets and, in final stages of senescence, only the tissues adjacent to major veins retained their green color (Moore, 1965).

MINERAL ELEMENTS

Growing leaves usually accumulate minerals. During leaf senescence, however, certain mineral elements are lost in appreciable amounts by translocation back into twigs and branches and by increased leaching from senescent cells. Losses by retranslocation are especially large. Whereas potassium, nitrogen, and phosphorus commonly are lost during leaf senescence, calcium and magnesium generally are retained (Moore, 1966). Nitrogen especially is lost in large amounts. In *Betula*, for example, leaves

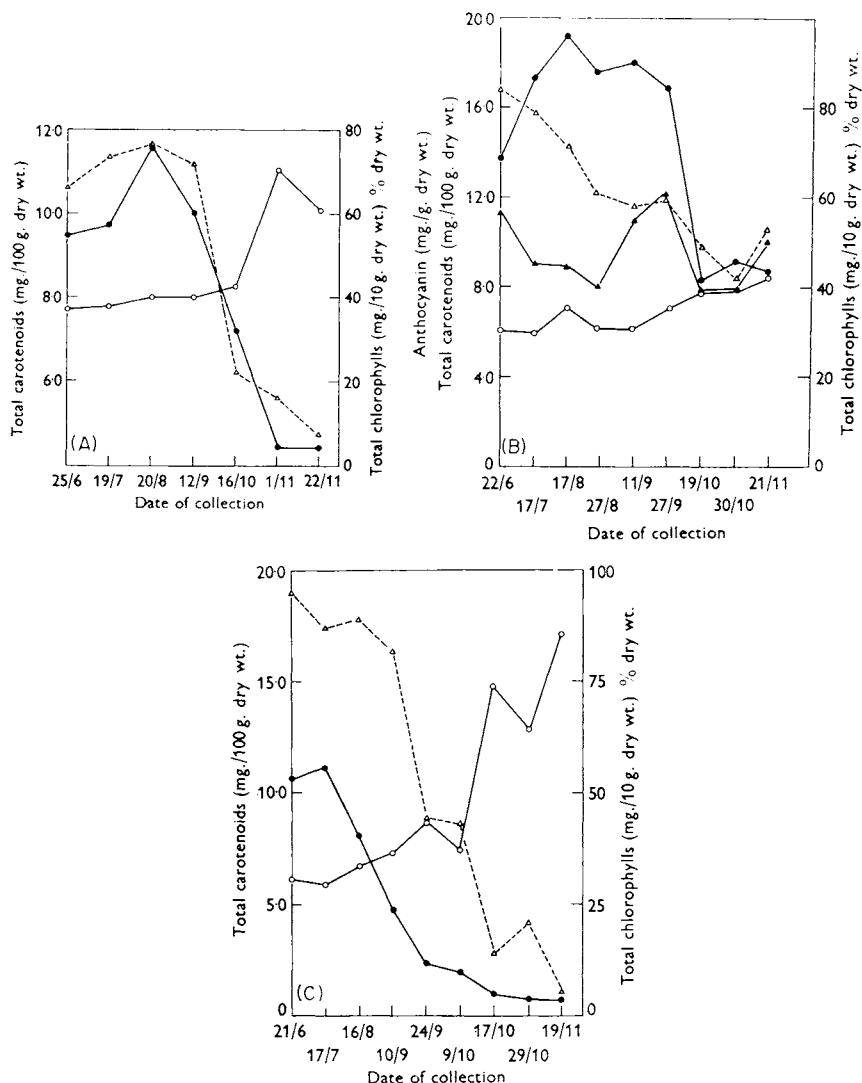


FIG. 6.11. Species variations in leaf dry weight and pigments during summer and autumn.
 (A) *Quercus robur*; (B) *Prunus nigra*; (C) *Acer pseudoplatanus*. ● — Total chlorophyll;
 △ — total carotenoids, ○ — dry weight, ▲ — anthocyanin. [From Goodwin (1958).]

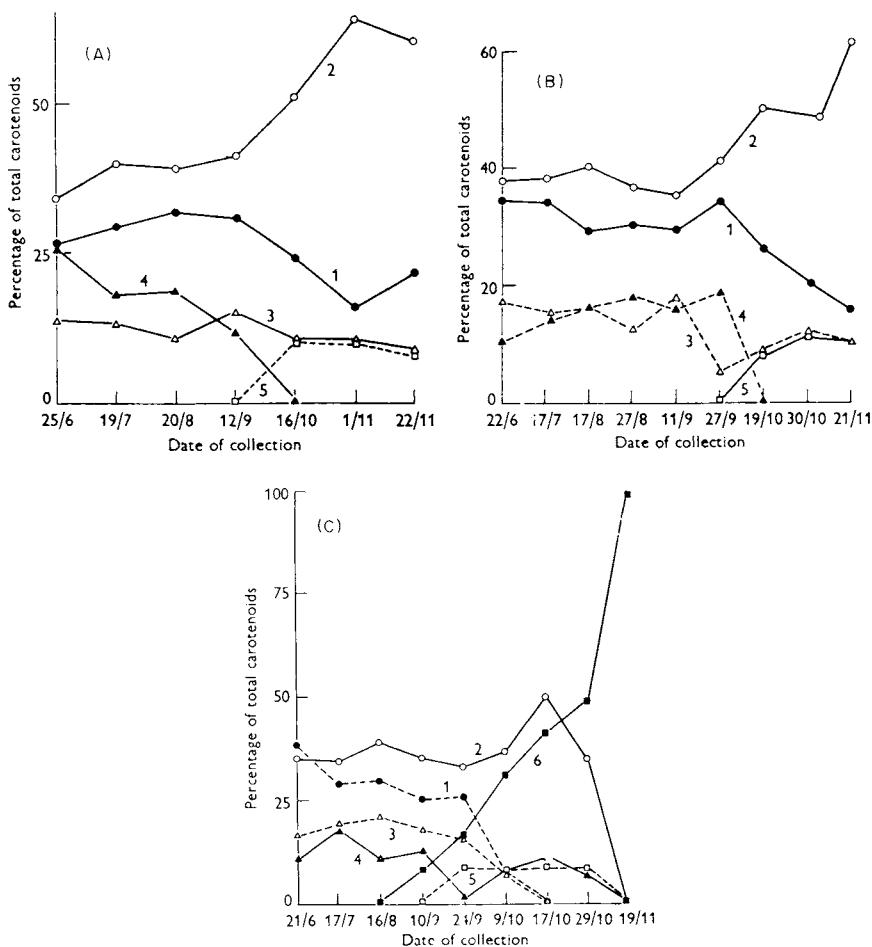


FIG. 6.12. Species variations in relative amounts of carotenoid pigments during summer and autumn. (A) *Quercus robur*; (B) *Prunus nigra*; (C) *Acer pseudoplatanus*. 1, carotene; 2, lutein; 3, violaxanthin; 4, neoxanthin; 5, lutein epoxide; 6, xanthophyll esters. [From Goodwin (1958).]

which began to yellow in the autumn lost from a third to a half of their nitrogen in approximately 2 weeks (Tamm, 1951). In *Malus*, 52, 27, and 36%, respectively, of the nitrogen, phosphorus, and potassium content were translocated from aging leaves to the twigs and branches. Dry weight of the leaves decreased by 16%. The major loss of dry matter and nitrogen began after the first week of October and took place in a 3- to 4-week period during

which the abscission layer was forming. Loss of minerals accounted for 40–50% of the decrease in leaf dry weight. Much of the remaining dry weight loss was accounted for by translocation into the bark of organic compounds such as carbohydrates. Since the loss of minerals from leaves was quantitatively a very steady process it was unlikely that leaching from the leaves accounted for a significant loss (Oland, 1963).

Increases in the amounts of certain elements lost by leaching occur as leaves become senescent. For example, in *Acer platanoides* loss of potassium by leaching from green leaves was low, with greater quantities of potassium leached from leaves showing some yellowing. Leaching experiments with detached leaves showed that the proportion of leaf potassium which could be removed by leaching increased as senescence progressed, with the amount leached proportional to the area of the leaf which had yellowed (Moore, 1966). As sodium was less readily removed from senescent leaves than potassium, there appeared to be a difference in the manner in which these ions were held by the leaf. These observations were in accord with evidence that senescence of a variety of tissues is accomplished by increased leakage of solutes from cells (Leopold, 1961, 1964).

Leaf senescence is characterized by decreases in nitrogen compounds. Osborne (1962), for example, reported decreases in levels of protein, RNA, and DNA in aging *Xanthium* leaves. Plaisted (1958) studied chemical changes in actively growing and aging *Acer pseudoplatanus* leaves. In very young leaves the amount of protein per leaf increased during the spring and early summer. Late in the summer, proteins reached a constant level and then rapidly declined in senescent leaves. The amount of soluble nitrogen tended to parallel protein content, except for the last few days before abscission, when it increased. The seasonal trend of amino acids divided them into three groups (Table 6.4): (A) aminobutyric acid and serine plus glycine followed a trend similar to that of protein, (B) aspartic acid, glutamic acid, and alanine decreased as the leaves aged, (C) glutamine, the leucines, phenylalanine, threonine, and valine increased in amount as the leaf senesced and abscission approached. Carbohydrates declined materially during senescence (Table 6.5).

Abscission of Leaves

Woody plants are defoliated periodically. Most angiosperms of the Temperate Zone shed their leaves in the autumn but they may lose them at any time during growth in response to injury, or unfavorable environmental conditions (Kramer and Kozlowski, 1960).

Some trees (e.g., *Citrus*) lose leaves continuously but have pronounced

TABLE 6.4
CHANGES IN AMINO ACIDS (AA) OF AGING *Acer platanoides* LEAVES^a

	Amount of AA (μg/leaf)	23	68	118	149	169	183	188	growth: 200
Aminobutyric acid	80	32	22 ± 4	144 ± 4	76 ± 2	36 ± 1	49 ± 2	37 ± 2	
Serine plus glycine	10	45	43 ± 5	91 ± 5	71 ± 1	34 ± 1	32 ± 5	45 ± 2	
Aspartic acid	17	18	33	10	8	4	5		T ^b
Glutamic acid	224	104	67 ± 6	47	61	— ^c	61	23	
Alanine	107	66	86 ± 16	62 ± 1	26 ± 1	18 ± 4	37 ± 1	27 ± 9	
Glutamine	58	15	39 ± 9	25	53	92	125	126	
Leucines	15	—	12	10	5	20	45 ± 1	57	
Phenylalanine	12	—	T	T	T	T	11	18	
Threonine	19	7	14 ± 1	17 ± 2	12 ± 3	10 ± 1	20 ± 3	28 ± 1	
Valine	T	5	9 ± 1	6	5	13 ± 3	23 ± 3	41 ± 15	

^a From Plaisted (1958).^b Trace.^c No determination made.

TABLE 6.5
CARBOHYDRATE CONTENT OF AGING *Acer platanoides* LEAVES^a

Days after beginning of leaf growth	Sucrose (mg/leaf)	Starch (mg/leaf)
149	21.0	11.9
169	16.8	8.6
189	12.1	5.9
200	7.6	6.0

^a From Plaisted (1958).

seasonal peaks of abscission. In Riverside, California, leaf fall of Washington Navel and Valencia orange trees was at a maximum during the bloom period in April. On the day of maximum leaf drop, Washington Navel orange trees lost more than 3200 leaves per tree. In contrast, only about 50 leaves were lost per day during periods of minimum abscission (Erickson and Brannaman, 1960).

LEAF ABSCISSION IN TROPICAL SPECIES

A variety of patterns of leaf abscission and leaf renewal occur in tropical trees. Numerous plants native to seasonal tropical areas, especially certain members of the Leguminosae, show seasonal shedding of foliage. Like many Temperate Zone trees, such plants cease forming new leaves and shed all

their foliage annually. In *Plumeria acuminata* plants in Hawaii, for example, there was an increase in the number of leaves from August to mid-October. Thereafter, net loss of leaves occurred until the plants were completely defoliated by late January. Abscission occurred in two stages, with slow initial leaf shedding up to mid-January and eventual and complete leaf drop toward the end of January (Murashige, 1966).

Leaf abscission of some tropical species is strongly controlled by hereditary factors and does not fluctuate greatly with small climatic changes. In other species, however, leaf fall occurs several times during the year in response to minor climatic changes, especially droughts. Leaf fall occurs over a period of a few weeks but in some instances this may take only a few days. In some species all or most leaves abscise quite some time before new leaves expand, leaving bare trees for extended periods. Examples are *Bombax flammeeum*, *B. malabaricum*, *Hymenaea courbaril*, *Koompassia malaccensis*, and *Terminalia superba*. In other species, the old leaves abscise only a short time before the new leaves expand.

Tropical species vary widely in their resistance to dry weather. In northwestern Brazil almost all deciduous trees of the "Caatinga" drop their leaves with the onset of drought and replace them when rains resume (Alvim, 1964). In Trinidad, several species including *Hymenaea courbaril*, *Platymiscium trinitatis*, *Copaisera officinalis*, and *Albizia caribea* have a short leafless period of a few days or weeks at the beginning of the dry season. These species are in leaf again at the time of maximum drought. All other deciduous species of Trinidad have relatively long leafless periods, with abscission occurring gradually with increasing water deficits. Many species do not lose all their leaves during the dry season, but abscission never occurs during the wet season (Beard, 1946).

Alvim (1964) stressed the importance of photoperiod in influencing abscission of tropical species. He found that in tropical latitudes with seasonal differences in daylength leaf abscission usually occurred during short days.

Holtum (1931, 1940) emphasized wide variability among leaf abscission patterns of tropical species. He placed species growing in Singapore, which has a very uniform climate and about 100 in. of rain per year, into the following groups:

(1) Deciduous species with annual leaf periods (*Kigelia pinnata*, *Hymenaea courbaril*, *Parkia javanica*, *Terminalia subspathulata*, *Canarium rufum*).

(2) Deciduous species with leaf periods greater than 12 months (*Cedrela glaziovii*, *Koompassia malaccensis*, *Caesalpinea ferrea*, *Homalium grandiflorum*, *Heritiera elata*, *H. macrophylla*).

(3) Deciduous species with leaf periods between 6 and 12 months (*Adenanthera pavonina*, *Cassia fistula*, *Cratoxylon formosum*, *Delonix regia*, *Ficus variegata*, *Lagerstroemia flos-reginae*, *Salmalia malabarica*, and *Sterculia macrophylla*).

(4) Deciduous species with irregular leaf periods (*Cassia nodosa*, *Dyera costulata*, *Ficus caulocarpa*, *Hevea brasiliensis*, *Mangifera indica*, *Sindora wallichii*, and *Sterculia carthagensis*).

In *Hevea* the intervals of leaf abscission vary among trees and they also change with tree age. Individual branches of *Mangifera* produce leaves at different times. Hence, leafing-out of a tree often occurs over a period of weeks. The pattern is similar to that in *Ceiba pentandra* in West Africa. Some branches of this species often are leafless while others are in full leaf (Richards, 1964).

(5) Evergreen species produce new leaves periodically, often at intervals of a few months. The old leaves generally do not abscise when new leaves have expanded, but remain on the tree for extended periods of time. Hence, growth of new leaves is stimulated by factors other than loss of old leaves.

THE MECHANISM OF LEAF ABSCISSION

Separation of leaves from a tree is achieved through physiological changes causing the formation of an abscission zone, mechanical factors, or a combination of both. In most trees leaf abscission involves cytolysis which weakens the cells of an abscission layer sufficiently so that the leaf falls. Cytolysis is not involved in mechanical separation.

Although most deciduous trees form an abscission layer and shed their leaves in the autumn, some marcescent species do not shed leaves until spring. In some oaks, for example, the leaves turn brown and die in the autumn but remain attached through the winter. In the spring formation of an abscission layer is completed and the leaves are shed.

Hoshaw and Guard (1949) found that abscission layers did not form at the petiole base of *Quercus palustris* or *Q. coccinea* leaves by the end of the summer. In *Q. coccinea* the first evidence of change was observed in winter (early January) when a lignified layer formed across the entire petiole base. In *Q. palustris* such a layer was first observed in late February. In the early period of leaf abscission, which began in March, no anatomical changes, other than the formation of a lignified layer, were noted. Early leaf abscission involved breaking of cell walls apparently because of mechanical forces. However, during late leaf-fall a softening of cell walls was observed. Thus, complete defoliation resulted from both mechanical forces and digestion of cell walls of the abscission layer.

The speed of shedding of marcescent leaves often varies considerably even among closely related species. For example, *Quercus coccinea* shed its leaves rapidly and uniformly since the vascular strands were small. Leaves of *Q. velutina* began to fall at about the same time as those of *Q. coccinea* but because the petioles of *Q. velutina* were larger, leaf abscission proceeded more

slowly. *Q. rubra*, with large vascular strands with heavy walls, shed its leaves more slowly than either *Q. coccinea* or *Q. velutina* (Berkeley, 1961).

FORMATION OF THE ABSCISSION LAYER

As mentioned, separation of most leaves from trees occurs at a discrete abscission zone. In simple leaves of angiosperms, the abscission zone forms along or at the base of the petiole. In compound leaves, individual abscission zones develop at the base of each leaflet as well as at the petiole of the whole leaf. As the abscission zone is mostly parenchymatous it has little strengthening tissue except for the vascular elements.

The abscission zone is made up of short and compact cells without inter-cellular spaces. The parenchyma cells of the abscission zone have thin walls and are unlignified. As the time for abscission approaches, several important changes occur, including development of tyloses, and blocking of vessels, increase in density of protoplasm, and starch deposition in the abscission layer. The cell walls swell and digestion of pectic and cellulosic materials takes place. Actual separation of leaves occurs between rows of cells, usually leaving a smooth scar. Shortly before or after actual separation occurs, a protective layer begins to form through deposition of various substances such as suberin and wound gum. In addition, some species develop protective periderm layers beneath the protective layer. These develop through meristematic activity of parenchyma cells of the abscission zone (Addicott, 1964).

According to Addicott and Lynch (1955), separation of leaves may result from dissolution of one or more layers of cells or cell parts. Three distinct types of dissolution have been reported: (1) the middle lamella between two layers of cells dissolves, but the primary walls remain intact, (2) both the middle lamella and primary cell walls between two layers of cells dissolve, and (3) entire cells of one or more layers dissolve.

Chemical changes in abscission zones include enzymatic conversions of calcium pectates to pectic acid, which in turn is converted to water soluble pectin (Facey, 1950). Yager (1960) duplicated the separation of cells observed normally during abscission by incubating plant tissue from the abscission zone with various pectic enzymes. Two possible roles of pectic enzymes in abscission were suggested: (1) factors which prevent activity of pectin methyl-esterase might cause abscission by allowing water-soluble pectin to accumulate, or (2) other pectic enzymes might be involved in producing pectin or otherwise causing chemical breakdown of the middle lamella.

It has been claimed that leaves of gymnosperms are lost by mechanical breakage rather than by chemical changes (Facey, 1956). Nevertheless, Sifton (1966) found that the abscission layer of *Picea* needles underwent the same pectic changes which took place during abscission of leaves of

deciduous species. In *Picea*, however the needles had strong vascular strands with considerable secondary tissues. These strands maintained attachment of leaves until they became brittle from drying.

CONTROL OF ABSCISSION

Under natural conditions leaves abscise when they become yellow and senescent. However, under extreme environmental stresses, such as drought, leaves often are shed when green, but physiological processes (e.g., protein synthesis) are reduced to levels similar to those in senescent leaves (Osborne, 1968).

A number of environmental factors including light, water, gases, minerals, and soil conditions either retard or accelerate abscission (Table 6.6). If the

TABLE 6.6

EFFECTS OF SOME ENVIRONMENTAL FACTORS ON PROMOTION OR RETARDATION OF ABSCISSION^a

Factors	Promotion →	Retardation ←
Temperature		
Moderate	→	
Light frost	→	
Extremes: heat or frost	←	
Light		
Photosynthetic: moderate	→	
deficiency or excess	←	
Photoperiodic: long days	←	
short days	→	
Water		
Drought or flooding	→	
High humidity	→	
Gases		
Oxygen	→	
< 20% oxygen	←	
Carbon dioxide	↔	
Ethylene	→	
NH ₃	→	
Mineral and soil factors		
Nitrogen	↔	
Deficiencies of N, Zn, Ca, S, Mg, K, B, Fe	→	
Excessive Zn, Fe, Cl, I	→	
Salinity and alkalinity	↔	
Biotic factors		
Insect or fungus injury to leaf blade	→	

^a From Addicott (1968).

abscission zone is sufficiently damaged by environmental extremes, such as heavy frost, the normal process of abscission cannot occur. Environmental changes influence abscission through the intermediation of various internal physiological processes and conditions (Table 6.7). Among the important

TABLE 6.7

SOME INTERNAL EFFECTS OF ENVIRONMENTAL FACTORS IN PROMOTION OR RETARDATION OF LEAF ABSCISSION^a

Factors	Internal effects	Promotion → Retardation ←
Temperature	Metabolism Respiration	{ →
Light		
Photosynthetic	Substrates Cell walls	{ →
Long day	Auxin Gibberellin Abscisic acid	{ → ←
Short day	Auxin Gibberellin Abscisic acid	{ ← →
Water		
Drought or flooding	Degenerative changes	→
High humidity	Solubilization of cell walls	→
Gases		
Oxygen	Respiration IAA-oxidase	{ →
Carbon dioxide	Respiration	←
NH ₃	Degenerative changes	→
Ethylene	Respiration Enzyme synthesis	{ →
Mineral factors		
Nitrogen	Amino acids Auxin Cytokinin	{ →
Calcium	Calcium pectate	→
Zinc	Tryptophan Auxin	{ →
Sulfur	Sulfhydryl compounds	→
Excessive Zn, Fe, I etc.	Degenerative changes	→
Biotic factors		
Insect or fungus	IAA-oxidase	→
injury to leaf blade	Ethylene Unknown abscission accelerants	{ →

^a From Addicott (1968).

internal factors involved in leaf abscission are hormones, sugars, pectins, cellulose, enzymes, amino acids, and purines (Addicott, 1968).

Abscission is prevented by substances produced in the leaf blade. Removal of a portion of a green blade or injury by insects or diseases causes senescence of the petiole and its earlier-than-normal abscission. Auxin apparently plays a key role in preventing abscission. Auxin levels are highest in young leaves and decrease as leaves senesce and abscise. However, as mentioned in the section on leaf senescence, other hormones also control senescence of leaves of various species.

Suggested Collateral Reading

- Addicott, F. T. (1968). Environmental factors in the physiology of abscission. *Plant Physiol.* **43**, 1471–1479.
- Berkeley, E. E. (1961). Marcescent leaves in certain species of *Quercus*. *Bot. Gaz.* **92**, 85–93.
- Carns, H. R. (1966). Abscission and its control. *Annu. Rev. Plant Physiol.* **17**, 295–314.
- de Laubenfels, D. J. (1953). The external morphology of coniferous leaves. *Phytomorphology* **3**, 1–20.
- Esau, K. (1965a). "Vascular Differentiation in Plants." Holt, New York.
- Esau, K. (1965b). "Plant Anatomy," Chapter 16. Wiley, New York.
- Foster, A. S. (1936). Leaf differentiation in angiosperms. *Bot. Rev.* **2**, 349–372.
- Humphries, E. C., and Wheeler, A. W. (1963). The physiology of leaf growth. *Annu. Rev. Plant Physiol.* **14**, 385–410.
- Leopold, A. C. (1967). The mechanism of foliar abscission. *Symp. Soc. Exp. Biol.* **21**, 507–516.
- MacDaniels, L. H., and Cowart, F. F. (1944). The development and structure of the apple leaf. *Cornell Univ., Agr. Exp. Sta., Mem.* **258**.
- Milthorpe, F. L., ed. (1956). "The Growth of Leaves." Butterworth, London and Washington, D.C.
- Mounts, B. T. (1932). The development of foliage leaves. *Iowa Univ. Stud. Nat. Hist.* **14**, 1–19.
- Osborne, D. J. (1968). Defoliation and defoliants. *Nature (London)* **219**, 564–567.
- Owens, J. N. (1968). Initiation and development of leaves in Douglas fir. *Can. J. Bot.* **46**, 271–278.
- Tetley, U. (1936). Tissue differentiation in some foliage leaves. *Ann. Bot. (London)* [N.S.] **50**, 523–557.

Chapter 7

VARIATIONS IN SHOOT GROWTH

Introduction

Shoot growth in woody plants is exceedingly variable with respect to rate and duration. The rate of growth of young trees and ultimate height achieved by adult trees often are not correlated and differ greatly among species. Within and among species the duration of shoot growth varies seasonally, diurnally, and with altitude and latitude. There is also marked variation in the amount and duration of shoot growth in different parts of the same tree, and from tree to tree. The present chapter will discuss these variations in shoot growth, with primary emphasis on internode elongation. As pointed out earlier, however, shoot growth usually involves growth of both internodes and leaves which may or may not be correlated.

Amounts of Shoot Growth

Trees vary greatly in amounts of seasonal and ultimate total shoot elongation during their lifetime. As a rule, during the first few years after seed germination, height growth of a tree rapidly increases a little each year until the maximum annual height growth is attained. Although the time of achieving maximum rate of height growth varies in different species of forest trees and on different sites, it is attained relatively early, usually when a tree is in the pole stage. After the maximum rate of height growth is attained, it is continued with but little variation for some years, and then decreases more or less rapidly.

In relatively young trees the amount of annual height growth varies greatly with the type of shoot produced in various species. Shoots of heterophyllous species usually tend to grow more than those of species with shoots fully preformed in the dormant bud. Recurrently flushing species, such as *Pinus taeda* and *P. radiata*, grow taller each year, when both achieve maximum

TABLE 7.1

VARIATIONS IN SIZE, GROWTH RATE, AND LIFE-SPAN OF NORTH AMERICAN GYMNOSPERMS.
THE VALUES ARE APPROXIMATE^a

Species	Stem diameter ^b at maturity (ft.)		Height at maturity (ft.)		Relative growth rate	Life- span (years)
	Average	Maxi- mum	Average	Maxi- mum		
<i>Abies amabilis</i>	2-4	6	140-160	250	Moderate	250-300
<i>balsamea</i>	1-1.5	3	40-60	85	Rapid	100-150
<i>concolor</i>	3-4	6	120-150	200	Moderate	150-400
<i>fraseri</i>	1-2	2.5	30-50	65	Moderate	200-300
<i>grandis</i>	2-4	6	120-160	250	Moderate	200-400
<i>lasiocarpa</i>	1.5-2	3	60-100	160	Moderate	150-200
<i>magnifica</i>	4-5	10	150-180	230	Moderate	250-400
<i>procera</i>	2.5-5	8	140-160	260	Rapid	300-500
<i>Chamaecyparis lawsoniana</i>	3.5-6	16	140-180	225	Moderate	300-500
<i>nootkatensis</i>	2-3	7	60-90	130	Slow	300-600
<i>thyoides</i>	1-2.5	5	50-80	120	Slow	100-200
<i>Cupressus arizonica</i>	1-2.5	5	50-60	90	Slow	100-300
<i>Juniperus deppeana</i>	1.5-3	6	30-50	60	Very slow	300-500
<i>occidentalis</i>	1-2.5	3	20-30	40	Slow	300
<i>osteosperma</i>	1-1.5	2.5	15-20	30	Very slow	150-300
<i>scopulorum</i>	1-2	3	20-40	55	Slow	100-300
<i>virginiana</i>	1-2	4	40-50	100	Slow	150-300
<i>Larix laricina</i>	1-2	3	40-80	100	Moderate	100-200
<i>occidentalis</i>	3-4	8	140-180	210	Slow	300-600
<i>Libocedrus decurrens</i>	2.5-4	11	80-110	190	Slow	300-400
<i>Picea engelmannii</i>	1-3	6	100-120	165	Slow	200-500
<i>glauca</i>	1.5-2	4	60-70	120	Slow	150-350
<i>mariana</i>	0.5-1	3	30-40	100	Slow	150-250
<i>pungens</i>	1-2	3	70-100	150	Slow	150-350
<i>rubens</i>	1-2	4	60-70	120	Slow	200-300
<i>sitchensis</i>	2-5	16	180-200	300	Rapid	400-750
<i>Pinus attenuata</i>	1-2	3	60-80	100	Rapid	100-150
<i>banksiana</i>	1-1.5	2	30-60	90	Rapid	80-150
<i>contorta</i>	1-2.5	3	30-70	150	Slow	120-300
<i>echinata</i>	2-2.5	4	80-100	150	Rapid	200-300
<i>edulis</i>	1-2	3	15-30	50	Very slow	150-400
<i>elliottii</i>	1-2	3	80-90	130	Rapid	150-250
<i>flexilis</i>	1.5-2.5	7	30-50	85	Slow	200-400
<i>glabra</i>	2-2.5	4	80-90	120	Rapid	75-150
<i>jeffreyi</i>	3-4	9	90-100	130	Moderate	300-500
<i>lambertiana</i>	2-4	10	160-180	250	Rapid	300-600
<i>monophylla</i>	1-2	3	20-30	50	Very slow	150-225

(continued)

TABLE 7.1 (*continued*)

Species	Stem diameter ^b at maturity (ft.)		Height at maturity (ft.)		Relative growth rate	Life- span (years)
	Average	Maxi- mum	Average	Maxi- mum		
<i>monticola</i>	2.5–3.5	8	150–180	120	Rapid	200–500
<i>palustris</i>	2–3	4	80–120	150	Rapid	300–400
<i>ponderosa</i>	3–4	9	100–180	235	Moderate	300–500
<i>resinosa</i>	2–3	5	50–80	120	Rapid	200–350
<i>rigida</i>	1–2	3	50–60	100	Rapid	100–200
<i>sabiniana</i>	1–2	4	40–50	90	Moderate	80–150
<i>strobos</i>	2–4	6	80–120	220	Rapid	300–500
<i>taeda</i>	2–2.5	5	90–110	190	Rapid	150–250
<i>virginiana</i>	1–1.5	3	30–40	100	Moderate	100–200
<i>Pseudotsuga menziesii</i>	4–6	15	180–250	385	Rapid	—
<i>Sequoia gigantea</i>	10–15	38	250–280	350	Rapid	2000–3000
<i>sempervirens</i>	6–12	20	150–275	365	Rapid	800–1500
<i>Taxodium distichum</i>	2–5	12	80–120	150	Slow	600–1200
<i>Taxus brevifolia</i>	1–1.5	2	20–40	65	Slow	250–350
<i>Thuja occidentalis</i>	2–3	6	30–50	125	Slow	300–400
<i>plicata</i>	4–8	20	150–200	250	Rapid	500–800
<i>Tsuga canadensis</i>	2–3	6	60–80	160	Slow	300–600
<i>heterophylla</i>	2–5	9	100–170	260	Moderate	300–600
<i>mertensiana</i>	2.3–3.5	5	70–100	130	Moderate	200–500

^a From Altman and Dittmer (1962).^b Measurement at breast height.

growth rates, than species such as *Pinus strobus*, which have predetermined shoots in the dormant bud. Some tropical trees such as the "foxtail" pines (e.g., *Pinus radiata*) have terminal leaders that grow more or less continuously during most of the year. Such foxtail trees often produce a much longer internode than the conventional recurrently flushing trees of the same species. When seasonal differences in internode length occur among trees within a multinodal species, or among shoots in the same tree of a multinodal species, the amount of elongation of a shoot generally is highly correlated with its seasonal duration of growth.

MAXIMUM HEIGHT GROWTH

Different species of trees vary greatly in the ultimate height attained (Tables 7.1 and 7.2). Among the world's tallest trees are those of the genus *Eucalyptus* in Australia and *Sequoia* in the western United States. Individual

TABLE 7.2
VARIATION IN SIZE, GROWTH RATE, AND LIFE-SPAN OF NORTH AMERICAN ANGIOSPERMS.
THE VALUES ARE APPROXIMATE^a

Species	Stem diameter ^b at maturity (ft.)		Height at maturity (ft.)		Relative growth rate	Life- span (years)
	Average	Maxi- mum	Average	Maxi- mum		
<i>Acer macrophyllum</i>	1-3	8	50-80	120	Rapid	150-300
<i>negundo</i>	1.5-3	6	40-50	75	Very rapid	75-100
<i>rubrum</i>	1-2.5	5	50-70	120	Rapid	80-250
<i>saccharinum</i>	2-3	7	60-80	120	Rapid	50-125
<i>saccharum</i>	2-3	5	60-80	135	Slow	200-300
<i>Aesculus glabra</i>	1-2	2.5	30-60	90	Moderate	—
<i>octandra</i>	2-3	4	70-90	100	Rapid	60-80
<i>Alnus rubra</i>	1-3	5	80-100	130	Rapid	60-100
<i>Arbutus menziesii</i>	1-2	4	40-80	125	Slow	—
<i>Betula alleghaniensis</i>	1-2	4	60-80	100	Rapid	150-300
<i>lenta</i>	1-2	5	50-60	80	Moderate	150-250
<i>nigra</i>	2-3	5	70-80	100	Rapid	—
<i>papyrifera</i>	1-2	5	50-70	120	Rapid	80-100
<i>populifolia</i>	0.6-1	1.5	20-30	60	Rapid	50
<i>Carya cordiformis</i>	1-2	4	50-60	85	Slow	175
<i>glabra</i>	1-2	4	60-80	120	Slow	200-300
<i>illinoensis</i>	2-4	6	90-120	180	Moderate	300
<i>laciniosa</i>	1-2	4	60-80	120	Slow	350
<i>ovata</i>	1-2	4	60-80	120	Slow	250-300
<i>tomentosa</i>	1-2.5	3.5	50-70	100	Slow	200-300
<i>Castanea dentata</i>	2-4	10	70-90	120	Rapid	100-300
<i>Castanopsis chrysophylla</i>	1-2.5	8	60-80	150	Rapid	200-400
<i>Catalpa speciosa</i>	1-3	5	30-60	120	Rapid	100
<i>Celtis laevigata</i>	1.5-2.5	5	60-80	130	Moderate	—
<i>occidentalis</i>	1-2	5	40-80	130	Rapid	75-150
<i>Cornus florida</i>	0.5-1	1.5	20-40	50	Slow	125
<i>nuttallii</i>	0.5-1	1.5	30-50	70	Slow	125
<i>Diospyros virginiana</i>	1-1.5	7	30-50	130	Slow	60-80
<i>Fagus grandifolia</i>	1-3	4	70-100	120	Slow	300-400
<i>Fraxinus americana</i>	2-3	6	60-80	125	Rapid	260-300
<i>latifolia</i>	2-3	5	60-80	130	Moderate	150-250
<i>nigra</i>	1-2	5	40-60	90	Slow	—
<i>pennsylvanica</i>	1-2	2.5	35-50	85	Rapid	—
<i>quadriangulata</i>	1-2	4	40-50	120	Rapid	200-300
<i>Gleditsia triacanthos</i>	2-3	6	70-80	140	Rapid	120
<i>Ilex opaca</i>	1-2	4	40-50	140	Slow	100-150
<i>Juglans cinerea</i>	1-2	3	40-60	110	Rapid	80
<i>nigra</i>	2-3	7	50-90	150	Rapid	150-250
<i>Liquidambar styraciflua</i>	2-5	6	80-140	200	Rapid	200-300

(continued)

TABLE 7.2 (continued)

Species	Stem diameter ^b at maturity (ft.)		Height at maturity (ft.)		Relative growth rate	Life- span (years)
	Average	Maxi- mum	Average	Maxi- mum		
<i>Liriodendron tulipifera</i>	2-5	12	80-120	200	Rapid	200-250
<i>Lithocarpus densiflora</i>	1-3	7	70-90	150	Moderate	150-300
<i>Maclura pomifera</i>	1-2	5	20-50	70	Moderate	75-100
<i>Magnolia acuminata</i>	2-3	5	70-90	100	Rapid	80-250
<i>grandiflora</i>	2-3	4.5	60-80	135	Moderate	80-120
<i>Morus rubra</i>	0.5-1	1.5	20-40	50	Moderate	125
<i>Nyssa aquatica</i>	3-4	5	80-100	120	Rapid	—
<i>sylvatica</i>	2-3	4	50-80	100	Rapid	—
<i>Ostrya virginiana</i>	1-1.5	1.5	30-40	55	Slow	—
<i>Platanus occidentalis</i>	2-5	14	80-120	175	Rapid	250-500
<i>Populus balsamifera</i>	1-2	5	60-80	100	Rapid	100-150
<i>deltoides</i>	3-4	11	80-100	175	Very rapid	60-100
<i>grandidentata</i>	1-2	3	60-70	80	Rapid	70-100
<i>sargentii</i>	2-3	5	50-80	110	Rapid	50-90
<i>tremuloides</i>	1-2	4.5	40-60	120	Very rapid	70-100
<i>trichocarpa</i>	3-4	8	80-120	225	Rapid	150-200
<i>Prunus serotina</i>	1.5-3	5	50-60	100	Rapid	100-200
<i>Quercus alba</i>	2.5-4	8	80-100	150	Slow	300-600
<i>agrifolia</i>	1-3	6	30-60	110	Slow	150
<i>bicolor</i>	2-3	7	60-70	100	Slow	300
<i>chrysolepis</i>	2-4	11	60-80	100	Slow	200-300
<i>coccinea</i>	2-3	4	70-80	110	Moderate	150
<i>douglasii</i>	1-2	3	50-80	130	Slow	—
<i>emoryii</i>	1-2	3	30-50	65	Slow	—
<i>falcata</i>	2-3	7	60-80	110	Moderate	200-275
<i>gambelii</i>	0.5-1	1.5	20-30	50	Slow	—
<i>garryana</i>	2-3	8	50-70	120	Slow	—
<i>kelloggii</i>	1.5-2.5	11	50-80	100	Slow	175-300
<i>laurifolia</i>	2-3	7	60-70	100	Moderate	—
<i>lobata</i>	3-5	10	50-90	130	Rapid	200-300
<i>lyrata</i>	1.5-2.5	4.5	40-70	110	Slow	300-400
<i>macrocarpa</i>	2-3	7	70-80	170	Slow	200-400
<i>marilandica</i>	0.5-1.5	2	20-30	55	Slow	100
<i>michauxii</i>	2-3	9	60-80	120	Slow	100-200
<i>muehlenbergii</i>	2-3	4	60-80	160	Rapid	—
<i>nigra</i>	1.5-3	5	60-70	125	Rapid	175
<i>nuttallii</i>	1-2	3.5	50-70	120	Moderate	—
<i>palustris</i>	2-3	5	60-80	120	Rapid	125-150
<i>phellos</i>	1.5-3	6	80-100	130	Moderate	—
<i>prinus</i>	2-3	6	50-60	100	Moderate	300-400
<i>rubra</i>	2-3	11	60-70	150	Rapid	200-400

(continued)

TABLE 7.2 (continued)

Species	Stem diameter ^b at maturity (ft.)		Height at maturity (ft.)		Relative growth rate	Life- span (years)
	Average	Maxi- mum	Average	Maxi- mum		
<i>shumardii</i>	4-5	8	80-100	180	Rapid	—
<i>stellata</i>	1-2	4	40-50	100	Slow	250
<i>velutina</i>	2-3	7	20-30	55	Moderate	150-200
<i>virginiana</i>	3-4	11	40-50	100	Moderate	200-300
<i>Rhamnus purshiana</i>	0.5-1	3	30-40	60	Rapid	40-50
<i>Robinia pseudoacacia</i>	1-2	5	40-60	100	Rapid	60-100
<i>Sabal palmetto</i>	1-1.5	2	30-50	90	Slow	50-80
<i>Salix amygdaloides</i>	1-1.5	3	20-40	60	Rapid	50-100
<i>nigra</i>	1-2	6	30-40	120	Rapid	50-125
<i>Sassafras albidum</i>	1-2.5	6	40-70	110	Rapid	100-500
<i>Swietenia mahogani</i>	0.5-1	1.5	30-40	60	Slow	150-200
<i>Tilia americana</i>	2-3	5	60-80	125	Rapid	100-140
<i>heterophylla</i>	1.5-2.5	3	60-80	125	Moderate	ca. 100
<i>Ulmus americana</i>	2-4	11	80-100	120	Rapid	150-300
<i>rubra</i>	1-2	4	50-70	90	Rapid	300
<i>thomasii</i>	1-2.5	5	50-70	100	Rapid	250
<i>Umbellularia californica</i>	1-3	6	60-100	175	Moderate	200

^a From Altman and Dittmer (1962).^b Measurement at breast height.

specimens more than 300 ft high have been recorded for both of these genera. Other tree species in the United States which exceed a height of 200 ft are *Pseudotsuga menziesii*, *Abies procera*, *Pinus lambertiana*, and *Pinus monticola*. Slightly shorter than these, but still very tall, are *Abies concolor*, *Pinus ponderosa*, and *Picea sitchensis*.

The ultimate height achieved by a tree often is more closely related to its longevity than to annual rate of growth of the young tree or the type of shoot produced. *Populus grandidentata* and *Populus tremuloides*, which often grow rapidly for a number of years, never achieve great height as they age rapidly and are relatively short-lived. In contrast, the slow growing, long-lived *Quercus alba* often achieves a height of 100 ft. This is true of gymnosperms also, with the rapid growing *Pinus rigida* growing to a height of only about 60 ft and the slow growing but relatively long lived *Libocedrus decurrens* growing to a height exceeding 110 ft. However, there are exceptions to these

generalizations and all species which attain great age do not necessarily achieve great height. For example, *Pinus aristata*, which is known for its longevity is not a particularly tall tree when mature.

The ultimate heights achieved during the entire life span of a tree bear little relation to whether its shoots are recurrently flushing, heterophyllous, or fully preformed in the dormant bud. The recurrently flushing species, *Pinus radiata* is a shorter tree at maturity than *Pinus lambertiana* which has a fully preformed shoot in the dormant bud and a short period of annual shoot elongation. The differences in ultimate height attained by these two species are traceable to the greater longevity of *Pinus lambertiana* and its capacity to continue appreciable shoot elongation for many more years than in *Pinus radiata*. The duration of shoot growth over a life-span of a tree has more to do with ultimate heights achieved than does duration of shoot elongation within the growing season. The rates of height growth of the recurrently flushing *Pinus taeda* and *P. echinata* trees were much greater for about 70 years than those of *Pinus monticola*. Nevertheless, *Pinus monticola* attained much greater height ultimately because it aged slowly and maintained a relatively fast rate of height growth for at least 120 years whereas height growth of *P. taeda* and *P. echinata* began to decline rapidly after about 50 years. Of course, species such as *Picea sitchensis* and *Pseudotsuga menziesii*, which have a fast rate of growth in their youth and, in addition, maintain fast growth for many years achieve great ultimate heights (Baker, 1950).

Many examples are available of unusually rapid growth of young trees. As may be seen in Fig. 7.1 *Populus nigra* grew to a height of 18 ft in 2 years from seed. In the Andaman Islands *Albizia moluccana* grew from seed to a height of 86 ft and a diameter of 9.8 in. in 7 years (Bradley, 1922). An example of rapid growth of *Pinus elliottii* in southern United States is shown in Fig. 7.2.

SEASONAL SHOOT GROWTH OF TEMPERATE ZONE SPECIES

Trees of the Temperate Zone show a rhythmic seasonal alternation of growth and dormancy. Species vary greatly in the time of initiation of shoot growth, rate and duration of shoot growth, capacity for recurrent growth flushes during periods of unusually favorable environments, and in the amount of shoot growth in different parts of the same tree.

Initiation of Shoot Growth

In a specific area most trees of the same species initiate annual shoot growth within a relatively short time span but they stop growing over a



FIG. 7.1. Two-year-old *Populus nigra* grown from seed in southern Italy. (Photo courtesy of A. dePhillipis.)



FIG. 7.2. Fast growing *Pinus elliottii* tree in Georgia. One internode is 12 ft long. (U.S. Forest Service photo.)

considerably longer period (Kozlowski, 1964a). For example, in the Adirondack Mountains of New York State, variation in time of growth initiation of individual trees of the same species was only 10 days or less, whereas it was as much as 30 days in time of growth cessation (Farnsworth, 1955). Although voluminous data are available on time of bud opening of various woody plants they often are difficult to evaluate and compare because the time of flushing varies with several factors such as temperature, species, age of tree, genetic factors, and various site factors. For example, *Acer* trees growing in the open initiated height growth later than those growing in a forest (Collins, 1960). According to Guzhev (1958), earliest bud burst of one-year-old tree seedlings of several species occurred under high soil moisture stress. Büsgen and Münch (1931) observed that 1- to 2-year *Picea* plants opened buds early. Thereafter, bud opening was inhibited with increasing age of trees and often occurred as much as a month later in 16- to 25-year-old trees than in very young ones. Büsgen and Münch (1931) also stated that *Fagus* buds which formed in the shade opened earlier than those grown in the light, further emphasizing the difficulty of comparing results of different investigators.

Differences in time of bud opening among species are well known. Büsgen and Münch (1931) gave the following order of flushing for European genera: *Larix*, *Betula*, *Alnus*, *Fagus*, *Quercus*, *Abies*, *Picea*. In the northeastern United States *Pinus resinosa* began height growth several weeks before *Picea abies* (Farnsworth, 1955). According to Friesner (1943), *Pinus resinosa*, *P. sylvestris*, and *P. banksiana* initiated shoot growth 3 weeks earlier than *Fagus grandifolia*, *Quercus alba*, *Ulmus americana*, *U. fulva*, and *Fraxinus americana*. Among the angiosperms *Acer saccharum* began shoot growth during the same week as the pines. In contrast, Kozlowski and Clausen (1965) found that buds of several species of gymnosperms growing in northern Wisconsin opened approximately 2 weeks later than those of several angiosperm species. It is not surprising that comparisons for species variations in time of bud break are not always consistent because they often represent data for trees of different ages and environmental conditions.

Duration of Shoot Growth

Species vary greatly in seasonal duration of shoot growth. Whereas shoots of some species elongate in only 2 to 6 weeks, those of other species may expand over a period up to several months. Nevertheless, in a large number of species a salient feature of shoot elongation in the Temperate Zone is that it begins relatively early and usually occurs over a shorter time than is involved in cambial growth or root elongation. Shoots generally start to elongate before the threat of frost is over, and their expansion is completed

during a relatively short part of the frost-free season. For example, in an average frost-free season in central Massachusetts, which extends from the beginning of May to mid-October (166 days), 95% of the height growth of *Betula papyrifera*, which had the longest duration of shoot growth of several species studied, was already completed by August 18. *Sorbus americana*, had already completed practically all its height growth before the end of June (Kozlowski and Ward, 1957b). These extremes show the marked variability in duration of shoot growth among species as well as relatively rapid shoot extension in many species.

Seasonal duration of shoot growth is genetically controlled and is highly correlated with the timing of development of shoot components in the bud. Many Temperate Zone species produce an annual shoot from opening and expansion of a single bud which in the spring contains a fully preformed and telescoped shoot. Shoot growth of such predetermined species is a two-year process involving bud differentiation the first year and extension of parts within the bud into a shoot the second year (Chapter 5). Such species characteristically expand their shoots very rapidly. However, such predetermined species may sometimes produce additional late-season lamas or proleptic shoots from opening of current-year buds. Hence, they may have two widely spaced seasonal growth bursts, with the second one extending late into the frost-free season.

Species which do not have fully preformed shoots in the winter bud expand their shoots for a much longer time during the growing season than those with preformed shoots. For example, height growth of *Aigeiros* poplars started at the time of leaf flushing and only 25% of seasonal height growth was completed by the end of June (Broekhuizen, 1962). About half of annual height growth was completed by the second half of July and three-fourths by mid-August. Height growth finally ceased in mid-September. The maximum rate of growth occurred in early August for certain clones, but not until the end of August for others (Table 7.3). Minckler and Woerheide (1968) studied seasonal height growth patterns of 72 young *Populus deltoides* trees. Height growth of most of the sample trees began in late April and continued into late September. Half of the sample trees were still growing after mid-September and some grew up to October 5 (Fig. 7.3). In Japan shoots of apple trees elongated from late May to early September (Mochizuki and Hanada, 1957).

Similarly, the heterophyllous genus *Liriodendron* expands its shoots for a long part of the frost-free season. Recurrently flushing species and gymnosperms with scale leaves which do not form true terminal buds and do not have a fully preformed shoot in the bud, such as *Juniperus*, *Thuja*, and *Seqnoia*, also expand their shoots for a much longer time than predetermined species.

TABLE 7.3
SEASONAL VARIATION IN GROWTH OF SHOOTS OF YOUNG *Populus* CLONES^a

Clone	Date of bud opening	Date of completion of 50% of growth	Date of completion of 100% of growth	Length of growing season (days)
"1214"	March 21	Aug. 2	Sept. 24	184
nigra "Italica"	March 24	Aug. 1	Sept. 22	182
"Heidmij"	March 24	July 24	Sept. 14	174
"Robusta"	March 25	July 20	Sept. 7	166
"Marilandica"	April 9	July 18	Sept. 13	157
"Regenerata"	April 8	July 20	Sept. 13	158
"Champagne"	April 11	July 20	Sept. 9	151
"Gelrica"	April 11	July 18	Sept. 7	149
"Serotina"	April 13	July 20	Sept. 9	149

^a From Broekhuizen (1962).

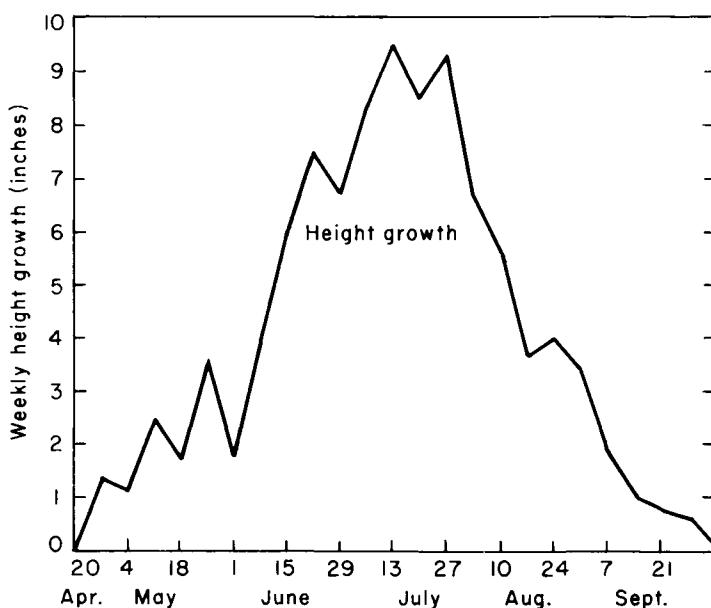


FIG. 7.3. Seasonal height growth in southern Illinois *Populus deltoides* plantation trees.
[From Minckler and Woerheide (1968).]

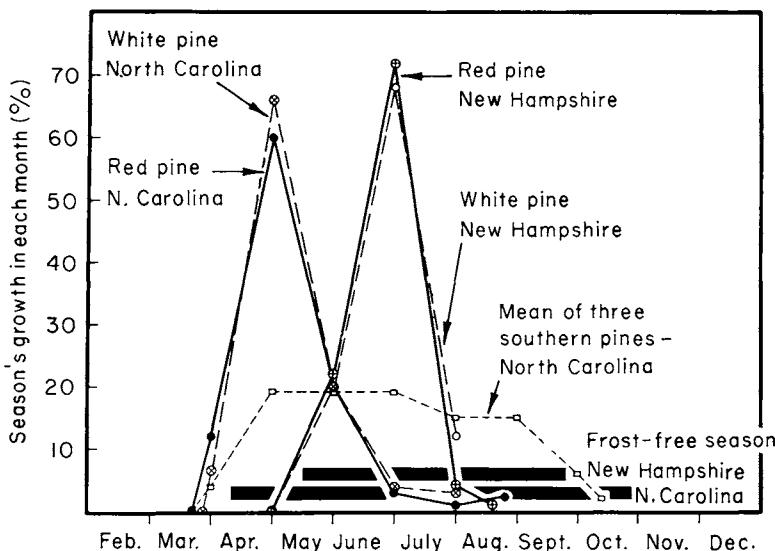


FIG. 7.4. Variations in seasonal height growth patterns of red pine (*Pinus resinosa*) and white pine (*P. strobus*) in North Carolina and in New Hampshire, and of three southern pines (*P. taeda*, *P. echinata*, *P. elliottii*) in North Carolina. The northern pines have preformed shoots and usually have one annual growth flush whereas the southern pines grow in recurrent flushes. [From Kramer (1943).]

The duration of shoot growth often varies greatly among different species of the same genus. For example, pines such as *Pinus resinosa* and *P. strobus* expanded their preformed shoots in only about 6 weeks (Table 7.4, Fig. 7.4). In contrast, the recurrently flushing southern pines such as *Pinus taeda*, *P. echinata*, and *P. caribaea* continued to elongate shoots in recurrent flushes for 5 months or more out of the year (Kramer, 1943). These three species made 15–20% of their seasonal height growth in each month from April to August. Close correlation between duration of shoot expansion and timing of development of shoot components in the bud has been demonstrated for many species in different regions (Cook, 1941a,b; Walters and Soos, 1963).

Kienholz (1941) divided deciduous species in Connecticut into 2 groups on the basis of their height growth characteristics. In the first group, height growth accelerated to a late May climax and ceased completely before the end of June. The entire growth period lasted only about 60 days, and 90% of annual shoot expansion was completed in a 4-week period which began 1 or 2 weeks after growth started. This group consisted of *Acer saccharum* and *Fagus grandifolia*, species with preformed shoots in the winter bud. In

TABLE 7.4
HEIGHT GROWTH EACH MONTH AS PERCENT OF TOTAL SEASONAL GROWTH IN DURHAM, NORTH CAROLINA^a

	<i>Pinus resinosa</i>		<i>Pinus strobus</i>		<i>Pinus taeda</i>		<i>Pinus echinata</i>		<i>Quercus alba</i>		<i>Liriodendron tulipifera</i>	
	1938	1939	1938	1939	1938	1939	1938	1939	1938	1939	1938	1939
March	16.0	8.0	13.0	0.0	5.0	2.0	2.0	3.0	6.0	0.0	0.0	0.0
April	66.0	55.0	67.0	65.0	21.0	14.0	24.0	16.0	57.0	45.0	20.0	20.0
May	8.0	32.0	10.0	32.0	15.0	27.0	13.0	22.0	6.0	5.0	25.0	
June	5.0	2.0	4.0	3.0	21.0	23.0	17.0	19.0	21.0	20.0	21.0	
July	3.0	0.0	6.0	0.0	15.0	14.0	16.0	14.0	7.0	20.0	23.0	
August	2.0	3.0	0.0	0.0	14.0	13.0	20.0	16.0	3.0	10.0	10.0	
September	0.0	0.0	0.0	0.0	5.0	6.0	7.0	8.0	0.0	0.0	1.0	
October	0.0	0.0	0.0	0.0	2.0	1.0	1.0	2.0	0.0	0.0	0.0	
Growing season (days)	140	150	127	115	210	210	200	200	140	135	160	

^a From Kramer (1943).

the second group, growth began at about the same time as in the first one, but did not accelerate as fast. The climax for this group occurred in mid-June and fell off to zero by the middle of August. About 90% of total shoot elongation in this group occurred in a 60-day period beginning 3 to 4 weeks after growth started. Characteristic species of this group included *Betula papyrifera*, *B. populifolia*, and *Populus tremuloides*, all heterophyllous species without fully preformed shoots in the winter bud.

Marked variations among seasonal height growth patterns of different species were shown for both gymnosperms and angiosperms growing in northeastern United States (Figs. 7.5 and 7.6). Among the gymnosperms, *Pinus resinosa*, *P. rigida*, and *P. banksiana* had very short periods of height growth (about 35 days), whereas *Thuja occidentalis* and *Larix* had long periods (about 140 days). The angiosperms also were divided into groups with short periods of height growth (*Fraxinus americana*, *Acer saccharum*) and those with long ones (*Populus* and *Betula*). For 7 consecutive years, each of these species retained its relative phenological position and shape of growth curve. Differences in the onset of spring in different years advanced or retarded the time of growth initiation somewhat. When shoot expansion once began, however, the course of growth was very similar from year to year. Significantly, all of the angiosperms and gymnosperms with very short periods of shoot expansion were species which had shoots fully preformed in the winter bud. Those with shoots which elongated for a long time were species which did not have preformed shoots in the dormant bud.

Seasonal height growth patterns of gymnosperms in British Columbia varied greatly (Walters and Soos, 1963). *Pinus monticola* was slower in

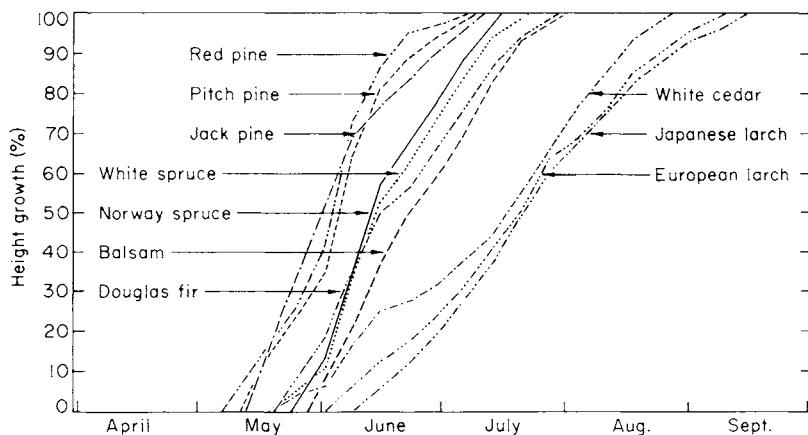


FIG. 7.5. Species variations in seasonal duration of height growth of gymnosperms. [From Cook (1941b).]

TABLE 7.5
AVERAGE SEASONAL ELONGATION OF TERMINAL LEADERS AND LATERALS OF CONIFERS IN BRITISH COLUMBIA DURING 1961^a

Date	Leader	Percent of season's shoot elongation					
		<i>Pseudotsuga menziesii</i>		<i>Tsuga heterophylla</i>		<i>Pinus monticola</i>	
		Lateral	Upper	Lateral	Upper	Lower	Leader
May 1	0.4	0.9	1.0				
May 15	1.4	3.0	3.4	0.7	0.5		1.5
May 29	13.7	27.6	30.1	11.2	11.9	10.2	14.2
June 19	50.2	71.0	77.1	45.4	57.5	50.1	77.3
June 26	60.8	80.6	85.9	56.9	72.0	62.7	96.7
July 3	72.0	87.8	92.7	67.6	83.4	76.5	99.1
July 10	86.4	95.4	97.8	78.7	93.2	88.4	100.0
July 24	97.5	99.5	100.0	91.7	99.2	97.2	
July 31	98.8	100.0		95.1	99.4	98.8	
Aug 7	99.4			98.0	99.4	100.0	
Aug 14	99.9			99.0	100.0		
Aug 28	99.9			99.7			
Sept 4	100.0			100.0			

^a From Walters and Soos (1963).

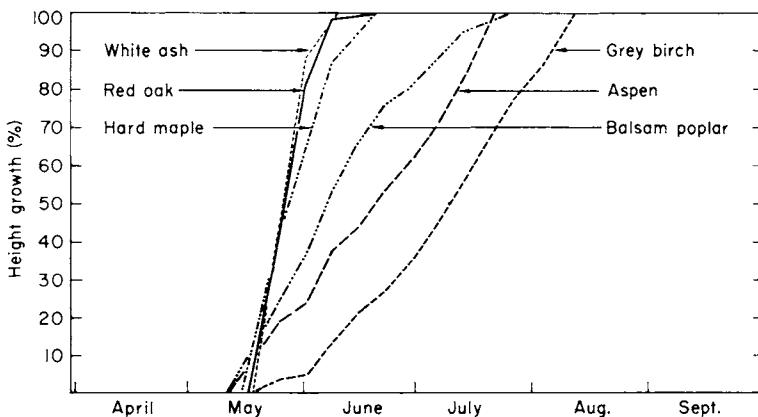


FIG. 7.6. Species variations in seasonal duration of height growth of angiosperms. [From Cook (1941b).]

beginning growth than *Pseudotsuga menziesii* or *Thuja plicata*, but growth of *Pinus monticola* increased rapidly and was completed first (Table 7.5). *Pseudotsuga* and *Tsuga heterophylla* had similar growth rates until June, but the former completed shoot elongation somewhat earlier. *Thuja*, with scale leaves and without a preformed shoot in the bud, had the longest growing season, which was about twice that of *Pinus monticola*, whose winter bud contained a preformed shoot.

Anic (1956) at Zagreb studied height growth patterns of 33 species of gymnosperms and angiosperms. Among those with the shortest season for leader growth were *Pinus sylvestris*, *Abies alba*, *Sorbus aucuparia*, and *Fraxinus ornus*. *Larix decidua* and *Populus nigra* had the longest growing seasons for the gymnosperm and angiosperm groups, respectively. Again, species with short growing seasons were those with shoots preformed in the dormant buds whereas those with long growing seasons were not.

The data of Kramer (1943) for North Carolina provide insight into the strong correlation between species patterns of development of leaf primordia and seasonal duration of shoot elongation (Table 7.4). The predetermined species, *Pinus resinosa* and *Pinus strobus*, expanded their shoots rapidly and made more of their growth in April than in all other months combined. In contrast, the heterophyllous species *Liriodendron tulipifera* and the recurrently flushing species *Pinus taeda* and *P. echinata* distributed seasonal shoot elongation over several months. *Quercus alba* also produced more than a single growth flush. The hereditary control of the pattern of seasonal height growth also is shown by the failure of many species to respond readily to small fluctuations in environment. Hence, height growth curves often are

quite similar from year to year. Although growth of several species began later in 1939 than in 1938 the duration of height growth generally was similar for each species in successive years. Kramer (1943) observed that even so drastic a change as resulted from transferring *Pinus resinosa* and *P. strobus* from New Hampshire to North Carolina increased somewhat the lengths of their growing seasons but did not change the relative lengths or shapes of their growth curves. Shoot growth of the heterophyllous species *Liriodendron tulipifera*, however, was influenced much more by environment as it produced shoots for a much longer time in the south than in the north.

Tree Age and Seasonal Shoot Growth Patterns

Within a species seasonal shoot growth patterns may vary considerably with age of the plants. Often the seasonal duration of height growth is shorter in mature trees than seedlings. For example, seedlings of *Robinia pseudoacacia* had a long growing season extending into autumn whereas tip growth of many shoots of mature trees stopped by the end of July (Wareing, 1956). The 2- and 3-year-old *Pinus taeda* seedlings studied by Kramer (1943) began shoot growth at about the same time as the 13-year-old trees of Young and Kramer (1952), but they continued growing longer. According to Turner (1956), 22- to 30-year-old *Pinus ponderosa* trees had a different seasonal pattern of shoot growth than 63- to 78-year-old trees. Lateral shoots in both young and old trees began elongating at about the same time but the younger trees grew more slowly at first. However, once the young trees began growing quickly, they maintained a fast growth rate for a long period of time and completed 95% of their total growth earlier than the old trees.

Relation of Amount to Duration of Shoot Growth

Relationships between the amount and duration of shoot growth are rather complicated. Within a tree there often is correlation between the total amount and duration of seasonal growth of individual shoots. For example, in species which have preformed shoots in the dormant bud, shoots on the upper crown grow more and expand for a longer time than those on the lower branches. Similarly, in recurrently flushing species such as pines of the southern United States, shoots in the upper stem grow more than those in the lower stem, but those in the upper stem often exhibit more seasonal flushes than those in the lower stem (Table 7.14). In contrast to these within-tree relations, comparisons of shoot growth among morphologically similar or dissimilar species very often show no correlation between the amount of shoot growth and its duration. In North Carolina, for example, *Fraxinus americana*, with a very short growing season, grew approximately as much as *Liriodendron tulipifera*, with an unusually long growing season (Kramer, 1943). The average growth period of *Abies balsamea*, which grew least of

five species of gymnosperms studied, was approximately as long as that of *Picea glauca* and *P. abies*. Shoots of *Pyrus americana*, with an unusually short growing season, grew two to three times as much as those of *Cornus florida*, a species with a very long growing season (Kozlowski and Ward, 1957a,b). Hanover (1963) found no positive relation between the amount of growth and length of growing season in various provenances of *Pinus ponderosa*.

SEASONAL SHOOT GROWTH OF TROPICAL AND SUBTROPICAL SPECIES

Shoot growth of tropical species is much more intermittent and occupies more of the year than it does in species of the Temperate Zone. In tropical species the time during which shoots expand in recurrent flushes often adds up to 6 to 11 months of the year and in some areas shoots grow throughout the year. Nevertheless, there is much variation in the duration of shoot growth of different species on the same site (Table 7.6).

A rigid classification of shoot growth characteristics of tropical trees is difficult to make because many species exhibit marked growth plasticity and respond to climatic variations, especially to seasonal distribution of rainfall. In tropical rain forests individual trees and variously located shoots of the same tree often are at different stages of development and show different growth patterns. Viewed broadly, however, the percentage of the entire flora of a tropical rain forest which is in a specific developmental phase remains more or less constant throughout the year. Richards (1964) considered tropical rain forests to grow continuously and to have no real seasonal aspects. Leaves remained green and some trees were in flower throughout the year. Nevertheless individual trees showed growth intermittency, which was characterized by variable rates of leaf production and flowering. The general continuity of flushing throughout the year contrasted strongly with the relatively short burst of shoot growth followed by a long period of bud dormancy of many Temperate Zone trees (Kozlowski, 1963b).

Trees of seasonal tropical climates often show growth periodicity. Even the tropical rain forest grows somewhat intermittently near its climatic limits. In southern Nigeria the climate is seasonal with distinct alternating dry and rainy seasons. At Ibadan, at the northern limit of the tropical rain forest, many species showed a sequential annual cycle of bud expansion, inactivity, leaf fall, and flowering. The period of leaf production often was confined to only a month and this was followed by a long period of bud dormancy. In addition flowering was a distinctly seasonal phenomenon (Njoku, 1963). Koriba (1958) also stressed that rigid classification of tropical trees on the basis of growth characteristics was difficult because growth patterns of a species varied greatly in different regions. For example, *Duabanga*

TABLE 7.6
VARIATIONS IN PATTERNS OF LEAF RENEWAL OF DECIDUOUS TROPICAL TREES GROWING IN SINGAPORE^a

Species	Species	Leaf period of 6 months	Leaf periods of 6 to 12 months		Leaf period of 12 months		Leaf period greater than 12 months		Period (months)
			Period (months)	Species	Species	Mean date	Species	Species	
<i>Cassia nodosa</i>	<i>Couroupita guianensis</i>		<i>Adenanthera pavonina</i>	7.25	<i>Kigelia pinnata</i>	Jan. 28	<i>Cedrela glaziovii</i>		12.5
<i>Dyera costulata</i>	<i>Peltiphyllum pterocarpum</i>		<i>Cassia fistula</i>	9.1	<i>Hymenaea courbaril</i>	Early Feb.	<i>Koompassia malaccensis</i>		12.7
<i>Ficus caudocarpa</i>	<i>Terminalia catappa</i>		<i>Cratoxylon formosum</i>	9.1	<i>Parkia javanica</i>	Feb. 23	<i>Caesalpinia ferrea</i>		14.2
<i>Hevea brasiliensis</i>			<i>Delonix regia</i>	8.8	<i>Terminalia subspathulata</i>	April 6	<i>Homalanthus grandiflorum</i>		13.7
<i>Mangifera indica</i>			<i>Ficus variegata</i>	6.5	<i>Canarium rufum</i>	May 9	<i>Parishia maingayi</i>		15.6
<i>Sindora wallichii</i>			<i>Lagerstroemia flor-regiae</i>	9.2	<i>Lecythis</i> sp.	Aug. 1	<i>Heritiera elata</i>		20.5
<i>Sterculia carthagagensis</i>			<i>Salmalia malabarica</i>	10.5			<i>Heritiera macrophylla</i>		32
			<i>Sterculia macrophylla</i>	6.9					

^a From Holtum (1940)

sonneratoides, *Thespasia populnea*, *Mimosa sepiaria*, and *Hibiscus tiliaceous* are all considered evergrowing in Singapore. Yet the same species of *Duabanga* and *Thespasia* are deciduous in India; *Mimosa* is semi-deciduous in San Paulo, Brazil and *Hibiscus* is classified as intermittent in East Java. Teak (*Tectona grandis*) tends to be deciduous in monsoon regions such as Burma and East Java, and evergreen in Singapore (Koriba, 1958). Alvim (1964) also emphasized that tropical trees classed as "evergrowing" evergreens exhibited some growth periodicity. *Coffea*, for example, an evergrowing species in some areas often shows two seasonal peaks of growth in other areas.

Most detailed growth studies of tropical trees have been conducted on deciduous species and, to a lesser extent, on intermittently growing evergreens (Alvim, 1964). According to K. A. Chowdhury (1958), broadleaved trees of India produce at least two flushes of shoot growth and some trees may show up to four. Shoot growth may precede radial growth at the stem base by 2 weeks to months. The first flush of shoot expansion occurs between February to April and the second begins sometime in July and August. When there is a third growth flush it takes place in October and November, with a fourth flush sometimes occurring in December and January.

Geographic Variation in Shoot Growth

Individuals or populations of trees within species with wide geographic ranges often vary greatly in shoot growth characteristics. Such geographic variation may be due to environmental as well as genetic factors and interactions among them.

Environmental regimes alone affect shoot growth of some species much more than others. For example, increase in length of the frost-free season affects the amount and duration of shoot growth in species which normally make a single annual flush of shoot growth, less than in recurrently flushing species. As mentioned earlier, shoot growth of *Pinus strobus* was affected less than that of *Liriodendron tulipifera* by moving these species into areas with a long frost-free season (Kramer, 1943). Shoot growth of recurrently flushing southern pines continued for about 100 days in New Jersey (Tepper, 1963a), for about 150 days in North Carolina (Kramer, 1943), and for about 200 days in Louisiana (Huberman, 1940), illustrating the plasticity of these multinodal species. Their greater duration of growth in more southerly latitudes was correlated with increased number of shoot growth flushes (Tepper, 1963a).

In addition to the influence of environmental effects alone, geographic variation in growth generally includes racial variation which is due to several mechanisms such as mutation, natural selection, hybridization, or

combinations of these. If the environment varies in different parts of the range of a species and some degree of reproductive isolation exists, racial variation is an inevitable result. Natural selection is the most important cause of racial variation, but chance fluctuations in gene frequencies leading to fixation of genes may also be involved. Such genetic drifts are most likely to occur in small, isolated populations and environmental differences are not a requisite for them (Squillace, 1966).

Geographic variations in shoot growth generally are greatest or most prevalent where the species range covers a wide geographical area. The character of geographic variation is important to growers because if differences are primarily genetic, seed sources must be carefully selected for planting. The existence of racial variation also provides excellent opportunity to produce superior trees.

To determine the presence and amount of provenance variation in growth within a species, growth on a common site in adjacent plots of seedlings from widely separated parts of the range has been studied. Viewed broadly, such plantings often show that southern provenances of a species usually extend their shoots faster and for a longer time, during the frost-free season, than northern provenances. According to Wright (1962), southern provenances also are less likely than northern ones to be injured by late spring or early autumnal frosts, but they are more susceptible to winter injury.

VARIATION IN DIFFERENT ASPECTS OF SHOOT GROWTH

Marked geographic variations in amounts of shoot growth have been documented. These may reflect differences in time of bud break, rate of growth, and seasonal duration of growth. A voluminous literature is available to illustrate these and only a few examples will be given of each.

Variation in Time of Bud Break

In a given experiment trees from northern regions often begin shoot growth earlier than trees from southern ones. Trees from high elevations also tend to leaf out earlier than those from low ones. However, deviations from these patterns may occur. For example, McNaughton (1967) collected woody plants of several species growing in Oregon at elevations from 60 to 1820 m. The plants were placed in a greenhouse and time of bud opening studied. Flushing occurred later in plants from intermediate altitudes than from extremely high or low ones. The late bud-bursting potential of intermediate altitude communities was related to conditions there which were conducive to marked cold air drainage.

Strong genetic control of time of bud break is well known and only a few examples will be given. Provenances of *Acer saccharum* grown in Wooster,

Ohio showed a clinal variation in time of spring growth initiation. Northern trees began growing earlier than southern ones. Both photoperiod and temperature showed some relation to the trend of bud opening but other influences also appeared to be important (Kriebel, 1957). In the USSR *Quercus robur* occurs in several types. The most common forms include the early (summer) oak and the late (winter) oak characterized by differences in time of bud break of up to 5 weeks. Both *Fagus* and *Fraxinus* have been classified into early, medium, and late flushing forms (Mikulka, 1955; Saks, 1956). Cottam (1954) noted very marked differences in time of flushing of *Populus tremuloides* var. *aurea* in Utah. In the Abajo Mountain and at Mt. Timpanogas of the Wasatch Range, early and late flushing forms apparently represented different genetic strains. Rehfeldt and Lester (1966) found that *Pinus resinosa* provenances which produced lamas shoots began shoot growth later in the spring and ended it later in the summer than trees with normal growth. The duration of shoot growth of these two groups was similar.

Variation in Amount and Duration of Shoot Growth

A rich literature is available to illustrate genetic variation in amount and duration of shoot growth. A few examples will be given here and others will be given in other sections of this chapter.

Height growth of *Pinus taeda* trees grown in Louisiana from local seed was greater than that of trees grown from Texas, Georgia, or Arkansas seed (Wakeley, 1961). After 14 years the greatest contrast was between the Louisiana and Georgia stock, with the former averaging 32.1 ft in height as against 26.1 ft for the latter. Critchfield (1957) collected seeds of *Pinus contorta* from various geographic origins. The seeds were stratified and then planted in the greenhouse in Berkeley, California. Seedlings from high latitudes or high elevations in the Rocky Mountain-Intermountain region were among the first to cease growing and form terminal buds. Seedlings from the coastal region showed greater differences in shoot growth than those of the Rocky Mountain-Intermountain region. Most Sierra Nevada seedlings grew for a longer time than those from other inland regions. Duration of growth in the coastal sources, which formed a continuous series, varied from 116 days for southeastern Alaska seeds to 214 days for the Mendocino County, California plants.

Perry *et al.* (1966) grew 31 widely separated provenances of *Pinus taeda* in Gainesville, Georgia. Under natural photoperiods, height growth varied greatly, with some provenances growing twice as much as others. For example, plants from Ocala, Florida grew almost 18 ft during the experiment whereas plants from a Maryland source grew only 7 ft. The northern sources produced only two annual flushes of shoot growth whereas southern sources

produced as many as six or seven. Under prolonged photoperiods, northern sources increased the number of nodes from two to four or more per year. Hence, the multinodal *Pinus taeda* exhibited racial variation in number of nodes formed. Southern sources of *Pinus taeda* continued to elongate buds throughout the winter, with some buds enlarging by as much as 10 cm. Large variations occurred in duration of shoot growth among provenances. Florida sources started growing 25 days earlier, and continued growing about 85 days longer, than Maryland sources. Duration of shoot growth of the Florida sources exceeded that of Maryland sources by about 110 days.

Genys (1960) evaluated height growth characteristics in New Hampshire of a number of provenances of *Larix decidua* (Table 7.7). Provenances from

TABLE 7.7

VARIATION IN HEIGHT AND DIAMETER GROWTH OF 12-YEAR-OLD *Larix decidua* OBTAINED FROM VARIOUS EUROPEAN SOURCES AND GROWN FROM SEED IN NEW HAMPSHIRE^a

Seed source	Elevation (m)	Average height (ft)	Average diameter at breast height (in)
Poland	200-450	23.3	3.07
Sudetenland	700	23.5	3.00
Slovakia	800-1000	21.6	2.50
Central Austria	600-950	18.6	2.45
Western Austria	750-900	18.4	2.37
Eastern Austria	550-800	17.4	2.30
Western Austria	1050-1900	17.2	2.25
Central Austria	1100-1700	17.1	2.25
Italy	900-1400	16.0	2.15
Switzerland	550-1500	14.2	2.05

^a From Genys (1960).

Poland, Sudetenland, and Slovakia grew faster than those from other sources. Slowest growing trees originated in Switzerland, Italy, and the higher elevations of Austria. Analyses of provenances from the Alps showed that trees originating from low elevations in Central Austria showed fastest height growth. Although the Slovakian provenances were not significantly greater in diameter than the slowest growing provenances, their height growth was greater.

When grown together at Corvallis, Oregon, seedlings of *Pseudotsuga menziesii* native to Corvallis differed in growth rate from those native to the coast range 25 miles west of Corvallis (Irgens-Moller, 1960). The Corvallis seedlings initiated growth 4 weeks earlier than those from the coast range, but the latter group grew considerably faster. Irgens-Moller speculated that

the early beginning of growth of the Corvallis seedlings may have reflected natural selection to complete growth early to avoid summer droughts.

Variation in Amount of Shoot Growth in Relation to Rate and Duration of Growth

Differences in amounts of shoot growth among provenances may be attributed in varying degrees to differences in rates of growth and to seasonal duration of growth. A few representative examples will be given.

Pinus banksiana provenances from areas of long growing season had a greater seasonal duration of shoot expansion, and started and finished shoot expansion later, than those from areas of short growing seasons. Most of the differences among provenances were accounted for by variations in duration of growth, not in rate of growth (Holst and Yeatman, 1961). Aldhous (1962) found similar results for *Picea sitchensis* provenances. Burley (1966a) found little variation in absolute rates of height growth among *Picea sitchensis* provenances. Variation in date of bud formation was considered the major factor in influencing provenance variation in height growth. Burley (1966b) found that shoot development in *Picea sitchensis* was basically a continuous process, but the timing of different phases varied greatly with seed sources. In New Haven, Connecticut, shoot elongation and needle initiation ceased in July for seedlings from Alaskan provenances and initiation of scale primordia began immediately. In plants from extreme northern sources, such as Kodiak Island, Alaska, scales were formed only after four needles were initiated. In plants from more southern sources, shoot elongation continued through the summer. In seed sources of extreme southerly origin, such as California, bud scales were not initiated until September. In northern sources needle initiation ceased by November. The primordia elongated until the terminal bud reached the resting stage. By comparison, needle initiation in plants from southerly origins continued into December. In extreme southerly origins a small number of leaf primordia were even initiated during early growth the following spring. Timing of bud formation, which was related to latitude of seed origin, varied over a three-month period in 47 *Picea sitchensis* provenances. Flushing in spring was controlled mainly by temperature, with time of flushing reflecting temperature regimes of the native habitats of different provenances. In England, Lines and Mitchell (1966) studied shoot growth characteristics of 12 *Picea sitchensis* provenances ranging from Alaska to Oregon. The most striking difference among provenances was the early cessation of shoot growth of those from northern Alaska which stopped growing in mid-summer, by which time the southern provenances had completed only half their annual height growth. Date of bud opening varied more among individual trees than among provenances.

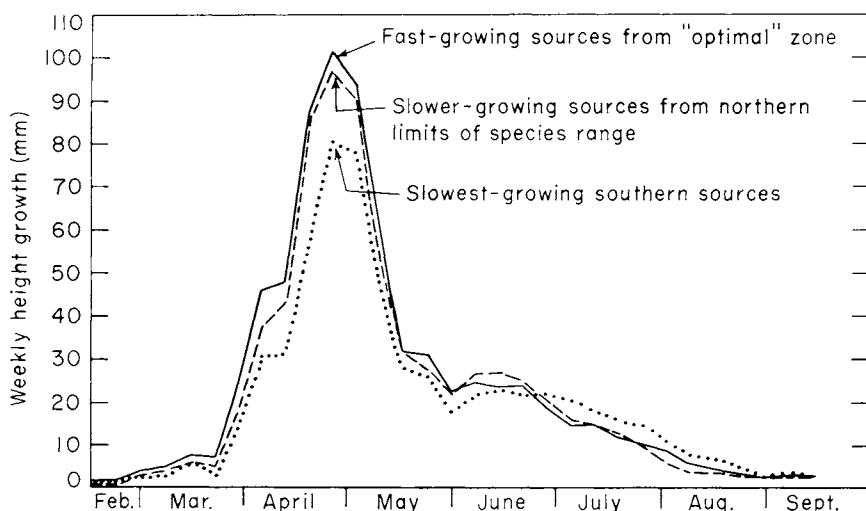


FIG. 7.7. Variations in weekly height growth of three representative seed source groupings of *Pinus elliottii*. [From Bengston *et al.* (1967).]

Several studies emphasized the importance of growth rate in influencing geographic variations in amounts of shoot growth. For example, Mirov *et al.* (1952) concluded that greater height growth of *Pinus ponderosa* trees from low altitudes, over those from high ones, was the result of more rapid growth rate as well as greater duration of growth of the former. Regression analyses of Perry *et al.* (1966) showed that differences in daily rate of growth of widely separated *Pinus taeda* provenances, which were tested in Gainesville, Florida, could account for about 60% of the variation in height growth, and differences in duration of seasonal growth, for about 30%.

Bengston *et al.* (1967) studied terminal growth phenology of 14 seed sources of 6-year-old *Pinus elliottii* trees. The test site in northeastern Florida was intermediate with respect to climatological extremes found within the species range. Differences among provenances in time of seasonal initiation of shoot growth were small. However, provenances from the north central portion (optimal climatic zone) expanded shoots faster early in the season than did those from extreme northern or southern areas. Southernmost sources grew somewhat faster than northern sources late in the season, but not enough faster to overcome the rapid early height growth of northern sources (Fig. 7.7). Total shoot growth during the year was greatest among sources from the north central region. Length of the dormant bud in February showed significant differences among sources and was a good estimator of both early-season height growth and of total seasonal height growth.

Rehfeldt and Lester (1966) noted that variation in duration and absolute rate of shoot elongation contributed about equally to variation in height growth among *Pinus resinosa* provenances. Hence, these several studies emphasize genetic variations in amounts and duration of shoot elongation.

TYPES OF GEOGRAPHIC VARIATION IN SHOOT GROWTH

Variation in shoot growth characteristics among provenances may be clinal, ecotypic, or random. Clinal variations are characterized by gradual transitions in shoot growth characteristics which parallel gradual changes in climatic or geographic features. Truly ecotypic variation, which is characterized by absence of continuity, occurs only in species which have geographical isolation and have become genetically adapted to a uniform habitat in regard to soil or exposure. A third type of genetic variation is random variation in which the real differences among stands of a species show no distinct trends such as clines or ecotypes.

Because the habitat within the range of a species, or parts of it, varies continuously, combinations of patterns of variation often occur. For example, in a species such as *Pinus ponderosa*, which occurred in isolated groups, ecotypes often were found. But as the climate varied continuously throughout the extensive range of this species, clinal variation occurred within and between the ecotypes. Combinations of patterns of geographic variation also occurred in height growth characteristics of *Pinus elliottii*. The pattern was largely random in the northern part of the range and clinal through Florida (Squillace, 1966).

There has been considerable disagreement on whether variation in many species should be classified as clinal or ecotypic. According to Squillace (1966), the presence or absence of these two types of variation often is a matter of degree and is subject to individual interpretations. The problem is also confounded by lack of standardized terminology as well as precise guidelines for classifying genetic variation. In dealing with provenance studies generally, Langlet (1962) cautioned against use of the term "ecotype" unless discontinuity of an ecological adaptation was clearly proved. He suggested that the ecotype concept be replaced by one of ecologic variability which could be in terms of clines. Referring to International Provenance Tests of *Pinus sylvestris*, Langlet emphasized that geographic variability of this species varied continuously with variation of the determining ecological factors. He stated that as latitude always and temperature usually varied continuously, resulting in ecological variability within a species, geographic continuity also existed. He acknowledged, however, that ecological variability was not always continuous. Discontinuities could arise from genetic or

environmental isolation, abrupt environmental change, or radically different edaphic conditions. In 1957 Wright and Baldwin grouped *Pinus sylvestris* in large parts of its European range into geographic ecotypes, since they believed discontinuity in variability existed. Langlet (1959a) reanalyzed their data and concluded that the variability was continuous to the same degree as the determining environmental factors varied continuously. Langlet (1959b) also criticized Sylven's distinguishing of subspecies of Norrland pine. Langlet concluded that Sylven's data indicated continuous clinal variability and did not justify the distinctions made by Sylven. Langlet's views were supported by Callaham (1962) who stated that variation in climate is essentially continuous and predictable, and since growth usually is related to climate, it essentially varies continuously in predictable patterns. Some examples of clinal and ecotypic variations will be discussed briefly.

TABLE 7.8

VARIATION IN AMOUNT OF LEADER GROWTH, TERMINAL BUD LENGTH, AND GROWTH RAPIDITY OF *Pinus ponderosa* OBTAINED FROM VARIOUS SOURCES^a

Mean total elongation		Mean terminal bud length		Rapidity of growth ^c	
Source	Feet ^b	Source	Feet	Source	Percent
Harney	0.93	Roosevelt	0.11	Santa Fe	37.9
Roosevelt	0.98	Ashley	0.12	Coconino	42.3
Payette	1.06	Coconino	0.13	Umatilla	43.5
Custer	1.08	Coloille	0.14	Payette	43.7
Bitterroot, 7200ft	1.11	Custer	0.14	Harney	44.6
Ashley	1.12	Santa Fe	0.14	Bitterroot, 5000ft	45.3
San Isabel	1.16	San Isabel	0.14	Bitterroot, 4000ft	45.6
Colville	1.22	Harney	0.15	Ashley	46.2
Helena	1.23	Payette	0.15	Lolo	47.1
Boise	1.23	Bitterroot, 7200ft	0.16	Siskiyou	47.3
Siskiyou	1.24	Bitterroot, 5000ft	0.16	San Isabel	47.6
Santa Fe	1.27	Boise	0.17	Whitman	48.0
Bitterroot, 4000ft	1.28	Bitterroot, 4000ft	0.18	Custer	48.6
Coconino	1.29	Siskiyou	0.20	Roosevelt	48.7
Kaniksu	1.33	Kaniksu	0.21	Colville	50.3
Bitterroot, 5000ft	1.37	Umatilla	0.23	Bitterroot, 7200ft	51.4
Whitman	1.43	Helena	0.23	Boise	51.9
Lolo	1.55	Whitman	0.24	Kaniksu	55.0
Umatilla	1.64	Lolo	0.24	Helena	58.1

^a From Hanover (1963).

^b Any two means not included within the same line appearing to the right of each ranking of sources are significantly different.

^c Percent of the total season's growth completed within the 2-week period of most rapid growth.

Clinal Variation

Nineteen races of *Pinus ponderosa* planted near Priest River, Idaho, showed continuous variations in date of leader growth initiation, date of growth cessation, total seasonal elongation, duration of growth, length of dormant apical bud, and growth rapidity (Tables 7.8 and 7.9). Neither beginning date, relative rapidity, duration of growth, nor ending date were related to total height growth, but a strong positive correlation existed between bud length and total elongation. Sources representing geographic regions in which September-June precipitation was low, began growth later and grew less than sources from areas of high precipitation. The period at which each tree and progeny achieved maximum rate of growth was related to local temperature (Hanover, 1963).

In studies conducted in Idaho, Oregon, and Washington, Squillace and

TABLE 7.9

VARIATIONS IN LEADER GROWTH INITIATION AND CESSATION AND LENGTH OF GROWING SEASON OF *Pinus ponderosa* OBTAINED FROM VARIOUS SOURCES^{a,b}

Mean initiation date		Mean cessation date		Mean duration	
Source	Day of year (From Jan. 1)	Source	Day of year (From Jan. 1)	Source	Days
Kaniksu	114	Bitterroot, 7200ft	153	Boise	35
Ashley	115	Siskiyou	155	Helena	36
Siskiyou	116	Lolo	156	Lolo	37
Bitterroot, 7200ft	117	Helena	156	Bitterroot, 7200ft	37
Umatilla	117	Boise	157	Custer	37
Bitterroot, 4000ft	118	Bitterroot, 4000ft	158	Bitterroot, 5000ft	38
Roosevelt	119	Kaniksu	158	Colville	39
San Isabel	119	Colville	158	Siskiyou	40
Colville	119	Custer	159	Whitmore	40
Lolo	120	Bitterroot, 5000ft	159	Bitterroot, 4000ft	40
Helena	120	San Isabel	160	San Isabel	41
Payette	120	Roosevelt	161	Payette	41
Harney	120	Payette	161	Harney	42
Santa Fe	120	Harney	162	Roosevelt	43
Bitterroot, 5000ft	121	Whitman	163	Kaniksu	44
Boise	121	Ashley	164	Santa Fe	49
Custer	122	Umatilla	167	Umatilla	50
Whitman	123	Santa Fe	169	Ashley	50
Coconino	124	Coconino	175	Coconino	52

^a Any 2 means not included within the same line to the right of each ranking of sources are significantly different.

^b From Hanover (1963).

Silen (1962) confirmed the existence of differences in shoot growth of 22 widely separated seed sources of *Pinus ponderosa*. Much of the inherent growth variation was associated with variations in characteristically continuous and specific climatic factors. A strong east to west gradient or cline in growth differences was identified. This gradient was clearly related to seasonal distribution of moisture. Trees from areas with large amounts of autumn, winter, and spring rainfall, or from areas which received much of their total rainfall during those seasons, had inherently rapid growth rates. A moderate latitudinal cline was found in a pattern related to temperature. A moderate altitudinal gradient in growth was also identified. Trees from high altitudes usually grew more slowly than those from low altitudes. The pattern appeared to be correlated with cool temperatures and unfavorable moisture conditions at high altitudes. A multiple correlation analysis showed that 76% of the variation in growth on a plot in northern Idaho was accounted for by September to June rainfall and May temperature.

Burley (1966c) reviewed seed source variation in many characters of both *Pinus elliottii* and *P. taeda*. Variation was more pronounced in *P. taeda* than *P. elliottii* but in both species within-provenance variability often obscured between-provenance differences. For some characters provenance variation was random, but for most traits the patterns of variability tended to be clinal with respect to latitude and longitude, resulting in a trend from northwest to southeast. The pattern was related to patterns of distribution of low temperature and warm-season rainfall, although plant responses could be regulated by photoperiod.

Ecotypic Variation

Vaartaja (1961) demonstrated ecotypic variation in shoot growth for several species of forest trees. Usually the differences in growth characteristics among ecotypes are related to the photoperiodic or thermoperiodic regime to which a race has become adapted. According to Billings (1957), ecotypic variation is related to environmental selection operating on mixed genotypes in local populations. Vaartaja (1959) considered a photoperiodic ecotype to be a population that during evolution "adapted to its seasonally changing environment through a photoperiodic stimulus in a way different from the adaptation elsewhere in other populations." Ecotypes have also been classified as "climatic" (J. Clausen, 1951), "edaphic" (Gregor, 1946), and "biotic" (Tadros, 1957). Habeck (1958) provided evidence of edaphic ecotypes, often within a small geographic area. In three combinations of soil and moisture, seedlings of *Thuja occidentalis* collected from upland habitats showed very different shoot and root growth characteristics than those from lowland habitats.

Apparently distinct ecotypes were found in *Pinus monticola* as little as

one-half mile apart in continuous stands in Idaho and Montana (Squillace and Bingham, 1958). Progenies of trees from moist, low elevations grew faster on good planting sites than those of trees from dry slopes or high elevations. Also, progenies of trees from high elevations grew relatively faster when planted at a high elevation than progenies of sources from low elevations. In the western United States, the rough topography and wide variations in local sites appear to provide selection pressures which may cause ecotypic variation within relatively continuous stands. This is in contrast to situations in the eastern and southern United States where clinal variation usually exists within local populations (Wright, 1944a,b, 1954; Pauley *et al.*, 1955). For example, in the southeastern United States, Wakeley (1961) noted clinal relations of height growth to latitude to be common to *Pinus taeda* and *P. elliottii*.

ADAPTATIONS OF SHOOT GROWTH TO LOCAL ENVIRONMENTS

Populations of trees tend to become adapted to local environments. In many cases the adaptations can be correlated with specific environmental factors. In others this is not readily accomplished because interpopulation migration, limited sizes of populations, and slow genetic response to selection pressure may obscure phenotype correlations (Hanover, 1963). This section will give some examples of adaptations of shoot growth to photoperiod, thermoperiod, and altitude.

Photoperiodic Adaptation

A large body of evidence is available which shows that genetically controlled variations in shoot growth involve adaptations to photoperiod (Kramer and Kozlowski, 1960). The beginning and cessation of shoot growth often are genetically fixed in relation to a given photoperiod. Such mechanisms probably evolved in response to a specific length of growing season. For example, Pauley and Perry (1954) observed genetic diversity in shoot growth characteristics of clonal lines of *Populus* when grown in the same daylength regime. There was a distinct tendency for clones of high latitude (or long day) origin to cease height growth early. Conversely, clones of low latitude (or short day) origin ceased terminal growth late when grown under the mid-latitude daylength regime of Weston, Massachusetts (Table 7.10). This experiment stressed the practical importance of seed source for planting in a particular photoperiodic regime. When seed from northern long-day races is planted in southern latitudes of long frost-free seasons, the resulting trees will cease shoot growth early and consequently will be relatively small. Also seed of ecotypes of long frost-free seasons should not be planted in

TABLE 7.10

HEIGHT GROWTH VARIATION IN CLONAL GROUPS OF *Populus* CLONES AT WESTON,
MASSACHUSETTS^a

Clonal group	Length of growing season (days)	Period of height growth cessation in various clones
Tacamahaca	158	June 20–Sept. 19 (91 days)
Deltoides	178	Aug. 15–Oct. 18 (64 days)
Trichocarpa	197	June 20–Oct. 28 (130 days)

^a From Pauley and Perry (1954).

habitats with short frost-free periods because of the susceptibility of the resulting trees to early frost damage.

Vaartaja (1954, 1957, 1959, 1960, 1961) tested the hypothesis of photoperiodic ecotypes of forest trees, using latitudinally distant seed sources. He established the common occurrence of ecotypes in tree species with wide north to south ranges in the northern hemisphere. At least 15 species out of 17 tested in 8 out of 9 genera (*Acer*, *Betula*, *Fraxinus*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Ulmus*) contained photoperiodic ecotypes. Greenhouse tests showed that the farther north the seed source, the greater was the response to test conditions, and the longer the maximum daylength which inhibited growth. Interactions of seed source and photoperiod were shown in duration of shoot elongation, amount of terminal shoot elongation, and development of lateral shoots. Under certain photoperiods, shoot elongation of northern seedlings ceased early whereas it continued for a long time in southern seedlings. There were no differences, or smaller differences in growth of northern and southern seedlings under other photoperiods. Heights and shoot weights of northern seedlings were much lower than those of southern ones under some photoperiods, and not others. The number of side branches and buds was low in northern seedlings exposed to short days.

Nienstaedt and Olson (1961) collected seeds of *Tsuga canadensis* from 30 locations throughout its latitudinal, longitudinal, and altitudinal range. Subsequently, the resulting seedlings were grown under varying photoperiods. For any given photoperiod, the seedlings from a region with a long frost-free season tended to form buds and stop shoot elongation later than those from an area with a short frost-free season. After 77 days, more than half the plants from a North Carolina source (frost-free season of 190 days) still had growing shoot tips under night lengths as long as 11 hours. In contrast, plants of most sources with growing seasons of less than 164 days ceased growing under night lengths of 9 hours or more. In fact many plants became dormant even under 8- and 4-hour night lengths. The 30 seed sources clearly showed a clinal variation in photoperiodic response.

Thermoperiodic Adaptation

Numerous studies show that the relation between day and night temperatures influences shoot growth of trees. Kramer (1957, 1958b), for example, grew *Pinus taeda* seedlings with various combinations of day and night temperatures. Shoot growth was related more to the difference between day and night temperature than to the actual temperatures used. Maximum shoot growth occurred with the greatest differences between day and night temperatures. Shoot growth was least when nights were as warm as days.

Thermoperiodic adaptations in shoot growth were reported by Callaham (1962). Growth of *Pinus ponderosa* from different parts of its range was measured under combinations of three day temperatures (30° , 23° , and 17°C) and three night temperatures (22° , 14° , and 7° or 10°C) with constant day-length of 16 hours. Trees from various geographic sources responded differently to different temperature combinations. In general, seedlings from east of the Rocky Mountains grew best with high night temperatures. Seedlings from a southwestern source made best growth with cold days and warm nights, whereas Pacific Coast seedlings showed vigorous growth at lower night temperatures.

Perry (1962) subjected *Acer rubrum* plants from different geographic sources to several day and night temperature treatments under controlled conditions. Daylength was maintained at 16 hours. The night and day temperature necessary for maximum shoot growth was different for each provenance. In general, it corresponded with the day and night temperature of the locale of the seed collection. The day temperatures required for optimum growth were higher than the night temperatures. Plants of northern provenances tended toward dormancy under night temperatures higher than 23°C and lower than 10°C . Northern provenances also tended to go into dormancy with low daylight intensity. In contrast, a Florida source was more tolerant of low light intensities. These observations suggested that temperature and low light intensity may counteract favorable photoperiod and cause dormancy in *Acer rubrum*.

Altitudinal Adaptation

Considerable study has been given in the western United States to altitudinal adaptations of height growth characteristics. For example, Mirov *et al.* (1952) studied growth of *Pinus ponderosa* trees derived from seed trees from 125 to 6919 ft above sea level on the west slope of the Sierra Nevada in California. Height growth was studied in test plantations at 960, 2730 and 5650 ft above sea level. Height growth of plants from 2 to 12 years old was greatest for seed trees from 1500 to 3500 ft above sea level. Callaham and Liddicoet (1961) remeasured the trees after 20 years and found that some changes had occurred over the early measurements. At 20 years, generally

local seed sources grew best at the three planting sites. The fastest growing 20-year-old progenies at low (960 ft) and medium (2730 ft) elevation plantations were from seed trees growing at elevations of 1000 to 2000 ft. Their height was greater than that of high elevation or very low elevation progenies. At the highest elevation test planting (5650 ft), height growth of the progenies from lower elevations was restricted.

Diurnal Variations in Shoot Growth

Distinct daily rhythms of shoot growth occur, with shoots often elongating more at night when cells are turgid than during the day (Mork, 1941). Under certain environmental conditions, however, growth during the day may exceed growth at night.

Shoot growth of several species, including *Pinus strobus*, *Picea abies*, *Prunus serotina*, *Fraxinus americana*, *Liriodendron tulipifera*, and *Quercus*, was measured separately during the day and night by Illick (1928). All species grew at approximately twice the rate at night as during the day. Kienholz (1934) compared shoot elongation of *Pinus resinosa* during the day and night from June 13 to 29 in New Hampshire. With the exception of two days, June 24 and 25, shoot expansion at night was greater than during the day. The average night growth was 5.93 mm and day growth was 4.47 mm. In North Carolina night growth exceeded day growth by about 100% in *Pinus taeda* and by 80% in *P. echinata* (Reed, 1939). In Australia, Fielding (1955) measured elongation of apical shoots of *Pinus radiata* at 3-hour intervals during the day and night in late October. Growth was consistently greater at night than during the day, with fastest growth during the 24 hours occurring between 3 PM and midnight.

Both turgor and temperature appear to influence diurnal periodicity of shoot growth. Some investigators have reported that shoots occasionally shrink longitudinally during the day because of low turgor. For example, Fielding (1955) noted that some *Pinus radiata* shoots showed shrinkage during the day, mostly in the spring of the year. On one day an extreme longitudinal shrinkage of 1 cm was recorded.

As the relationship between day and night shoot growth is influenced greatly by temperature conditions, it varies with season. Kienholz's data (1934) showed that during the 2 days when growth of shoots during the day surpassed growth at night the minimum temperatures were low. Tolsky (1914) found that early in the growing season night growth of shoots was inhibited by low temperatures and day growth was greater. In Placerville, California, early season height growth (April 18 to 25) by *Pinus attenuata* and *Pinus sabiniana* was greater during the day than at night, (Table 7.11).

TABLE 7.11

DAY AND NIGHT HEIGHT GROWTH OF *Pinus attenuata* AND *P. sabiniana* TREES, IN APRIL, 1962 AT PLACERVILLE, CALIFORNIA^a

Date	Growth (mm)			
	<i>P. attenuata</i>		<i>P. sabiniana</i>	
	Day	Night	Day	Night
April				
18-19	4.0	3.0	4.5	3.5
19-20	2.0	0.0	1.0	0.0
20-21	4.0	1.0	5.0	3.0
21-22	9.0	5.0	4.5	3.0
22-23	7.0	6.0	7.0	7.0
23-24	6.0	5.0	7.5	2.5
24-25	2.0	2.0	2.5	2.0
Total	34.0	22.0	32.0	20.5

^a From Lanner (1964).

Growth of both species was closely related to accumulated heat units. This relation applied to day versus night growth, growth for consecutive 24 hour periods, and growth during the course of a single day. *Pinus sabiniana* was less sensitive to temperature change than *P. attenuata*, and it made most of its shoot growth and reached maximum growth later than the latter species (Lanner, 1964). In Norway a correlation of 0.90 between daily shoot elongation and mean temperature of the 6 warmest hours of the day was found by Dahl and Mork (1959).

Within-Tree Variations in Shoot Growth

The amount and seasonal pattern of growth of shoots on the same tree often differ greatly for a variety of reasons. Such variations often are traceable to differences in expandable bud contents or variations among shoots in the number of growth flushes they undergo in the same year. Differences in growth of long and short shoots within the same tree in genera such as *Larix*, *Ginkgo*, and *Cercidiphyllum* reflect substantial internodal growth of long shoots and lack of internodal extension in short shoots. As emphasized in Chapter 4, within-tree variations in shoot growth of these genera vary considerably with tree age. To a large extent, variations in shoot elongation in *Populus* are related to the presence of three morphologically different types

TABLE 7.12
GROWTH DURING 1967 OF LEAVES AND INTERNODES OF LONG SHOOTS OF UNEARTHED TREES AND STUMP SPROUTS OF *Acer rubrum*
TREES CUT AT DIFFERENT TIMES OF YEAR^a

Time of cutting	Leaf pairs produced per week	Leaf length (mm)		Internode length (mm)		Maximum height growth (mm/week)
		Maximum	Maximum elongation per week	Maximum	Maximum elongation per week	
Uncut tree						
Autumn 1966	1.0-1.3	87-116	20-30	78-86	25-40	79-126
May 31, 1967	1.3-2.3	180-208	44-66	107-183	50-88	202-306
June 14, 1967	1.0-1.6	c				87-141
June 30, 1967	0.8-1.5					70-133
July 28, 1967	1.0-1.3					114-170
August 24, 1967	1.0-1.5					10-86
			1.0 ^b			3

^a From Wilson (1968).

^b Only one stump sprouted: the one bud produced one leaf pair.

^c For stumps cut May 31 to August 24 data were taken only on the rate of leaf pair production and rate of height growth.

of shoots; those with early leaves only, those with early and late leaves, and those with late leaves only (Chapters 5 and 6).

Sprout shoots often grow faster than shoots of nonsprout origin. For example, the rates of leaf production, leaf elongation, and internode elongation, the final size of leaves and internodes, and seasonal duration of leaf and internode elongation were greater in *Acer rubrum* sprouts of trees cut the previous winter than in long shoots of uncut trees (Table 7.12). The sprouts grew faster from the time of their emergence, even before mature leaves had developed and continued at approximately that rate until shortly before shoot growth ceased in the autumn. Sprouts from stumps cut later in the season did not grow as fast or as tall as from those cut in the winter. In fact, they grew only slightly more than control long shoots (Wilson, 1968).

Some species of trees show more or less systematic variation in within-tree shoot growth. For example, many gymnosperms with fully preformed shoots in the dormant bud produce one annual burst of shoot growth, with the amount of growth of individual shoots decreasing more or less regularly from the top of the tree downward. In contrast, many species do not show such pronounced apical dominance and exhibit wide and unpredictable variations in growth of shoots. In some orchard trees, for example, one branch may show continuous growth all season, another may show an early growth flush and early cessation, a third may show two flushes of rapid growth separated by a period of slow growth, and a fourth may exhibit two or more distinct flushes of shoot growth (Glock *et al.*, 1964). Sometimes variations in shoot growth within trees are caused by production of lammas or proleptic shoots from bursting of current-year buds on some branches, or by production of variously located epicormic shoots. There is considerable evidence of both hereditary and environmental control over differences in shoot growth within the same tree.

The excurrent growth form is widely considered to be an expression of strong apical dominance and the deliquescent or decurrent form of weak apical dominance. However, apical dominance as originally used referred to bud inhibition by an active apex on currently elongating shoots. C. L. Brown *et al.* (1967) pointed out that the patterns of bud inhibition in excurrent and deliquescent trees are really the opposite of what they should be according to the accepted usage of apical dominance. They noted that in decurrent angiosperms practically all lateral buds on the current year's growth are inhibited in a pattern conforming to strong apical dominance. In contrast, in excurrent trees such as many gymnosperms and a few angiosperms (i.e., *Liriodendron tulipifera*), the lateral buds on current year's twigs elongate in varying amounts, an expression of weak apical dominance. It is during the second season that the uppermost vigorous lateral buds of deliquescent

trees elongate more rapidly than the terminal bud and hence produce excessively branched stems. The concept that apical dominance is strong in excurrent trees and weak in deliquescent ones apparently resulted from translating early experiments with herbaceous plants to woody plants without studying patterns of bud inhibition in the latter group. Because decapitation of herbaceous plants caused branching and a bushy growth habit, it was assumed that decurrent or deliquescent trees lost apical dominance. The present widely entrenched and somewhat erroneous association of strong apical dominance with excurrent trees and weak apical dominance with deliquescent ones is the result of applying the term to tree form rather than to bud inhibition on individual shoots.

C. L. Brown *et al.* (1967) suggested that the term *apical control* be used for the physiological condition determining the excurrent or decurrent growth pattern. The excurrent growth habit could then be explained in terms of strong apical control reflecting initial weak apical dominance or incomplete bud inhibition. In such a system the terminal leader maintains control each year over the suppressed branches below and conical-shaped crowns are thereby maintained. In contrast, decurrent or deliquescent trees show strong apical dominance and completely inhibit buds along the elongating terminal leader. Such trees lose apical control quickly because the inhibited lateral buds can successfully compete with the terminal buds during the next season of shoot extension. In many decurrent species the terminal leader eventually abscises resulting in a sympodial branching habit. Hence, a previously inhibited lateral bud may gain dominance for a season or two, but it is soon replaced by one of the upper, inhibited lateral buds.

APICAL REGULATION OF SHOOT GROWTH IN GYMNOSPERMS

Many species of gymnosperms show very marked inhibition of lateral shoots, especially those in the lower stem (Fig. 7.8). Kozlowski and Ward (1961) found that total annual shoot growth of primary and secondary stem axes by 6-year-old trees was in the following order: *Pinus resinosa* > *Pinus strobus* > *Picea glauca* > *Picea mariana*. All of these species showed strong correlative growth inhibition. The primary axis (terminal leader) grew more than a secondary axis; a secondary axis grew more than a tertiary axis; and a tertiary axis grew more than a quaternary one (Table 7.13). Growth of secondary axes was greatest at the uppermost whorl and decreased progressively in the whorls below it. The amount of growth of tertiary and quaternary axes also decreased downward in the trees. When there were two sets of the same axis on the same branch, for example, tertiary axes on third and fourth whorls, the more distal tertiary axis grew more than the more proximal one. Hence, the amount of annual shoot elongation decreased

TABLE 7.13
VARIATIONS IN SHOOT ELONGATION DURING 1960 ON DIFFERENT LOCATIONS OF STEMS OF 6-YEAR-OLD CONIFERS GROWN AT WISCONSIN RAPIDS,
WISCONSIN^{a,b}

Primary axis (Terminal leader)	Secondary axis whorl number				Tertiary axis whorl number				Quaternary axis whorl number			
	1		2		3		4		Upper		Lower	
	set	set	set	set	set	set	set	set	set	set	set	set
<i>Pinus</i>	57.7	34.6	32.5	27.7	15.4	17.1	15.3	13.7	11.5	8.1	6.2	4.7
<i>resinosa</i>	± 6.2	± 7.7	± 4.9	± 5.4	± 8.0	± 5.8	± 5.4	± 4.5	± 4.9	± 4.8	± 2.7	± 2.5
<i>Pinus</i>	44.3	25.5	24.8	19.1	14.1	12.3	10.5	9.5	7.8	7.3	4.3	3.0
<i>strobus</i>	± 7.6	± 8.2	± 7.0	± 4.1	± 2.2	± 5.1	± 3.4	± 3.4	± 8.4	± 3.7	± 0.6	± 0.5
<i>Picea</i>	33.5	19.8	17.4	15.3	11.8							
<i>glauca</i>	± 5.7	± 4.1	± 3.5	± 2.8	± 3.0							
<i>Picea</i>	23.8	17.3	16.5	14.1	10.0							
<i>mariana</i>	± 6.4	± 3.5	± 2.5	± 3.3	± 3.2							

^a All measurements are in centimeters.

^b From Kozlowski and Ward (1961).

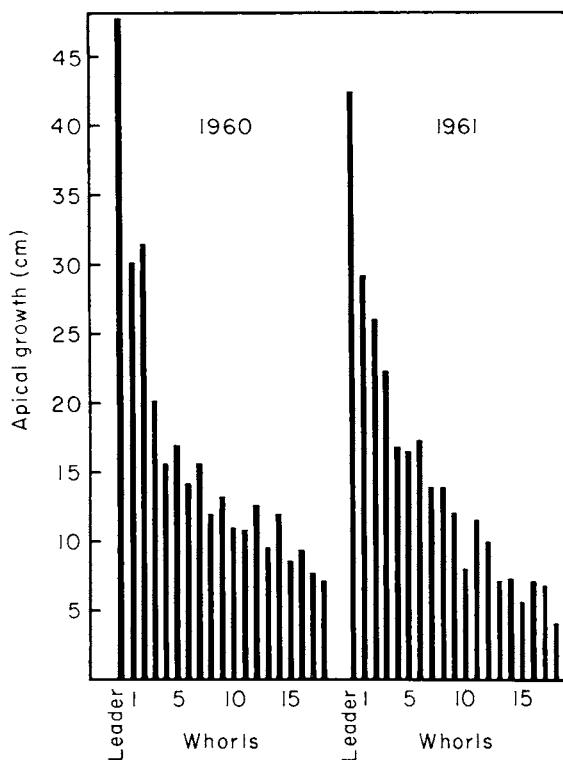


FIG. 7.8. Apical dominance in *Picea glauca*. Total apical growth is shown for the terminal leader and 18 whorls on a 9-m-high tree for 1960 and 1961. [From Fraser (1962).]

progressively downward and inward in the tree. Terminal leaders elongated an average of almost 12 times as much as the quaternary branches of the fourth whorl down from the top of the tree. Fraser (1962) demonstrated strong apical control of shoot growth in *Picea glauca*. Total shoot elongation was greatest in the terminal leader, with the four side branches in the first two whorls averaging about two thirds as much growth as the leader. In lower whorls there was a general decrease in growth (Fig. 7.8). The degree of apical control of shoot growth often changes with physiological tree age. In *Pinus radiata*, for example, apical control was weak in trees up to 6 years old and strong thereafter (Fielding, 1960).

In recurrently flushing pines the number of seasonal growth flushes of lateral shoots varies with shoot location. Shoots in the upper crown generally show more annual growth flushes than those in the lower crown. Some buds of lower branches may not open at all (Table 7.14). Boyer (1970) found wide

TABLE 7.14

NUMBER OF SHOOT GROWTH FLUSHES AT DIFFERENT HEIGHTS IN *Pinus taeda* AND *Pinus caribaea*^{a,b,c}

Whorl location	<i>Pinus taeda</i>				<i>Pinus caribaea</i>				
	Number of growth flushes	0	1	2	3	Number of growth flushes	0	1	2
Topmost		5	6	5		14	24		
Second		3	8	4		10	19	7	
Third		3	10	2		12	11	1	
3rd above middle		6	2			1	7		
2nd above middle		2	3			3	3	1	
1st above middle		15	3			18	19		
1st above middle		12	2			15	10		
2nd above middle		6				3	2		
4th from bottom		9				12			
3rd from bottom		2	8			2	25	1	
2nd from bottom		4	10			3	29		
Lowest		4	5			12	20		

^a The trees were 10 to 15 ft tall and grew in Covington, Louisiana.

^b The numbers indicate how many shoots elongated in each category.

^c From Eggler (1961).

within-tree variations in shoot growth of *Pinus taeda* seedlings and saplings in North Carolina. The number of annual growth flushes, amount of secondary branching, and average shoot length all declined with increasing distance from the tree top. All seedling terminal shoots had three growth flushes and half of them had four. Forty percent of seedling lateral shoots had three growth flushes, 55% had two, and 5% had one. A small number of buds did not expand at all. The number of buds failing to develop into shoots was low for the first seasonal growth flush, but much higher for the third and fourth growth flushes of terminal shoots and the second and third flushes of lateral shoots.

Some gymnosperms do not show strong apical control of shoot growth. In contrast to the situation in *Pinus* and *Picea*, second-order branches of *Araucaria excelsa* apparently lack the inherent capacity to assume apical dominance. Removal of the apical shoot is not followed by formation of a new leader by one of the lateral branches (Brink, 1962). Rooted cuttings of this species grow horizontally, and Wareing (1959) mentioned that rooted cuttings from a first order side branch of *Araucaria* grew horizontally for at least 50 years. Although many species of *Pinus* exhibit strong apical control of shoot elongation for a long time, some species such as *Pinus pinea*, often lose such control rather early (Fig. 7.9).

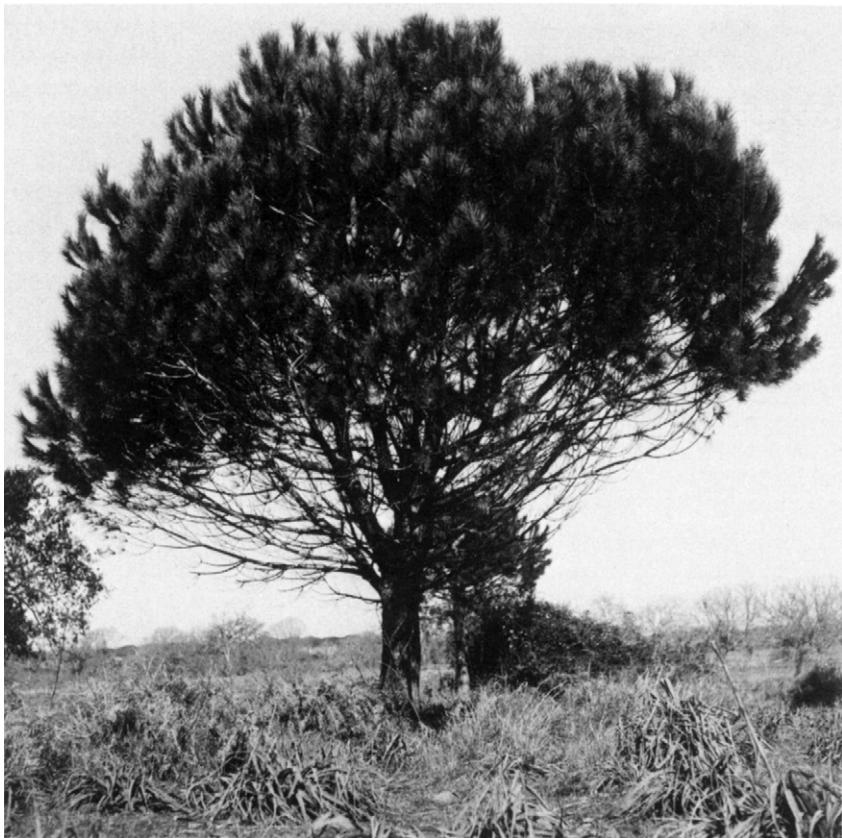


FIG. 7.9. Sixteen-year-old *Pinus pinea* showing lack of apical dominance (Photo courtesy of A. de Phillipis.)

There is some evidence of genetic regulation of apical control of shoot growth. For example, Fielding (1953) showed that certain clones of *Pinus radiata* had a tendency for subterminal shoots to develop faster than terminals and to overtop them. In other clones the terminal shoot was always dominant. Fielding (1960) cited an interesting case of two adjacent clones of *Pinus radiata* on similar sites and raised by cuttings from trees of the same age. In one clone 100% of the trees had leading shoots overtopping the branch shoots, in contrast to only 12% in other clones. Very weak apical control of shoot growth may occur in certain fastigiate gymnosperms. For example, fastigiate variants develop rather commonly in *Pinus radiata* plantations in Australia. They lack a main stem and are characterized by several competing, vertically growing branches. As the terminal buds lack apical control, the fascicle buds at the ends of vigorous shoots elongate into long branches.

Branchless Pines or "Foxtails"

A very interesting and extreme form of apical control of shoot growth is that shown by recurrently flushing tropical or subtropical pines which sometimes produce unusually long, unbranched terminal leaders. Leading shoots up to 20 ft long, without branches, are commonly produced by these species and sometimes the terminal leaders may be up to 40 ft long. These shoots represent the cumulative growth of several years. Among species reported to form foxtail shoots are *Pinus radiata*, *P. caribaea*, *P. merkusii*, *P. oocarpa*, *P. canariensis*, *P. cembroides*, *P. insularis*, *P. tropicalis*, *P. palustris*, *P. taeda*, *P. elliottii*, and *P. echinata*.

In Malaysia various degrees of foxtailing were observed in *Pinus caribaea* var. *hondurensis* trees up to 15 years of age (Kozlowski and Greathouse, 1970). For example: (1) in some trees continuous growth of the terminal leader occurred without pause after field planting, resulting in a single stem with no side branches; (2) foxtailing began at the time of field planting and



FIG. 7.10. Five-year-old normal branched trees and branchless foxtail forms of *Pinus caribaea* var. *hondurensis* in Malaysia. [From Kozlowski and Greathouse (1970).]

ceased after a few years. Thereafter a normal, recurrently flushing pattern of shoot growth occurred; (3) trees grew normally in recurrent flushes for a few years and then foxtailed; and (4) foxtailing began at the time of field planting, ceased after a few years, and subsequently resumed in the terminal leader. Thus, conversions from continuous shoot elongation to a recurrently flushing pattern, as well as the reverse, were observed. Often the alternation of the normal recurrently flushing habit and the abnormal foxtailing pattern produced individual trees of grotesque form (Fig. 7.10). Many examples of foxtailing of lateral shoots, in trees which had flushed recurrently, were observed. Hence, whorl branches sometimes also exhibited continuous growth. Either gradually or abruptly, such lateral shoots became vertically oriented (Fig. 7.11). Like the terminal leaders of strongly foxtailing trees, these branches did not produce any branch shoots.

Lanner (1966) distinguished between "true foxtails" whose long terminal



FIG. 7.11. Marked apical dominance in lateral shoots of foxtailing *Pinus caribaea* var. *hondurensis* in Malaysia. [From Kozlowski and Greathouse (1970).]

leaders were branchless because no buds formed on them and "false foxtails" whose leaders were branchless because branch buds which formed aborted before they could elongate.

A typical true foxtail of *Pinus radiata* is shown in Fig. 7.12 growing in Hawaii as described by Lanner (1966). This tree was 22 ft high and had several whorls or branch scars up to a height of only 3.5 ft. The 18.5 ft long terminal shoot lacked branch scars or lateral buds over its entire length. As the only sterile-scale zone occurred immediately above the branch whorl at the base of the foxtail, the terminal shoot was made up primarily of elongated internodes between dwarf shoots. Beginning at a height of 2 ft above ground, a 4 ft section of the stem had a bearded appearance as a result of extensive proliferation of needle fascicles. Needle fascicles along the foxtail were regularly spaced. This was in contrast to the systematic variation in normal annual shoot increments of many pines in which internodes are short at the shoot base, longer in the middle, and again short at the distal end.

Unlike the terminal bud of most pines that of the true foxtail consisted only of primary leaves subtending needle fascicles. As true foxtails form from continuous growth the character of the bud does not change seasonally



FIG. 7.12. *Pinus radiata* foxtail in Hawaii. Five and one-half years after planting the tree was 22 ft high and had 18.5 ft of unbranched terminal leader. [From Lanner (1966).]

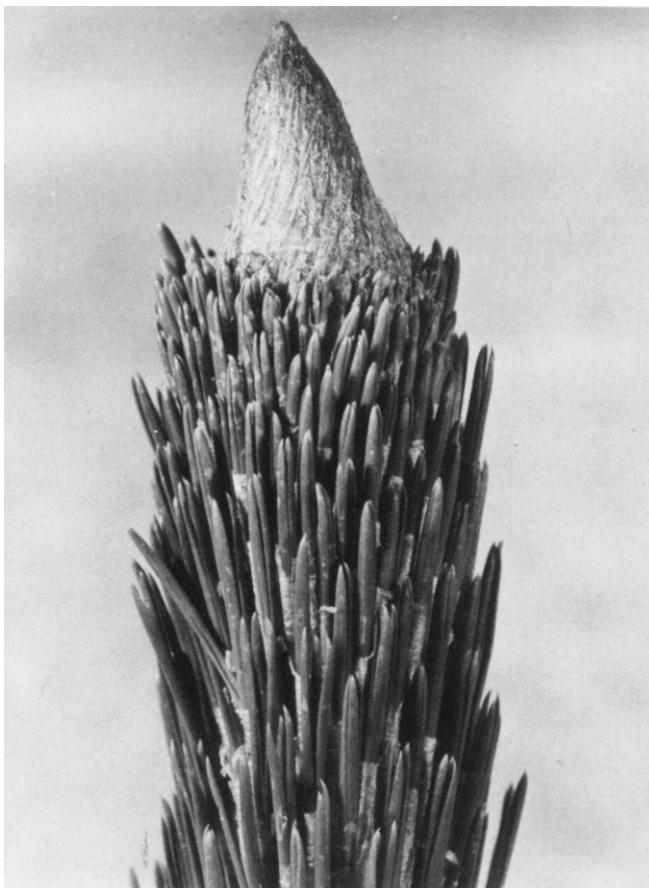


FIG. 7.13. Tip of continuously growing *Pinus radiata* foxtail showing a continuous series of scales subtending needle fascicles and absence of sterile bud scales. [From Lanner (1966).]

(Fig. 7.13). Needles of all sizes and stages of development are found throughout the year. The shoot tip consists of tightly packed needles within unbroken sheaths. Below them occur needles penetrating sheaths and needles free of sheath which gradually increase in size to an abnormal length. According to Forde (1964) needles of normal *Pinus radiata* trees averaged 11 to 15 cm in length and those of foxtails closer to 20 cm. Needles on branches of foxtail-bearing trees are of normal length. The xylem laid down by a shoot of a true foxtail is typically earlywood, without annual rings.

False foxtails differ from true foxtails in several respects. As in a normal pine stem, the terminal shoot of a false foxtail has alternating series of bud scales, sterile scales, and dwarf shoots. The base of each sterile-scale zone usually has a whorl of very small dormant buds unless these have aborted (Fig. 7.14). The terminal bud is normal and is enclosed in sterile bud scales during the dormant season. When dormancy is broken a false foxtail shoot exhibits a typical sigmoid growth pattern. Needles of false foxtails are similar in length to those of normal pines. Cambial growth is seasonal, and both earlywood and latewood are formed in the terminal shoot.



FIG. 7.14. False foxtail of *Pinus palustris* in Hawaii. The exposed part of the stem bears sterile scales which have never borne needle fascicles. Below this is a whorl of aborted buds and branches, one of which is visible. [From Lanner (1966).]



FIG. 7.15. Shaping of *Pinus sylvestris* trees by cutting back of shoots. (A) Spindly, control tree; (B) Well-shaped and bushy tree which had been sheared. (U.S. Forest Service Photo.)



Control of Foxtailing

The characteristic foxtailing of tropical pines appears to be a strongly inherited growth phenomenon, with its expression modified considerably by site and environmental factors. In Australia, an unselected crop of *Pinus caribaea* var. *hondurensis* had a much higher frequency of foxtails than unselected crops of var. *caribaea* or var. *bahamensis*. However, progeny from selected var. *hondurensis* parents had a lower incidence of foxtailing,

with the amount of reduction depending on the degree of control of the parentage (Slee and Nikles, 1968). In South Africa, Luckhoff (1964) noted low incidence of foxtailing at high elevations and latitudes with cool temperatures. For example, along the coast of Zululand (average altitude of 150 to 200 ft) foxtails of *Pinus caribaea* var. *hondurensis* averaged 43%; at Ntsubane (altitude approximately 1500 ft) 26%; and at Dargal in the Natal Midlands (altitude approximately 4000 ft) 13%. In Queensland, Australia, Slee and Nikles (1968) recorded a higher incidence of *Pinus caribaea* foxtails at Beerwah than at Bowenia and attributed the difference to the more favorable environment at Beerwah.

Practical Implications in Loss of Apical Dominance

Natural loss of apical dominance in trees following injury often is harmful as it degrades logs by causing a forking of the main stem when the apical meristem of the terminal leader is destroyed. For example, apical control of eastern white pine (*Pinus strobus*) often is at least temporarily destroyed by the white pine weevil (*Hylobius pales*) which bores into the terminal bud cluster and lays eggs. After the young grubs emerge they kill the leading shoot. Eventually one of the lateral branches assumes dominance and suppresses its neighboring shoots in the same whorl. The killing of tops of *Abies balsamea* trees by spruce budworm (*Choristoneura fumiferana*) often is followed by one of the lateral branches turning upward and becoming the leading branch of the tree (Stillwell, 1956).

The loss of apical dominance may also have very useful practical implications, as in improvement of quality of Christmas trees. Outplanted gymnosperms grow slowly for the first few years and much more rapidly thereafter. When long internodes start to form on the main stem and the secondary axes of a fast growing tree, it assumes a spindly appearance that inevitably lowers its quality as a Christmas tree. For this reason, many growers routinely "shape" rather young Christmas trees by modifying apical control by inhibiting internodal growth of the main stem and its major branches. This is accomplished by cutting back current shoots, or sometimes 1-year-old growth as well. Shearing of the terminal leader and current-year laterals, or removal of buds at the tips of these shoots, stimulates expansion of dormant buds and formation and expansion of new buds into branches which grow at various angles from the treated shoots. The end result of such treatment is a decrease in internodal growth of the major axes and an increase in the number and development of shoots of subordinate axes. A well-shaped and bushy Christmas tree results from altering normal apical dominance relations by shearing (Fig. 7.15).

The shoots which are newly stimulated by shearing form fascicle buds between the needles that make up the needle fascicles. As many as 15 such buds formed in *Pinus sylvestris* terminal shoots in response to shearing (Lentz, 1965). Trees can be sheared at various times during the year, but when this is done after annual shoot growth ceases, the formation of fascicle buds is delayed. For example, if shoots are cut back early in the growing season, i.e., before they harden, fascicle buds usually develop within a month to 6 weeks. However, if shearing is delayed until late summer, autumn or winter, the fascicle buds usually do not appear until the following spring. More fascicle buds form as a greater length of shoot is removed by shearing. Practical aspects of shearing Christmas trees are discussed by Cunningham and Winch (1962).

Suggested Collateral Reading

- Alvim, P. de T. (1964). Tree growth periodicity in tropical climates. In "The Formation of Wood in Forest Trees" (M. H. Zimmermann, ed.), pp. 479-496. Academic Press, New York.
- Burley, J. (1966). Review of variation in slash pine (*Pinus elliotii* Engelm.) and loblolly pine (*P. taeda* L.) in relation to provenance research. *Commonw. Forest. Rev.* **45**, 322-338.
- Callaham, R. Z. (1962). Geographic variability in growth of forest trees. In "Tree Growth" (T. T. Kozlowski, ed.), Chapter 20. Ronald Press, New York.
- Hanover J. W. (1963). Geographic variation in ponderosa pine leader growth. *Forest Sci.* **9**, 86-95.
- Kozlowski, T. T. (1964). Shoot growth in woody plants. *Bot. Rev.* **30**, 335-392.
- Kozlowski, T. T., and Keller, T. (1966). Food relations of woody plants. *Bot. Rev.* **32**, 293-382.
- Kozlowski, T. T., and Ward, R. C. (1961). Shoot elongation characteristics of forest trees. *Forest Sci.* **7**, 357-368.
- Kramer, P. J. (1943). Amount and duration of growth of various species of tree seedlings. *Plant Physiol.* **18**, 239-251.
- Langlet, O. (1962). Ecological variability and taxonomy of forest trees. In "Tree Growth" (T. T. Kozlowski, ed.), Chapter 23. Ronald Press, New York.
- Richards, P. W. (1964). "Tropical Rain Forest." Cambridge Univ. Press, London and New York.
- Squillace, A. E. (1966). Geographic variation in slash pine. *Forest Sci. Monogr.* **10**.
- Vaartaja, O. (1959). Evidence of photoperiodic ecotypes in trees. *Ecol. Monogr.* **29**, 91-111.
- Wright, J. W. (1962). Genetics of forest tree improvement. *FAO Forest. Forest Prod. Stud.* **16**.

Chapter 8

CONTROL OF SHOOT GROWTH

Introduction

The growth of shoots reflects an integrated response to a host of impinging climatic, edaphic, and biotic factors which, by influencing internal physiological processes, contribute variously to formation and expansion of shoot primordia. As growth is controlled by an ecological nexus, it is extremely difficult to appraise the specific contributions of individual environmental factors to shoot growth because they are interacting and interdependent (Kozlowski, 1949). Among the most important environmental components which affect shoot growth are light, water, temperature, mineral supply, composition of the atmosphere above and below ground, soil physical and chemical properties, insects, other plants, and various animals. Shoot growth is also greatly modified by cultural practices and by reproductive growth. The influences of genetic factors and aging of trees on shoot growth are superimposed on those of environmental regimes.

Environmental Control of Shoot Growth

The environment influences shoot growth mainly by regulating the expansion of primordia previously laid down and by influencing the production of new primordia to be expanded later, often in the subsequent year. Hence, both rapid and gradual responses of various phases of shoot growth to environmental regimes are recognized. A warm spell early in the spring often causes buds to open rapidly. Late in the growing season, however, prevailing temperatures may influence the number of leaf primordia which are laid down and thereby place a limitation on shoot expansion during the subsequent year. Whereas, early-season droughts often inhibit leaf expansion, late-season droughts may restrict the number of primordia laid down in the new bud. The effect of a late-summer drought, therefore, may not be obvious until

the following year when shoots expand in an amount which reflects the number of primordia contained in the winter bud.

The complexity of environmental control of growth is further illustrated by shifting in importance of individual environmental factors on various phases of shoot development. For example, temperature predominates early in the season in controlling bud opening whereas, late in the season, drought often is much more important than temperature in controlling leaf expansion or formation of new leaf primordia. To illustrate some ways in which environmental factors may influence shoot growth the effects of a few will be discussed in the next section.

Light

Shoot growth of trees is affected by light intensity, duration of exposure to light or photoperiod, and light quality or wavelength. Under natural conditions shoot growth is influenced much more by light intensity and photoperiod than by light quality.

LIGHT INTENSITY

The light intensity to which trees are exposed varies greatly in different habitats and with age of tree stands. It also varies greatly in different parts of the crown of a given tree. For example, light intensity in the interior of tops of citrus trees varied from as little as 0.5–2% of full sunlight. The light intensities in tree crowns also differed greatly among citrus varieties, with those having dense crowns, such as Marsh seedless grapefruit and Clementine mandarin, being much darker than those of Shamouti orange (Monselise, 1951).

Species vary greatly in shoot growth response to light intensity (Kramer and Kozlowski, 1960; Gatherum *et al.*, 1963). For example, shading reduced shoot growth in *Pinus taeda* more than in *Quercus lyrata* (Kozlowski, 1949). Logan (1965, 1966a,b) compared shoot growth of seedlings of several species of angiosperms and gymnosperms in full light and in shelters admitting 45, 25, or 13% light. In general, heavy shading reduced shoot growth of the gymnosperms more than that of angiosperms (Tables 8.1 and 8.2). Height growth of *Betula papyrifera*, *B. alleghaniensis*, *Acer saccharinum*, and *A. saccharum* was not adversely affected by reducing light intensity to 45% of maximum (Table 8.1). However, further reduction in light intensity caused decreases in various aspects of shoot growth. Shoot growth of *Acer saccharum* was affected least by reduction in light intensity. Maximum height growth of this species extended over a wide range from 45–13% of full light. In contrast to shoot weight of other species of angiosperms, weight of *Acer saccharum*

TABLE 8.1
EFFECT OF SHADING FOR FIVE YEARS ON SHOOT GROWTH CHARACTERISTICS OF ANGIOSPERM SEEDLINGS^{a,b}

	Height (in.) at light intensity		Dry weight of shoots (gm) at light intensity			Dry weight of foliage (gm) at light intensity		
	13%	25%	45%	100%	13%	25%	45%	100%
<i>Betula papyrifera</i>	71	80 ²	89 ³	60 ⁴	90.7 ¹	156.7 ²	318.5	243.4 ⁴
<i>Betula alleghaniensis</i>	60 ¹	77 ²	84 ³	59 ⁴	88.1 ¹	154.8 ²	237.6 ³	236.2 ⁴
<i>Acer saccharinum</i>	44	48	47	30	34.2	44.2	54.5 ³	50.7
<i>Acer saccharum</i>	59 ¹	57	72	55 ⁴	56.4	76.6	171.2	235.0 ⁴
							32.7 ¹	
							43.3 ³	77.7 ^{4,5}
							27.5	34.0
							18.5	50.4

^a From Logan (1965).

^b Lines connect treatments in which a species showed no significant differences; common numerals denote the species in each column that did not differ significantly in various aspects of shoot growth.

TABLE 8.2
EFFECT OF SHADING FOR FIVE YEARS ON SHOOT GROWTH CHARACTERISTICS OF GYMNOSPERM SEEDLINGS^{a,b,c}

	Height (in.) at light intensity			Dry weights of shoots (gm) at light intensity			Dry weight of foliage (gm) at light intensity		
	13%	25%	100%	13%	25%	45%	100%	13%	25%
									45%
<i>Larix laricina</i>	30	44	68	67	4.2	10.2	30.3 ³	40.7	—
<i>Pinus banksiana</i>	16	29	39	44	2.7 ¹	16.2	32.1 ³	52.7	—
<i>Pinus strobus</i>	11	15	22	22	2.6 ¹	5.4 ²	17.3	22.7 ⁴	5.4
<i>Pinus resinosa</i>	6	12	15	16	1.4	4.4 ²	12.1	23.5 ⁴	1.7
								10.1 ¹	22.3
									38.5

^a From Logan (1966a).

^b Lines connect treatments in which species showed no significant differences; common numerals denote the species in each column that did not differ significantly in various aspects of shoot growth.

^c Data on dry weight of shoots are given after 4 years.

shoots was not reduced by a decrease from full light to 25% of full light (Logan, 1965).

Light intensity had only a limited effect on shoot elongation of *Tilia americana* seedlings. Dry weights of the main stem and leaf area also were not influenced appreciably by changes in light intensity between 25% and full light. By comparison, *Ulmus americana* seedlings showed an increase in height and stem weight as light intensity was increased up to 45% of full light (Logan, 1966b).

Low light intensities greatly decreased shoot growth of *Larix laricina*, *Pinus banksiana*, *P. strobus*, and *P. banksiana* seedlings (Table 8.2, Figs. 8.1 and 8.2). By the fourth year the seedlings of all four species at the two lowest light intensities (13 and 25% of full light) were smaller than those in 45–100% of full light. Five-year-old *Pinus banksiana* plants required full light for maximum height growth but height growth of the other species was not greatly different at the two highest light intensities. Nevertheless, shoot dry weight of each of the four species was reduced by each shading treatment. Shading depressed shoot growth in *Pinus resinosa* more than in *P. strobus* (Logan, 1966a).

Light intensity affects growth of shoots both directly and indirectly. Direct effects are exerted on photosynthesis, stomatal opening, and chlorophyll synthesis. The influence of light on cell enlargement and differentiation, through effects on plant metabolism and especially hormone synthesis, is reflected in changes in height growth, leaf size, and structure of leaves and stems (Kramer and Kozlowski, 1960). Indirect effects of light on shoot growth may be reflected in leaf desiccation as a result of excessive transpiration under exposure to high light intensities. In appraising the effects of light intensity on shoot growth, it is important to recognize the separate effects of the persistent and consistently decreasing light intensity in plantations or forests as trees age from the influences of short-time changes in light intensity from day to day and at different times during a day. The specific effects of changes in light intensity are not easily assessed because increases in light intensity often are accompanied by higher temperatures which, in turn, influence each of the physiological processes already mentioned, and respiration as well.

The persistent effects of decreasing light intensity are most important in controlling species composition of tree communities. Trees vary greatly in their capacity to survive in shade, a characteristic often expressed in "tolerance" ratings. For example, among gymnosperms *Tsuga canadensis*, *Abies balsamea*, and *Thuja plicata* are considered very tolerant of shade; *Picea rubens*, *P. glauca*, *P. sitchensis*, and *Abies concolor* are tolerant; *Pinus strobus*, *P. monticola*, *P. lambertiana*, and *Sequoia sempervirens* are intermediate; *Pinus resinosa*, *P. taeda*, and *P. ponderosa* are intolerant; and *Pinus*

palustris, *P. banksiana*, and *Larix laricina* are very intolerant of shade. Among the angiosperms *Fagus grandifolia*, *Acer saccharum*, and *Cornus florida* are very tolerant of shade; *Acer rubrum*, *A. saccharum*, and *Tilia americana* are tolerant; *Betula alleghaniensis*, *Quercus alba*, and *Fraxinus americana* are intermediate; *Liriodendron tulipifera*, *Betula papyrifera*, and *Prunus serotina* are intolerant; and *Populus tremuloides*, *Betula populifolia*, and *Robinia pseudoacacia* are very intolerant (Baker, 1950).

The differences among species in shoot growth response to shading often are correlated with effects of light intensity on photosynthesis. For example, several species of pines showed increased photosynthesis with added light up to full light intensity, whereas a number of species of broadleaved trees achieved maximum photosynthesis at relatively low light intensity (Kramer and Decker, 1944; Kozlowski, 1949). Photosynthesis of *Pinus taeda* increased with light intensity up to the highest intensity used, which was almost that of full sunlight. In contrast, photosynthesis of *Quercus rubra*, *Q. alba*, and *Cornus florida* reached a maximum at approximately one-third of full sunlight and showed a slight decrease at higher light intensities. These results indicated that lack of sufficient light for maximum photosynthesis was an important factor in ability of intolerant pine seedlings to compete with more tolerant angiosperm seedlings in dense forest stands.

As mentioned earlier, in many species the ultimate length of shoots often is correlated with the size of the bud and the number of shoot primordia that were present in the dormant bud. The low light intensities of lower and inner branches of trees undoubtedly influence physiological processes, especially food and hormone synthesis, sufficiently to limit production of shoot primordia and thereby impose a limitation on shoot development. Subsequently, expansion of shoots with a given number of primordia is further influenced by the light intensity to which shoots are exposed. J. J. Clausen and Kozlowski (1967b) observed, for example, that shading of *Larix* shoots at various times during the growing season affected their elongation.

In addition to influencing the formation and extension of shoot primordia, natural shading often induces death of lower branches on tree stems. The degree of such natural pruning in response to the low light intensities of dense tree stands varies among species, with some (e.g., *Pinus palustris*) losing their lower branches in shade much more readily than other species (e.g., *Pinus coulteri*). A common response to opening of stands by thinning or of pruning branches and suddenly exposing trees to increased light intensities is stimulation of epicormic shoots (Chapter 5).

Sun and Shade Leaves

Leaf structure in angiosperms often varies greatly within the same tree because of mutual shading of leaves and variable exposure of leaves to light.

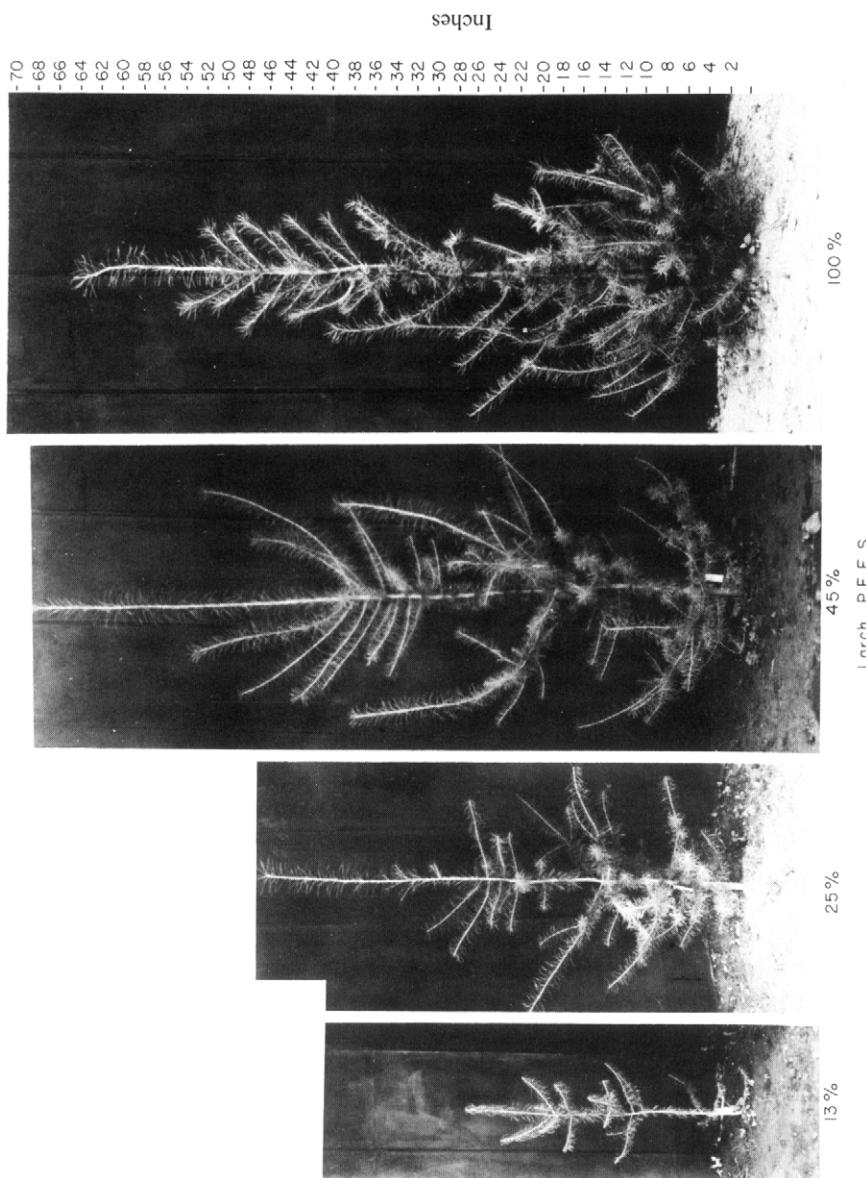
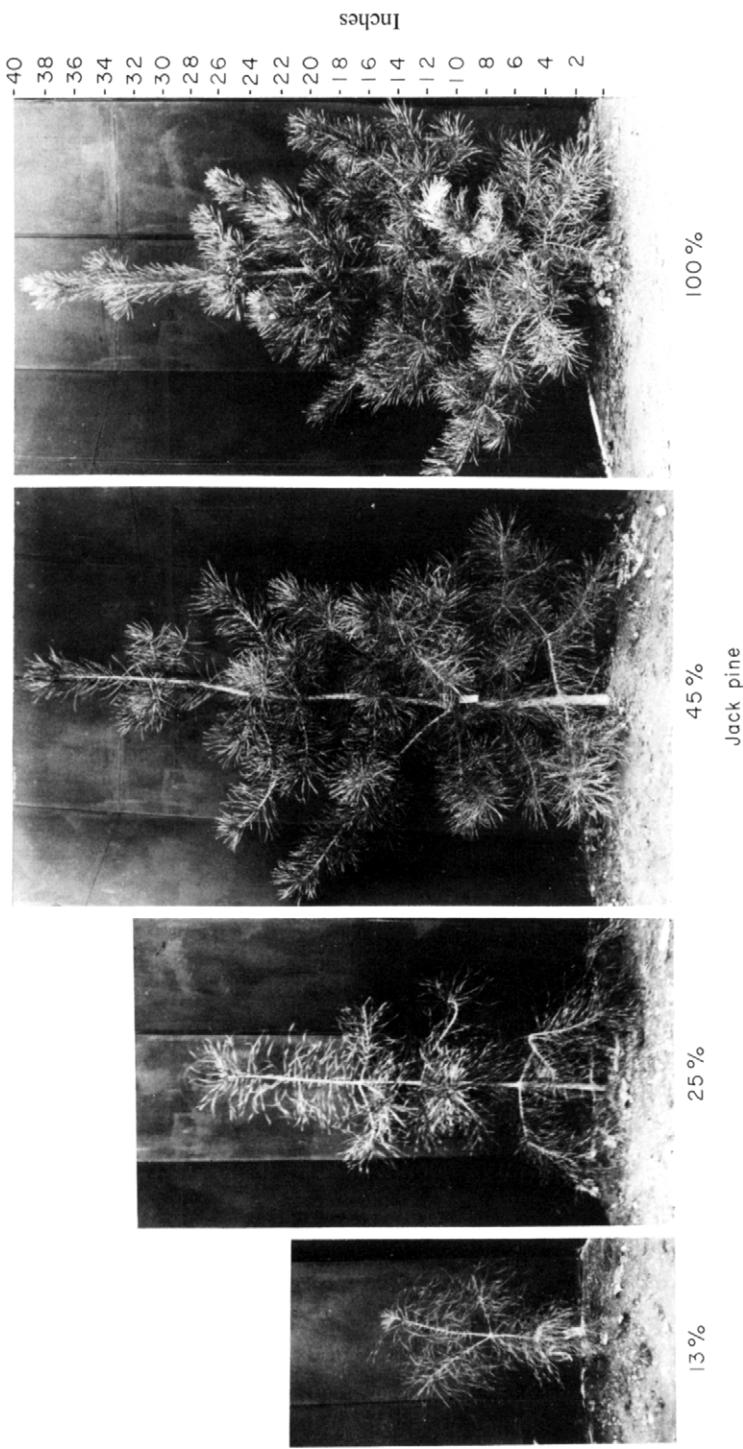


FIG. 8.1. *Larix laricina* and *Pinus banksiana* seedlings grown for 5 years in 13, 25, 45, and 100% of full light. [From Logan(1966a).]



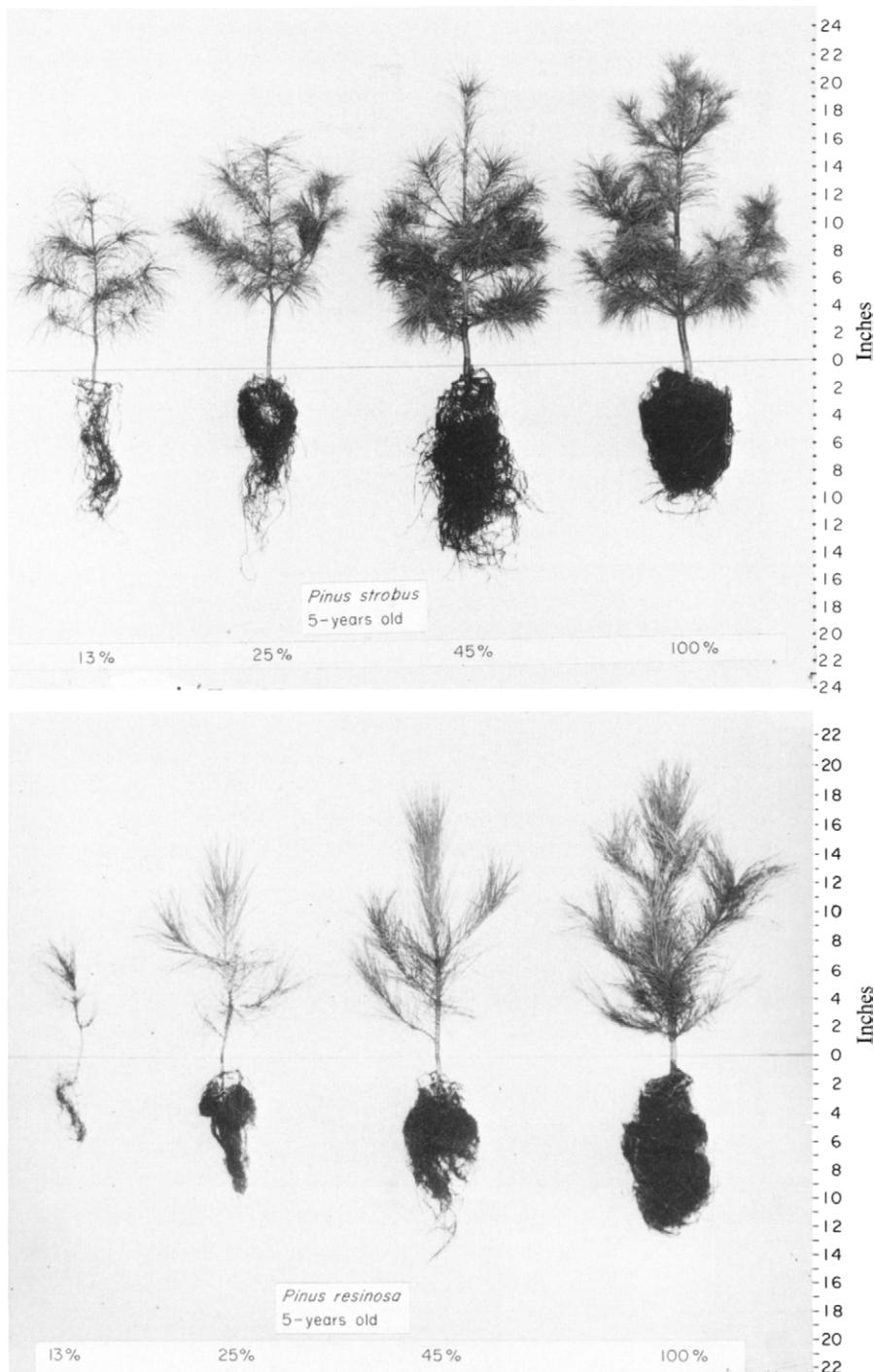


FIG. 8.2. *Pinus strobus* (upper) and *P. resinosa* (lower) seedlings grown for 5 years in 13, 25, 45, and 100% of full light. [From Logan (1966a).]

A characteristic feature of sun-grown leaves is the prevalence of palisade parenchyma, whereas spongy mesophyll is found in greater abundance in shade leaves. There is a tendency for mesophyll cells of sun leaves to elongate in a direction perpendicular to the surface of the leaves. In addition, sun-grown leaves are smaller and thicker than shade leaves and they often are more deeply-lobed (Fig. 8.3). The conducting and mechanical tissues also are more strongly developed in sun-grown leaves, and the epidermal cells have thicker walls (Wylie, 1949, 1951; Talbert and Holch, 1957; Kramer and Kozlowski, 1960).

The number of stomates per unit of surface area usually is greater in sun leaves than in shade leaves. For example, sun leaves of *Fagus sylvatica* had 416 stomates/mm² and shade leaves had 113; corresponding values in *Carpinus betulus* were 365 for sun leaves and 170 for shade leaves; in *Acer pseudoplatanus* 860 for sun leaves and 215 for shade leaves (Schramm, 1912).

Wylie (1949) observed wide variations in structure of *Acer platanoides* leaves collected from two locations in the crown periphery and two in the crown interior. Leaves in the interior of the crown were only a third to a fourth as large as the sun leaves in the crown periphery (Table 8.3). Blade thickness

TABLE 8.3

VARIATIONS IN STRUCTURE OF *Acer pseudoplatanus* LEAVES COLLECTED FROM FOUR LOCATIONS IN THE CROWN^a

Leaf type and location	Thickness (μ)					
	Blade	Upper epidermis	Total epidermis	Spongy mesophyll	Palisade mesophyll	Vein spacing
Sun, south	198	22.8	33.5	57.3	106.6	129
Sun, north	148	22.0	31.3	44.5	72.6	158
Shade, lower interior	91	23.6	33.2	26.1	35.4	183
Shade, deep interior	77	23.2	34.2	23.9	22.4	227

^a From Wylie (1949).

and that of both palisade and spongy mesophyll was much greater in sun than in shade leaves. The epidermal layers were of about the same thickness in all leaves. The peripheral sun leaves were more compact and had longer palisade cells and less distinctive spongy mesophyll than the shade leaves. Vein spacing and the separation of vein extensions increased with shading also.

In another study Wylie (1951) compared structure of leaf tissues taken

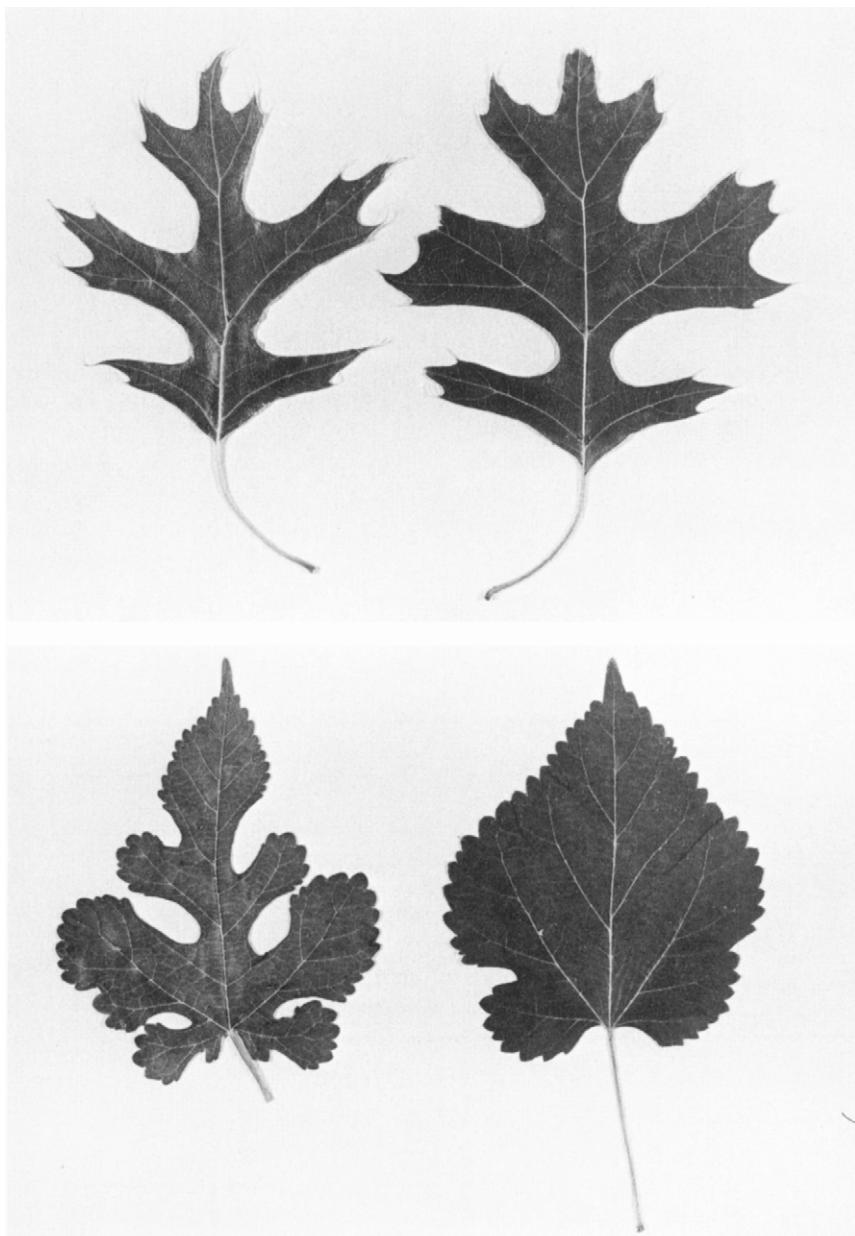


FIG. 8.3. Sun and shade leaves of *Quercus velutina* (upper photo) and *Morus pendula* (lower photo). [From Talbert and Holch (1957).]

TABLE 8.4
MEASUREMENTS OF LEAF TISSUES COLLECTED IN THE CROWN PERIPHERY (SUN LEAVES) AND IN THE INTERIOR OF THE CROWN (SHADE LEAVES)^a.

Species	Blade thickness(μ)		Upper epidermis (μ)		Lower epidermis (μ)		Palisade layer (μ)		Spongy mesophyll (μ)		Tissue ratio ^b		Vein spacing (μ)	
	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade
<i>Acer saccharum</i>	132	84	18.6	15.7	15.4	12.8	62	34	36	22	1.13	1.49	159	187
<i>Acer platanoides</i>	198	91	22.7	23.6	10.8	9.6	107	35	57	26	0.85	1.69	129	183
<i>Catalpa speciosa</i>	342	116	26.6	19.2	14.7	16.0	155	33	147	51	1.22	2.61	168	199
<i>Fraxinus americana</i>	186	132	12.8	12.4	12.8	10.0	93	57	69	52	1.02	1.30	106	131
<i>Liquidambar styraciflua</i>	192	148	19.2	16.2	13.1	11.5	80	53	77	69	1.37	1.82	108	145
<i>Lonicera tatarica</i>	175	79	16.0	19.0	15.7	12.0	68	23	75	26	1.57	2.50	103	134
<i>Prunus serotina</i>	220	147	16.7	15.2	14.7	12.6	97	32	91	87	1.26	3.59	90	139
<i>Quercus macrocarpa</i>	144	82	20.8	18.0	9.6	8.0	73	25	42	32	0.99	2.32	71	124
<i>velutina</i>	190	98	32.6	21.0	14.2	11.0	92	43	50	23	1.05	1.28	71	122
<i>Ulmus americana</i>	209	93	28.0	19.4	16.0	9.4	102	27	58	37	1.00	2.44	64	98
Means	197	107	21.4	18.0	13.7	11.2	93	36	70.2	42.5	1.15	2.10	107	146

^a From Wylie (1951).

^b Combined volume of spongy mesophyll and epidermis divided by total volume occupied by palisade tissue.

from the periphery and interior of the crowns of ten species of angiosperms. Most of the sun leaves were somewhat xeromorphic, but shaded leaves were greatly modified and often abnormally developed (Table 8.4). Mean blade thickness was decreased about 54% by shading; mean volume of palisade tissue decreased by 60%; of mesophyll by 40%; and total epidermis by 17%. Vein spacing widened as a result of shading and tissue ratios (combined volume of spongy mesophyll divided by total volume occupied by palisade tissue) also increased with shading.

L. W. R. Jackson (1967) found considerable variation in leaf structure of deciduous forest trees of different tolerance classes (Table 8.5). Leaf structure of intolerant species was altered more by shading than was structure of tolerant species. Species considered tolerant of shade usually had thinner

TABLE 8.5

BLADE THICKNESS, TISSUE RATIO, AND NUMBER OF ROWS OF PALISADE CELLS IN SUN AND SHADE LEAVES OF TOLERANT, INTERMEDIATE, AND INTOLERANT FOREST TREES^a

Species	Blade thickness (μ)		Sun-leaf/shade-leaf ratio		Rows of palisade cells	
	Sun	Shade	Palisade	Spongy mesophyll	Sun	Shade
Tolerant						
<i>Acer rubrum</i>	100	88	1.45	0.92	1	1
<i>Nyssa sylvatica</i>	141	118	1.43	1.13	1	1
<i>Ostrya virginiana</i>	74	60	1.22	1.38	1	1
<i>Fagus grandifolia</i>	113	102	1.12	1.21	1	1
<i>Cornus florida</i>	111	91	1.05	1.29	1	1
Intermediate						
<i>Ulmus americana</i>	105	79	1.44	1.10	1	1
<i>Quercus alba</i>	113	81	1.42	1.42	2	1
<i>Castanea dentata</i>	118	90	1.37	1.35	2	1
<i>Quercus velutina</i>	109	81	1.27	1.29	2	1
<i>Fraxinus pennsylvanica</i>	123	107	1.19	1.17	3	2
Intolerant						
<i>Liquidambar styraciflua</i>	218	112	3.12	1.52	2	1
<i>Platanus occidentalis</i>	188	93	2.68	1.90	1	1
<i>Prunus serotina</i>	184	106	2.14	1.69	2	1
<i>Populus deltoides</i>	197	123	2.10	1.36	1	1
<i>Liriodendron tulipifera</i>	156	98	1.90	1.65	3	1

^a From L. W. R. Jackson (1967).

sun leaves and less reduction in thickness in shade than did intolerant species. The thickness of the palisade layer was greatest in intolerant and least in tolerant species. Shading reduced the thickness of both the palisade layer and the spongy mesophyll, but thickness of the latter was reduced less. In a number of intolerant species the normal two or three layers of palisade cells were reduced to one layer in shade leaves.

Turrell (1936) measured internal and external exposed cell surfaces of leaves. He found the ratio of the internal to the external surface to be low for shade leaves (6.8–9.9), intermediate for mesomorphic leaves (11.6–12.9), and high for xeromorphic sun leaves (17.2–31.3). A sunleaf of *Syringa vulgaris*, selected at random had 96% more internally exposed surface than a shade leaf of the plant. Turrell (1944) postulated that since the Dalton equation showed the importance of the water surface on rate of evaporation, the exposed area of a plant ought to affect transpiration greatly. Turrell found highly significant correlations between internal-external surface ratios of angiosperm leaves and transpiration rates.

The chemical composition of sun leaves often is different than that of shade leaves. For example, on a dry weight basis the shade leaves of *Fagus sylvatica atropunicea* had higher concentrations of major elements (Mg, K, N, P, S) and minor elements (B, Fe, Zn, Cu, Mn, Mo) than sun leaves (Haas *et al.*, 1968). The amino acid contents of sun and shade leaves also were different. Shade leaves contained more tyrosine, phenylalanine, and methionine and less lysine, histidine, arginine, valine, isoleucine, and proline than sun leaves (Haas, 1969).

Differences in structure of sun-grown and shade-grown leaves of gymnosperms also have been shown. McLaughlin and Madgwick (1968) studied the structure of needles of *Pinus taeda* in different portions of tree crowns. Needles produced in the outer crown, which received full sunlight, were larger and weighed more than needles produced in shaded inner portions of the crown. Sun needles also were thicker and had more stomates per unit area than shade-grown needles. Needles in the upper crown, which were well lighted, were heavier, thicker, and had more stomates per unit area than needles in the more shaded, lower crown positions (Table 8.6).

Mutual Shading and Adaptation to Light Intensity

Leaves on the same tree show marked differences in photosynthetic efficiency because of variations in shading and exposure among leaves. Leaf adaptations to sun and shade also influence their photosynthetic capacity over a wide range of light intensities. Leaves adapted to shade are darker green than those adapted to light, and the former usually absorb light more efficiently (Kramer and Kozlowski, 1960).

TABLE 8.6
GROWTH OF *Pinus taeda* NEEDLES IN VARIOUS PARTS OF TREE CROWNS^a

	Crown position					
	Top		Middle		Bottom	
	Outer	Inner	Outer	Inner	Outer	Inner
Length (cm)	16.8	15.8	18.5	14.0	16.2	13.5
Weight (mg)	39.3	36.1	42.4	21.9	35.2	16.0
Surface area (mm ²)	612	573	677	451	572	358
Number of stomates $\times 10^{-3}$	57.1	52.7	57.5	34.1	48.7	25.0

^a From McLaughlin and Madgwick (1968).

Several investigators have emphasized high photosynthetic efficiency at low light intensities of shade-adapted leaves of both gymnosperms and angiosperms. Only a few examples will be given. Bourdeau and Laverick (1958) found that chlorophyll and nitrogen contents of *Pinus resinosa* and *P. strobus* needles generally increased with shading. Shade needles of both species had higher photosynthetic rates than sun needles on a unit needle weight basis.

Ostretkov (1957) noted that under high illumination the sun needles of *Pinus* had rates of photosynthesis about 50% higher than those of shade needles. In weak light, however, shade needles were as efficient as sun needles, and sometimes even more so.

Complexity of light effects on net photosynthesis was demonstrated by Pisek and Tranquillini (1954) who measured CO₂ uptake in different parts of *Picea abies* and *Fagus sylvatica* crowns. During the summer, parts of the crown reached maximum net photosynthesis at 20,000 lux. Direct sunlight never was fully used except at low sun positions. High light intensities caused leaf temperatures to increase; and subsequent increase in transpiration influenced photosynthesis by stomatal regulation. The rise of leaf temperature caused an increase of respiration and up to half of the photosynthate often was rapidly consumed by respiration. This accounted for a double-peaked diurnal curve for CO₂ uptake. Especially favorable for high photosynthesis were conditions of diffuse light under an overcast sky and changing, moderate light intensities. In closed stands only small parts of the crowns received full sunlight because of mutual shading of trees.

In *Fagus sylvatica* shade leaves used weak light very efficiently, with net CO₂ uptake recorded even in deep shade. Photosynthesis of shade leaves at 500 to 1000 lux was four to five times greater than that of sun leaves, on

a dry weight basis. Sun leaves were less efficient probably because of their lower chlorophyll content (Tranquillini, 1954).

It should be remembered that the magnitude of the differences in photosynthetic efficiency of sun and shade leaves depends greatly on how rates of photosynthesis are expressed. Some of the large differences in photosynthetic efficiency may disappear if photosynthesis is expressed on a chlorophyll weight basis rather than on a leaf dry weight basis.

PHOTOPERIOD

Shoot growth of many woody plants is greatly influenced by length of day (Kramer and Kozlowski, 1960). Although species vary greatly in their response to a given daylength or photoperiod, short days usually stop shoot growth and long days cause it to continue. Some species can even be kept in a state of more or less continuous shoot growth if days are long enough. As shoot elongation slows under short-day conditions, successively shorter internodes usually are produced until growth eventually ceases (Figs. 8.4 to 8.6). Like Temperate Zone species, those of the tropics also are responsive to short days except that under short days many tropical trees neither stop shoot elongation completely nor set dormant buds. A few species of the



FIG. 8.4. Growth of white spruce (*Picea glauca*) after 4 months on photoperiods of 12, 14, 16, and 24 hours (left to right). [From Downs (1962). Copyright ©, The Ronald Press Co., New York.]



FIG. 8.5. Growth of Douglas fir (*Pseudotsuga menziesii*) after 12 months on photoperiods of 12 hours, 12 hours plus a 1-hour interruption near the middle of the dark period, and 20 hrs (left to right). [From Downs (1962). Copyright ©, The Ronald Press Co., New York.]

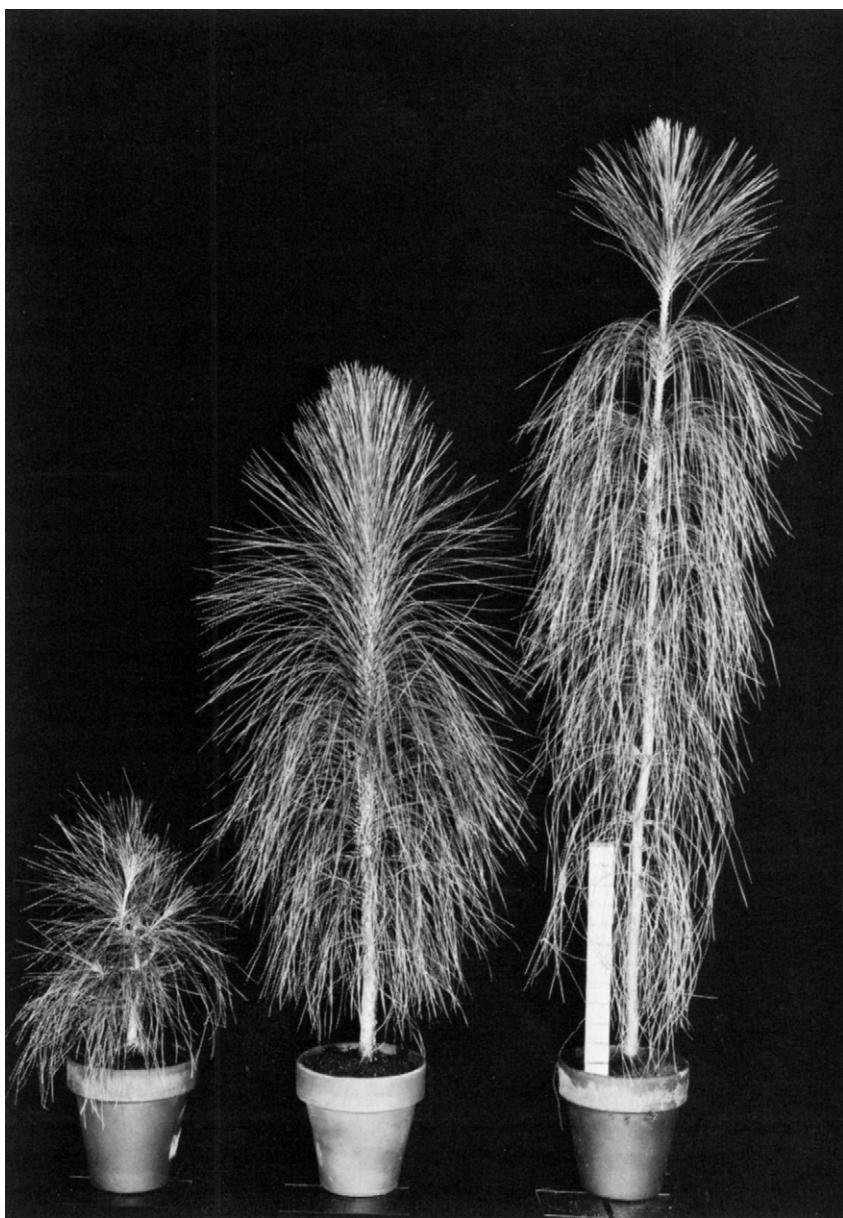


FIG. 8.6. Growth of slash pine (*Pinus elliottii*) after 15 months on photoperiods of 12, 14, and 16 hrs (left to right). [From Downs (1962). Copyright ©, The Ronald Press Co., New York.]

Temperate Zone, for example *Sequoia sempervirens* and *Pinus radiata*, react to short days somewhat like tropical species (Downs, 1962). The role of daylength on shoot growth is discussed further in the section on control of bud dormancy in this chapter.

LIGHT QUALITY

Experiments performed under artificial illumination indicate that light quality or wavelength may influence shoot growth of trees by controlling plant processes, especially photosynthesis. For example, expansion of leaf blades is reduced in green light, intermediate in blue light, and greatest in white light (Kramer and Kozlowski, 1960). Under natural conditions, however, trees are subjected to a very wide range of visible and invisible radiation rather than to narrow spectral bands. In forests, therefore, the influences of light intensity and photoperiod on shoot growth have been more obvious and definite than have changes in light quality. Daubenmire (1959) considered light quality to have a relatively unimportant influence on growth under natural conditions. He stated that each physiological process was sensitive to all wavelengths of light, the influence of wavelength differed so much among species that generalizations are difficult, and variations in light quality in natural plant communities usually were too small to be critical. Nevertheless, some evidence is available that the quality of light under broadleaved trees varies considerably from that in the open, whereas under coniferous trees the light quality is little altered. For example, Vezina and Boulter (1966) found the light under *Acer saccharum* trees to be low in blue, high in green, low in red, and very rich in the far red while under *Pinus resinosa* there was no great change in light quality over that in the open. Under a hardwood forest canopy where light intensity frequently is low the effect of the quality of the shade light on photosynthesis and on shoot growth has not been investigated adequately and more research is needed.

Temperature

Various aspects of shoot growth are influenced by temperature in terms of its degree and duration. When temperature changes are small alterations in shoot growth are associated with changes in photosynthesis, transpiration, hormone synthesis, respiration, chlorophyll synthesis, enzymatic activity, and cell division and elongation. However, when temperature changes are large considerable injury can occur to unhardened shoots as a result of freezing of tissues, direct heat injury, or excess transpiration (Kramer and Kozlowski, 1960).

The influences of temperature on phenology are well known, with bud

opening and subsequent shoot expansion responding to temperature regimes. That temperature is an exceedingly important environmental factor influencing bud opening is shown by variations among years in time of growth initiation of a given species in a specific area. For example, a difference of as much as 21 days from one year to another in the date of growth initiation of *Platanus occidentalis* was noted in response to temperature variations (Kaszkurewicz and Fogg, 1967). Büsgen and Münch (1931), cited differences of 39 days in time of bud opening in different years for *Aesculus*, 36 days for *Fagus*, and 24 days for *Quercus*. The importance of temperature on bud opening is also emphasized by variation in time of growth initiation of the same species at different latitudes. For example, *Pinus strobus* and *P. resinosa* trees began shoot growth in North Carolina in the latter part of March, but did not start growing in New Hampshire until the first day of May (Kramer, 1943).

Tranquillini and Unterholzener (1968) demonstrated the greatly limiting effect of decreasing temperatures on growth of gymnosperm shoots. *Larix* seedlings of uniform mountain provenance that had been grown at an elevation of 1000 m were transported in pots to three nurseries at different altitudes (700, 1300, and 1950 m) where annual shoot growth was studied. At 1300 m, the needles started to grow 29 days later, and at 1950 m 80 to 90 days later, than at 700 m. Total height growth of seedlings was greatly decreased as elevation increased (and temperature regimes lowered). Height growth at 1300 m was 60%, and at 1950 m only 17% of height growth at 700 m.

Several investigators have related the time of bud opening to prevailing temperature and identified differences among species in critical temperatures for initiation of shoot growth. For example, Ahlgren (1957) noted that *Pyrus americana*, *Populus tremuloides*, *Betula lutea*, and *B. papyrifera* began growing in the first spring warm period when minimum temperatures were still below freezing. Buds of *Picea glauca*, *P. mariana*, and *Pinus resinosa* became active after minimum temperatures reached at least 30°F. By comparison, *Ulmus americana* and *Acer rubrum* began to grow only after minimum temperatures reached at least 60°F. whereas *Fraxinus nigra*, *F. pennsylvanica*, *Abies balsamea*, and *Pinus strobus* began shoot growth only after maximum temperature reached at least 70°F. Bud opening of *Tilia americana*, *Quercus macrocarpa*, *Populus grandidentata*, and *Acer saccharum* appeared to be unrelated to specific temperatures.

Kaszkurewicz and Fogg (1967) found that variation with latitude in the length of the growing season of *Populus deltoides* and *Platanus occidentalis* was the result of both a delay in bud opening and an early cessation of shoot growth at the higher latitudes. Although temperature influenced bud opening, no single temperature was decisive in initiation of shoot growth since

temperatures sometimes were satisfactory for growth at one latitude but not at another latitude.

In Japan Yanagisawa (1954) identified *Sorbus aucuparia* and *Betula latifolia* as early-flushing species. *Ulmus japonica* and *Betula maximowicziana* were considered medium-flushing species. Late-flushing species included *Picea jezoensis*, *Abies sachalinensis*, *Quercus crispula*, and *Fraxinus mandshurica*. Buds opened in the early-flushing group when mean air temperature for the previous ten days reached 6 to 8°C; in the medium flushing group 8 to 11°C; and in the late flushing group 11 to 13°C.

Growth of trees occurs over a wide temperature range, but within this range temperature conditions exist which promote optimal growth for various species (Kramer and Kozlowski, 1960; Kozlowski, 1967). Thermoperiodic studies also show that the distribution of temperatures during the day and night greatly influences shoot growth (see Chapter 7).

FROST HARDINESS

The cold resistance or frost hardiness of trees shows remarkable periodicity throughout the year. It increases during the autumn as temperatures drop, reaches a maximum in winter, and decreases in the spring to a summer minimum. Although trees are rapidly killed in summer when artificially exposed to temperatures only a few degrees below freezing, they can withstand super low temperatures during midwinter.

Seasonal increase and decrease in frost hardiness, which develop rather rapidly, are induced primarily by temperature changes but, as will be mentioned later, photoperiodic effects also appear to be involved. Exposure of trees to low temperatures increases hardiness whereas high temperatures decrease hardiness. However, only dormant trees can develop a very high degree of cold resistance on exposure to low temperatures. When growing trees are exposed to low temperatures, they become somewhat more hardy but they will not withstand really low temperatures without injury. The pre-conditioning effect of the temperature at which plants are growing influences their ability to resist sudden frosts. For example, a freeze following a period of warm weather injures trees more than frost which follows a period of cold weather.

As growing trees are not particularly frost hardy and they do not develop pronounced hardiness when chilled, some investigators believed that the development of dormancy in plants was prerequisite to cold resistance. Chandler (1954), for example, postulated that substances were translocated into the bark of trees in autumn as precursors of substances which induce cold hardiness but that these materials could not accumulate until a state of deep-seated dormancy was reached. However, Irving and Lanphear (1967a)

presented evidence that development of cold hardiness was independent of induction of bud dormancy. They obtained appreciable levels of cold hardiness by exposing *Acer negundo* and *Viburnum plicatum tomentosum* plants to long days and low temperatures, without development of dormancy as a prerequisite.

Development of frost-hardiness, which is also associated with desiccation resistance, has been related to increases in (1) water-soluble proteins, (2) RNA, (3) sulfhydryl levels, (4) anthocyanins, and (5) various sugars and related compounds (Parker, 1963, 1969). Studies of changes associated with frost-hardiness in the living bark and needles of *Pinus resinosa* indicated that variations in soluble protein and rate of incorporation of leucine into protein were correlated with changes in hardiness (Pomeroy *et al.*, 1970).

Sakai (1962) studied internal changes in twigs during the development of frost hardiness. Shortly after twig growth ceased, important changes occurred in the cortical regions of twigs: (1) Water content and activity of cambial cells decreased, and (2) sucrose and osmotic concentration increased. These changes appeared to be necessary for development of frost hardiness as without them the cortical cells were not cold resistant nor could they be further hardened by chilling. His data showed that when chilling of parenchyma cells was not accompanied by increase in sucrose concentration they could not be hardened further by chilling. He concluded that low temperature itself, although it induced hardiness, had no direct effect on increasing frost hardiness whereas the accompanying increase in sugar in cells appeared to be the primary factor in frost hardiness. In addition to sugars, some polyhydric alcohols and acetoamide contributed to frost hardiness of certain plants.

Cold hardiness appears to be a photoperiodic phenomenon. For example, Irving and Lanphear (1967a) showed that increasing weeks of short days, followed by a low temperature hardening period in darkness, caused a progressive increase in hardiness of *Acer negundo* and *Viburnum plicatum tomentosum* plants. Long days reversed the short-day stimulus. After 6 weeks of exposure to short days, the rate of hardening in darkness at 5°C was more than twice that of plants which had been previously exposed to long days.

There is some evidence of hormonal involvement in hardiness. For example, short photoperiods followed by low temperatures induced cold hardiness in *Acer negundo*, *Viburnum plicatum tomentosum*, and *Weigela florida*. Long days and natural autumn temperatures also resulted in development of hardiness provided the leaves were removed. Also removal of leaves from plants exposed to long days at 5°C caused rapid hardening. These observations suggested that leaves contained a hardiness inhibitor which was counteracted by short days or leaf removal (Irving and Lanphear, 1967b).

Gibberellin appears to block induction of cold hardiness. Various

compounds which show antigibberellin or growth-retarding properties, were effective in inducing hardness of *Acer negundo* plants under long days, presumably by counteracting the influence of endogenous gibberellin (Irving and Lanphear, 1968). Extraction of leaves previously exposed to short days showed lower levels of gibberellinlike compounds and higher levels of inhibitors than extraction of leaves exposed to long days. Irving (1969) extracted an inhibitor from short-day-treated *Acer negundo* leaves and found its chromatographic properties to agree closely with those of abscisic acid. Treatment of *Acer negundo* plants under nonhardening preconditions (e.g., long days) with either the inhibitor or abscisic acid increased cold hardness. Such observations suggest that long days inhibit hardness through high gibberellin activity whereas short days promote hardness by accumulation of an inhibitor which can counteract gibberellin.

LOW TEMPERATURE INJURY TO SHOOTS

Unhardened or partially hardened shoots often are injured by spring or autumn frosts. The nature and amount of injury vary with the severity and duration of the frost as well as the degree of hardness induced in trees by the time of occurrence of the frost. Spring frosts injure certain shoots of a tree more than they damage others because of considerable variation in dehardening of variously located shoots. Different degrees of injury to shoots may also occur within trees because various shoots may be exposed to different temperatures.

Frost hardness of shoots disappears in the spring before buds actually open. Often frosts which occur before buds open damage only the buds as they generally are in a more advanced stage of dehardening than are expanded shoots. When buds or young leaves are killed by spring freezes, surviving dormant buds become active and a new crop of leaves emerges. Spring frosts which occur after seasonal bud opening, generally damage both the leaves and succulent shoots. Mild injury may result in withering of leaf or needle tips. Frost damage to *Picea glauca* needles, consisting of collapse of mesophyll cells and coagulation of cytoplasm, is shown in Fig. 8.7. As sudden killing of leaves by frosts prevents abscission layers from forming, the dead leaves usually remain attached to the tree.

Early autumn frosts injure only succulent shoots. Thus, such injury tends to be most common to late-season growth flushes (e.g., lammas shoots, proleptic shoots, or late-season flushes of recurrently-flushing species). Irrigation or addition of fertilizers late in the growing season sometimes stimulates and prolongs seasonal shoot growth sufficiently to increase susceptibility of trees to autumn frost injury or to winter killing as such trees may not have sufficient time to harden adequately against low temperatures.

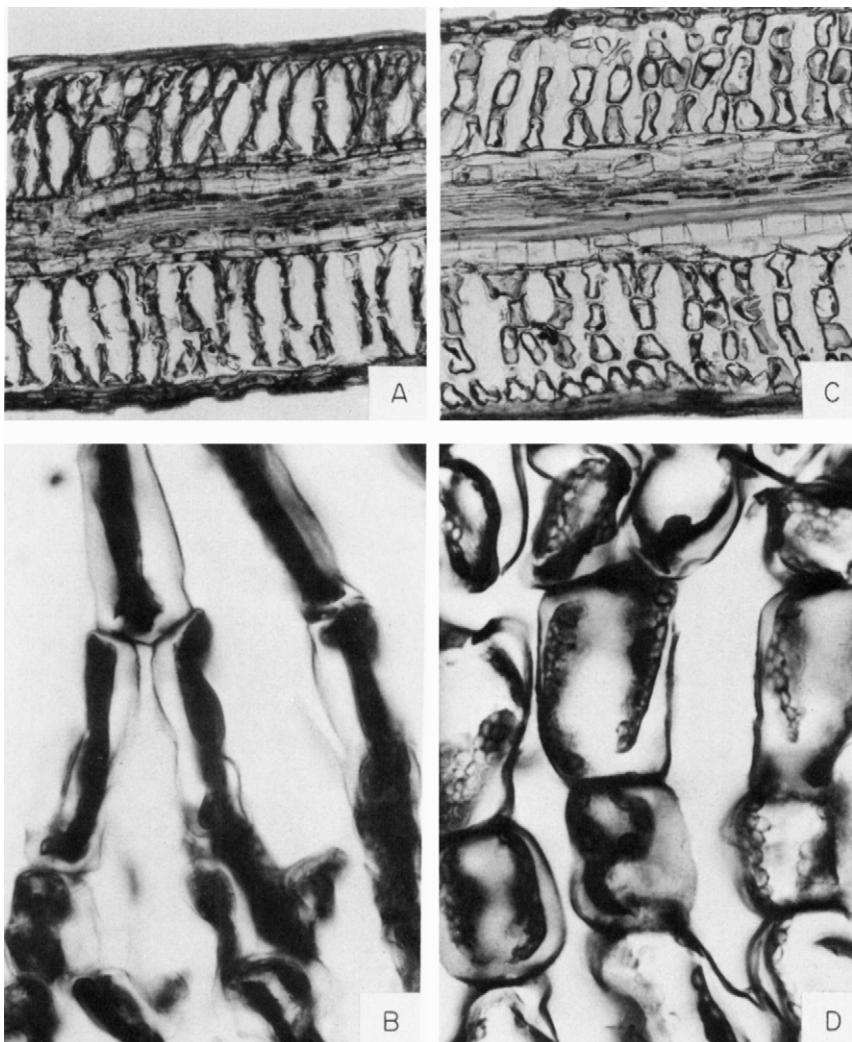


FIG. 8.7. Frost damage to *Picea glauca* needles. (A) Longitudinal section through a frost-damaged needle. Mesophyll cells are collapsed and cytoplasm is coagulated, $100\times$; (B) Longitudinal section through frost-damaged needles showing a few damaged mesophyll cells, $425\times$; (C) Longitudinal section through normal needle; (D) Longitudinal section through a normal needle showing arrangement of a few mesophyll cells. Note cell turgidity. $550\times$. [From Glerum and Farrar (1965).]

DESICCATION INJURY ASSOCIATED WITH LOW TEMPERATURES

Much winter injury to gymnosperms is the result of shoot desiccation rather than direct thermal injury (Kozlowski, 1968a,b). In many parts of the world transpirational losses from frost-hardened trees are appreciable during the winter and spring especially during the afternoons of relatively warm days. As the soil is cold or frozen, the trees cannot absorb water fast enough to replace transpirational losses and shoots consequently become desiccated and often killed. Such injury is very common and sometimes has been erroneously considered to be the result of direct frost damage to tissues. Winter desiccation injury to shoots of gymnosperms in the United States was described by Curry and Church (1952) who observed entire mountainsides covered with discolored trees. *Picea rubens*, *Tsuga canadensis*, *Pinus strobus*, and *Abies balsamea* showed both browning of leaves and defoliation. About half the stands examined showed such injury, with large portions of the tree crowns dead as a result of desiccation of tops. Sakai (1968) described extensive winter desiccation injury to *Picea* and *Cryptomeria* trees growing in frozen soil and wind-swept areas of Japan. Whereas desiccation injury was severe to trees on northern slopes it was slight or negligible on southern slopes. In many areas examined, the soil of northern slopes was frozen during the winter, but that of southern slopes was not. However, in northern-most parts of Japan the soil remained frozen all winter on both northern and southern slopes, and desiccation injury to shoots occurred commonly in all wind-swept areas irrespective of slope. When trees were protected by a windbreak their shoots were damaged much less than at some distance from the windbreak.

Site

Over a period of years the amount of height growth of a species is influenced by interactions of climatic, edaphic, and biotic factors of a particular site (Kozlowski, 1964a). Foresters commonly express the quality of site in terms of site index or the average height of dominant trees at age 50. Site quality can be readily determined in fully stocked stands of appropriate age. Techniques also are available for estimating the quality of a site which lacks trees. The methods used have emphasized analysis of soil properties because site quality within moderately broad geographic areas appears to be controlled more by soil characteristics than by climatic factors (Coile and Schumacher, 1953). According to Zahner (1968), site quality often is closely correlated with physical factors of the soil which influence moisture and aeration. Stoeckeler (1960) observed that mechanical properties of the soil, such as silt plus clay content or moisture equivalent, were better related than

were available nutrients to growth of *Populus tremuloides* in the Lake States. These observations placed great importance on the role of favorable water relations in growth of trees.

It should be emphasized that the specific limiting factors of site on height growth vary in different areas. For example, in the northwest United States nutrient content of forest soils did not limit height growth (Tarrant, 1949), whereas, in contrast, chemical properties of Carolina Coastal Plain soils were critical (Woodwell, 1958). Various components of site may also exert an interactive effect on height growth. Chrosciewicz (1963) noted, for example, that site index of *Pinus banksiana* varied markedly with soil moisture regime, soil texture, soil petrography, regional macroclimate, and various combinations of these. Hence, over a period of years the character of height growth is influenced to variable degrees by many site factors.

The amount of height growth of trees has been shown to be very sensitive to interactions among various site components of specific habitats. For example, Wilde (1964) analyzed *Pinus resinosa* plantations on a variety of sites in Wisconsin. Irregularities in the rate of height growth were traceable to deficiency of minerals in surface soil layers depleted by fires and cultivation, severe podzolization, variation in mineral supply of substrate, position of the ground water, and weed growth. Plantations established on reasonably weed-free areas generally showed rapid height growth for 10 to 12 years. However, a few years after closing of the canopy, height growth usually began to decline because of increased competition of larger trees for water and minerals. Height growth generally was retarded in soils low in water and mineral supply, intermediate in fertile soils resulting from weed suppression by the closed canopy, and high on infertile but naturally subirrigated soils in which there was a contact of tree roots with the capillary fringe.

Competition and Cultural Conditions

Both the amount of shoot growth and the length of the growing season during which shoot growth occurs can be modified considerably by plant competition. Maples in the open initiated height growth later but grew faster and for a longer time than those in a forest (Collins, 1960). Catrina and Moisiuc (1958) noted that *Crataegus monogyna* and *Ligustrum vulgare* grown on the steppe showed much greater root, shoot, and leaf growth than when grown under a forest canopy. According to Brender and Barber (1956), height growth of *Pinus taeda* in the Piedmont of Georgia was inhibited by a relatively small amount of overtopping vegetation. Effect of competition also was emphasized by L. W. R. Jackson (1959) who measured height growth of *Pinus echinata* and *P. taeda* seedlings under a series of over-story opening diameters ranging from 5 to 55 ft. After 6 years the average

height of trees had increased in proportion to opening diameter, from 18.6 to 66.7 in. for *P. echinata*, and from 11.6 to 31.2 in. for *P. taeda*.

The duration of shoot growth of some species can be prolonged materially by high water availability, high mineral availability, or both. Data of Merrill and Kilby (1952) showed that, on the average irrigated tung (*Aleurites fordii*) trees completed only 38% of their annual shoot growth by July 10, whereas unirrigated trees completed 66% of growth by the same date (Table 8.7). Irrigation increased growth of both primary and secondary branches, but growth of secondaries was increased most.

TABLE 8.7

EFFECT OF IRRIGATION AND FERTILIZER APPLICATION ON AMOUNT OF SHOOT GROWTH, LENGTH OF GROWING SEASON, AND PRODUCTION OF BRANCHES IN TUNG (*Aleurites fordii*) TREES GROWN IN MISSISSIPPI DURING 1947^a

	Added fertilizer (8-8-6) per tree (lb)	Total to July 10 (cm)	% of annual total completed by July 10	Primary branches October 30 (cm)	Secondary branches October 30 (cm)
Unirrigated	1	94	77	107	15
	2	112	56	125	74
	3	101	65	121	35
Irrigated	1	158	44	178	183
	2	231	36	286	357
	3	166	33	243	256

^a From Merrill and Kilby (1952).

Shoot-Growth Responses to Prior-Year and Current Weather

Rowe (1964) presented evidence of environmental preconditioning which modifies the effect of current environment on phenology. The time of bud opening, for example, is affected by inherited control interacting with current temperature and light regimes. Rowe (1964) cited examples of *Picea glauca* seedlings, grown the previous season under cool nights, opening buds later than those grown under warm nights. The time of bud opening may also be influenced by timing of exposure to low temperatures during the dormant period and by mineral availability during the previous season.

The importance of predetermination during the year of bud formation on growth of shoots of some species is emphasized by studies which show closer correlation between shoot elongation and environment of the year of bud

formation than with the environment of the year of expansion of the bud into a shoot. Mikola (1962), for example, concluded that annual height growth of *Pinus sylvestris* in Finland was determined mainly by temperature of the preceding summer. In eastern Canada high correlation was found between height growth of *Pinus strobus* and mean air temperature of the previous summer (MacHattie and K. W. Horton, 1963). Motley (1949) reported that low rainfall in May to November of 1940 and 1944 was reflected in low amounts of height growth of *Pinus resinosa* in 1941 and 1945. Conversely, large amounts of rain during a growing season were reflected in increased shoot elongation the following year. May to November of 1945 had more than twice as much rain as the same period the previous year. This was reflected by more than doubling of shoot elongation in 1946 over 1945. The control of height growth by bud differentiation also was pointed up by Duff and Nolan (1953). They reported that *Pinus resinosa* trees left in a plantation from which many trees had been removed showed no greater height than before thinning of the stand. Earlier Friesner (1943) found that heavy rainfall in June failed to check decreasing shoot growth of pines. K. W. Horton (1958b) could find no correlation between current season rainfall and leader extension of *Pinus contorta* in Alberta, Canada, but Friesner and Jones (1952) noted significant correlations between shoot growth of gymnosperms and May-November precipitation of the preceding year. Muelder and Schaeffer (1962) observed shoot growth of *Pinus ponderosa* in California to be closely related to June-July precipitation of the previous year. These several observations stress the controlling influence of environment of the season of bud formation on shoot growth of many species during the following year. It should be emphasized, however, that this carry-over effect pertains primarily to species with short growing seasons and with unexpanded foliar organs of shoots already predetermined in the unopened bud. And even in these species, environmental stresses of the current year sometimes inhibit shoot expansion in the same year. This was illustrated by regression analyses of Zahner and Stage (1966) which showed that water deficits during mid-June to October of the previous year accounted for as much reduction in height growth of young *Pinus resinosa* stands as the water deficit from May to mid-July of the current year.

Shoot growth of many Temperate Zone species is completed early in the frost-free season and often escapes mid- or late-season environmental stresses such as severe drought. In arid regions, however, shoot growth of all species including those with preformed shoots, often is responsive to weather of the current year. Pearson (1918) found that *Pinus ponderosa* in northern Arizona depended largely on rain stored during the previous winter and spring for height growth. If winter rain provided the only supply of water small amounts of shoot growth occurred. But if April and May

rains supplemented winter rainfall, the amount of height growth was much greater. Another study in Arizona showed a close relationship between height growth and current-season rainfall. There was three times as much rain in May through October in 1940 as in 1939. Leader growth of junipers was 69 mm in 1940 and only 15 mm in 1939. Early in the season height growth began but ceased when moisture supplies were exhausted. However, height growth was resumed each year after rains in August (Herman, 1956).

In nonarid regions the effects of current-season environment on shoot growth are most apparent on species with long growing seasons. These include heterophyllous species which do not contain a fully preformed shoot in the winter bud (e.g., *Populus*, *Betula*, *Eucalyptus*, *Liriodendron*) and recurrently flushing species such as *Pinus taeda* and *P. radiata*. Abundant late-season precipitation may also affect shoot growth in species which have preformed shoots and a short season of shoot expansion by stimulating them to produce late-season lamas or proleptic shoots.

Internal Control of Shoot Growth

Shoot growth is regulated by complex internal mechanisms of control of various sequential phases such as breaking of bud dormancy, opening of buds, elongation of internodes, expansion of leaves, and bud formation. Internal control and correlation of these often overlapping growth phases require a food supply, various hormonal growth regulators (including growth promoters and inhibitors), water, minerals, and other substances. As mentioned in Chapter 1, internal control of shoot growth involves close interdependency between roots and shoots as sources of essential growth controlling factors. Internal regulation of shoot growth in the tropics is somewhat different and perhaps less complex than in temperate regions because many tropical species do not show annual lapses into protracted periods of true dormancy.

Carbohydrates

Although growth requires large amounts of available carbohydrates several lines of evidence show that cessation of shoot expansion generally is not due primarily to carbohydrate deficiency (Kozlowski, 1969). When annual shoot growth slows down a substantial carbohydrate reserve usually is present (Kozlowski, 1962a). C. A. Priestley (1962a,b) showed that only about a third of the extractable carbohydrate supply was depleted during growth of apple trees. Kramer (1958a) emphasized that shoots of *Pinus taeda* seedlings did not grow continuously in growth chambers under conditions of adequate light, water, and minerals. Furthermore, shoot growth

of many species is greatly increased with long photoperiods even when the added light is of such low intensity that it does not materially affect the food supply. These observations suggest that food supply often is adequate but growth is inhibited because utilization of food is controlled by other internal regulatory mechanisms. In the discussion to follow, emphasis will be placed on variations in use of foods in shoot growth rather than on the importance of food supply in directly controlling shoot growth.

Both stored carbohydrates and products of current photosynthesis are used in shoot growth. The variety of shoot growth patterns observed among species, among age classes of the same species, among trees in different environments, and even among shoots in different parts of the same tree indicate that variations occur in amounts of carbohydrates, and in proportion of reserve and currently produced carbohydrates, that are mobilized during shoot growth. The quantity and proportions of reserve and currently produced carbohydrates used in leaf expansion often differ from those used in internode elongation. For example, in *Pinus resinosa* the expansion of needles, which lags far behind internode elongation, utilizes products of current photosynthesis late into the summer and after internode elongation has ceased (Larson, 1964).

In many trees of the Temperate Zone the preformed shoot primordia contained in winter buds, which expand into leaves and internodes of shoots during the subsequent growing season, are comprised in part of structural carbohydrates representing photosynthate produced during the year before bud expansion occurs.

During early stages of shoot expansion many deciduous trees of the Temperate Zone must depend on carbohydrate reserves accumulated during the previous season. Later when the newly expanded leaves begin to produce carbohydrates they first use them for their own growth and eventually export carbohydrates for growth of subtending internodes and other tissues.

Evidence for the use of reserve carbohydrates in shoot expansion comes from many observations of seasonal depletion of stored carbohydrates from twigs as buds open and shoots expand (Kraybill *et al.*, 1931; Smyth, 1934; Siminovitch *et al.*, 1953; C. A. Priestley, 1962a,b; Kozlowski, 1962a,b, 1964a). A few examples will be given.

In most deciduous forest trees of the Temperate Zone, carbohydrate reserves decrease sharply during spring shoot growth and they increase in late summer to an autumn peak. For example, sucrose in twigs of *Betula populifolia* showed a regular annual fluctuation, rising to a maximum in December and remaining high until March. A rapid decrease occurred in spring and lowest concentrations were reached in May when shoots were growing rapidly. Sucrose increased slowly during the summer to the high winter values (Gibbs, 1940). An unusual case of early dependency of shoot

growth on reserve carbohydrates was cited by Schimper (1903) who recorded an early shoot expansion of 2.6 cm/day in a *Brownia* tree when it was leafless.

Woods, *et al.* (1959) noted rapid utilization of carbohydrates during the spring flush of growth of *Quercus laevis* and *Q. incana* trees. Minimum carbohydrate levels occurred when the leaves attained maximum size. Total carbohydrate reserves at that time were approximately half as great as during the dormant season. After the low value was reached, carbohydrate reserves increased steadily into autumn.

Direct evidence of use of reserve foods in expanding shoots of young *Malus* trees was provided by Quinlan (1969) who treated leaves with $^{14}\text{CO}_2$ in the autumn (October) after shoot extension had ceased. In the following spring (May 20th) ^{14}C was detected in all new leaf and shoot growth, emphasizing mobilization of stored reserves. The root system and the old stem appeared to be the main sources of reserves for shoot growth.

Although evergreen species already have a functioning photosynthetic system when shoots begin to elongate they also deplete reserve carbohydrates during early phases of shoot expansion. Krueger (1967), for example, showed that carbohydrates stored in 1-year-old *Pseudotsuga menziesii* shoots contributed substantially to expanding shoots. From April to early June, when new shoots were expanding rapidly, the concentration of carbohydrates in 1-year-old shoots decreased rapidly. Both the concentration and quantity of carbohydrates in the new shoots increased from the time of bud opening to mid-June, by which time carbohydrates reached a level about equal to that in the 1-year-old shoots. Some evidence is also available which shows that carbohydrates stored in old needles of some gymnosperms may be mobilized early in the season and used in shoot growth. For example, 1-year-old needles of basal shoots of *Pinus resinosa* decreased in dry weight as new shoots began to expand, suggesting mobilization of carbohydrates from the old needles by the growing shoots (J. J. Clausen and Kozlowski, 1967a).

When old needles of *Pinus resinosa* were exposed to $^{14}\text{CO}_2$ late in the growing season, some of the ^{14}C was fixed in reserves. A portion of the reserve ^{14}C was translocated from the leaves and used in shoot expansion during the next growing season (Schier, 1970; Gordon and Larson, 1970).

An important consideration in when new leaves begin to contribute current photosynthate to development of subtending internodes and other internodes is the rate of leaf expansion. Some investigations with broadleaved species have shown that young, rapidly expanding leaves did not export appreciable photosynthetic products. However, after some critical leaf size was attained, export of photosynthetic products predominated. For example, when top leaves of vigorous shoots of apple trees were exposed to $^{14}\text{CO}_2$ the subsequent distribution of ^{14}C -photosynthate varied with the date of treatment. During July, when shoot growth was vigorous, more than 80%

of the ^{14}C was retained in the shoot, mainly in the treated leaves. If leaves were exposed to $^{14}\text{CO}_2$ in August, when shoot extension was nearing completion, a large percentage of the labeled carbohydrate was translocated from the shoot. Thus, young growing leaves retained the majority of the photosynthate for their further growth. About 30–35% of the ^{14}C applied in July was incorporated into methanol-insoluble substances, indicating considerable incorporation of the carbohydrates into shoot tissues. By comparison, at least three-fourths of the ^{14}C taken up by the mature leaves disappeared from them and only 4–9% was recovered in the methanol-insoluble component (Hansen, 1967b).

SPECIES CHARACTERISTICS

Trees which exhibit a single seasonal shoot growth flush of short duration use less of the total current photosynthate for shoot expansion than do species with shoots that continue to expand late into the summer, (Kozlowski, 1962a; Kozlowski and Winget, 1964; Kozlowski and Keller, 1966). Among species of the Temperate Zone whose shoots grow late into the frost-free season are those with heterophyllous shoots which do not contain a fully preformed shoot in the winter bud (e.g., *Populus*), recurrently flushing species, and species which have preformed shoots in the winter bud but which also produce late-season lamas or proleptic shoots (Chapter 5).

Kozlowski and Clausen (1966) presented evidence for use of considerable current photosynthate during shoot expansion of the heterophyllous species, *Betula papyrifera*. Experiments on covering early and late leaves separately showed that the contributions of the two types of leaves to shoot expansion differed. Covering or removal of early leaves at various times in the growing season inhibited shoot elongation. The early leaves were fully grown within a few weeks after buds opened and, when mature, appeared to contribute current photosynthate for subsequent shoot expansion. Late leaves, which had not yet completed expansion, apparently received assimilates from other tissues. Hence, their covering or removal from the tree at various times during the growing season did not appreciably alter shoot elongation.

According to Heinicke and Childers (1937), the new shoots of young McIntosh apple trees at first used stored carbohydrates, but about 6 weeks after buds opened they became independent of reserves. C. A. Priestley (1962b) cited evidence of Bolas that apple leaves began to supply carbohydrates to shoot growth after they achieved about half their size. Mochizuki and Hanada (1957) divided growth of apple shoots into two phases. They concluded that during the first phase when about 12 leaves were produced, shoot growth depended on carbohydrate reserves accumulated the previous year. During the second phase, about eight additional leaves formed and

current photosynthate appeared to be mobilized for their growth. As C. A. Priestley (1962b) emphasized, fruit trees on different rootstocks grow at different rates and, therefore, the proportion of current photosynthate mobilized by expanding shoots may be expected to vary somewhat from tree to tree.

In many tropical species in areas of seasonal climates, the first growth flush of the season utilizes carbohydrate reserves for the first part of shoot expansion but new shoots soon begin to utilize currently produced carbohydrates. In *Antiaris africana*, a tropical deciduous species of Nigeria, trees started shedding leaves in February and March. A new leaf flush in March and April rapidly depleted reserve carbohydrates but, with onset of photosynthesis in the new leaves, carbohydrates rapidly accumulated again (Olofinboba, 1969).

Much evidence is available which shows that citrus trees use both reserve and currently produced carbohydrates for shoot expansion. Use of stored carbohydrates in shoot growth of citrus is shown by marked depletion of reserves. For example, orange trees in California showed a reduction in starch in twigs and small branches shortly after the beginning of shoot growth. Starch was then depleted from the phloem and, in some instances, from the outer xylem of adjacent branches (Cameron and Schroeder, 1945). In Florida, sugars fluctuated in expanded Valencia orange leaves. The largest decline occurred immediately following the beginning of the spring growth flush. Starch, which was present in smaller amounts, was almost totally exhausted during growth flushes but carbohydrates reaccumulated between growth flushes (P. F. Smith *et al.*, 1952). Similarly, in Arizona a rapid decrease in carbohydrates in old leaves of Valencia orange in March was associated with development of large numbers of leaves and blossoms. The decrease was entirely in reducing and nonreducing sugars. After the spring growth flush, all carbohydrate fractions increased (Hilgeman *et al.*, 1967). Sharples and Burkhardt (1954) also showed a rapid utilization and redeposition of starch that was correlated with shoot growth cycles of Marsh grapefruit trees. Stored starch was rapidly converted into readily usable soluble carbohydrates during spring growth. Reserve carbohydrates were first exhausted in regions of the tree nearest to the meristems.

Kriedemann (1969) showed that citrus trees used considerable current photosynthate, in addition to reserves, during shoot expansion. During the initial seasonal growth flush, ^{14}C -assimilates were drawn from fully expanded old leaves on the same shoot as well as from mature leaves on adjacent shoots. The expanding leaves of new shoots did not export labeled assimilates. However, once the expanding leaves achieved full size and hardened, they also became contributing organs, but even then a nearby sink such as adjacent fruit was necessary to ensure export of labeled photosynthate.

Gymnosperms vary greatly in the amount of total current photosynthate used in shoot expansion. For example, recurrently flushing species of the tropics use currently produced carbohydrates in shoot growth for much of the year. Each growth flush depletes recently produced carbohydrates. Some of the "foxtail" pines of the tropics (Chapter 7) which exhibit continuous shoot growth throughout the year are constantly depleting recently formed carbohydrates in expansion of the terminal leader.

Recurrently flushing pines of the Temperate Zone use current photosynthate for shoot growth over a period of several months. In North Carolina, shoots of *Pinus taeda* and *P. echinata* started growing in March and then divided shoot expansion over a period of about five months (Kramer, 1943; Young and Kramer, 1952). These species flush several times during the year. In *Pinus taeda* a significant excess of photosynthesis over respiration was not measured until April and even then it was quite low (McGregor and Kramer, 1963). The first seasonal growth flush of this species in March and April utilized carbohydrate reserves as well as current photosynthesis. During July, August, and September photosynthesis greatly exceed respiration and large amounts of current photosynthate were used in extension of shoots of the second and subsequent growth flushes.

Several investigators have demonstrated that pines of the Temperate Zone which have preformed shoots in the winter bud and usually one seasonal growth flush of short duration (e.g., *Pinus resinosa*, *P. strobus*) utilize current photosynthate from the old leaves during early phases of shoot expansion, in addition to stored carbohydrates. For example Dickmann and Kozlowski (1968) demonstrated early-season transport of currently produced ^{14}C -photosynthate from old needles to the newly expanding shoots of *Pinus resinosa*. During the first week of May, when terminal buds of shoots were just beginning to open, the 1-year-old needles were contributing most of the current photosynthate to the expanding bud. By June 8, the shoots were in the "candle" stage with internodes partially expanded and needles only very slightly elongated. At that time the 1-year-old needles again contributed the largest amounts of current photosynthate to the expanding shoots, with less supplied by 2-year-old needles and only a small amount by 3-year-old needles. In the latter part of June, the 2- and 3-year-old needles supplied more current photosynthate to expanding shoots than they had earlier. The supply of current photosynthate to new shoots from the three age classes of old needles declined late in the season as increasingly more carbohydrates were produced by the now mature current-year needles. These findings were reinforced by Gordon and Larson (1968) who also noted that old needles of young *Pinus resinosa* trees rapidly lost much of the ^{14}C applied to them early in the season. Translocation of ^{14}C -photosynthate from the old needles was rapid during the grand period of shoot elongation

and early stages of new needle development. Translocation of labeled assimilates from the old needles was greatest when the new needles began elongating. At that time a larger proportion of the ^{14}C translocated was rapidly converted to alcohol-insoluble material in the new needles, showing incorporation into protoplasm and cell wall constituents. Later in the season, when the new needles were offered $^{14}\text{CO}_2$, they also produced ^{14}C -photosynthate, an appreciable portion of which was incorporated into the structure of the new needles within a few weeks after shoot expansion began. Similarly Ursino *et al.* (1968) found that the old needles of *Pinus strobus* seedlings that were offered $^{14}\text{CO}_2$ in April and May in Ontario, Canada, translocated appreciable amounts of labeled carbohydrates to expanding new shoots. By mid July, when growth of the new shoots was virtually completed, the new needles had replaced the old needles both as the primary photo-assimilating parts of the plant and as exporters of carbohydrates.

In expanding shoots of heterophyllous species a very young, rapidly developing leaf near the apex does not export carbohydrates and at first depends on carbohydrates provided by an exporting leaf below it. The carbohydrates produced by a very young leaf are used almost completely for its own growth. By the time such a leaf is fully expanded it becomes a major exporter of carbohydrates, most of which are translocated upward in the shoot. When a number of leaves in different stages of maturity are present on such a shoot, the upper leaves translocate carbohydrates primarily to younger leaves above, the lower leaves to the lower stem and roots, and intermediate leaves may translocate carbohydrates both upward and downward. Such patterns have been described for *Populus deltoides* (Larson and Gordon, 1969) and *Malus* (Hansen, 1967a,b). In *Malus* the leaves on short side shoots (spur shoots) which developed relatively early in the season were capable of exporting photosynthates early for growth of other shoots. By comparison, the terminal leaves of long shoots did not export carbohydrates until very late in the season (Hansen, 1967a,b), further emphasizing variable patterns of utilization of currently produced carbohydrates in shoot growth.

LOCATION OF SHOOTS

Whereas growth of root suckers and stump sprouts utilizes large amounts of reserves, other shoot types appear to use considerably more current photosynthate for their expansion. Shoots in the upper parts of gymnosperm trees use more of the total currently produced carbohydrate supply than do shoots lower down in the stem. This is so because the duration of expansion of a given growth flush, as well as the number of seasonal growth flushes, decrease progressively from the top of the tree downward (Kozlowski,

1964a). For example terminal leaders of pines expand for a longer time than do leading shoots of lateral branches (Kozlowski, 1964a).

Friesner (1943) reported that secondary axes of *Pinus strobus* and *P. resinosa* had a shorter duration of elongation from the uppermost whorl downward. Fielding (1955) also showed that growth cessation of *Pinus radiata* shoots occurred later in the upper stem than near the base. In recurrently flushing pines of the United States (e.g., *Pinus taeda*) the number of growth flushes often varies from as many as four in upper branches to one or none in lower branches, emphasizing a greater total consumption of current photosynthate by the upper branches.

J. J. Clausen and Kozlowski (1967a) noted that even in *Pinus resinosa* which has a fully preformed shoot in the spring bud, the carbohydrate economy of variously located shoots differed. One-year-old needles of basal shoots decreased in dry weight beginning early in the growing season, indicating they were a carbohydrate source for the new shoots. In contrast, 1-year-old needles of the upper stem did not decrease in dry weight until about a third of shoot growth was completed, indicating that they were less important than needles lower down on the stem, as a carbohydrate source for early-season growth of new shoots.

RESPIRATORY CONSUMPTION OF CARBOHYDRATES BY SHOOTS

Growing shoots consume large amounts of carbohydrates in respiration. Young, rapidly expanding leaves with a high proportion of protoplasm to cell wall material respire more rapidly per unit of dry weight than old mature leaves with thick cell walls. Koch and Keller (1961) noted that fully developed leaves of *Populus* had the highest apparent photosynthesis and low respiration. The rate of actual photosynthesis (net CO₂ uptake plus respiratory CO₂ evolution) to respiration increased from 1.5 to 2 for young, to 4 for old, and to 6 for middle-aged mature leaves.

Buds consume some carbohydrates in respiration during the dormant season but the rate increases rapidly as dormancy is broken. Hence, considerable carbohydrate reserve is consumed in respiration at the time of year when carbohydrate production is low. Respiration of *Pinus strobus* buds increased greatly at the time of shoot unfolding, emphasizing the importance of reserves as a respiratory substrate (Kozlowski and Gentile, 1958). Flushing of shoots of *Picea excelsa*, *Pseudotsuga menziesii*, and *Pinus sylvestris* was characterized by high respiration leading to a negative CO₂ balance. As new shoots increased in length, the amount of CO₂ used in photosynthesis eventually reached and surpassed that produced in respiration (Neuwirth, 1959).

Shortly after buds opened the new needles of *Abies balsamea* and *Picea glauca* released more CO₂ in respiration than they absorbed in

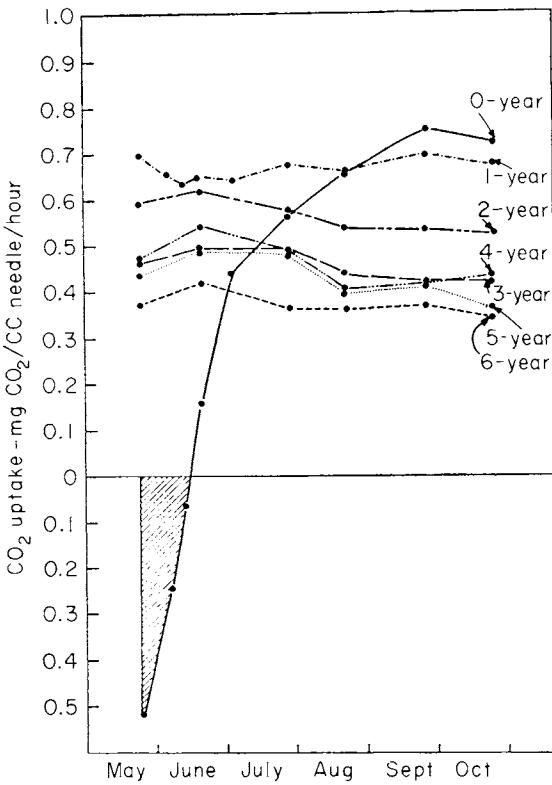


FIG. 8.8. Seasonal variations in photosynthetic capacities of *Abies balsamea* needles of varying age. [From Clark (1961).]



FIG. 8.9. Effect of fertilizers on shoot growth of *Pinus banksiana*. The branch at the left is from a control tree which did not receive fertilizer and the branch at the right from a tree which had been fertilized. Note increased foliage density and greater needle retention as a response to added fertilizer. [From Swan (1965).]

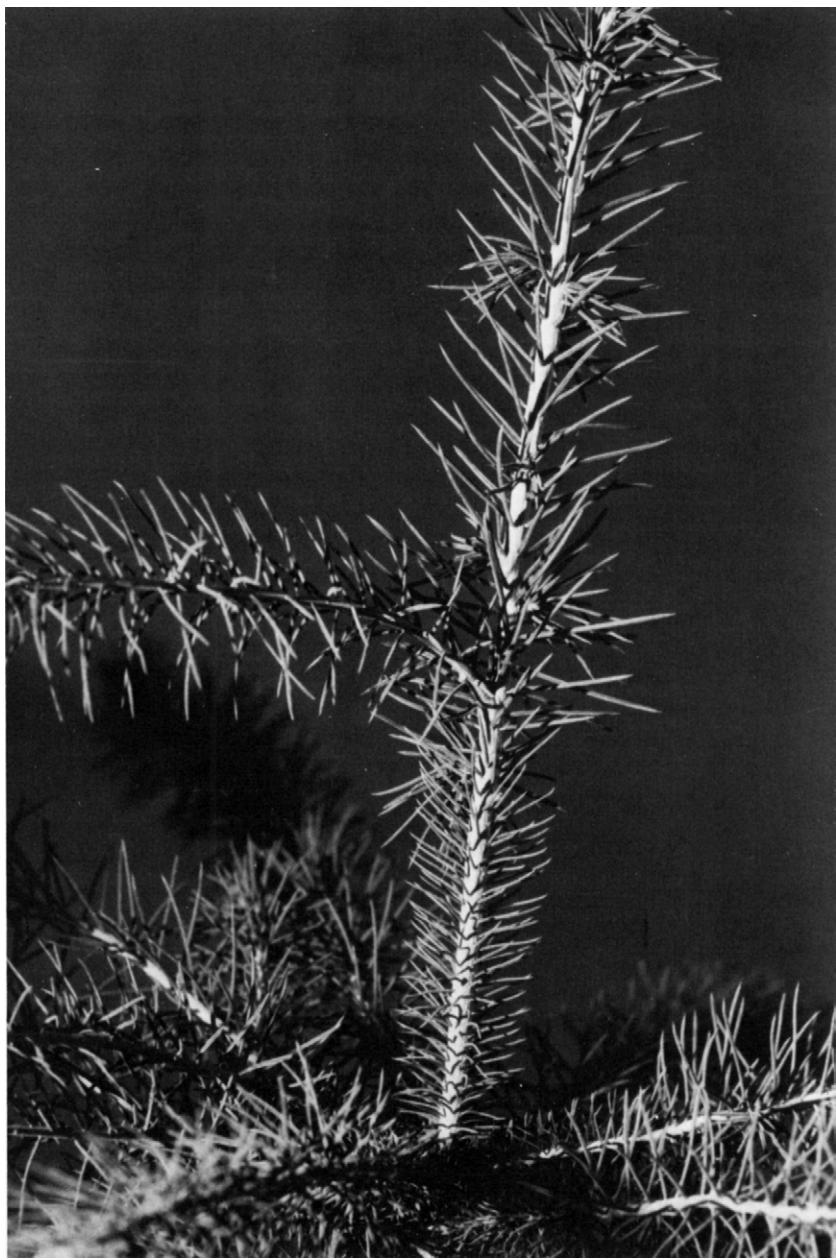


FIG. 8.10. Response of *Picea mariana* to mineral supply. The short needles on the lower part of the stem were produced under mineral deficiency. The longer, more widely spaced needles were produced when the seedling was supplied with a complete nutrient solution. (Photo courtesy of Pulp and Paper Research Institute of Canada.)

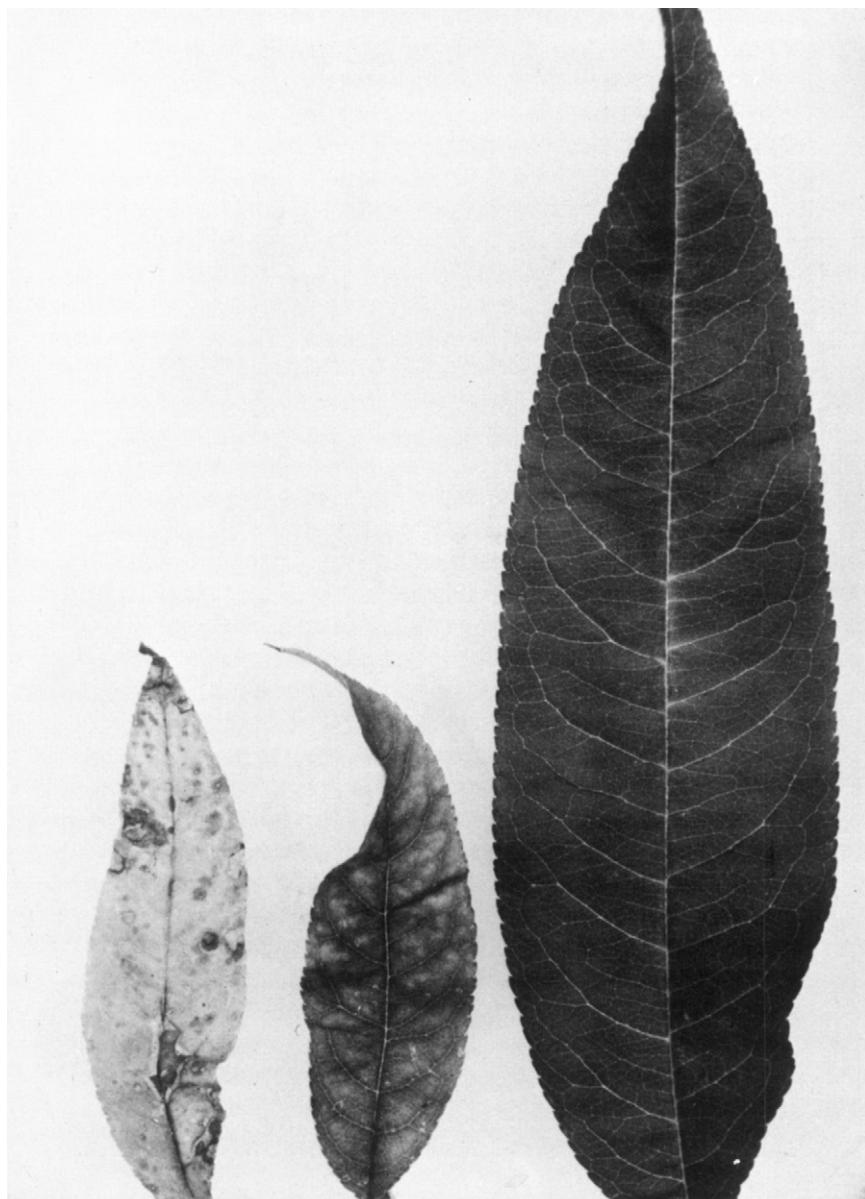


FIG. 8.11. (*Left to right*). Nitrogen deficiency in first two leaves and control leaf in peach. (Photo courtesy N. F. Childers.)

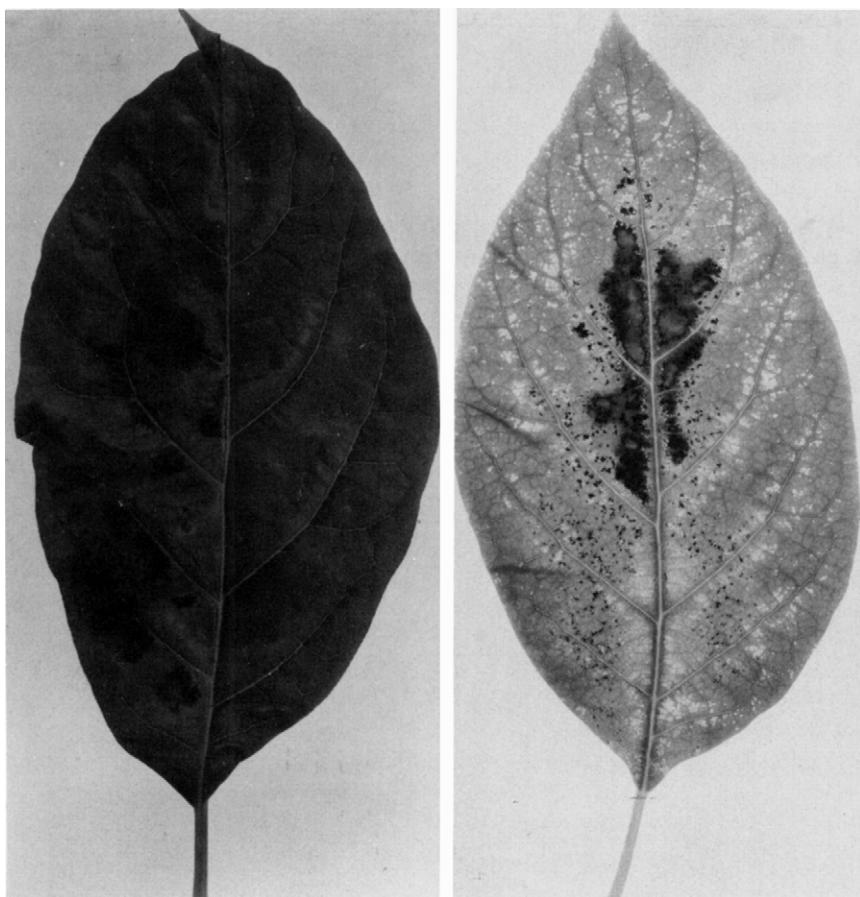


FIG. 8.12. Phosphorous deficiency in avocado. (*Left*) early burning and (*right*) advanced necrosis and chlorosis. [From Childers (1966a).]

photosynthesis. By June 15 the currently produced needles accounted for no net loss or gain of CO_2 . However, it was not until late August that the new foliage showed a net CO_2 uptake as high as that of 1-year-old needles (Fig. 8.8).

The consumption of food in respiration at different times of the growing season may vary greatly among individual leaves of some species. In species with shoots fully predetermined in the winter bud all leaves usually expand rather rapidly. Their respiration rate is high early in the season and it slows down greatly within a few weeks as cell walls thicken. In contrast, leaves of species with heterophyllous shoots such as *Populus* and *Betula* mature at

different rates. Late in the growing season there often are young expanding leaves with high respiration rates on the same shoots which bear leaves that matured several weeks earlier and have low respiration.

Minerals

It is well known that mineral deficiency impedes shoot growth of trees. For example, Schomaker and Rudolph (1964) showed that deficiency of mineral elements was limiting height growth of *Liriodendron tulipifera* in southwestern Michigan. Height growth of this species varied greatly in two parts of a plantation. Foliar analyses showed highly significant differences



FIG. 8.13. (Left to right). Control leaf and 3 leaves of peach with various stages of potassium deficiency. (Photo courtesy N. F. Childers.)

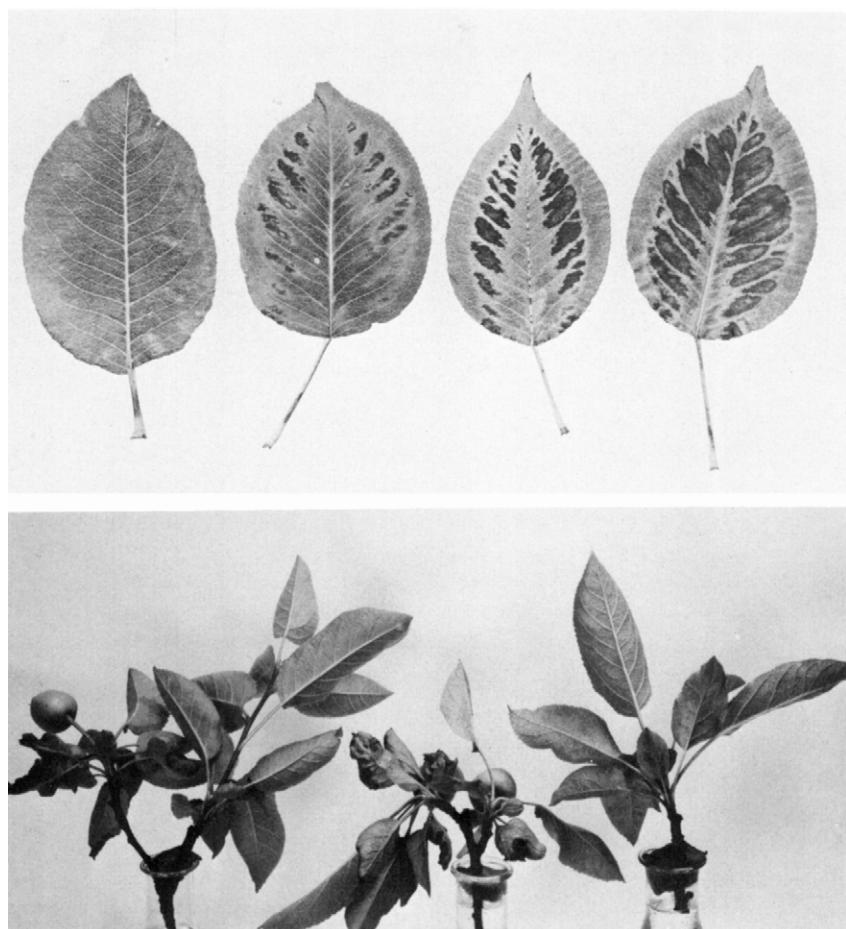


FIG. 8.14. Magnesium deficiency. (*Upper*) different degrees of interveinal chlorosis in pear in mid to late season. (*Lower*) marginal and interveinal chlorosis early in season on spur leaves of apple. [From Childers (1966a).]

between mineral element concentration of leaves from trees in the area of high growth rate and the area of low growth rate. Differences were found for every element analyzed, except boron and magnesium (Table 8.8). The most outstanding differences were found for nitrogen and phosphorus concentrations, with nearly twice as high a concentration in the leaves from the area of rapid growth as from the area of slow growth. Both nitrogen and phosphorus concentrations were highly correlated with tree height, emphasizing that they were important factors limiting height growth. Leaf concentrations of nitrogen, phosphorus, and potassium throughout the study area were well below levels of luxury consumption.

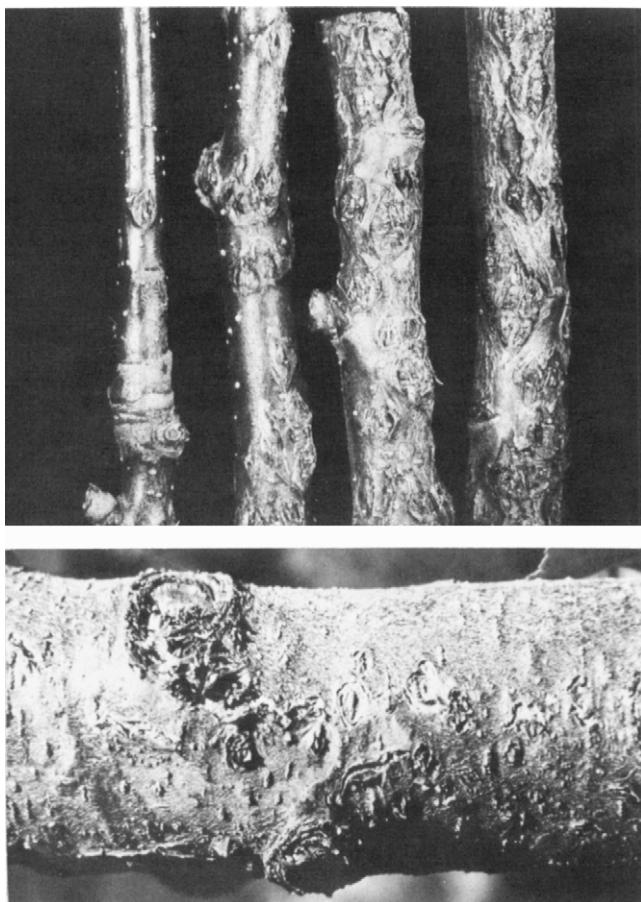


FIG. 8.15. Boron deficiency in apple. Injury to young twigs (*upper*) and older twigs (*lower*) of Delicious. [From Childers (1966a).]

The nature and amount of shoot growth inhibition varies with the degree of mineral deficiency and the particular elements involved. Deficiencies of some elements not only reduce growth of leaves and internodes by impeding formation of shoot primordia and their subsequent expansion, but also cause necrosis of leaves, branches, and other tissues (Figs. 8.9 to 8.21). Additional details on effects of mineral deficiencies on shoots of fruit trees are available in the books by Childers (1961, 1966a,b).

The most commonly observed symptom of deficiency of any of several mineral elements is leaf chlorosis caused by interference with chlorophyll synthesis. Photosynthetic capacity of affected leaves usually is greatly reduced (Kramer and Kozlowski, 1960; Kozlowski and Keller, 1966).

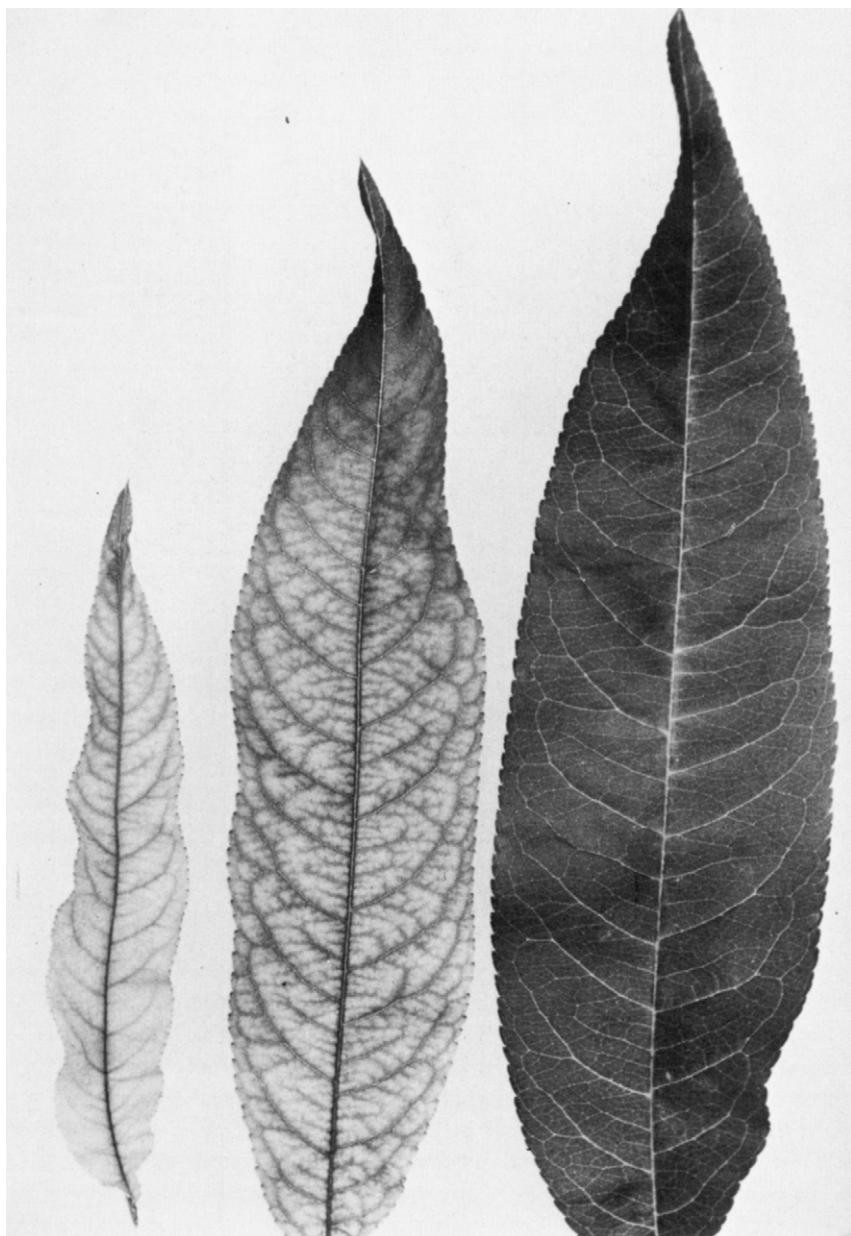


FIG. 8.16. (*Left to right*). Iron deficiency in first two leaves and control leaf in peach.
(Photo courtesy N. F. Childers.)

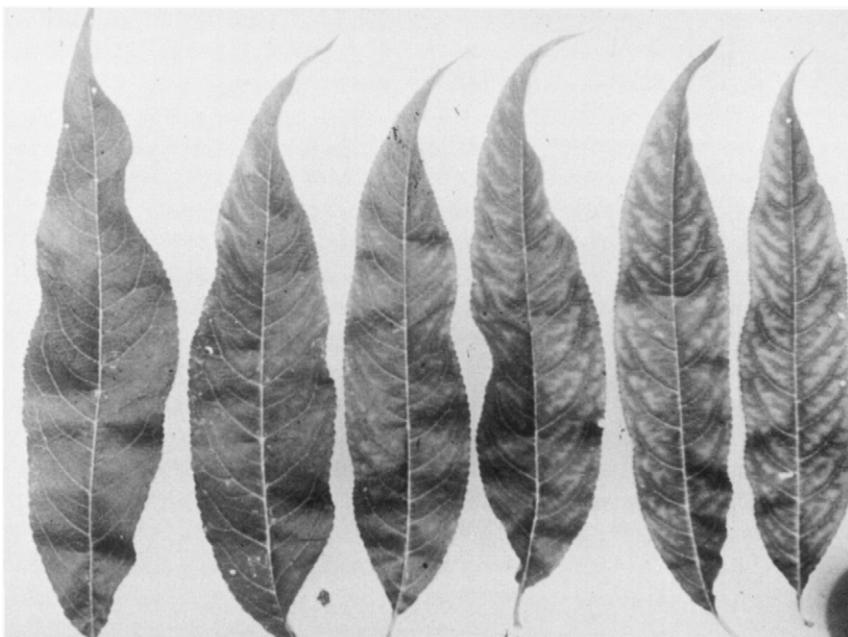


FIG. 8.17. Mild manganese deficiency in peach. Leaves show a herringbone effect with green areas next to major veins. [From Childers (1966a).]

The essential mineral elements classified as macronutrients usually are required in available amounts exceeding 1 ppm. whereas micronutrients are needed in very much smaller amounts, often less than 1 ppm. The macronutrients include nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur. Important micronutrients are boron, iron, manganese, zinc, copper, molybdenum, and chlorine. Many plant physiologists consider an element necessary for growth only if it meets the following conditions (Arnon and Stout, 1939): (1) deficiency of the element prevents completion of the vegetative or reproductive phase of the life cycle of a plant; (2) the deficiency is identified with a particular element and can be prevented or corrected only by this element; and (3) the element is directly involved in nutrition of the plant irrespective of its influence in correcting some unfavorable condition of the soil or growth medium.

Mineral elements have several important physiological functions in plants (B. S. Meyer and Anderson, 1952). They serve as (1) constituents of plant tissues (e.g., calcium in cell walls, nitrogen and sulfur in proteins, magnesium in chlorophyll); (2) catalysts (e.g., iron, manganese, copper, and zinc as activators of enzymes); (3) buffers (e.g., phosphate buffer systems); (4)



FIG. 8.18. Copper deficiency. (*Upper*) defoliation shoots from tip and shoot dieback in pear. (*Lower*) early stages of copper deficiency in apple starting at shoot tips. [From Childers (1966b).]



FIG. 8.19. Zinc deficiency in Stayman apple shoots. (*Left*) control shoots. (*Right*) affected shoots. Note narrow, crinkled, chlorotic leaves with wavy margins. [From Childers (1966b).]



FIG. 8.20. Zinc deficiency in peach. [From Childers (1966a).]



FIG. 8.21. Sulfur deficiency in peach. (*Left*) control shoot. (*Right*) affected shoot. [From Childers (1966b).]

TABLE 8.8

VARIATIONS IN GROWTH AND MINERAL CONTENT OF FOLIAGE OF *Liriodendron tulipifera* IN TWO PARTS OF A PLANTATION IN MICHIGAN^a

Tree characteristic	Tree location	
	Area of good growth	Area of poor growth
Height	57.5 ft.	26.6 ft.
Diameter	7.38 in.	3.99 in.
Mineral Content of Leaves	Oven-dry leaf weight (%)	
Nitrogen	1.75	0.95
Potassium	0.89	0.67
Phosphorus	0.20	0.10
Calcium	3.18	2.76
Magnesium	0.32	0.29
	Oven-dry leaf weight (ppm)	
Manganese	471	345
Iron	122	87
Copper	10	8
Boron	72	73
Zinc	32	27
Molybdenum	12	10
Aluminum	402	437

^a From Schomaker and Rudolph (1964).

controllers of permeability (monovalent ions increase permeability of cell membranes and calcium and other divalent ions decrease permeability); (5) osmotic regulators; (6) antagonists (one element can reverse the action of another one); (7) toxic agents (aluminum and mercury are toxic and some essential micronutrients are toxic if present in more than minute quantities). This section will briefly discuss some of the specific roles of the more important mineral elements in trees and effects of their deficiencies on shoot development.

MACRONUTRIENTS

Nitrogen

This element is an important constituent of proteins and of the chlorophyll molecule. It also occurs in purines, alkaloids, and vitamins. Demands for nitrogen by trees are very high and response to lack of nitrogen probably is the most widespread form of mineral deficiency in trees. During bud swelling in spring a mobilization of nitrogen to buds occurs and is accompanied by a sharp decrease in total nitrogen in older shoots and branches, suggesting that protein hydrolysis occurs and that soluble nitrogen is translocated from these tissues to the developing meristems. Taylor (1967) found that nitrogen, which accumulated in peach trees after shoot growth ceased in late summer, was mobilized for shoot growth during the next growing season. Taylor and May (1967) also observed that the amount of shoot growth in peach trees

TABLE 8.9

INFLUENCE OF ROOT APPLICATIONS OF NITROGEN AND PHOSPHORUS THE PREVIOUS SEASON ON THE NUTRIENT CONTENT OF DORMANT *Taxus* PLANTS, ON GROWTH DURING THE FOLLOWING SPRING, AND ON MINERAL CONTENT OF NEW GROWTH^a

Fertilizer Treatment (mg)	Nutrient concentration of dormant plants (% dry wt)	Spring growth (gm fresh wt)	Mineral content of new growth (% dry wt)
Nitrogen			
0	1.54	19.67	1.49
45	1.95	29.57	1.67
90	2.18	36.50	1.69
135	2.37	38.19	1.77
Phosphorus			
0	0.157	26.52	0.206
175	0.193	31.46	0.258
350	0.209	34.97	0.266

^a From M. M. Meyer and Tukey (1965).

during the first half of the growing season was positively correlated with the level of storage nitrogen in tree tissues, whereas late in the season it depended on external nitrogen supply. About two-thirds of the storage nitrogen in dormant, two-year-old peach trees was held in root tissues. Storage nitrogen in dormant trees consisted mostly of soluble organic nitrogen, with free arginine as its main component. The level of arginine in dormant trees was a sensitive indicator of the nitrogen status of the tree.

The work of M. M. Meyer and Tukey (1965) provides a good example of the importance of nitrogen reserves to shoot growth. Nitrogen fertilizers affected shoot growth only slightly during the year of application, but greatly during the subsequent year (Table 8.9). The increased growth due to added nitrogen was attributed to nitrogen reserves within the plant because (1) the nitrogen content of dormant *Taxus* plants was increased by nitrogen applications the previous year, and (2) the nitrogen content of the new growth was similar at all nitrogen levels the previous season, but the growth was very different and was greatest at the highest nitrogen levels.

Mochizuki and Hanada (1958) evaluated the role of reserve and currently absorbed nitrogen on shoot growth of apple trees (Tables 8.10 and 8.11).

TABLE 8.10

ELONGATION OF APPLE SHOOTS WITH AND WITHOUT N FERTILIZER APPLIED IN EARLY APRIL^{a,b}

Treatment	Date					
	May 27	June 12	June 27	July 12	July 27	August 12
Minus nitrogen	9.1	17.9	20.3	20.3	20.3	20.3
Plus nitrogen	9.2	19.6	22.1	26.8	32.0	32.0

^a Shoot lengths are given in cm.

^b From Mochizuki and Hanada (1958).

TABLE 8.11

INTERNODE LENGTH^a BETWEEN VARIOUS APPLE LEAVES^b

Treatment	Internode length at leaves numbered:				
	1-5	5-9	9-13	13-17	17-21
Minus nitrogen	0.5	2.5	10.8	6.5	0
Plus nitrogen	0.6	2.4	10.3	10.6	8.1

^a In centimeters.

^b From Mochizuki and Hanada (1958).

The addition of fertilizer nitrogen at the beginning of April had little effect on shoot length until June 27. At that time the shoots which had not received added nitrogen ceased growing whereas those receiving nitrogen continued to grow. Internode length from the first to the 13th leaf from the base was approximately the same in both fertilized and unfertilized plots. The differences in final shoot length shown in Table 8.10 were attributed to differences of internodes from the 13th to the terminal leaf. Mochizuki and Hanada concluded that reserve nitrogen determined the area of the first 12 leaves whereas currently absorbed nitrogen controlled growth of the 14th to the terminal leaf on a shoot.

Shoot growth was greatly influenced by adding nitrogen fertilizers to young *Picea abies* stands in Finland (Viro, 1965). The chlorophyll content of needles increased significantly during the year after fertilization (Table 8.12). How-

TABLE 8.12

EFFECT OF NITROGEN FERTILIZATION ON RELATIVE QUANTITIES OF CHLOROPHYLL IN NEEDLES AND SHOOT GROWTH OF *Picea* FOR FIVE YEARS AFTER TREATMENT^{a,b}

Year after adding Nitrogen	Relative weight					
	Chlorophyll		Needles		Shoots	
	Current	2-year	Current	2-year	Current	2-year
1	142	153	104	108	107	108
2	177	143	150	111	158	137
3	140	155	133	138	146	158
4	111	128	113	127	118	140
5	95	105	100	107	101	117

^a Data are given as percent of controls (minus nitrogen).

^b From Viro (1965).

ever, the quantity of needles and shoots did not increase until the second year after adding fertilizer. In the second year, the weight of new needles was 48% greater on fertilized plots than on unfertilized ones. The effect on the weight of 2-year-old needles was much less obvious. The influence of nitrogen fertilizer began to decrease after the second year. It was significant in the fourth but not the fifth year. In the third, fourth, and fifth year after treatment, the effect of adding nitrogen on the weight of 2-year-old needles was greater than on current needles, indicating the waning effect of fertilization. The trend of shoot weight was correlated with needle weight. Armsom (1966) found that *Picea glauca* seedlings in the nursery that were given fertilizers several times during the growing season in their second year showed greatly

stimulated height growth during the same year. An increased number of secondary needles was associated with the greater height of the fertilized trees. At the end of the season fertilized trees had a mean of 180 needles and unfertilized trees had only 94 needles.

Experiments by Maki (1961) showed marked shoot growth responses of *Pinus taeda* trees to nitrogen fertilizers. Needles turned dark green within two weeks after treatment. Heavy nitrogen application (160 lb N/acre) increased average needle length by an inch or more. Furthermore, in years of abundant moisture, nitrogen fertilization also increased the volume of foliage because of a high proportion of fascicles having four or more needles.

Nitrogen deficiency in trees is associated with reduction in shoot growth and pale leaf color. The symptoms usually are noticeable over the entire crown and individual leaves also show a uniformly pale color. Chlorosis becomes increasingly marked as the season advances, often causing early defoliation. Apple and plum trees often show more yellowing than cherry, peach, or pear trees. Nitrogen deficiency also occurs commonly in many forest trees and in nurseries. It frequently is caused by competition between trees and other vegetation such as grass or heather. Nitrogen deficiency often is reflected more in impeded growth than in clear and definite deficiency symptoms.

Phosphorus

Trees require phosphorus in relatively large amounts. Phosphorus is a part of nucleoproteins and phospholipids. The high energy bonds of phosphate groups are important in energy transfer.

M. M. Meyer and Tukey (1965) demonstrated the importance of phosphorus reserves to shoot growth in *Taxus* and *Forsythia*. More than three-fourths of the phosphorus in the new growth of *Taxus* and more than half of the phosphorus in new growth of *Forsythia* came from reserves. Application of phosphorus during one growing season increased the reserve content and greatly stimulated growth during the next year (Table 8.9).

Phosphorus deficiency often occurs in young gymnosperms. As a result of anthocyanin production the affected trees usually show purplish foliage which eventually withers (Hobbs, 1944). In phosphorus-deficient *Thuja plicata* the youngest foliage remained green whereas the old leaves were at first purplish but subsequently turned brown and died (R. B. Walker *et al.*, 1955). In coniferous nurseries, purplish discoloration of pines and spruces often indicates phosphorus deficiency.

A deficiency of phosphorus is very uncommon in fruit trees. When it does occur, however, the young leaves and shoots develop a purple color along the margins of leaves and lower sides of the major veins. Deficiency symptoms are most obvious early in the summer and they tend to be reduced later as absorption of phosphorus by roots increases.

Potassium

Trees require potassium in large amounts. Potassium appears to catalyze cellular reactions and a deficiency of it impedes nitrogen metabolism and translocation of carbohydrates. When deficiencies occur potassium moves from older tissue to growing points. Hence, deficiencies are most obvious in older tissue. Luxury consumption without apparent injury to trees occurs commonly.

Potassium deficiency, which occurs often in fruit trees, causes marginal scorching of old leaves together with reduction in shoot length and leaf size. The color of the scorched margins varies from dark brown in apple leaves to grey in cherry and peach leaves. Before actual development of marginal necrosis the leaves of peach, cherry, and pear often curl upward. Chlorosis sometimes also precedes the marginal scorching. Symptoms usually are much less severe in young leaves than in old ones.

Potassium deficiency occurs commonly in forest trees, with symptoms varying greatly among species. For example, potassium-deficient *Prunus serotina* leaves had bright red margins, those of *Betula populifolia* had chlorotic margins, and those of *Acer rubrum* were uniformly chlorotic (L. C. Walker, 1956).

Gymnosperms usually show various types of chlorosis in response to potassium deficiency. Young needles of potassium-deficient *Picea abies*, were green at the base and yellow or brown at their tips (Ingestad, 1959). Generalized chlorosis was followed by browning and eventual death of needles in *Pinus resinosa*, *P. strobus*, *Picea abies*, and *P. glauca* in response to potassium deficiency (Heiberg and White, 1951). Shoot growth also was depressed.

Magnesium

As magnesium is a constituent of the chlorophyll molecule a deficiency would be expected to cause chlorosis. Magnesium is also important in certain enzyme systems. Magnesium is rather mobile in plants and when deficiencies occur it may move from old to young growing tissues. Therefore, symptoms of deficiency often, but not always, are detected first in mature tissues.

Magnesium deficiency in orchard trees is well known by patches of chlorosis or necrosis between the veins of old leaves. Yellowing occurs first at the ends of the smallest veins. In most species these areas become chlorotic; in others they may darken and die. More severe symptoms are found on basal leaves than on tip leaves of a shoot. Magnesium-deficient leaves have a v-shaped green area which is centered along the midrib. In advanced stages of deficiency the area outside the green zone may become necrotic. Deficiency symptoms usually intensify toward late summer and the more severely affected leaves may abscise.

Magnesium deficiency occurs commonly in gymnosperms and usually is identified by characteristic tip chlorosis (Hobbs, 1944; Voigt *et al.*, 1958). Magnesium deficiency caused yellowing of tips of current-year needles, especially in the upper crown, of pines of the northeastern United States (E. L. Stone, 1953a).

Calcium

The precise role of calcium in trees is vague. It appears to be involved in nitrogen metabolism and affects membrane permeability. It occurs together with pectates in cell walls.

Calcium deficiency in broadleaved trees causes shoot dieback and inward rolling of leaves. In fruit trees leaf margins may have thin chlorotic margins with some spotting and brown scorching. Growing points often are stubby and die back. Symptoms of calcium deficiency in gymnosperms resemble those caused by lack of magnesium. In calcium-deficient *Picea* the young needles were yellow and had yellow-brown tips (Ingestad, 1959), whereas calcium-deficient *Pinus taeda* seedlings had small buds and stem tips and small leaves (Davis, 1949). In *Thuja plicata*, calcium deficiency caused death of shoot and root tips (R. B. Walker, *et al.*, 1955).

Calcium is most important in tree nutrition largely because, when it is abundant, it decreases availability of other elements causing "lime-induced" chlorosis. Low uptake of manganese or iron is commonly attributed to excess calcium but absorption of other elements is impeded also. For example, lime-induced potassium deficiency has been described in *Picea* (Björkman, 1953) and iron deficiency in *Fagus* (W. R. Day, 1946). The most severe lime-induced chlorosis occurs on fine-textured, poorly aerated, and cold soils where conditions do not favor mineral uptake.

MICRONUTRIENTS

Most symptoms of micronutrient deficiency are specific for species, yet the same deficiency does not cause the same symptoms in different species. If two or more micronutrients are deficient the symptoms may not be typical for either element, as one may obscure the effect of the other. Some typical roles of micronutrients and symptoms of their deficiencies will be described briefly.

Boron

A deficiency of boron in fruit trees has been well documented. According to E. L. Stone (1968), boron deficiency also appears to be the most common microelement deficiency in forest plantations. Symptoms of boron deficiency include chlorosis, reduced leaf size, "rosetting," dieback of shoots, much-branched roots, and multiple buds. Anatomical effects usually are reduced

growth, necrosis, and changes in cell wall thickness. Boron-deficient angiosperm leaves often are blistered or curled especially in the affected terminals. Petioles and stems may show cracking and necrotic spots as well as deposits of gum or resin.

Boron deficiency in pines causes stunted growth as well as death of growing shoots and root tips. Boron deficiency of *Pinus radiata* was distinctly seasonal in occurrence, with shoots appearing normal until midsummer. Thereafter, shoot expansion was inhibited, the apex usually died, and lateral or fascicle buds proliferated below the damaged portion. Expression of dieback symptoms varied greatly and the range of symptom patterns was grouped into "shoot dieback" and "tip dieback." The latter condition appeared to result from more gradual onset of boron deficiency or less acute deficiency (E. L. Stone and Will, 1965). Features of boron deficiency in *Thuja plicata* were listed by R. B. Walker *et al.* (1955). Branchlets of boron-deficient plants were grouped into a "strap" type and a "club" type. Straplike branches had fewer than normal laterals, slightly larger internodes, and divergent rather than appressed leaf tips. The club-shaped tips involved excessive branching followed by dieback.

Iron

This element appears to be part of an enzyme system involved in chlorophyll synthesis. It also occurs in peroxidases and cytochrome oxidase.

Iron deficiency occurs commonly in fruit trees and angiosperm and gymnosperm forest trees. It often occurs together with deficiencies of other elements. High soil pH renders iron unavailable to plants and iron deficiency often is found in trees on chalk and limestone soils. As iron is relatively immobile and not readily translocated from old leaves, iron deficiency usually develops in young leaves at shoot tips as an interveinal chlorosis. Usually the midrib and fine veins are green against a background of yellow green to almost white interveinal tissue. In extreme cases the small veins eventually become chlorotic and apical or marginal scorching may follow. Usually the youngest leaves are affected most, with old leaves frequently appearing normal or only slightly chlorotic.

Iron deficiency also occurs commonly in gymnosperms, especially in nurseries. The new foliage of affected trees becomes chlorotic while the old needles remain dark green. When iron deficiency is severe, needle tips or whole needles may turn brown and abscise. However, when iron deficiency is slight the chlorotic new needles slowly assume a greener color.

Manganese

Like iron, manganese is associated with chlorophyll formation. It is also involved in activation of enzyme systems.

Manganese deficiency occurs commonly in orchard trees and shade trees, but has been reported only rarely in deciduous forest trees. Lack of manganese causes a leaf chlorosis somewhat between the pattern traceable to magnesium deficiency and that caused by lack of iron. In contrast to iron deficiency, symptoms of manganese deficiency are not found on the youngest leaves and the very fine veins are not outlined. Also, in contrast to magnesium deficiency, lack of manganese usually does not cause interveinal chlorosis. Furthermore, the deficiency may occur on all mature leaves and there is no discernible gradient in severity in leaves along a shoot. Under moderate, well-developed manganese deficiency the larger green veins have fairly wide bands of green tissue along both sides. Symptoms usually appear shortly after leaf expansion is completed. Generalized necrosis is not associated with manganese deficiency, but some species may have necrotic spots in the chlorotic tissue. As symptoms of manganese deficiency develop late in leaf development, expansion of internodes and leaves usually is not greatly impeded. However, leaves may be shed when deficiency is severe.

Manganese deficiency has been reported in several gymnosperms. In *Pinus radiata*, for example, lack of manganese caused retarded shoot growth, with buds turning brown and needles becoming chlorotic. Tip needles sometimes showed exudation of resin (M. E. Smith, 1943). According to Wilde and Voigt (1952), manganese deficiency caused generalized chlorosis of gymnosperm seedlings whereas only terminal needles showed chlorosis under iron deficiency.

Copper

This element is a constituent of such enzymes as ascorbic acid oxidase and tyrosinase.

As copper is required in very small quantities, deficiencies in fruit and forest trees are uncommon, except on leached sands. The use of copper fungicides in orchards may prevent deficiency symptoms from developing. When copper deficiency occurs in orchards it sometimes is referred to as "exanthema."

Symptoms of copper deficiency in broadleaved trees include early termination of shoot growth followed by defoliation and shoot dieback. A bushy appearance often results from release of buds below dead shoots, resulting in a condition called "witches broom." Terminal internodes usually are short and the small upper leaves may exhibit marginal scorching or necrosis and interveinal chlorosis. Often the leaves grade abruptly from those which apparently are normal to severely affected, small terminal leaves. Benzian and Warren (1956) described symptoms of copper deficiency in *Picea sitchensis*. Symptoms appeared during summer droughts and included yellowing of needle tips.

Zinc

This element is involved in synthesis of tryptophane, a precursor of indole-acetic acid. Zinc deficiency is not very common in fruit trees or broadleaved forest trees. When it occurs in orchards, zinc deficiency sometimes is referred to as "rosette" or "littleleaf." The most pronounced symptoms include chlorosis of young leaves in tops of shoots, shedding of older leaves, shortening of internodes toward shoot tips, and small narrow leaves which are cupped upward from the midrib. Terminal rosettes of small, abnormal leaves are characteristic. Severe deficiency causes shoot dieback.

Zinc deficiency is well known in *Pinus radiata* plantations in Australia (Stoate, 1950). When deficiency occurs early the trees may be severely stunted. Characteristic symptoms in pines include shoot dieback, shortening of internodes and needles, as well as generalized chlorosis and shedding of needles that are more than 2 years old.

Molybdenum

Deficiencies of molybdenum occur in citrus. Otherwise they are rare in orchard and forest trees. Except in nitrogen-fixing species, the requirement for molybdenum is very low, usually less than 1 ppm. The element is especially important for nitrogen fixing species because it is required in large amounts by nitrogen fixing bacteria and hence by nodulated nonlegumes. Pot culture experiments by Becking (1961a,b) with *Alnus* and G. Bond and Hewitt (1961) with *Myrica gale* showed that molybdenum deficiency caused symptoms usually associated with nitrogen deficiency.

Hormonal Growth Regulators

Balances among various endogenous growth promoters and inhibitors play an important role in regulating shoot growth by controlling division, expansion, and differentiation of cells. Differentiation of bud tissues, release of bud dormancy, expansion of leaves and internodes, leaf senescence, apical dominance, leaf abscission, and onset and release of bud dormancy all appear to be variously controlled by endogenous growth regulators.

At least five major groups of endogenous hormonal growth regulators are involved in control of plant growth. These include such growth promoters as auxins, gibberellins, and cytokinins as well as such inhibitors as abscisic acid (ABA) and ethylene.

Auxins play a major role in influencing a wide variety of growth phenomena such as cell enlargement, root initiation, bud inhibition, gall formation, and tropisms. Auxins occur in greatest amounts in rapidly expanding tissues, such as young stems and leaves, and they decrease to low levels in old and

senescent tissues. They are translocated basipetally in the stem where they are inactivated by various metabolic reactions. Hence, there often is a decreasing concentration of auxin from young to old tissues. Gibberellins also are found in both young and old tissues, but their concentration usually is highest in apical buds and young expanding leaves. Some idea of the complexity of hormonal growth control may be gained from the fact that more than two dozen different gibberellins have been identified. Various plants respond differently to each of these gibberellins. The auxins and gibberellins are readily mobile for when they are applied to one part of a shoot, growth usually is influenced in aerial tissues located some distance from the point of application. The cytokinins are characterized by their capacity to stimulate cell division.

Although some specific effects can be assigned to individual growth promoters or inhibitors, normal growth is the end result of balances of various growth regulators and synergistic effects among them. Various proportions of growth promoters can produce different ratios of cell division and expansion, thereby regulating growth and differentiation. As the concentration of a given phytohormone varies with time, an increase or decrease in concentration influences plant response caused by the other growth regulators present in the system. The presence of nonmobile inhibitors in certain tissues can check their growth, whereas in other tissues which lack the inhibitor, growth often is unimpeded (Galston and Davies, 1969).

Environmental factors often influence growth by controlling the amounts and kinds of phytohormones present by regulating their synthesis, translocation, or destruction. Although the mode of action of phytohormones is not fully understood, it appears that many enzyme and physiological systems are involved. Much evidence is available which shows that plant hormones act on the nucleic acid system, somewhere between DNA and messenger RNA (van Overbeek, 1966).

In the light of much evidence for the importance of endogenous inhibitors on development of bud dormancy, attention is being given to inhibitory compounds as components of the endogenous system controlling growth. Perhaps the most important of these inhibitors is abscisic acid (ABA). This widely distributed compound appears to be involved in many growth responses including (a) acceleration of abscission in fruits and leaves, (b) induction and maintenance of dormancy in shoots of deciduous trees, (c) prolonging seed dormancy (Chapter 2), abortion of young fruits, and (d) leaf senescence. Although knowledge of the influence of ABA on enzymatic synthesis is incomplete, some evidence shows that ABA can inhibit GA-induced synthesis of enzymes. ABA is also able to promote biochemical changes of senescence and abscission (Addicott and Lyon, 1969). This section will discuss the role of hormonal growth regulators on bud

development, shoot expansion, leaf senescence, and leaf abscission. The important role of endogenous growth regulators in control of bud dormancy will be discussed in another section.

OTHER GROWTH REGULATORS

There is considerable evidence that endogenous compounds which cannot be classified as auxins, cytokinins, gibberellins or inhibitors may play a role in growth control (Romberger, 1963). For example, inositol, leucoanthocyanins, and vitamins, among other substances, may variously affect growth of woody plants.

It appears that plant cells require inositol to build into phospholipid molecules and probably in synthesizing cell wall polysaccharides (L. Anderson and Wolter, 1966). The cyclic alcohols occur widely in woody plants as D-, L-, or *myo*-inositol, as methyl ethers (pinitol, sequoiatol, lirodendritol, quercitol, scyllitol), as phosphate (phytic acid), and as the complex lipids, liposolts (Romberger, 1963). Inositol were found in dormant buds and the amount increased greatly during bud opening (Burkholder and McVeigh, 1945). Tissue cultures from woody plants often show a requirement for or growth response to inositol. For example, callus tissue of *Fraxinus pennsylvanica* was grown in a medium of sucrose, inorganic salts, and supplemented with *myo*-inositol, pyridoxine, 2,4-D, and kinetin. *Myo*-inositol, pyridoxine, and an auxin were essential for growth, with naphthaleneacetic acid (NAA) an effective alternate auxin. Kinetin and gibberellic acid increased yield whereas thiamine had no effect (Wolter and Skoog, 1966). Maximal growth was obtained with 10 mg/liter of inositol, and in its absence the tissues soon died. Effects of other cyclitols were tested on *Picea* callus (Steinhart *et al.*, 1962). Growth was promoted by sequoiatol as much as by *myo*-inositol, and to a lesser degree, by *scyllo*-inositol, (+)-pinitol, and D-inositol.

The leucoanthocyanins, which are widely distributed in wood, leaves, and buds of woody plants, may also have considerable physiological significance. In *Eucalyptus* the amount of leucoanthocyanins decreased with increasing maturity of different leaves on a stem (Hillis, 1956). The amount of leucoanthocyanin in the cambial zone also decreased as the season progressed. These observations, in addition to correlation between cell proliferation following wounding and leucoanthocyanin content, were interpreted as suggesting an association between cell division and leucoanthocyanins.

That certain vitamins play a role in control of plant growth is indicated by participation of vitamins of the B complex (thiamine, riboflavin, pyridoxine, niacin, pantothenic acid, biotin, and adenine) as prosthetic groups of enzymes (J. Bonner and Galston, 1959). Tissue culture experiments also

point to a role of vitamins in growth. For example, pantothenic acid stimulates growth of some tissues of *Crataegus* (Morel, 1946) but not those of *Vitis* or *Parthenocissus* (Gautheret, 1955). This discrepancy may merely indicate that tissues of the latter two genera synthesize sufficient amounts for growth.

Vitamin contents often vary during different phases of shoot development. Purohit and Nanda (1966) studied the course of recurrent shoot flushing of *Callistemon viminalis* in relation to ascorbic acid (AA) content of tissues. AA was depleted during each flush of shoot growth and was accumulated during intervening periods of inactivity. In addition the level attained by peaks of AA content decreased gradually with time. The low content of AA during periods of shoot growth was traceable to a high utilization rate even though the rate of synthesis was also high. The accumulation of ascorbic acid between periods of shoot growth appeared to result from a low rate of utilization.

DISTRIBUTION OF GROWTH REGULATORS

The kinds and amounts of hormonal growth regulators vary widely in different parts of trees, as well as at various times during the growing season. Buds and young leaves of trees often contain both growth promoters and inhibitors (Ogasawara, 1960; Clark and Bonga, 1963; Blommaert, 1955; Giertych, 1964).

Whereas dormant buds contain little auxin, swollen or opening buds contain large amounts (Czaja, 1934). In some species the initial auxin supply comes from the bud and young leaves but after shoots start to grow auxin often is produced by the shoot itself (Kramer and Kozlowski, 1960). Ogasawara (1961a) found IAA and an inhibitor in buds and needles of *Pinus densiflora*. He also found three growth promoters and two inhibitors in buds and needles of *P. thunbergii* (Ogasawara, 1961b). *Pinus palustris* seedlings had at least one inhibitor and four growth promoters (R. M. Allen, 1960). Buds of *Pinus resinosa* had three growth promoters and an inhibitor. The ratio of these growth regulators changed during shoot elongation (Giertych and Forward, 1966). Most identifications of growth regulators involved *Avena* bioassays of bud and leaf extracts. Such extracts apparently contain many substances, some of which have not yet been adequately identified (Giertych, 1964).

W. A. Zimmermann (1936) found that buds from the upper crowns of trees had more auxin than buds from the lower crowns. However, in *Pinus resinosa*, Giertych and Forward (1966) found highest levels of growth promoters in the lower or middle part of the crown. But there also were higher levels of inhibitors in the lower or midcrown than in the upper crown,

suggesting that the upper crown had a balance in favor of growth promoters. The levels of growth promoters usually are higher in terminal buds than in lateral buds as demonstrated for *Tilia* (Zimmermann, 1936), *Picea abies*, and *Pseudotsuga menziesii* (Fröhlich, 1958) and *Pinus resinosa* (Giertych and Forward, 1966).

HORMONAL CONTROL OF BUD FORMATION

Several investigators have emphasized the importance of a balance of endogenous growth regulators for bud growth. Work with herbaceous plants showed an important contributory role of adenine in formation and growth of buds. Auxins exerted an inhibitory effect, but the inhibition could be overcome by high concentrations of adenine (Skoog and Tsui, 1951). Skoog and Miller (1957) concluded that a balanced supply of purine and pyrimidine compounds, IAA, and possibly other substances such as amino acids was required for optimal bud growth in herbaceous plants. Skoog (1955) suggested that control of bud growth might be exerted primarily through purines and pyrimidines which are essential constituents of nucleic acids and nucleoproteins. When grown in culture, the buds of all species of plants do not have identical requirements for endogenous factors. Buds of *Ulmus campestris* growing on cambial tissue in culture appeared to depend on a critical balance between a supply of adenine and meso-inositol (Jacquot, 1955).

HORMONAL CONTROL OF SHOOT EXPANSION

There is considerable evidence that expansion of both leaves and internodes is variously regulated by endogenous growth regulators. Experiments with herbaceous plants show, for example, that when expanding leaves are placed in nutrient solutions containing inorganic salts and sucrose they grow little, but when also supplied with extracts of mature leaves they readily expand (J. Bonner and Galston, 1959). Although both auxin and gibberellin stimulate cell enlargement, they appear to have different modes of action for effects on cell enlargement to be expressed. Hence, auxin and gibberellin interact in control of cell enlargement, probably through their separate influences on the cell (Kefford and Goldacre, 1961).

There is some evidence that growth of various leaf tissues is controlled by different endogenous factors. For example, auxins appear to have a greater effect on growth of veins than on mesophyll tissue. Work with herbaceous plants showed that virus diseases or compounds allied to 2,4-D suppressed growth of mesophyll, suggesting that these widely different causes may act by blocking the supply of a phyllokaline which appeared to stimulate mesophyll growth (Went, 1951). Auxins and cytokinins also influence division of stomatal mother cells and hence control the ratio of stomates to other epidermal cells of the leaf (Zucker, 1963).

If specific growth regulators play an important role in shoot elongation they should show a relation to seasonal timing of growth and ample evidence exists of such a relation. For example, auxin yields were proportional to vegetative growth in *Prunus persica* (Shalucha, 1946). Hatcher (1959) found an increase in auxin content in apple shoots in the spring as shoots began to expand. Auxin levels declined during the growing season and the decrease was followed by a deceleration of shoot growth. In *Ginkgo* the production of long shoots appears to be correlated with high auxin production, first at the apex and later in lower internodes (Gunckel and Thimann, 1949). Such correlations have often tempted postulating direct control of shoot growth by auxin alone. However, in *Ginkgo* maximum amounts of auxin occur in internodes which have already passed their maximum growth rate. Furthermore, most species have a changing complement of various growth regulators and, as mentioned, there is increasing evidence that a balance among various growth promoters and inhibitors is more important in controlling growth than is the amount of individual growth regulators.

Exogenous applications of GA have been shown to increase shoot elongation in a variety of woody angiosperm species, with the degree of stimulation also influenced by the physiological condition of the plant (Marth *et al.*, 1956; Wiggans and Martin, 1961). Nanda and Purohit (1964a) treated apices of *Salmania malabarica* with GA (0.0 to 100 ppm) in June, August, September, or October. Stem elongation was stimulated by GA and the effect was greater as GA concentration was increased. GA was most effective when applied early in the growing season until by November it was ineffective. In another study Nanda and Purohit (1964b) found that the effect of GA on extension growth of individual internodes of *Salmania* varied with dosage, position of the internode on the stem, and photoperiod. Upper internodes were affected most but at high concentrations of GA (100 ppm) expansion growth of even the lower internodes was stimulated. The more pronounced effect of increased concentration of GA on total internode extension reflected both a higher rate of growth of individual internodes as well as a greater number of internodes in the plant which responded to treatment (Nanda and Purohit, 1965). Bachelard (1969a) showed that effects of GA on internode extension of *Eucalyptus camaldulensis* seedlings varied with internode position. The relatively limited expansion of lower internodes was the result of cell elongation whereas proportionally greater expansion of upper internodes resulted primarily from cell division.

In contrast to growth stimulation in angiosperms by short-time treatments of GA, the effects of applied gibberellin on gymnosperms generally have been disappointing. Westing (1959) concluded that the effects of gibberellins on various aspects of growth of gymnosperms were very small in comparison to those on angiosperms. B. R. Roberts *et al.* (1963) suggested that there may be some problems with uptake by gymnosperms of applied gibberellin. They

studied long-term effects of gibberellic acid on *Pinus taeda* seedlings by treating them monthly for 9 months with GA in aqueous solutions (10, 100, and 1000 ppm) and in hydrous lanolin paste (25, 50, and 75 mg of lanolin containing 1% gibberellic acid). Spray applications of GA produced significant increases in height growth, (observed for 17 months). After treatment was discontinued, however, the difference between treated and control seedlings decreased.

HORMONAL CONTROL OF LEAF SENESCENCE

Although various chemical changes which occur in senescing leaves have been characterized for many plants, the question of why senescent cells eventually die is not fully understood. According to Osborne (1959), changes in enzymatic activity during aging of leaves are subject to control by hormones. In fact, a considerable body of evidence shows that natural senescence of leaves results from hormone deficiency. Senescence in leaf tissues has been retarded by treatment with various growth regulators including auxins, cytokinins, and gibberellins. However, there apparently are variations among species in deficiencies of specific senescence-retarding hormones. For example, senescence in cherry leaves was retarded by applied auxin but not by kinetin (Osborne and Hallaway, 1960a). Brian *et al.* (1959) sprayed branches of a variety of deciduous trees with 0.005% gibberellic acid and found that some species were not affected, whereas others responded by delaying autumn coloration and leaf fall. In *Fraxinus excelsior*, *Prunus avium*, and *Acer pseudoplatanus* the leaves of treated branches retained a bright green color and did not abscise by November 21, whereas all leaves on untreated branches had fallen by that date.

Numerous examples in the literature show that senescence of leaves of tropical and Temperate Zone trees can be postponed by treatment with hormones and only a few examples will be given. Application of 2,4,5-T to leaf blades of certain tropical trees produced differential aging in various parts of treated leaves. With appropriate dosages the leaf area just below the point of 2,4,5-T application remained green and healthy whereas surrounding areas aged and yellowed progressively (Osborne, 1958). When 2,4-D was applied to attached cherry leaves early in autumn the treated area stayed green even after the leaves abscised (Hallaway, 1960). The sequence of aging in the treated area was postponed for about 2 weeks. Treated areas not only remained green but retained high photosynthetic capacity longer than the rest of the leaf. The breakdown of protein, which is typical of senescence, did not begin until about 16 days after it was initiated in the rest of the leaf. Respiration drifts characteristic of aging leaves also were postponed for 14 to 16 days. After Osborne (1959) treated attached leaves of *Prunus*

serrulata senriko with 2,4-D in autumn, normal yellowing and senescence were observed in untreated areas. In contrast, in cells of tissues below the treated areas, plastids retained their chlorophyll. At the time of normal leaf fall the treated area was an isolated green spot. In detached leaves the untreated leaves remained green for an additional 10 to 20 days. Treated leaves had a higher level of alcohol-insoluble nitrogen in the green, 2,4-D treated areas than was found in the yellow tissue, emphasizing a hormonal control of protein metabolism.

Senescent leaves of both Temperate Zone and tropical woody plants contained an abscission promoting factor which was not present in healthy leaves (Osborne, 1955, 1958). During the period of autumn leaf fall Osborne (1955) compared diffusates from petioles of yellow leaves which abscised and from attached green leaves. Abscission was accelerated by the diffusates obtained from abscised leaves of several species (Table 8.13). *Rhododendron* leaves in their first year of growth do not normally abscise and diffusates from such leaves do not promote leaf fall, but they sometimes retard it. In contrast, diffusates from senescent *Rhododendron* leaves in their second or third year accelerate abscission. According to Osborne (1955), the diffusible factor from senescent leaves counteracted retardation of abscission which followed treatment with IAA. It was not clear, however, whether the abscission-promoting factor from senescent leaves accelerated abscission directly or indirectly by altering hormone levels in the abscission zone.

Leaf Senescence and Protein Metabolism

Although a variety of changes occur during aging of leaves, a decreased ability of cells to synthesize RNA and protein appears to be a crucial malfunction which promotes senescence. With repression of DNA the synthesis of proteins and chlorophyll declines. This sequence of events appears to be involved in the basic mechanism of leaf senescence (Leopold, 1961; Osborne, 1965).

When Osborne and Hallaway (1960b) treated parts of *Euonymus* leaves with 2,4-D, high rates of metabolism persisted in the cells of the treated area which also maintained high protein levels (Table 8.14). The treated parts of leaves appeared to function as metabolic sinks to which nitrogen and possibly carbon compounds migrated, thereby, presumably causing premature senescence in untreated cells. Osborne (1962) noted that changes of senescence, such as decline in levels of protein, RNA, DNA, and chlorophyll in detached *Xanthium* leaves, could be temporarily arrested with kinetin and high ratios of RNA (or protein) to DNA maintained. The kinetin effect was direct and not dependent on translocated metabolites. Kinetin appeared to retard senescence by sustaining synthesis of nucleic acid and proteins.

The dependency of protein synthesis on additional auxin is determined

TABLE 8.13

TIME (IN HOURS) FOR ABSCISSION OF BEAN EXPLANTS TREATED WITH DIFFUSATES FROM PETIOLES OF ATTACHED OR ABSCIDED LEAVES^a

Species	Control	Diffusate from attached green leaves	Diffusate from abscised leaves
<i>Ulmus glabra</i>	102	77	48
<i>Ligustrum ovalifolium</i>	758 ^b	759 ^c	44
<i>Rhododendron sutchuense</i>	67	777 ^d	55

^a From Osborne (1955).

^b Abscission had not occurred in 25% of the explants when the experiment was terminated at 96 hours.

^c Abscission had not occurred in 15% of the explants when the experiment was terminated in 96 hours.

^d Abscission had not occurred in 35% of the explants when the experiment was terminated at 144 hours.

TABLE 8.14

RESPIRATION RATE AND NITROGEN FRACTIONS OF DETACHED *Euonymus* LEAVES 19 DAYS AFTER TREATMENT WITH 2,4-D OR ETHANOL^a

Treatment	Respiration μlO ₂ /hr/gm fresh wt.	Nitrogen fractions, mg N/gm fresh wt		
		Total	Alcohol insoluble	Alcohol soluble
Control leaves	—	3.72	3.21	0.43
Ethanol-treated area of control leaves ^b	108	3.81	3.22	0.73
2,4-D Treated area of leaves (green) ^b	195	4.38	3.33	0.99
2,4-D Untreated area of leaves (yellow) ^b	164	2.83	2.11	0.49

^aFrom Osborne and Hallaway (1960b)

^bDetached for 19 days

by the age of the leaf. In very young, excised *Prunus serrulata* leaves in which the content of endogenous auxin should be high, 2,4-D had no effect on the protein nitrogen-total nitrogen ratio until the value had fallen by 20% (Osborne and Hallaway, 1964). As leaves aged, however, there was an increasing sensitivity of protein metabolism to auxin.

To determine if auxin influenced the protein nitrogen-total nitrogen ratio

by regulating protein synthesis, Osborne and Hallaway (1964) examined the ability of leaf discs from auxin-treated and control leaves of *Prunus serrulata* collected in November to incorporate radioactive amino acid into protein. There was no net loss of chlorophyll from leaf blades treated with 2,4-D. In contrast, over half the chlorophyll was degraded in controls. Variations in rates of leaf senescence were shown in ability to synthesize protein. The rate of incorporation of ^{14}C -leucine into protein was maintained at a high level in leaf tissues supplied with 2,4-D, whereas it was reduced to less than half of the initial rate in leaf parts receiving no additional auxin.

Bud Dormancy

Buds of woody plants of the Temperate Zone exhibit a rhythmic seasonal alternation of growth and inactivity. This temporary growth suspension during the winter is called "dormancy." However, it is difficult to establish clearly the period during which buds are truly dormant because their development from an active state to a truly dormant one, and subsequent release from it, occur very gradually.

At one extreme a simple type of reversible growth inactivity is recognized, in adequately predisposed buds, as a result of unfavorable environmental conditions. Various terms have been used to describe such an early phase of reversible dormancy including "unfreiwillige Ruhe" (Molisch, 1922), "imposed rest" (Stiles, 1950), "imposed dormancy" (Doorenbos, 1953), and "quiescence" (Romberger, 1963). At the other extreme is a deep-seated, state of dormancy which cannot be broken by reversal of the environmental conditions which caused it. Buds in this condition may be predisposed to grow and the external environment may be generally favorable for growth, but unfavorable internal physiological conditions inhibit bud growth. Such a state, sometimes called "true dormancy" is entered rather gradually. The tissues are in such a state of deep dormancy only during a middle phase of the overall rest period. The first phase of the overall rest period is called "prerest" and plants in it often are described as "predormant." When plants are in the predormant condition they still have the capacity for growth, but only in a narrower range of environmental conditions than when they were fully active. Ordinarily the range of environmental conditions in which plants retain capacity for growth becomes narrower with time after predormancy has once developed. The state of dormancy then continues to deepen until a condition of true dormancy is attained. Once this state has been reached, shoot apices cannot be induced to elongate even under the most favorable environmental conditions. Subsequently, true dormancy is terminated and a transition to a condition of "afterrest" or post dormancy

occurs. During post dormancy the tissues are again able to resume growth, at first under very narrow environmental limits, and later under wider ones. Finally, a state is reached in which the tissues are completely released from dormancy. At that time the environmental limits in which growth can occur are widest (Vegis, 1964).

Kawase (1961) visualized dormancy as a quantitative state. When *Betula* plants stopped growing following exposure to short days, subsequent short-day treatment did not further modify growth. However, the degree of dormancy depended on the number of photoperiods which were shorter than a critical threshold. The number of long days required for breaking dormancy in plants which had become dormant under the influence of short days, increased as the duration of short-day treatment was increased. Hence, the dormancy promoting effect of short days accumulated in the plant, emphasizing that development of dormancy was a phasic process.

Many buds considered to be dormant exhibit some growth. Perry and Simons (1967), for example, reported some growth of bud scales and leaves of several species of woody angiosperms during each month of the winter in Raleigh, North Carolina. Externally, the sequential phases leading to development of dormancy are characterized by slowing down and finally ending of internode expansion. Internally, however, the onset of dormancy is characterized by accelerated meristematic activity. Finally a group of primordia are developed on a short axis in the dormant bud. After true dormancy is attained these primordia cannot grow even if placed in a controlled environment normally adequate for growth. In the development toward the persistent, deep-seated dormant state the bud tissues undergo biochemical changes which render them cold hardy.

Considerable evidence is available of increasing cell division and decreasing cell enlargement during phasic development of bud dormancy. In *Abies concolor*, for example, as shoot expansion ceased in late summer, needle primordia continued to form until late September (Parke, 1959). When rapid growth of the shoot apex of *Pinus lambertiana* ceased at the end of the summer a number of cataphylls were produced which would be the terminal bud scales of the following year's bud (Sacher, 1954). In England Frampton (1960) found considerable winter activity in apical meristems of *Larix decidua*. Changes occurred in the size and shape of the apex, which were associated with early stages in initiation of bud scales for the next winter's bud. At the height of bud dormancy meristematic activity is considerably reduced over that of early phases of dormancy development. In California *Araucaria* buds showed no period of complete dormancy. Mitotic figures were found in apical meristems during each month of the year, but from November to March cell elongation and mitotic activity were greatly reduced over that in other months (Griffith, 1952). Sterling (1945) found only a few mitoses in

dormant buds of *Sequoia sempervirens* collected in the San Francisco Bay area in December and January.

Some data show that reproductive buds continue development during the winter. For example, ovulate cones of *Pinus ponderosa* continued to grow at a low rate through the winter and early spring in Placerville, California (Gifford and Mirov, 1960). Mergen and Koerting (1957) found the ovulate strobilus of *Pinus elliottii* in Florida to grow through the winter. In southern Canada growth during the winter of the megasporangiate cone primordium of *Pinus resinosa* was described by Duff and Nolan (1958). In October and November the cone in the bud had little differentiated tissues and its surface was smooth. By January, however, the cone increased slightly in size and its body was covered with small, protruding early primordia of cone scales.

ENVIRONMENTAL CONTROL OF BUD DORMANCY

Dormancy can be induced in most plants by altering their environment, especially by changing temperature, photoperiod, light quality, mineral availability, or water supply. However, the specific environmental factors which impede growth and accelerate dormancy in nature vary for different species. These variations often reflect differences among species in adaptations to climates in which the unfavorable season represents different environmental combinations. Some species may become adapted to survive in cold winters; others to hot, dry summers; and still others to both cold winters and hot, dry summers. Because of repeated crossings cultivated varieties do not adapt as well as indigenous plants to different environmental conditions (Vegis, 1964).

Dormancy can be readily induced in a wide variety of woody plants by low temperatures or short days. In fact, the use of short days is probably the most common experimental tool for inducing dormancy. It should not be assumed, however, that cold or short days are the primary environmental factors causing dormancy in all species. Many woody plants cease growing long before seasonal temperatures are sufficiently low to stop growth. Dormancy in many species is induced when days are too long to promote it. Thus, various combinations of unfavorable environments appear to alter the internal physiological conditions which induce dormancy.

Chilling

In nature bud dormancy is most commonly broken by the low temperatures of winter or seasonal spells of cold weather. Complete removal of dormancy requires exposure of buds to a critical number of hours of a low threshold temperature. That buds can accumulate the dormancy breaking effects of chilling is shown by greater expansion of buds as the duration of chilling is

increased (Darrow, 1942). Freezing temperatures are not necessary for breaking dormancy but they remove dormancy sooner than low temperatures above freezing (Weinberger, 1950). Temperatures much below freezing are not required and they often cause serious injury to bud tissues. Dormancy may also be broken by alternating warm and cold periods, but continuous chilling usually eliminates the dormant state faster. Release from dormancy by exposure to cold is not followed by shoot expansion until the temperature is substantially increased.

The length of exposure to cold necessary for removal of bud dormancy varies greatly among species, varieties, and even among different buds on the same tree. Eggert (1951) reported the order of breaking dormancy among hardy fruit plants to be as follows: red raspberry, black raspberry, blackberry, prune, peach, currant, sweet cherry, pear, sour cherry, apple, grape, and blueberry. He emphasized that this order might well have been changed if different varieties had been evaluated. According to Samish (1954), the chilling requirement for breaking bud dormancy of peach may vary from 200 to 1150 hours below 45°F, depending on variety. However, it is very difficult to define specific chilling requirements for any variety because these vary greatly in different locations. When seedlings of *Acer rubrum* from different geographic origins were brought to Gainesville, Florida and subjected to different cold treatments, both racial and local variations in chilling requirements were shown. Plants from very cold parts of the range required considerable chilling to break dormancy, whereas those from warm parts of the range required little or no chilling. The responses to chilling were correlated with the frost-free seasons which prevailed in the native habitats of the experimental plants (Perry and Wang, 1960). Eggert (1951) emphasized variations in chilling requirements among different buds on the same tree when he found that flower buds required less chilling than leaf buds, and terminal buds less than lateral buds.

The chilling requirement for breaking dormancy prevents successful cultivation of many woody species in warm areas (Kramer and Kozlowski, 1960). Horticulturists have been especially concerned about the failure of orchard trees to break dormancy and fruit properly after mild winters. For example, following the mild winter of 1948–49 in South Carolina, the blossoms of peach trees appeared later than normally and they were small. Leaf buds also were late and opened after flowers emerged. Some terminal buds remained dormant and others died. Fruits of some varieties abscised probably because the leaves emerged too late to support the rapidly growing fruits. The number of fruit buds formed for the following year's crop also was much lower than normal (Higdon, 1950). Samish (1954) summarized in considerable detail the effects of mild winters on growth of fruit trees in the Temperate Zone. When dormancy is insufficiently broken, the buds may

start to open but the shoot later dies. Leaf deformation, multiple pistils, failure of the style to develop, and poor pollen development also are likely results. With inadequate chilling the abscission of buds or parts within them often occurs. In pome fruits the primordial flowers or part of the cluster may abscise so a mixed bud produces a small flower cluster or only a leafy spur. In stone fruits the entire bud often abscises. Because of these difficulties plant breeders are attempting to modify the chilling requirements of important varieties of trees by introducing genes with low chilling requirements from tropical varieties (Perry and Wang, 1960).

Photoperiod

As pointed out earlier, short days can cause many woody species to stop shoot expansion and begin a phasic development to a dormant state, whereas long days delay or prevent dormancy. The cessation of vegetative growth by short days can be brought about in different ways. For example, in *Populus*, *Cornus*, and *Platanus* grown under short days, the leaf primordia developed into scales instead of leaves, and in *Rhus* and *Syringa* the terminal meristem died and abscised (Nitsch, 1957a). Generally the induction of dormancy by short days leads to formation of a terminal resting bud in monopodial species and to abscission of the shoot apex in sympodial ones. Some species, such as *Liriodendron tulipifera*, *Liquidambar styraciflua*, *Fagus sylvatica*, *Betula pubescens*, *Larix europaea*, and *Pinus* spp, which are induced to a dormant state under short days, will resume growth if placed under long day conditions. That these are true photoperiodic responses is shown by shoot expansion of even leafless dormant trees of these species under long days, whereas they are maintained in a dormant state under short days. Wareing (1953) has shown that photoperiodic sensitivity resides in the very young leaf primordia of resting buds of these species.

Species vary widely in their photoperiodic sensitivity. *Liriodendron tulipifera* and *Robinia pseudoacacia* can be induced to grow continuously for at least 13 months under long days. In other species growth stops more rapidly even under continuous illumination. For example, *Pinus sylvestris*, *Acer pseudoplatanus*, and *Phellodendron amurense*, entered dormancy after a certain period even when illuminated continuously (Wareing, 1956).

Shoots of seedlings of species which normally tend to grow in flushes, such as some oaks, respond to long days by elongating in several recurrent flushes rather than by growing continuously. Some species of pines, which normally exhibit a single growth flush, often respond to long days or continuous illumination by expanding in a series of flushes. Still other species such as *Sorbus aucuparia*, *Syringa vulgaris*, and some species of *Fraxinus* and *Rosa* appear to have little or no photoperiodic sensitivity (Wareing, 1956).

The following useful classification of variations in photoperiodic sensitivity is that of Nitsch (1957b) who, following Chouard, distinguished between species in which long days caused continuous growth and those in which long days could not prevent the onset of dormancy:

	Class
I. Long days prevent onset of dormancy	
1. Short days cause dormancy	
a. Long days cause continuous growth	A <i>Weigela</i>
b. Long days cause intermittent growth	B <i>Quercus</i>
2. Short days do not cause dormancy	C <i>Juniperus</i>
II. Long days do not prevent onset of dormancy	D <i>Syringa</i>

As emphasized by Kramer and Kozlowski (1960), various degrees of intergradation exist among the various classes set up by Nitsch. Rigorous classification for species may not hold because the photoperiodic response of a given species often depends on the geographic origin of the seeds or other propagating material (Chapter 7).

Breaking of Dormancy

Species vary greatly in their capacity to break bud dormancy under continuous illumination. For example, bud dormancy of *Fagus* seedlings can be broken at any time by continuous light and this can be accomplished whether the plants have leaves or not. In other species dormancy can be broken by photoperiod only if the buds are in a relatively mild state of dormancy. *Pinus sylvestris* buds in a state of quiescence or summer dormancy, which normally would not have expanded until the following spring, opened prematurely after exposure to continuous illumination. However, when buds of species were in a state of deep winter dormancy, continuous illumination was ineffective in inducing shoot growth (Wareing, 1956). Similarly, long-day treatments often induce shoot growth in oaks as long as buds are in a mild state of summer dormancy but not when buds are in a truly dormant winter condition.

In some species long days generally are ineffective in breaking dormancy. For example, when dormancy was induced by short days in buds of *Acer pseudoplatanus* and *Robinia pseudoacacia*, they subsequently could not be induced to grow even after eight to ten weeks of continuous light (Wareing, 1954).

Interactions of Chilling and Photoperiod

There undoubtedly are various interactions of chilling and photoperiod on breaking of bud dormancy. Buds of *Fagus sylvatica* did not respond to

chilling and their photoperiodic requirements were not altered after prolonged exposure to low temperatures (Wareing, 1953). In contrast, *Betula pubescens* buds readily responded to cold and, after chilling, broke dormancy readily even under short days (Wareing, 1956). In plants such as *Robinia pseudoacacia*, *Acer pseudoplatanus*, and *Populus* which do not break dormancy in response to photoperiod when unchilled, bud break often occurs faster under long than under short days (Wareing, 1956).

Site of Photoperiodic Perception

The locus of photoperiodic sensitivity varies among species and may be in very young leaf primordia, in resting buds, in partially expanded leaves, or in mature leaves.

In *Fagus sylvatica* the photoperiodic perception arises in the buds. When dormant buds were covered and twigs exposed to continuous illumination dormancy was not broken. In contrast, continuous illumination of buds promoted their growth, even in the absence of bud scales, emphasizing a direct effect of light on the primordial tissue. Approximately 0.7% of the incident light was transmitted through the bud scales to leaf primordia in *Fagus sylvatica* and that was adequate for a photoperiodic response (Wareing, 1953).

Wareing (1954) found that originally dormant *Betula pubescens* buds receiving short days remained dormant, whereas buds exposed to continuous light resumed growing in both leafy and defoliated plants. When the leaves alone were exposed to continuous illumination while the buds were maintained in darkness, no growth occurred. Hence, only direct exposure of the buds to long days broke dormancy, whether leaves were present or absent (Table 8.15). However, if the leaves were exposed to short days, normal bud expansion did not take place, emphasizing that under short days the leaves had an inhibitory effect on bud development.

In actively growing seedlings of *Betula pubescens*, growth occurred when the shoot apical regime was exposed to long days and the leaves to short days. Thus, a growing apex could overcome the inhibitory effects of leaves under short days. When an active apex was exposed to short days, dormancy occurred even when the leaves were continuously illuminated. These observations indicated that an actively growing bud was directly controlled by the day length conditions to which it was exposed.

Whereas the shoot apex of *Betula pubescens* showed extreme photoperiodic perception, that of *Acer pseudoplatanus* and *Robinia pseudoacacia* did not. In these species the primary site of photoperiodic perception was in the mature leaves. This was shown by experiments in which dormancy was rapidly induced when the leaves were exposed to short days, even when the apex received long day treatment. When the apex was exposed to short days and the leaves to long days dormancy was not induced although internode

TABLE 8.15

LOCUS OF PHOTOPERIODIC PERCEPTION FOR BUD EXPANSION IN DORMANT
Betula pubescens SEEDLINGS^a

Treatment		
Buds	Leaves	Results
Long day ^b Continuous	Long day	Buds resumed growth
—	Long day	Buds remained dormant
Short day ^c	Long day	Buds remained dormant
Long day	—	Buds resumed growth
Short day	Short day	Buds remained dormant
Short day	—	Buds remained dormant

^a From Wareing (1954).

^b Continuous illumination.

^c Eight to nine hours of daylight or illumination of 10,000 lux from fluorescent tubes.

extension of *Acer pseudoplatanus* was reduced. The primary role of mature leaves in photoperiodic induction of dormancy in *Acer* and *Robinia* was somewhat comparable to the control of flowering by the photoperiod to which mature leaves of herbaceous plants are exposed.

Durkin (1965) showed that the subtending leaf exerted strong control over dormancy of the axillary bud in Better Times rose. When the uppermost axillary bud on shoots failed to grow, removal of the subtending leaf caused buds to grow in about 95% of the shoots, whereas only 26% of the buds on control shoots grew. The amount of leaf tissue necessary to control bud growth was small.

INTERNAL CONTROL OF BUD DORMANCY

The influence of environmental fluctuations on dormancy is mediated through internal controls. As H. Smith and Kefford (1964) stated, an overall theory of the mechanism of internal regulation of dormancy should account for three primary phases of bud development. These include (1) phasic development of dormancy culminating in a truly dormant state, (2) breaking of dormancy leading to a nondormant state, and (3) growth initiation in the spring leading to a steady-state development. Such a scheme also encompasses various transitional phases among the three primary ones (Fig. 8.22).

For many years the regulation of bud dormancy was assumed to be a single process rather than a series of transitional ones. Many early theories proposed that the overall process was limited by a single endogenous chemical regulator.

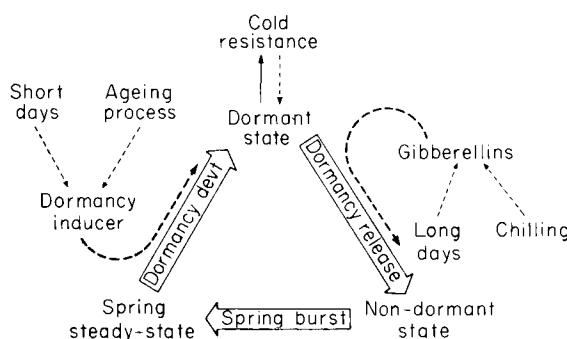


FIG. 8.22. Model of the relationship of dormancy phases of bud development to the annual cycle of Temperate Zone trees. The three steady states are in heavy lettering and the transitional phases in enclosed arrows. Mediation of environmental and internal factors is shown by broken arrows. [From H. Smith and Kefford (1964).]

Much emphasis was placed on regulation of development of lateral buds on shoots by auxin levels alone. Kozlowski (1964a) reviewed the literature on these early theories. It now appears that the mechanism of control of bud dormancy is considerably more complicated than previously supposed.

Over the years primary attention was given to 2 main theories of control of bud dormancy: (1) that bud scales interfere with oxygen uptake of internal tissues causing them to enter a dormant state after prolonged anaerobiosis, and (2) that bud dormancy is controlled by availability and balance between endogenous hormonal growth inhibitors and promoters. Whereas interference with oxygen uptake might sometimes be important in seed dormancy, the evidence now available suggests it is unlikely to play a major role in bud dormancy. As Eagles and Wareing (1964) emphasized, gaseous exchange cannot be blocked until buds are formed. Morphological changes involved in formation of resting buds occur before gaseous exchange is restricted. The buds induced in *Betula* by short days often are lax and not completely enclosed by scales. Furthermore, removal of scales from fully dormant buds usually does not induce growth. For these reasons primary attention will be given to the role of growth regulators in control of dormancy.

Hemberg (1949) was among the first to evaluate the mechanism of bud dormancy in terms of specific endogenous growth inhibitors. He found growth inhibitors in terminal buds of *Fraxinus* and noted that they decreased in amount as buds were released from dormancy. Subsequently growth inhibitors were found in buds of a variety of species of woody plants, often together with growth promoting substances (Blommaert, 1955; Hendershott and Bailey, 1955; Nitsch, 1957b; Phillips and Wareing, 1958a; Ogasawara, 1961a; Y. Kondo and Ogasawara, 1962).

Certain difficulties were recognized in early inhibitor theories which ascribed to one chemical all the changes which must be accounted for in the overall development and release of dormancy. Dormancy tests often were unsuitable for demonstration of inhibitors. The plant response checked often was growth of tissues other than those from which the inhibitors were extracted. H. Smith and Kefford (1964) criticized early inhibitor theories because bioassays measured only cell enlargement and did not account for other phases of dormancy development such as alteration of meristematic activity. Early theories also were based on correlations of inhibitor levels with dormancy stages. As Wareing (1961) cautioned, some of the early data could be interpreted to show that dormancy was induced by specific inhibitors or that the inhibitor levels might even be the result of changes in dormancy. Wareing (1961) emphasized that inhibitors occurred widely even in actively growing shoot apices. In peach flower buds inhibitor levels were reported to decrease as buds were released from dormancy (Hendershott and Bailey, 1955; Blommaert, 1955; Hendershott and Walker, 1959a,b). However, Dennis and Edgerton (1961) showed that the correlation between dormancy release and decrease in inhibitors may have been an artifact produced by the method of extraction. The inhibitor, which was localized in the scale leaves, did not change quantitatively with release of dormancy. An apparent decrease had been reported because entire buds were extracted and the inhibitor content was expressed on a whole bud basis.

THEORIES OF CONTROL OF BUD DORMANCY

Considerable evidence now shows that regulation of bud dormancy is the result of a balance and interaction among endogenous growth promoters and inhibitors. At least three major and several minor phases of bud development are recognized, with each controlled by growth regulator patterns in the buds. Inhibitors, auxins, gibberellins, and cytokinins appear to be variously involved. A key role of inhibitors (e.g., abscisic acid) in promoting development of dormancy is indicated, whereas growth promoters, especially gibberellinlike substances, appear to play a major role in dormancy release. Interactions among various growth promoters and inhibitors probably also are important in regulating the overall dormancy phenomenon.

Regulation of Development of Dormancy

An impressive body of evidence has accumulated which stresses the importance of endogenous inhibitors on the development of bud dormancy and a less important role in the breaking of dormancy. The primary evidence indicating that development of dormancy is largely regulated by endogenous inhibitors may be summarized as follows: (1) under short-day conditions the leaves of many woody plants inhibit growth of the shoot tip, (2) greater

amounts of inhibitors are found in leaves and buds of many woody plants under short-day than under long-day conditions, and (3) when inhibitors are extracted from leaves of a dormant woody plant and reapplied to plants of the same species, which were not dormant prior to the application of inhibitor, shoot elongation stops and sequential development toward a dormant state is initiated (Wareing, 1965b).

Phillips and Wareing (1958a) investigated seasonal changes in inhibitors and demonstrated a strong correlation between amounts of inhibitors in buds and leaves of *Acer pseudoplatanus* and the state of dormancy. The greatest amounts of inhibitors were found during the time of year when the tissues were most dormant and least amounts when the apex was actively growing. The increase in the amount of inhibitor in leaves up to August 20 was accompanied by an increase of inhibitors in the apex. The amount of inhibitors did not increase after August 20 and it decreased only after leafless plants were exposed to winter conditions. These observations suggested that inhibitors were produced in the leaves and translocated to the apex.

Eagles and Wareing (1963, 1964) induced dormancy in *Betula verrucosa* by application of an inhibitor which had been extracted from dormant buds of the same species. Plants treated with the inhibitor stopped growing within 12 days whereas control plants grew for the duration of the experiment. In apical buds of treated plants the stipular scales were closed around the apex and expanding leaves were absent. Hence, the bud resembled that of dormant plants maintained under short days. In contrast, buds of control plants had reflexed stipules and young, expanding leaves. Application of gibberellin to inhibitor-arrested buds caused them to grow again, emphasizing that the failure of buds to grow had not been caused by toxicity.

Phillips and Wareing (1958b) found that the concentration of inhibitors in leaves of *Acer pseudoplatanus* was always less than a fifth as much as in the apical tissues. Kawase (1961) also found that inhibitors increased in the growing points of *Betula pubescens* seedlings with an increase in the duration of short days, and they decreased in proportion to the duration of long days to which they were exposed after they had become dormant (Fig. 8.23). Growth ceased when inhibitors reached a critical threshold level. Inhibitors were found throughout the seedlings but were most concentrated in growing points. For example, when inhibitor activity was expressed as total inhibitory activity per 100 mg dry weight, the following data were obtained:

Plant part	Total inhibitory activity (%)
Growing points	1258
Upper leaves	243
Stems	119
Roots	80

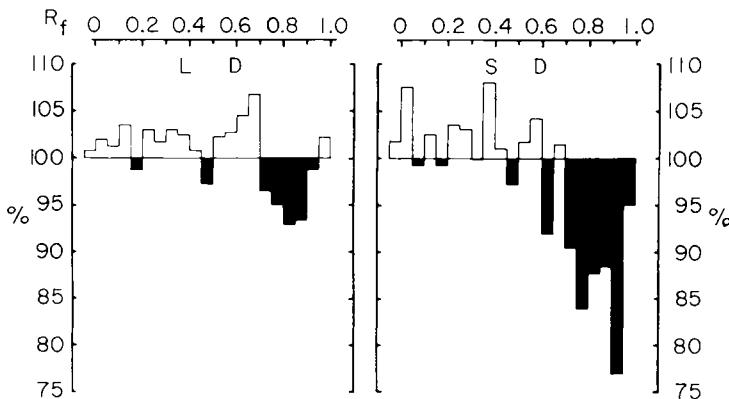


FIG. 8.23. Histograms indicating the growth-promoting and growth-inhibiting activities in extracts of *Betula pubescens* which had grown under long days (LD) and short days (SD). The ordinate values represent elongation as percent of controls. Abscissa values represent R_f values in 80% isopropanol. [From Kawase (1961).]

These observations were consistent with those of Wareing (1964a) who concluded that exposure of apical buds of *Betula pubescens* dominated in inducing dormancy. When mature leaves were removed and apical buds exposed to long days dormancy was broken.

Other evidence for importance of inhibitors in promoting dormancy comes from plant responses following defoliation (Nitsch, 1957a). In many species removal of leaves stimulates buds which have ceased growing to grow again even under short days, prevents abscission of terminal meristems, or causes leaf primordia to become foliage leaves rather than cataphylls. *Syringa* leaves, which contain strong inhibitors, often suppress growth so much that the terminal meristem is killed.

The term "dormin" was given to the specific growth inhibitor which was synthesized under short days and induced dormancy (Eagles and Wareing, 1963). Subsequently Cornforth *et al.* (1965) isolated a dormin from *Acer pseudoplatanus* and established its identity with abscisic acid which had been isolated from cotton by Addicott *et al.* (1964).

Regulation of Release from Dormancy

Both growth promoters and inhibitors are present during various transitional phases of dormancy. Whereas inhibitors appear to play a primary role in promoting dormancy the breaking of dormancy apparently is associated largely with activity of growth promoters, especially gibberellinlike substances. Possibly other growth promoters are involved, and balances and interactions among them play a role in dormancy release. The observations that

chilling of dormant seeds increases gibberellin activity of extracts, and that long days increase levels of growth promoters in buds, are consistent with these conclusions (Frankland and Wareing, 1962; Nitsch, 1957b). Inhibitors do not always decrease with release from dormancy.

Eagles and Wareing (1963) postulated that dormancy release involved activity of endogenous gibberellins which increased in response to chilling. They envisioned an alteration of existing patterns of regulators at the apex as a result of gibberellin accumulation. Developmental changes in meristems occur following application of gibberellin (Robbins, 1960). Evidence also is available that other growth regulators have a role in influencing break of dormancy. For example, Domanski and Kozlowski (1968) studied levels of kinetinlike activity in dormant buds of *Betula papyrifera* and *Populus balsamifera* as well as in buds at various stages of release from dormancy. The amount of kinetinlike activity was determined by observing effects of bud extracts on senescence (chlorophyll retention) of suitable test plants. Kinetinlike activity was absent in dormant buds of both *Betula* and *Populus* and was present in various amounts after dormancy was broken. Kinetinlike activity was greater in nondormant buds of *Populus* than in those of *Betula*. However, the trend of variation in activity with time after breaking of bud dormancy was similar in both species. After bud dormancy was broken, kinetinlike activity in both species increased progressively until shortly after buds opened, and it decreased thereafter.

Release from bud dormancy may be promoted by applying cytokinins. Weaver (1963) released buds of cuttings of *Vitis vinifera* from dormancy with 6-benzyladenine. In one experiment, buds on 53% of the cuttings treated with benzyladenine opened before any buds on controls opened. Pieniazek (1964) broke bud dormancy in 8-month-old apple seedlings with single applications of kinetin at 100 μ g/l. Treated buds were stimulated to grow within 2 weeks. Various stages of dormancy were readily overcome and dormant seedlings treated in October, November, December, or January responded to treatment. Breaking of dormancy of unchilled embryos of woody plants by kinetin also suggests the possible role of cytokinins in the overall dormancy-break mechanism (Frankland, 1961).

Evidence of interactions of abscisic acid and growth promoting regulators also is available. Studies of partially purified abscisic acid from *Acer pseudoplatanus* indicated it did not interact competitively with IAA in coleoptile tests. This was consistent with the observation that IAA did not overcome bud dormancy. On the other hand, there is evidence that abscisic acid antagonizes the action of endogenous gibberellins in plants. Thus gibberellin will overcome the dormancy of buds induced by short days in several woody species. Furthermore, *Betula* seedlings which had been induced to form resting buds by externally applied inhibitors resumed growth if

gibberellic acid then was applied. If gibberellic acid was applied at the same time as the inhibitor, active growth was continued, emphasizing the nullifying of the inhibitor effect by gibberellic acid (Wareing, 1965b). De Maggio and Freeberg (1969) showed that abscisic acid not only inhibited gibberellin-stimulated bud growth in *Acer platanoides* but also suppressed the photoperiodically stimulated growth of apices.

An *Avena* coleoptile expansion test showed that coleoptiles did not respond to gibberellic acid in the absence of the inhibitor, but in its presence they required gibberellic acid. Another test showed that the inhibitor checked cell division. Thus, gibberellic acid appeared to counteract the effect of the inhibitor. Conversely the inhibitor countered the effect of the gibberellic acid. These experiments suggested that the inhibitor may function as a gibberellin antagonist in the plant (T. H. Thomas *et al.*, 1965).

Internal Water Deficits

Shoot growth is suppressed by internal water deficits in a complex manner, with the degree of growth inhibition varying greatly among tree species, severity and time of drought, shoot location on a given tree, and with different aspects of shoot growth such as internode elongation and leaf expansion (Kozlowski, 1955, 1958, 1964a, 1968b, 1970). Internal water stress influences shoot growth both by its effects on cell expansion of preformed shoot primordia and on development of new primordia. Therefore, as mentioned earlier, internal water deficits in each of two successive seasons variously modify growth of shoots. Some aspects of shoot growth are sensitive to relatively low soil moisture tension (Sands and Rutter, 1959; Jarvis and Jarvis, 1963).

The effects of water deficits on shoot growth appear to be exerted both indirectly through influences on cell metabolism and directly via control of cell expansion by turgor (Zahner, 1968; Kozlowski, 1968a,b). As turgor of guard cells controls stomatal opening, it also causes changes in transpiration and photosynthesis, which eventually are reflected in growth changes. Water deficits can influence new tissue development by inhibiting hydrolysis and translocation of stored carbohydrates (Lotan and Zahner, 1963). Internal water stress can also depress RNA levels and consequently retard growth and hasten leaf senescence and abscission.

Direct effects of low turgor have been shown to decrease cell size and thereby reduce leaf area in both herbaceous and woody plants. Wadleigh and Gauch (1948), for example, observed that turgor pressure and expansion of cotton leaves were closely related, with leaf elongation ceasing at approximately zero turgor pressure. Using relatively nonpermeating mannitol and

permeating NaCl, Ordin (1958, 1960) created water deficits of similar magnitudes, but different internal values of osmotic pressure and turgor pressure, in cells of *Avena coleoptiles*. Cell expansion was inhibited more by mannitol than by NaCl, emphasizing that turgor had an important direct role in cell enlargement. Reduced turgor inhibited incorporation of ^{14}C in cell walls, whereas an increase in osmotic pressure in the cells did not. Similar results were obtained by Plaut and Ordin (1961) for *Helianthus annuus* and *Prunus amygdalus* leaves.

Although it was emphasized earlier that duration and amount of internode elongation of species with shoots wholly preformed in the winter bud often are unaffected by severe late-summer droughts which occur after annual stem elongation has ceased, there is considerable evidence that such droughts suppress leaf expansion in the same species. As Zahner (1968) emphasized, internal water deficits during the period of shoot expansion cannot influence the predetermined number of leaves which mature, but they often result in small leaves which are spaced closer together than normally along the shoot. Internode expansion is affected less than leaf elongation by some droughts because the period of internode expansion may be much shorter than that of leaf expansion. Indeed, considerable evidence is available that when protracted droughts occur during the time when both internode elongation and leaf expansion are taking place, both aspects of shoot growth are inhibited, but internode elongation often is affected less than leaf expansion. For example, Sands and Rutter (1959) found that needle elongation of *Pinus resinosa* seedlings was decreased by soil moisture tensions as low as 0.5 atm (Table 8.16). Drought did not reduce the duration of leaf growth,

TABLE 8.16

EFFECT OF SOIL MOISTURE TENSION ON NEEDLE ELONGATION OF *Pinus sylvestris*^a

Duration of treatment	Mean needle length (cm) at			
	0.1	0.5	1.5	5.0
June 7–Sept 4	—	5.85	4.80	3.75
April 14–Sept 4	5.05	4.25	4.20	3.40
June 1–Sept 4	4.95	4.35	4.25	3.75
June 1–July 24	5.00	4.50	4.80	4.00
Mean	5.00	4.35	4.40	3.70

^a From Sands and Rutter (1959)

and needles under all treatments continued to expand until the beginning of September. Apical shoot length also was decreased. The final mean length of the apical shoot in plants exposed to varying degrees of water deficit from April 14 on was as follows:

Maximum soil moisture tension (atm)	0.1	0.5	1.5	> 5.0
Apical shoot length (cm)	17.6	16.7	13.5	13.5

Kaufmann (1968) studied growth of buds and needles of *Pinus taeda* and *P. strobus* seedlings during a series of soil drying cycles. As mean soil water potential decreased, the growth of buds and needles decreased (Fig. 8.24). Seedlings were subjected to three watering regimes: daily watering for 21 days, three 5-day drying cycles, and three 7-day drying cycles. Figure 8.25 shows the mean daily growth of needles and percentage of total growth of each drying cycle. Growth decreased as the severity of the watering regimes increased. Needle growth of plants watered daily was reduced during the third measuring period. As these needles grew rapidly the reduction in growth reflected needle maturation. Under the most severe water deficits (7-day drying cycles) the growth of needles was uniform for each of the three periods.

Lister *et al.* (1967) maintained potted *Pinus strobus* seedlings under moisture stress for much of the growing season. Water deficit caused only a slight reduction of internode elongation and a proportionally greater decrease in needle length. Both the rate and duration of needle expansion were decreased

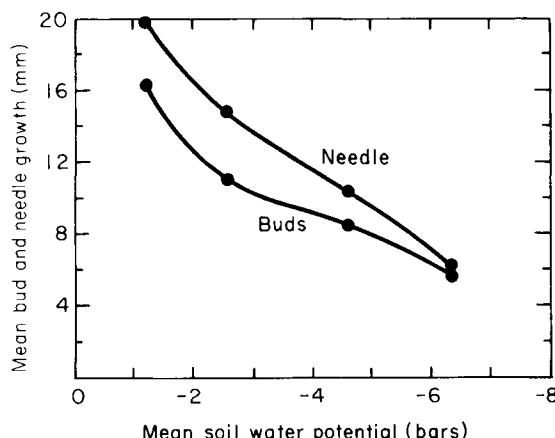


FIG. 8.24. Effect of soil water potential on needle and bud extension of *Pinus taeda*. [From Kaufmann (1968).]

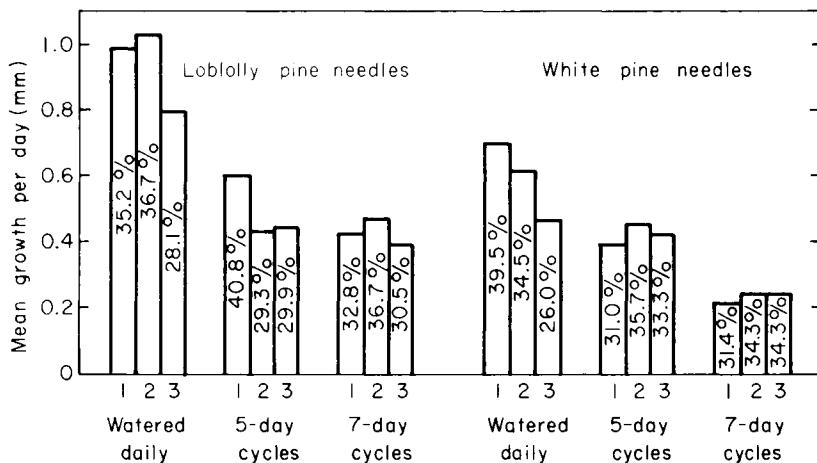


FIG. 8.25. Mean daily needle growth of Loblolly pine (*Pinus taeda*) and White pine (*P. strobus*) seedlings during each of three drying cycles in three watering regimes. [From Kaufmann (1968).]

by prolonged water stress. It should be remembered that the duration of needle elongation in *Pinus strobus* is about twice as great as that of internode expansion.

Leaf thickness and intervacular intervals often are affected by water deficits. Turrell and Turrell (1943) compared leaves of several species of herbaceous and woody plants developed in Iowa during the unusually hot, dry summer of 1934 and the normal summer of 1935. Leaves of most species generally were thinner and the intervacular intervals smaller in the drought year than in the normal one.

In heterophyllous and recurrently flushing species, internal water stress during the growing season often inhibits both internode elongation and leaf expansion (Kozlowski, 1968b). For example, Stransky and Wilson (1964) showed that shoot elongation of seedlings of the recurrently flushing species, *Pinus taeda* and *P. echinata* was decreased when moisture tension in drying soil reached 2.5 atm. When soil moisture tension reached 3.5 atm, all seedlings stopped growing (Fig. 8.26). By the time soil moisture tension increased to 15 atm all the experimental seedlings died. It should be remembered that in recurrently flushing species variously located shoots on the stem exhibit different numbers of seasonal growth flushes (see Chapter 7). Therefore, shoots on the lower stem, which flush only once or not at all during a season, may not be affected by late-season droughts, whereas those in the upper stem, which flush several times, will be responsive to such late-season water deficits.

As mentioned, internal water deficits often affect shoot growth by limiting

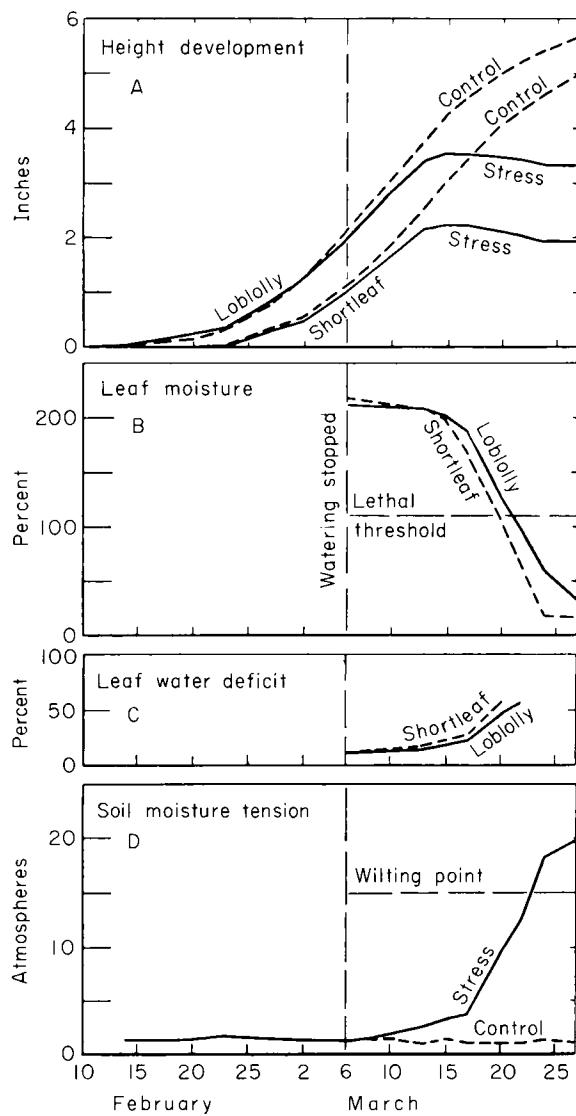


FIG. 8.26. Effect of drought on height growth, leaf water deficit, and soil water tension in Loblolly pine (*Pinus taeda*) and Shortleaf pine (*P. echinata*) trees. [From Stransky and Wilson (1964).]

development of leaf primordia which form in the developing bud. Hence, in recurrently flushing species a drought in midsummer often does not have a marked effect on the first seasonal growth flush which preceded the drought, but it may decrease the number of primordia which are forming in the new bud and will expand in a late-season flush of shoot growth. Hence, the second seasonal flush of shoot expansion may be greatly limited by the reduced number of primordia, and if the drought continues into the period of the second growth flush, the expansion of these primordia may also be inhibited.

Differences among species in height growth response to water deficits are shown by comparing the studies of Zahner (1962) on *Pinus taeda* and Lotan and Zahner (1963) and Clements (1970) on *Pinus resinosa*. Whereas height growth of *Pinus taeda*, which makes several growth flushes in the same growing season and has an unusually long growing season, was markedly affected by late-summer weather, that of *Pinus resinosa*, which does not flush recurrently and completes height growth early, was influenced less. Even when subjected to very severe extremes of soil moisture stress during the growing season, all *Pinus resinosa* trees set buds at approximately the same time and ceased elongating within a week of each other. Lotan and Zahner (1963) were indeed able to show quantitative differences in current height growth of *Pinus resinosa* by exposing trees to extremely high or low soil moisture stress early in the growing season. Under unusually severe drought the elongation of individual cells already present in the bud and of those being currently formed in the apical meristem probably was inhibited. Nevertheless, in many areas the degree of early-season moisture stress in forests is considerably lower than was experimentally imposed on trees by Lotan and Zahner (1963). The work of Clements (1970) emphasized the marked effect of internal water deficits during the period of bud formation on subsequent shoot growth. Irrigation of 5-year-old *Pinus resinosa* trees in late summer caused large buds to form. Next spring these produced large shoots with many needle fascicles. Fascicles on long shoots were widely spaced. Late-summer droughts resulted in small buds which produced small shoots with few needle fascicles during the subsequent year. In contrast to the marked influence of late-summer irrigation on shoot growth, spring irrigation did not appreciably influence shoot growth.

Internal Control of Within-Tree Variations in Shoot Growth

Internal correlation of growth of shoots in different parts of a tree appears to be complicated and involve interacting hormonal and nutritional aspects. It is widely accepted that most of the growth factors which control shoot growth originate elsewhere than in the cells in which they exert their major

influence. Such growth control of organs and tissues from distant sites is a general feature of growth control in trees.

Theories of the mechanism of correlative inhibition of shoot growth within trees should account for control of several growth phases such as bud initiation, determination of structures produced by bud meristems, and expansion of buds into shoots. It is difficult to postulate a common theory of shoot growth control because variations in amounts of growth in different parts of trees are traceable to marked differences in morphogenic development of shoots in different species. Furthermore, there appear to be wide variations among species in the site of control of growth of lateral shoots. Growth of certain shoots may be inhibited by heavy fruiting (see Volume II, Chapter 8). Apical dominance of species with shoots fully preformed in the dormant bud often reflects variations in bud contents and in duration of shoot expansion. Terminal leaders often expand for a longer time than do leading shoots of lateral branches, and there often is a corresponding progressive decrease in duration of shoot growth from the top of the tree downward. For example, in *Pinus strobus* and *P. resinosa* shoot elongation began almost simultaneously on all branches of the tree. The primary axis grew more than secondary or tertiary axes. Secondary axes showed shorter total growth in length, shorter duration of growth, and a lower growth rate from the uppermost whorl downward in the tree (Friesner, 1943; Friesner and Jones, 1952). In *Picea glauca* the terminal leader also maintained a high rate of elongation for a longer time than did shoots lower down on the stem. Whereas annual terminal growth in *Thuja occidentalis* reached a maximum during the last half of July, the growth of lateral shoots was greatest early in the growing season and declined steadily after midJune (Silver, 1956).

The differences in duration of growth of different shoots often are correlated with variations in bud size and in numbers of leaves contained in the dormant bud. Both the amount of shoot growth and the size of buds of pines decreased from the apex toward the base and from the top to the base of individual branches (Szymanski and Szczerbinski, 1955). Burley (1966a) also demonstrated high correlation between bud size and shoot growth of *Picea sitchensis* seed sources. The amount of annual height growth of seedlings was greater as terminal buds increased in size. Bud size also reflected the number of enclosed needle primordia, and Burley (1966a) concluded that these determined ultimate shoot length. The number of lateral branches also was greater with increasing seedling height. Seedlings of comparable height often had similar bud dimensions, but seedlings of different provenances usually had different average bud dimensions associated with provenance differences in height growth.

The amount of shoot growth in heterophyllous species may also be correlated with bud size and shoot content. Size of buds was a reasonably

TABLE 8.17

RELATION BETWEEN SIZE OF BUD AND NUMBER OF LEAF PRIMORDIA IN STARK APPLE TREES^a

Sampling date	Bud size	Mean number of primordia
April 7, 1944	>4 mm	7
	2-4 mm	5.5
	<2 mm	4
June 9, 1944	>4 mm	5.6
	2-4 mm	5.4
	<2 mm	4.8
March 15, 1945	>4 mm	8
	2-4 mm	6
	<2 mm	4.6

^a From Felber (1948).

dependable measure of the number of leaf primordia differentiated in *Malus* buds (Table 8.17). Although large buds tended to produce vigorous shoots with many leaves, the ultimate development of shoots depended on a growth stimulus after the dormant period, in addition to the number of leaf primordia in the bud (Felber, 1948). Bud length of *Populus tremuloides* was closely correlated with the length of the branch that developed from it (Maini, 1966a,b).

Apical dominance in recurrently flushing pines is correlated both with differences in duration of bud expansion and in variable numbers of growth flushes in different parts of the tree. In *Pinus radiata* spring growth of variously located shoots began at about the same time, except for third order shoots and those near the ground, which began to grow later. The cessation of shoot growth occurred later in the upper than in the lower stem (Fielding, 1955). Upper shoots of recurrently flushing pines form and open more buds than do lower shoots during the same year. The number of growth flushes in southern pines of the United States varied from none to one in lower branches to as many as four in upper branches (Boyer, 1970).

The complexity of the apical dominance mechanism is emphasized by evidence that inhibition of shoot growth does not reside in the same tissues in all species. Strong inhibition of growth of lateral shoots may be exerted by terminal buds or, in some cases, by leaves. In guayule, (*Parthenium argentatum*), for example, old leaves had a stronger inhibitory effect than the terminal bud on development of axillary buds. A single adult leaf per branch inhibited new growth of stems (P. F. Smith, 1944). Allary (1958) showed that inhibition of axillary buds might be caused by incompletely developed apical leaves in

Prunus avium, *P. padus*, and *Euonymus europaeus*, fully grown leaves in *Acer platanoides*, *Fraxinus excelsior*, and *Salix caprea*, or a combination of both in *Acer pseudoplatanus*, *Lonicera xylosteum*, and *Cornus sanguinea*.

Usually an inhibitory action is exerted on buds below the apical meristem, but there is ample evidence of correlative inhibition of growth acting both up and down a plant axis (Audus, 1959). Champagnat's defoliation experiments (1955) showed that in *Betula papyrifera* and *Syringa* the leaves inhibited buds higher up on the stem, but in *Sambucus nigra* and *Prunus padus* the inhibitory effect was exerted only on buds lower down.

ROLE OF NUTRITION

Several investigators provided evidence of an important role of nutritional factors in correlative growth inhibition. Gregory and Veale (1957), for example, believed the degree of apical dominance was dependent on nitrogen and carbohydrate supplies. Their view was that under deficiency conditions lateral buds were inhibited. At low nitrogen levels there was not enough nitrogen to maintain activity in more than one meristem. Basal buds might begin activity, but later they competed with more buds below the apex as well as with the apical bud, and growth inhibition consequently followed. At high nitrogen levels all buds tended to remain active and apical dominance was poorly expressed, if at all. Gregory and Veale (1957) visualized auxin as having an indirect role in apical dominance and controlling development of vascular traces to axillary buds. They believed that high auxin content might inhibit formation of provascular strands to axillary buds, thereby impeding translocation of nutrients into them and inhibiting growth.

Wareing and Nasr (1958, 1961) also emphasized importance of nutritional factors in apical dominance. When uppermost lateral shoots of woody plants were trained horizontally and the lower ones vertically, the usual apical dominance relations were reversed. Attributing the reduced growth of leading shoots to large auxin supplies from the laterals would require acropetal auxin transport. Their results suggested an indirect role of auxin in correlative growth inhibition. They found that lateral buds grew at the point nearest the root at which the shoot was turned from the vertical. A mechanism of apical dominance was postulated in which nutrients were diverted to the highest upwardly directed meristem. Booth *et al.* (1962) showed that ^{14}C -sucrose moved into decapitated internodes or mature leaves to which auxin was applied. Kozlowski and Winget (1964) noted that a supply of reserves from the old needles of *Pinus resinosa* was necessary early in the growing season to maintain dominance of the terminal leader over lateral branches. Such data suggested that auxin-directed translocation might redistribute nutrients from storage tissues to young growing tissues and exert a role in correlative inhibition of lateral buds.

Pruning and ^{32}P injection experiments by Moorby and Wareing (1963) suggested that a rapid increase in the number of growing shoots as the branches increased in complexity resulted in competition among them for available nutrients. In intact *Pinus sylvestris* plants more minerals were obtained by leading shoots than by laterals. When distal parts of a branch were removed by pruning, increased growth of the laterals followed. Pruning also was followed by increased availability of minerals to the remaining lateral branches. These experiments emphasized the disadvantages of the laterals in competing for nutrients with leading shoots in intact plants.

ROLE OF GROWTH REGULATORS

The mechanism of inhibition of laterals by terminal meristems has been widely investigated and debated. Although auxins appear to be much involved in apical control of shoot growth there has not been general agreement on whether their role is direct or indirect. Three primary mechanisms of control of apical dominance have received attention. They are: (1) direct auxin inhibition of lateral buds because of their extreme sensitivity to auxin, (2) indirect effects of auxin, and (3) the blocking of transport hypothesis of van Overbeek (1938) which relates lack of activity in lateral buds to impeded nutrient translocation through the vascular system. The indirect effect of auxin theory involves two possibilities: (1) that under the influence of auxin produced in actively growing regions there is preferential translocation of nutrients to this region, and (2) auxin is converted to or catalyzes the formation of an inhibitor.

Thimann (1952) stated that most available data pointed to lateral bud inhibition as directly traceable to auxin but that the mechanism involved formation of an inhibitor under the influence of auxin. Vardar (1955) related apical dominance directly to total auxin levels. Inhibition in laterals was weakened when natural auxin from the terminal bud was blocked by TIBA (2,3,5-triiodobenzoic acid), and hence the auxin level was decreased. Conversely, apical inhibition was increased when total auxin level in intact plants was increased by giving them IAA solution through the roots. Kuse (1954) also supported a direct theory of auxin inhibition. He found that the inhibitory effect of bracts on growth of axillary buds was eliminated when the transport of auxin from the lamina of the bract was blocked by TIBA.

Several investigators have questioned that auxin alone can wholly account for apical dominance. For example, Camus (1949) showed that apical buds checked growth of lateral buds, yet auxin contents of apical and lateral buds were not significantly different. Furthermore, Champagnat (1955) showed that large leaves of *Syringa vulgaris*, which contained little auxin, arrested growth of lateral buds, and that terminal buds, which had a high auxin content, had a negligible inhibitory effect.

C. L. Brown, *et al.* (1967) stated that a balance of growth regulators exerted primary control over bud inhibition and that nutritional factors were less important. They were able to release the inhibition of second-order axillary buds of *Liriodendron tulipifera* and *Liquidambar styraciflua* trees by decapitating the terminal bud of the lateral shoots, or by releasing a single inhibited bud by notching the stem above it. These observations suggested that hormonal factors diffusing basipetally from the apical region above kept lateral buds from opening. They reasoned that once such inhibition was removed the lateral buds obtained sufficient nutrients and carbohydrates to undergo some degree of internodal elongation.

Thimann (1959) placed considerable emphasis on the importance of auxin in apical control of growth but suggested that the mechanism actually involved interrelations between auxin and another growth regulator, presumably kinetin or a related substance. This conclusion was based on work by Wickson and Thimann (1958) who found that several auxins inhibited growth more or less completely. However, when kinetin was applied together with auxin at physiological concentrations, the inhibition was cancelled. Higher concentrations of kinetin were needed with higher auxin concentrations to remove the inhibiting effect. Kinetin also caused bud development when the inhibiting auxin came from the intact apex, suggesting an interaction of auxin and a kinetinlike substance. Further evidence for interacting roles of kinetin and auxin was provided by Sachs and Thimann (1967). They found that kinetin released lateral buds from the inhibition of the growing apex, whereas auxin primarily influenced internodal extension, only after removal of the initial inhibition. Buds released by kinetin from the inhibition of the apex did not elongate as much as uninhibited control buds except when they were given auxins. C. L. Brown *et al.* (1967) emphasized that many observed variations in tree form could be explained by modifying influences of nutrition and vigor on interacting growth factors such as cytokinins and auxins.

C. H. A. Little (1970) demonstrated that removal of shoots from a whorl in *Pinus strobus* induced compensatory growth in the remaining shoots. Treatments that impeded movement of auxin (e.g., triiodobenzoic acid, girdling) or decreased auxin production (e.g., defoliation, decapitation) also induced compensatory growth and, at the same time, inhibited growth of the treated shoot. Application of indoleacetic acid (IAA) in lanolin to a decapitated and defoliated shoot maintained diameter growth in the shoot and prevented compensatory growth. C. H. A. Little (1970) concluded that the shoots in a whorl competed for nutrients translocated from the preceding internode. The amount of nutrients mobilized by a shoot, and its growth, depended on the capacity of the shoot to produce hormonal growth regulators.

As emphasized in the section on bud dormancy, there is evidence of an

important role of endogenous inhibitors in bud growth (Kefford, 1955; Hemberg, 1961). Libbert (1954a,b, 1955a,b,c) stressed the indirect suppression of buds by inhibitor action. According to this view, a specific inhibitor is formed under the influence of auxin in apical buds and this inhibitor suppresses the growth of axillary buds. As pointed out earlier, the differences in length of shoots in upper and lower stems sometimes are correlated with differences in the number of seasonal growth flushes as in southern pines of the United States. In at least such species, and probably others, it appears likely that growth inhibitors as well as growth promoters play a role in correlative growth inhibition.

Suggested Collateral Reading

- Childers, N. F. (1966). "Nutrition of Fruit Crops." Horticultural Publ., New Brunswick, New Jersey.
- Downs, R. J. (1962). Photocontrol of growth and dormancy in woody plants. In "Tree Growth" (T. T. Kozlowski, ed.), Chapter 7. Ronald Press, New York.
- Giertych, M. (1964). Endogenous growth regulators in trees. *Bot. Rev.* **30**, 292-311.
- Kozlowski, T. T. (1949). Light and water in relation to growth and competition of forest tree species. *Ecol. Monogr.* **19**, 207-231.
- Kozlowski, T. T. (1964). Shoot growth in woody plants. *Bot. Rev.* **30**, 335-392.
- Kozlowski, T. T., ed. (1968a). "Water Deficits and Plant Growth," Vol. I. Development, Control, and Measurement. Academic Press, New York.
- Kozlowski, T. T., ed. (1968b). "Water Deficits and Plant Growth," Vol. II. Plant Water Consumption and Response. Academic Press, New York.
- Kozlowski, T. T., and Keller, T. (1966). Food relations of woody plants. *Bot. Rev.* **32**, 293-382.
- Kramer, P. J., and Kozlowski, T. T. (1960). "Physiology of Trees," Chapters 15 and 16. McGraw-Hill, New York.
- Leopold, A. C. (1964). "Plant Growth and Development." McGraw-Hill, New York.
- Osborne, D. J. (1967). Hormonal regulation of leaf senescence. *Symp. Soc. Exp. Biol.* **21**, 305-311.
- Osborne, D. J. (1968). Defoliation and defoliants. *Nature (London)* **219**, 564-567.
- Parker, J. (1965). Mineral deficiencies. *Advan. Front. Plant Sci.* **12**, 181-222.
- Smith, H., and Kefford, N. P. (1964). The chemical regulation of the dormancy phases of bud development. *Amer. J. Bot.* **51**, 1002-1012.
- Swan, H. S. D. (1965). Reviewing the scientific use of fertilizers in forestry. *J. Forest.* **63**, 501-508.
- Talbert, C. M., and Holch, A. E. (1957). A study of the lobing of sun and shade leaves. *Ecology* **38**, 655-658.
- Vegis, A. (1964). Dormancy in higher plants. *Annu. Rev. Plant Physiol.* **15**, 185-224.
- Viro, P. J. (1965). Estimation of the effect of forest fertilization. *Comm. Inst. Forest. Fennica* **59.3**, 5-42.
- Wareing, P. F. (1965). Dormancy in plants. *Sci. Progr. (London)* **53**, 529-537.

BIBLIOGRAPHY

- Aaron, I. (1956). Dormant and adventitious buds. *Science* **104**, 329.
- Abbott, H. (1961). White pine seed consumption by small mammals. *J. Forestry* **59**, 197-201.
- Addicott, F. T. (1964). Physiology of abscission. *Encycl. Plant Physiol.* **15**, Part 2, 1094-1126.
- Addicott, F. T. (1968). Environmental factors in the physiology of abscission. *Plant Physiol.* **43**, 1471-1479.
- Addicott, F. T., and Lynch, R. S. (1955). Physiology of abscission. *Annu. Rev. Plant Physiol.* **6**, 211-238.
- Addicott, F. T., and Lyon, J. L. (1969). Physiology of abscisic acid and related substances. *Annu. Rev. Plant Physiol.* **20**, 139-164.
- Addicott, F. T., Carns, H. R., Lyon, J. L., Smith, O. E., and McMeans, J. L. (1964). "Regulateurs naturels de la croissance végétale." *C. N. R. S.*, Paris.
- Addoms, R. M. (1946). Entrance of water into suberized roots of trees. *Plant Physiol.* **21**, 109-111.
- Ahlgren, C. E. (1957). Phenological observations of nineteen native tree species. *Ecology* **38**, 622-628.
- Aldhous, J. R. (1962). Provenance of sitka spruce: An account of the nursery stage of experiments sown in 1958. *Rep. Forest Res.* pp. 147-154.
- Aldrich-Blake, R. N. (1929). Recent research on root systems of trees. *Forestry* **3**, 66-70.
- Aldrich-Blake, R. N. (1930). The root system of the Corsican pine. *Oxford Forest. Mem.* **12**, 1-64.
- Allary, S. (1958). Remarques sur l'inhibition des bourgeons axillaires de la pousse herbacée des végétaux ligneux. *C. R. Acad. Sci.* **246**, 1071-1073.
- Allen, G. S. (1962). Factors affecting the viability and germination behavior of coniferous seed. V. Seed moisture content during stratification and secondary storage, *Pseudotsuga menziesii* (Mirb.) Franco. *Forest. Chron.* **38**, 303-308.
- Allen, R. M. (1960). Changes in acid growth substances in terminal buds of longleaf pine saplings during the breaking of winter dormancy. *Physiol. Plant.* **13**, 555-558.
- Allen, R. M., and McGregor, W. H. D. (1962). Seedling growth of three southern pine species under long and short days. *Silvae Genet.* **11**, 43-45.
- Allen, R. M., and Scarbrough, N. M. (1969). Development of a year's height growth in longleaf pine saplings. *U.S. Forest Serv., Res. Pap. SO-45*.
- Altman, P. L., and Dittmer, D. S. (1962). "Growth, including reproduction and morphological development." Federation of American Societies for Exptl. Biology. Washington, D.C.
- Alvim, P. de T. (1964). Tree growth periodicity in tropical climates. In "The Formation of Wood in Forest Trees" (M. H. Zimmermann, ed.), pp. 479-496. Academic Press, New York.
- Amen, R. D. (1963). The concept of seed dormancy. *Amer. Sci.* **51**, 408-424.
- Amen, R. D. (1968). A model of seed dormancy. *Bot. Rev.* **34**, 1-31.

- Anderson, A. B., Scheffer, T. C., and Duncan, C. C. (1962). Chemistry of heartwood decay on ageing in incense cedar (*Libocedrus decurrens* Torrey). *Chem. Ind. (London)*, pp. 1289–1290.
- Anderson, L., and Wolter, K. E. (1966). Cyclitols in plants: Biochemistry and physiology. *Annu. Rev. Plant Physiol.* **17**, 209–222.
- Anderson, R. F. (1944). The relation between host condition and attacks by the bronzed birch borer. *J. Econ. Entomol.* **37**, 588–596.
- Anic, M. (1956). Rhythmus des Höhenwachstums bei Pflanzen verschiedener Holzarten im Laufe ihrer Vegetationsperiode. *12th Congr. Int. Union Forest Res. Org.*, 1956 IUFRO No. 56/11/101.
- Anonymous (1948). Woody-plant seed manual. *U.S., Dep. Agr., Misc. Publ.* **654**.
- Armson, K. A. (1966). The growth and absorption of nutrients by fertilized and unfertilized white spruce seedlings. *Forest. Chron.* **42**, 127–136.
- Arnon, D. I., and Stout, P. R. (1939). The essentiality of certain elements in minute quantity for plants with special reference to copper. *Plant Physiol.* **14**, 371–376.
- Asakawa, S. (1956). Thermoperiodic control of germination of *Fraxinus mandshurica* var. *japonica* seeds. *J. Jap. Forest. Soc.* **38**, 269–272.
- Asakawa, S. (1959). Germination behaviour of several coniferous seeds. *J. Jap. Forest. Soc.* **41**, 430–435.
- Ashby, E. (1948). Studies in morphogenesis of leaves. I. An essay on leaf shape. *New Phytol.* **47**, 153–176.
- Ashby, W. C. (1962). Root growth in American basswood. *Ecology* **43**, 336–339.
- Audus, J. L. (1959). Correlations. *J. Linn. Soc. (Bot.)* **56**, 177–187.
- Bachelard, E. P. (1969a). Effects of gibberellic acid on internode growth and starch contents of *Eucalyptus camaldulensis* seedlings. *New Phytol.* **68**, 1017–1022.
- Bachelard, E. P. (1969b). Studies on the formation of epicormic shoots on Eucalypt stem segments. *Aust. J. Biol. Sci.* **22**, 1291–1296.
- Bachelard, E. P., and Stowe, B. B. (1963). Rooting of cuttings of *Acer rubrum* L. and *Eucalyptus camaldulensis* Dehn. *Austr. J. Biol. Sci.* **16**, 751–767.
- Baker, F. S. (1950). "Principles of Silviculture." McGraw-Hill, New York.
- Balch, R. E., and Prebble, J. S. (1940). The bronze birch borer and its relation to the dying of birch in New Brunswick forests. *Forest. Chron.* **16**, 179–201.
- Baldwin, H. I. (1934). Germination of red spruce. *Plant Physiol.* **9**, 491–532.
- Ball, E. (1941). The development of the shoot apex and of the primary thickening meristem in *Phoenix canariensis*, with comparisons to *Washingtonia filifera* and *Trachycarpus excelsa*. *Amer. J. Bot.* **28**, 820–832.
- Barlow, H. W. B. (1959). Root/shoot relationships in fruit trees. *Sci. Hort.* **14**, 35–41.
- Barton, L. V. (1935). Storage of some coniferous seeds. *Contrib. Boyce Thompson Inst.* **7**, 379–404.
- Barton, L. V. (1945a). A note on the viability of seeds of Maga, *Montezuma speciosissima*. *Contrib. Boyce Thompson Inst.* **13**, 423–426.
- Barton, L. V. (1945b). Viability of seeds of *Fraxinus* after storage. *Contrib. Boyce Thompson Inst.* **13**, 427–432.
- Barton, L. V. (1947). Effect of different storage conditions on the germination of seeds of *Cinchona ledgeriana* Moens. *Contrib. Boyce Thompson Inst.* **15**, 1–10.
- Barton, L. V. (1953). Seed storage and viability. *Contrib. Boyce Thompson Inst.* **17**, 87–103.
- Barton, L. V. (1961). "Seed Preservation and Longevity." Wiley (Interscience), New York.
- Beal, J. A. (1943). Relation between tree growth and outbreaks of the Black Hills beetle. *J. Forest.* **41**, 359–366.
- Beard, J. S. (1946). The natural vegetation of Trinidad. *Oxford Forest. Mem.* **20**.
- Becking, J. H. (1961a). Molybdenum and symbiotic nitrogen fixation by alder (*Alnus glutinosa* Gaertn.). *Nature (London)* **192**, 1204–1205.

- Becking, J. H. (1961b). A requirement of molybdenum for the symbiotic nitrogen fixation in alder (*Alnus glutinosa* Gaertn.). *Plant Soil* **15**, 217-227.
- Beckmann, C. H., Kuntz, J. E., Riker, A. J., and Berbee, J. G. (1953). Host responses associated with the development of oak wilt. *Phytopathology* **43**, 448-454.
- Becquerel, P. (1934). La longéité des graines macrobiotiques transmise par Louis Mangin. *C. R. Acad. Sci.* **199**, 1662-1664.
- Bengston, G. W., McGregor, W. H. D., and Squillace, A. E. (1967). Phenology of terminal growth in slash pine: Some differences related to geographic seed source. *Forest Sci.* **13**, 402-412.
- Benzian, B., and Warren, R. C. (1956). Copper deficiency in Sitka spruce seedlings. *Nature (London)*, **178**, 864-865.
- Benzie, J. W. (1960). Viability of balsam fir seed depends on age of tree. *U.S., Forest Serv. Lake States, Forest Exp. Sta., Tech. Note* **591**.
- Berkley, E. E. (1961). Marcescent leaves of certain species of *Quercus*. *Bot. Gaz.* **92**, 85-93.
- Berlyn, G. P. (1967). The structure of germination in *Pinus lambertiana* Dougl. *Yale Sch. Forest. Bull.* **71**.
- Billings, W. D. (1957). Physiological ecology. *Annu. Rev. Plant Physiol.* **8**, 375-392.
- Bishop, D. M. (1962). Lodgepole pine rooting habits in the blue mountains of northeastern Oregon. *Ecology* **43**, 140-142.
- Björkman, E. (1953). Om "Granens gulspetssjuka" i plantskolor. *Sv. Skogsvardsfoeren. Tidskr.* **51**, 211-229.
- Black, M., and Wareing, P. F. (1955). Growth studies in woody species. VII. Photoperiodic control of germination in *Betula pubescens* Ehrh. *Physiol. Plant.* **8**, 300-316.
- Black, M., and Wareing, P. F. (1959). The role of germination inhibitors and oxygen in the dormancy of the light-sensitive seed of *Betula* spp. *J. Exp. Bot.* **10**, 134-145.
- Blair, D. S., MacArthur, M., and Nelson, S. H. (1956). Observations in the growth phases of fruit trees. *Proc. Amer. Soc. Hort. Sci.* **67**, 75-79.
- Blais, J. R. (1952). The relationship of the spruce budworm (*Choristoneura fumiferana*, Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.) *Can. J. Zool.* **30**, 1-29.
- Blais, J. R. (1958). The vulnerability of balsam fir to spruce budworm attack in northwestern Ontario with special reference to the physiological age of the tree. *Forest Chron.* **34**, 405-422.
- Blommaert, K. L. J. (1955). The significance of auxins and growth inhibiting substances in relation to winter dormancy of the peach. *S. Afr. Dep. Agr. Sci. Bull.* **368**, 1-23.
- Blum, B. M. (1963). Excessive exposure stimulates epicormic branching in young northern hardwoods. *U.S., Forest Serv., Res. Note NE-9*.
- Blumer, J. C. (1910). The vitality of pine seeds in serotinous cones. *Torreya* **10**, 108-111.
- Bond, G., and Hewitt, E. J. (1961). Molybdenum and the fixation of nitrogen in *Myrica* root nodules. *Nature (London)* **190**, 1033-1034.
- Bond, T. E. T. (1942). Studies in the vegetative growth and anatomy of the tea plant (*Camellia thea* Link.) with special reference to phloem. I. The flush shoot. *Ann. Bot. (London)* [N.S.] **6**, 607-629.
- Bond, T. E. T. (1945). Studies in the vegetative growth and anatomy of the tea plant (*Camellia thea* Link.) with special reference to the phloem. II. Further analysis of flushing behavior. *Ann. Bot. (London)* [N.S.] **9**, 183-216.
- Bonner, F. T. (1968). Water uptake and germination of red oak acorns. *Bot. Gaz.* **129**, 83-85.
- Bonner, J. (1962). Summary and observations. In "Proceedings Plant Science Symposium," pp. 213-223. Campbell Soup Co., Camden, New Jersey.
- Bonner, J., and Galston, A. W. (1959). "Principles of Plant Physiology." Freeman, San Francisco, California.

- Booth, A., Moorby, J., Davies, C. R., Jones, H., and Wareing, P. F. (1962). Effects of indolyl-3-acetic acid on the movement of nutrients within plants. *Nature (London)* **194**, 204–205.
- Borchert, R. (1969). Unusual shoot growth pattern in a tropical tree, *Oreopanax* (Araliaceae). *Amer. J. Bot.* **56**, 1033–1041.
- Bormann, F. H. (1958). The relationships of ontogenetic development and environmental modification to photosynthesis in *Pinus taeda* seedlings. In "The Physiology of Forest Trees" (K. V. Thimann, ed.), Chapter 10. Ronald Press, New York.
- Bormann, F. H. (1963). Ontogenetic relationships of the primary leaf of *Pinus taeda* L. and *P. echinata* Mill. *Bull. Torrey Bot. Club* **90**, 320–332.
- Bormann, F. H. (1965). Changes in the growth pattern of white pine trees undergoing suppression. *Ecology* **46**, 269–277.
- Bosse, G. (1960). Die Wurzelentwicklung von Apfelkernen und Apfelsämlingen während der ersten drei Standjahre. *Erwerbssitzbach* **2**, 26–30.
- Bosshard, H. H. (1965). Aspects of the aging process in cambium and xylem. *Holzforschung* **19**, No. 3, 65–69.
- Bourdeau, P. F., and Laverick, M. L. (1958). Tolerance and photosynthetic adaptability to light intensity in white pine, red pine, hemlock, and ailanthus seedlings. *Forest Sci.* **4**, 196–207.
- Boyce, J. S. (1954). Forest plantation protection against disease and insect pests. *FAO Forest. Develop. Pap.* 3.
- Boyer, W. D. (1970). Shoot growth patterns of young loblolly pine. *Forest Sci.* (in press).
- Bradbeer, J. W. (1968). Studies in seed dormancy. IV. The role of endogenous inhibitors and gibberellin in the dormancy and germination of *Corylus avellana* seeds. *Planta* **78**, 266–276.
- Bradbeer, J. W., and Pinfield, N. J. (1967). Studies in seed dormancy. III. The effects of gibberellin on dormant seeds of *Corylus avellana*. *New Phytol.* **66**, 515–523.
- Bradley, J. W. (1922). A plantation of remarkable growth. *Indian Forest* **48**, 637–640.
- Bray, J. R., and Gorham, E. (1964). Litter production in forests of the world. *Advan. Ecol. Res.* **2**, 101–157.
- Brazier, J. D., and Franklin, G. L. (1961). Identification of hardwoods. *Forest Prod. Res. Bull.* **46**, London.
- Brender, E. V., and Barber, J. C. (1956). Influence of loblolly pine overwood on advance reproduction. *U.S. Forest Serv., Southeast. Forest Exp. Sta., Sta. Pap.* **62**.
- Brian, P. W., Petty, J. H. P., and Richmond, P. T. (1959). Effects of gibberellic acid on development of autumn color and leaf-fall of deciduous woody plants. *Nature (London)* **183**, 58–59.
- Brink, R. A. (1962). Phase change in higher plants and somatic cell heredity. *Quart. J. Biol.* **37**, 1–22.
- Broekhuizen, J. T. M. (1962). Over net groeritme van populieren. *Comm. Inst. Forest. Res. Wageningen* No. 5.
- Brown, A. B. (1935). Cambial activity, root habit and sucker development in two species of poplar. *New Phytol.* **34**, 163–179.
- Brown, C. L. (1964). "The Seedling Habit of Longleaf Pine." Georgia Forest Research Council and School of Forestry, Univ. of Georgia, Athens, Georgia.
- Brown, C. L., and Kormanik, P. P. (1967). Suppressed buds on lateral roots of *Liquidambar styraciflua*. *Bot. Gaz.* **128**, 208–211.
- Brown, C. L., McAlpine, R. G., and Kormanik, P. P. (1967). Apical dominance and form in woody plants: A reappraisal. *Amer. J. Bot.* **54**, 153–162.
- Brown, R. T. (1967). Influence of naturally occurring compounds on germination and growth of jack pine. *Ecology* **48**, 542–546.

- Browning, B. L., ed. (1963). "The Chemistry of Wood." Wiley, New York.
- Bubrjak, I. I. (1961). Concerning the flowering and fruiting of tea in Transcarpathia. *Agrobiologiya*. (Russ.) **2**, 301-303.
- Burkholder, P. R., and McVeigh, I. (1945). The B vitamin content of buds and shoots of some common trees. *Plant Physiol.* **20**, 276-282.
- Burley, J. (1966a). Genetic variation in seedling development of Sitka spruce, *Picea sitchensis* (Bong.) Carr. *Forestry* **39**, 68-94.
- Burley, J. (1966b). Provenance variation in growth of seedling apices of Sitka spruce. *Forest Sci.* **12**, 170-175.
- Burley, J. (1966c). Review of variation in slash pine (*Pinus elliottii* Engelm.) and loblolly pine (*P. taeda* L.) in relation to provenance research. *Comm. Forest. Rev.* **45**, 322-338.
- Büsgen, M., and Münch, E. (1931). "The Structure and Life of Forest Trees" (transl. by T. Thomson), 3rd ed. Wiley, New York.
- Callaham, R. Z. (1962). Geographic variability in growth of forest trees. In "Tree Growth" (T. T. Kozlowski, ed.), Chapter 20. Ronald Press, New York.
- Callaham, R. Z., and Liddicote, A. R. (1961). Altitudinal variation at 20 years in Ponderosa and Jeffrey pines. *J. Forest.* **59**, 814-820.
- Campbell, A. I. (1961). Shortening the juvenile phase of apple seedlings. *Nature (London)* **191**, 517.
- Cameron, S. H., and Schroeder, C. A. (1945). Cambial activity and starch cycle in bearing orange trees. *Proc. Amer. Soc. Hort. Sci.* **46**, 55-59.
- Camus, G. (1949). Recherches sur le rôle des bourgeons dans les phénomènes de morphogenèse. *Rev. Cytol. Biol. Veg.* **11**, 1-100.
- Cannon, J. R., Corbett, N. H., Haydock, K. P., Tracey, J. G., and Webb, L. J. (1962). An investigation of the effect of the dehydroangustione present in the leaf litter of *Backhousia angustifolia* on the germination of *Araucaria cunninghamia*—an experimental approach to a problem in rain-forest ecology. *Aust. J. Bot.* **10**, 119-128.
- Carns, H. R. (1966). Abscission and its control. *Annu. Rev. Plant Physiol.* **17**, 295-314.
- Carroll, W. J. (1956). History of the hemlock looper *Lambdina fiscellaria fiscellaria* (Guen.) (Lepidoptera: Geometridae) in Newfoundland, and notes on its biology. *Can. Entomol.* **88**, 587-599.
- Carter, M. C., and Jones, L. (1962). The effect of hydrogen peroxide on the germination of loblolly and slash pine seed. *U.S. Forest Serv., Southeast. Forest Exp. Sta., Sta. Pap.* **141**.
- Carvell, K. L. (1956). Summer shoots cause permanent damage to red pine. *J. Forest.* **54**, 271.
- Catrina, I., and Moisiuc, G. (1958). Caracterele cresterii paducelului si lemmuli curesc in dona statiuni deferite. *Rev. Padurilor* **4**, 202-204.
- Cayford, J. H., and Waldron, R. M. (1967). Effects of captan on the germination of white spruce, jack, and red pine seed. *Forest. Chron.* **43**, 381-384.
- Chalk, L. (1934). Annual rings in transplants and seedlings. *Quart. J. Forest.* **28**, 220-224.
- Champagnat, P. (1955). Les correlations entre feuilles et bourgeons de la pousse herbacée du lis. *Rev. Gen. Bot.* **62**, 325.
- Chandler, W. H. (1947). "Deciduous Orchards." Lea & Febiger, Philadelphia, Pennsylvania.
- Chandler, W. H. (1954). Cold resistance in horticultural plants: A review. *Proc. Amer. Soc. Hort. Sci.* **64**, 552-572.
- Chattaway, M. M. (1949). The development of tyloses and secretion of gum in heartwood formation. *Aust. J. Sci. Res. Ser., B* **2**, 227-240.
- Chattaway, M. M. (1952). The sapwood-heartwood transition. *Aust. Forest.* **16**, 25-34.

- Chattaway, M. M. (1953). The occurrence of heartwood crystals in certain timbers. *Aust. J. Bot.* **1**, 27-38.
- Childers, N. F. (1961). "Modern Fruit Science." Hort. Publ. Rutgers Univ., New Brunswick, New Jersey.
- Childers, N. F. (1966a). "Fruit Nutrition." Hort. Publ., Rutgers Univ., New Brunswick, New Jersey.
- Childers, N. F., ed. (1966b). "Nutrition of Fruit Crops." Hort. Publ., Rutgers Univ., New Brunswick, New Jersey.
- Ching, T. M. (1959). Activation of germination in Douglas-fir seed by hydrogen peroxide. *Plant Physiol.* **34**, 557-563.
- Ching, T. M. (1963a). Change of chemical reserves in germinating Douglas-fir seed. *Forest Sci.* **9**, 226-231.
- Ching, T. M. (1963b). Fat utilization in germination of Douglas-fir seed. *Plant Physiol.* **38**, 722-728.
- Ching, T. M. (1966). Compositional changes of Douglas-fir seeds during germination. *Plant Physiol.* **41**, 1313-1319.
- Chowdhury, C. R. (1962). The embryogeny of conifers: A review. *Phytomorphology* **12**, 313-338.
- Chowdhury, K. A. (1958). Extension and radial growth in tropical perennial plants. *Mod. Develop. Plant Physiol., Proc. Delhi Univ. Semin. 1957* pp. 138-139.
- Chrosciewicz, Z. (1963). The effects of site on jack pine growth in northern Ontario. *Can., Dep. Forest. Publ.* **1015**.
- Church, T. W., Jr., and Godman, R. M. (1966). The formation and development of dormant buds in sugar maple. *Forest Sci.* **12**, 301-386.
- Clark, J. (1961). Photosynthesis and respiration in white spruce and balsam fir. *State Univ. Coll. Forest., Syracuse, New York, Tech. Publ.* **85**.
- Clark, J., and Bonga, J. M. (1963). Evidence for indole-3-acetic acid in balsam fir, *Abies balsamea* (L.) Mill. *Can. J. Bot.* **41**, 165-173.
- Clark, J., and Gibbs, R. D. (1957). Studies in tree physiology. IV. Further investigations of seasonal changes in moisture content of certain Canadian forest trees. *Can. J. Bot.* **35**, 219-253.
- Clausen, J. (1951). "Stages in the Evolution of Plant Species." Cornell Univ. Press, Ithaca, New York.
- Clausen, J. J., and Kozlowski, T. T. (1967a). Food sources for growth of *Pinus resinosa* shoots. *Advan. Front. Plant Sci.* **18**, 23-32.
- Clausen, J. J., and Kozlowski, T. T. (1967b). Seasonal growth characteristics of long and short shoots of tamarack. *Can. J. Bot.* **45**, 1643-1651.
- Clausen, J. J., and Kozlowski, T. T. (1970). Observations on growth of long shoots of *Larix laricina*. *Can. J. Bot.* **48**, 1045-1048.
- Clausen, K. E., and Rudolph, P. O. (1958). Germination of 29-year-old red pine seed. *Minn. Forest. Notes* **72**.
- Clements, J. R. (1970). Shoot responses of young red pine to watering applied over two seasons. *Can. J. Bot.* **48**, 75-80.
- Clowes, F. A. L. (1950). Root apical meristems of *Fagus sylvatica*. *New Phytol.* **49**, 249-268.
- Clowes, F. A. L. (1961). "Apical Meristems." Oxford Univ. Press, London and New York.
- Coile, T. S., and Schumacher, F. X. (1953). Relation of soil properties to site index of loblolly and shortleaf pines in the Piedmont region of the Carolinas, Georgia and Alabama. *J. Forest.* **51**, 739-744.
- Collins, S. (1960). Seasonal elongation of red maple (*Acer rubrum* L.) in an open field and the understories of non-defoliated and defoliated woodlands. *Bull. Ecol. Soc. Amer.* **41**, 127.

- Cook, D. B. (1941a). Five seasons' growth of conifers. *Ecology* **22**, 285-296.
- Cook, D. B. (1941b). The period of growth in some northeastern trees. *J. Forest.* **39**, 957-959.
- Cornforth, J. W., Milborrow, B. V., Ryback, G., and Wareing, P. F. (1965). Chemistry and physiology of 'dormins' in sycamore. *Nature (London)* **205**, 1269-1270.
- Cossmann, K. F. (1939). Citrus roots: Their anatomy, osmotic pressure, and periodicity of growth. *Palestine J. Bot. Hort. Sci.* **3**, 3-41.
- Coté, W. A., Jr. (1963). Structural factors affecting the permeability of wood. *J. Polymer Sci. Part C*, **n2**, 231-242.
- Coté, W. A., Jr., ed. (1965). "Cellular Ultrastructure of Woody Plants." Syracuse Univ. Press, Syracuse, New York.
- Coté, W. A., Jr. (1967). "Wood Ultrastructure." Univ. of Washington Press, Seattle, Washington.
- Cottam, W. P. (1954). Prevernal leafing of aspen in Utah mountains. *J. Arnold Arboretum Harvard Univ.* **35**, 239-250.
- Coulter, J. M., and Chamberlain, C. J. (1917). "Morphology of Gymnosperms." Univ. of Chicago Press, Chicago, Illinois.
- Cox, L. G. (1942). A physiological study of embryo dormancy in the seed of native hardwoods and iris. Ph.D. Dissertation, Cornell University.
- Critchfield, W. B. (1957). Geographic variation in *Pinus contorta*. *Maria Moors Cabot Found., Publ.* **3**.
- Critchfield, W. B. (1960). Leaf dimorphism in *Populus trichocarpa*. Amer. J. Bot.
- Crutchfield, W. B. (1960). Leaf dimorphism in *Populus trichocarpa*. Amer. J. Bot.
- Crocker, W. (1938). Life span of seeds. *Bot. Rev.* **4**, 235-274.
- Crocker, W. (1948). "Growth of Plants." Reinhold, New York.
- Crocker, W., and Barton, L. V. (1957). "Physiology of Seeds." Chronica Botanica, Waltham, Massachusetts.
- Cross, G. L. (1940). Development of the foliage leaves of *Taxodium distichum*. *Amer. J. Bot.* **27**, 471-482.
- Cross, G. L. (1942). Structure of the apical meristem and development of the foliage leaves of *Cunninghamia lanceolata*. *Amer. J. Bot.* **29**, 288-301.
- Cummings, W. H. (1941). A method for sampling the foliage of a silver maple tree. *J. Forest.* **39**, 382-384.
- Cunningham, G. R., and Winch, F. E., Jr. (1962). Shaping Christmas trees for quality. *Cornell Ext. Bull.* **1080**.
- Curry, J. R., and Church, T. W. (1952). Observations on winter drying of conifers in the Adirondacks. *J. Forest.* **50**, 114-116.
- Czaja, A. T. (1934). Der Nachweis des Wuchsstoffes bei Holzpflanzen. *Ber. Deut. Bot. Ges.* **52**, 267-271.
- Dadswell, H. E. (1957). Tree growth characteristics and their influence on wood structure and properties. *7th Brit. Comm. Forest. Conf. CSIRO Melbourne*, pp. 1-19.
- Dadswell, H. E., and Hillis, W. E. (1962). Wood. In "Wood Extractives" and their Significance to the Pulp and Paper Industries (W. E. Hillis, ed.), Chapter 1. Academic Press, New York.
- Dahl, E., and Mork, E. (1959). Om sambandet mellom temperatur, ånding og vekst hos gran (*Picea abies* (L.) Karst.). *Medd. Nor. Skogforsoksv.* **16**, 81-93.
- Darrow, G. M. (1942). Rest period requirement for blueberries. *Proc. Amer. Soc. Hort. Sci.* **41**, 189-194.
- Daubenmire, R. F. (1959). "Plants and Environment." Wiley, New York.
- Davis, D. E. (1949). Some effects of calcium deficiency on the anatomy of *Pinus taeda*. *Amer. J. Bot.* **36**, 276-282.

- Day, M. W. (1944). The root system of the aspen. *Amer. Midl. Natur.* **32**, 502–509.
- Day, W. R. (1946). The pathology of beech on chalk soils. *Quart. J. Forest.* **40**, 72–82.
- Day, W. R. (1959). Observations on Eucalypts in Cyprus. Root development in relation to soil conditions. *Emp. Forest. Rev.* **38**, 186–197.
- De Bruyne, A. S. (1952). Wood structure and age. *Proc. Kon. Ned. Akad. Wetensch., Ser. C.* **55**, 282–286.
- de Laubenfels, D. J. (1953). The external morphology of coniferous leaves. *Phytomorphology* **3**, 1–20.
- Delisle, A. L. (1954). The relationship between the age of the tree and rooting of cuttings of white pine. *Proc. Indiana Acad. Sci.* **64**, 60–61.
- De Maggio, A. E., and Freeberg, J. A. (1969). Dormancy regulation: hormonal interaction in maple (*Acer platanoides*). *Can. J. Bot.* **47**, 1165–1169.
- Dennis, F. G., Jr., and Edgerton, L. J. (1961). The relationship between an inhibitor and rest in peach flower buds. *Proc. Amer. Soc. Hort. Sci.* **77**, 107–116.
- Desch, H. E. (1968). "Timber, its Structure and Properties." Macmillan, New York.
- De Sloover, J. (1958). Recherches sur l'histogenèse des tissus conducteurs. II. Le sens longitudinal de la différenciation du procambium, du xylème et du phloème chez *Coleus*, *Ligustrum*, *Anagallis* et *Taxus*. *Cellule* **59**, 55–202.
- Dickmann, D. I., and Kozlowski, T. T. (1968). Mobilization by *Pinus resinosa* cones and shoots of C¹⁴-photosynthate from needles of different ages. *Amer. J. Bot.* **55**, 900–906.
- Doak, C. C. (1935). Evolution of foliar types, dwarf shoots, and cone scales of *Pinus*. *Ill. Biol. Monogr.* **13**, No. 3.
- Domanski, R., and Kozlowski, T. T. (1968). Variations in kinetin-like activity in buds of *Betula* and *Populus* during release from dormancy. *Can. J. Bot.* **46**, 397–403.
- Doorenbos, J. (1953). Review of the literature on dormancy in buds of woody plants. *Landbouwhogeschool Wageningen Med.* **53**, 1–24.
- Doorenbos, J. (1954). "Rejuvenation" of *Hedera helix* in graft combinations. *Proc. Kon. Ned. Akad. Wetenschap., Ser. C.* **57**, 99–102.
- Doorenbos, J. (1955). Shortening the breeding cycle of Rhododendron. *Euphytica* **4**, 141–146.
- Downs, R. J. (1962). Photocontrol of growth and dormancy in woody plants. In "Tree Growth." T. T. Kozlowski, ed. Chapter, 7. Ronald Press, New York.
- Duff, G. H., and Nolan, N. J. (1953). Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in *Pinus resinosa* Ait. *Can. J. Bot.* **31**, 471–513.
- Duff, G. H., and Nolan, N. J. (1958). Growth and morphogenesis in the Canadian forest species. III. The time scale of morphogenesis at the stem apex of *Pinus resinosa* Ait. *Can. J. Bot.* **36**, 687–706.
- Dunning, D. (1928). A tree classification for the selection forests of the Sierra Nevada. *J. Agr. Res.* **36**, 755–771.
- Dure, L., and Waters, L. (1965). Long-lived messenger RNA: Evidence from cotton seed germination. *Science* **147**, 410–412.
- Durkin, J. (1965). Bud dormancy in the Better Times Rose. *Proc. Amer. Soc. Hort. Sci.* **86**, 798–805.
- Eagles, C. F., and Wareing, P. F. (1963). Dormancy regulators in woody plants. Experimental induction of dormancy in *Betula pubescens*. *Nature (London)*, **199**, 874–875.
- Eagles, C. F., and Wareing, P. F. (1964). The role of growth substances in the regulation of bud dormancy. *Physiol. Plant.* **17**, 697–709.
- Eames, A. J. (1961). "Morphology of the Angiosperms." McGraw-Hill, New York.
- Eggert, F. P. (1951). A study of rest in several varieties of apple and in other fruit species grown in New York State. *Proc. Amer. Soc. Hort. Sci.* **57**, 169–178.

- Eggler, W. A. (1961). Stem elongation and time of cone initiation in southern pines. *Forest Sci.* **7**, 149-158.
- Eglinton, G., and Hamilton, R. J. (1967). Leaf epicuticular waxes. *Science* **156**, 1322.
- Eichenberger, W., and Grob, E. C. (1962). The biochemistry of plant plastids. 1. A study of autumn coloring. *Helv. Chim. Acta* **45**, 974-981.
- Eliasson, L. (1961). The influence of growth substances on the formation of shoots from aspen roots. *Physiol. Plant.* **14**, 150-156.
- Elliott, J. H. (1937). The development of the vascular system in evergreen leaves more than one year old. *Ann. Bot. (London)* [N.S.] **1**, 107-127.
- Engstrom, A. (1948). Growing cottonwood from seed. *J. Forest.* **46**, 130-132.
- Erdtman, H. (1955). The chemistry of heartwood constituents of conifers and their taxonomic importance. *Experientia Suppl.* **2**, 156-180.
- Erickson, L. C., and Brannaman, B. L. (1960). Abscission of reproductive structures and leaves of orange trees. *Proc. Amer. Soc. Hort. Sci.* **75**, 222-229.
- Ermeev, G. N. (1960). The growth of the absorbing roots of fruit trees in relation to soil conditions. *Dokl. Akad. Nauk SSSR* **130**, 678-681.
- Esau, K. (1945). Vascularization of the vegetative shoots of *Helianthus* and *Sambucus*. *Amer. J. Bot.* **32**, 18-29.
- Esau, K. (1960). "Anatomy of Seed Plants." Wiley, New York.
- Esau, K. (1965a). "Vascular Differentiation in Plants." Holt, New York.
- Esau, K. (1965b). "Plant Anatomy." Wiley, New York.
- Evenari, M. (1949). Germination inhibitors. *Bot. Rev.* **15**, 153-194.
- Evenari, M. (1956). Seed germination. *Radiat. Biol.* pp. 518-549.
- Ewart, A. J. (1908). On the longevity of seeds. *Proc. Roy. Soc. Victoria* **21**, 1-210.
- Facey, V. (1950). Abscission of leaves in *Fraxinus americana*. *New Phytol.* **49**, 103-116.
- Facey, V. (1956). Abscission of leaves in *Picea glauca* (Moench) Voss and *Abies balsamea* L. *Proc. N. Dak. Acad. Sci.* **10**, 38-43.
- Fahn, A. (1967). "Plant Anatomy." Pergamon Press, Oxford.
- Fahn, A., and Arnon, N. (1963). The living wood fibers of *Tamarix aphylla* and the changes occurring from sapwood to heartwood. *New Phytol.* **62**, 99-104.
- Farmer, R. E., Jr., and Bonner, F. T. (1967). Germination and initial growth of eastern cottonwood as influenced by moisture stress, temperature, and storage. *Bot. Gaz.* **128**, 211-215.
- Farnsworth, C. E. (1955). Observations of stem elongation in certain trees in the western Adirondacks. *Ecology* **36**, 285-292.
- Felber, I. M. (1948). Growth potentialities of vegetative buds on apple trees. *J. Agr. Res.* **77**, 239-252.
- Fielding, J. M. (1952). The moisture content of the trunks of Monterey pine trees. *Austr. Forest* **16**, 3-21.
- Fielding, J. M. (1953). Variations in Monterey pine. *Aust. Forest. Timber Bur., Bull.* **31**.
- Fielding, J. M. (1955). The seasonal and daily elongation of the shoots of Monterey pine and the daily elongation of the roots. *Aust. Forest. Timber Bur., Leaflet.* **75**.
- Fielding, J. M. (1960). Branching and flowering characteristics of Monterey pine. *Aust. Forest. Timber Bur., Bull.* **37**.
- Forde, M. B. (1964). Variation in natural populations of *Pinus radiata* in California. Part 2. Needle characters. *N. Z. J. Bot.* **2**, 237-257.
- Forward, D. F., and Nolan, N. J. (1964). Growth and morphogenesis in the Canadian forest species. VII. Progress and control of longitudinal growth of branches in *Pinus resinosa* Ait. *Can. J. Bot.* **42**, 932-950.
- Foster, A. S. (1936). Leaf differentiation in angiosperms. *Bot. Rev.* **2**, 349-372.
- Foster, A. S. (1941). Comparative studies on the structure of the shoot apex in seed plants. *Bull. Torrey Bot. Club* **68**, 339-350.

- Foster, A. S., and Gifford, E. M., Jr. (1959). "Comparative Morphology of Vascular Plants." Freeman, San Francisco, California.
- Fowells, H. A. (1965). Silvics of forest trees of the United States. U.S. Forest Service, Agriculture Handbook No. 271.
- Frampton, C. V. (1960). Some aspects of the developmental anatomy of the 'long' shoot in *Larix decidua*. Mill. with particular reference to seasonal periodicity. *New Phytol.* **59**, 175-191.
- Frank, H., and Renner, O. (1956). Über Vergungung bei *Hedera helix* L. *Planta* **47**, 105-114.
- Frankland, B. (1961). Effect of gibberellic acid, kinetin, and other substances on seed dormancy. *Nature (London)* **192**, 678-679.
- Frankland, B., and Wareing, P. F. (1962). Changes in endogenous gibberellins in relation to chilling of dormant seeds. *Nature (London)* **194**, 313-314.
- Fraser, D. A. (1962). Apical and radial growth of white spruce (*Picea glauca*) (Moench Voss) at Chalk River, Ontario, Canada. *Can. J. Bot.* **40**, 659-668.
- Fraser, D. A., Belanger, L., McGuire, D., and Zdrrazil, Z. (1964). Total growth of the aerial parts of a white spruce tree at Chalk River, Ontario, Canada. *Can. J. Bot.* **42**, 159-179.
- Freeland, R. O. (1952). Effect of age of leaves upon the rate of photosynthesis in some conifers. *Plant Physiol.* **27**, 685-690.
- Frey-Wyssling, A., and Bosshard, H. H. (1959). Cytology of the ray cells in sapwood and heartwood. *Holzforschung* **13**, 129-137.
- Friesner, R. C. (1943). Correlation of elongation in primary, secondary and tertiary axes of *Pinus strobus* and *P. resinosa*. *Butler Univ. Bot. Stud.* **6**, 1-9.
- Friesner, R. C., and Jones, J. J. (1952). Correlation of elongation in primary and secondary branches of *Pinus resinosa*. *Butler Univ. Bot. Stud.* **10**, 119-128.
- Fritzsche, R. (1948). Untersuchungen über die Jugendformen des Apfel-und Birnbaumes und ihre Konsequenzen für die Unterlagen-und Sortenzüchtung. *Ber. Schweiz. Bot. Ges.* **58**, 207-267.
- Fröhlich, H. J. (1958). Grundlagen und Voraussetzungen der autovegetativen Vermehrung. *Silvae Genet.* **8**, 49-58.
- Furr, J. R., Cooper, W. C., and Reece, P. C. (1947). An investigation of flower formation in adult and juvenile citrus trees. *Amer. J. Bot.* **34**, 1-8.
- Galston, A. W., and Davies, P. J. (1969). Hormonal regulation in higher plants. *Science* **163**, 1288-1297.
- Gardner, R. C. B. (1937). Storage of acorns. *Quart. J. Forest.* **31**, 32-33.
- Garner, R. J., and Hatcher, E. S. J. (1958). Aspects of rootstock propagation. V. The behaviour of root cuttings from plants of different age of establishment. *Ann. Rept., E. Malling Res. Sta., Kent* pp. 57-61.
- Garrison, R. (1949a). Origin and development of axillary buds: *Syringa vulgaris* L. *Amer. J. Bot.* **36**, 205-213.
- Garrison, R. (1949b). Origin and development of axillary buds: *Betula papyrifera* Marsh. and *Euptelea polyandra*. Sieb. et Zucc. *Amer. J. Bot.* **36**, 379-398.
- Garrison, R. (1955). Studies in the development of axillary buds. *Amer. J. Bot.* **42**, 257-266.
- Garrison, R., and Wetmore, R. H. (1961). Studies in shoot tip abortion: *Syringa vulgaris*. *Amer. J. Bot.* **48**, 789-795.
- Gashwiler, J. S. (1967). Conifer seed survival in a western Oregon clearcut. *Ecology* **48**, 431-438.
- Gatherum, G. E., McComb, A. L., and Loomis, W. E. (1963). Effects of light and soil moisture on forest tree seedling establishment. *Iowa, Agr. Exp. Sta., Res. Bull.* **513**, 776-792.
- Gautheret, R. J. (1955). The nutrition of plant tissue cultures. *Annu. Rev. Plant Physiol.* **6**, 433-484.

- Genys, J. B. (1960). Geographic variation in European larch. *Fox Res. Demonstration Forest Bull.* **13**.
- Gerry, E. (1914). Tyloses: Their occurrence and practical significance in some American woods. *J. Agr. Res.* **1**, 445–469.
- Ghent, A. W., and Thomas, J. B. (1960). Regularity in distribution of supernumerary needles on the terminal growth of young jack pine trees. *Forest Sci.* **6**, 331–333.
- Gibbs, R. D. (1940). Studies in tree physiology. II. Seasonal changes in the food reserves of field birch (*Betula populifolia* Marsh.). *Can. J. Res.* **18**, 1–9.
- Giertych, M. M. (1964). Endogenous growth regulators in trees. *Bot. Rev.* **30**, 292–311.
- Giertych, M. M., and Forward, D. F. (1966). Growth regulator changes in relation to growth and development of *Pinus resinosa* Ait. *Can. J. Bot.* **44**, 718–738.
- Gifford, E. M., Jr. (1954). The shoot apex in gymnosperms. *Bot. Rev.* **20**, 477–529.
- Gifford, E. M., Jr., and Mirov, N. T. (1960). Initiation and ontogeny of the ovulate strobilus in Ponderosa pine. *Forest Sci.* **6**, 19–25.
- Glerum, C., and Farrar, J. L. (1965). A note on internal frost damage in white spruce needles. *Can. J. Bot.* **43**, 1590–1591.
- Glock, W. S., Agerter, S. R., and Studhalter, R. A. (1964). Tip growth in trees of west Texas and Maryland. *Advan. Front. Plant Sci.* **9**, 15–106.
- Goo, M. (1952). When cell division begins in germinating seeds of *Pinus thunbergii*. *J. Jap. Forest Soc.* **34**, 3.
- Goodin, J. R. (1965). Anatomical changes associated with juvenile-to-mature growth phase transition in *Hedera*. *Nature (London)* **208**, 504–505.
- Goodwin, T. W. (1958). Studies in carotenogenesis, 24. The changes in carotenoid and chlorophyll pigments in the leaves of deciduous trees during autumn necrosis. *Biochem. J.* **68**, 503–511.
- Gordon, J. C., and Larson, P. R. (1968). Seasonal course of photosynthesis, respiration, and distribution of ^{14}C in young *Pinus resinosa* trees as related to wood formation. *Plant Physiol.* **43**, 1617–1624.
- Gordon, J. C., and Larson, P. R. (1970). Redistribution of ^{14}C -labeled reserve food in young red pines during shoot elongation. *Forest Sci.* **16**, 14–20.
- Graham, K. (1963). "Concepts of Forest Entomology." Reinhold, New York.
- Graham, S. A., Harrison, R. P., and Westell, C. E., Jr. (1963). "Aspens." Univ. of Michigan Press, Ann Arbor, Michigan.
- Greenwood, M., and Posnette, A. F. (1950). The growth flushes of cacao. *J. Hort. Sci.* **25**, 164–174.
- Gregor, J. W. (1946). Ecotypic differentiation. *New Phytol.* **45**, 254–270.
- Gregory, F. G., and Veale, J. A. (1957). A reassessment of the problem of apical dominance. *Symp. Soc. Exp. Biol.* **11**, 2–20.
- Griffith, M. M. (1952). The structure and growth of the shoot apex in *Araucaria*. *Amer. J. Bot.* **39**, 253–263.
- Gulisashvili, V. Z. (1947). Periodichnost' i ritm rosta sredizemnomorskikh sozen kak priznak rodstvennoy svyazi ikh mezhdu soboy. *Dokl. Akad. Nauk SSSR* **57**, 955–158; *Forest. Abstr.* **9**, No. 2148 (1948).
- Gunckel, J. E., and Thimann, K. V. (1949). Studies of development in long shoots and short shoots of *Ginkgo biloba* L. III. Auxin production in shoot growth. *Amer. J. Bot.* **36**, 145–151.
- Gunckel, J. E., and Wetmore, R. H. (1946a). Studies of development in long shoots and short shoots of *Ginkgo biloba* L. I. The origin and pattern of development of the cortex, pith, and procambium. *Amer. J. Bot.* **33**, 285–295.
- Gunckel, J. E., and Wetmore, R. H. (1946b). Studies of development in long shoots and short shoots of *Ginkgo biloba* L. II. Phyllotaxis and the organization of the primary vascular system; primary phloem and primary xylem. *Amer. J. Bot.* **33**, 532–543.

- Gunckel, J. E., Thimann, K. V., and Wetmore, R. H. (1949). Study of development in long shoots and short shoots of *Ginkgo biloba* L. IV. Growth habit, shoot expression and the mechanism of its control. *Amer. J. Bot.* **36**, 309–318.
- Guzhev, Y. L. (1958). Izmenenie srokov nachala vegetatsii u seyantsev plotovykh Kultur i duba putem regulirovaniya vlazhnosti pochvy. *Iv. Akad. Nauk SSSR, Ser. Biol.* pp. 104–111.
- Haas, W. (1969). Die Aminosäurenzusammen-setzung der Proteine von Sonnen-und Schattenblättern der Blutbuche (*Fagus sylvatica* L. cv. *Atropunicea*). *Planta* **87**, 95–101.
- Haas, W., Barth, K., and Kausch, W. (1968). Spurenelemente und Nährelemente in Sonnen- und Schattenblättern der Blutbuche (*Fagus sylvatica* L. cv. *Atropunicea*). *Z. Pflanzenphysiol.* **58**, 385–394.
- Haasis, F. W. (1931). Notes on the growth period of Monterey pine leaves. *Bull. Ecol. Soc. Amer.* **12**.
- Habeck, J. R. (1958). White cedar (*Thuja occidentalis*) ecotypes in Wisconsin. *Ecology* **39**, 457–463.
- Hahne, B. (1926). The origin of secondary dormant buds in deciduous fruit trees. *Univ. Calif. Pub. Berkeley, Bot.* **13**, 125–127.
- Haig, I. T., David, K. P., and Weidmann, R. H. (1941). Natural regeneration in the western white pine type. *U.S. Dep. Agr., Tech. Bull.* **769**.
- Hale, J. D., and Clermont, L. P. (1963). Influence of prosenchyma cell-wall morphology on basic physical and chemical characteristics of wood. *J. Polymer Sci. Part C No. 2*, 253–261.
- Hall, G. S. (1965). Wood increment and crown distribution relationships in red pine. *Forest Sci.* **11**, 438–448.
- Hallaway, M. (1960). Ageing in higher plants. *New Sci.* **8**, 1243–1245.
- Haller, J. R. (1962). Variation in needle number in *Pinus ponderosa*. *Amer. J. Bot.* **49**, Part 2, 675–676.
- Hanover, J. W. (1963). Geographic variation in ponderosa pine leader growth. *Forest Sci.* **9**, 86–95.
- Hansen, P. (1967a). ^{14}C -studies on apple trees. I. The effect of the fruit on the translocation and distribution of photosynthates. *Physiol. Plant.* **20**, 382–391.
- Hansen, P. (1967b). ^{14}C -studies on apple trees. II. Distribution from top and base leaves from extension shoots. *Physiol. Plant.* **20**, 720–725.
- Harler, C. R. (1964). "The Culture and Marketing of Tea." Oxford Univ. Press, London and New York.
- Harris, J. M. (1954). Heartwood formation in *Pinus radiata* (D. Don.). *New Phytol.* **53**, 517–524.
- Harrison, B. J., and McLeish, J. (1954). Abnormalities of stored seed. *Nature (London)* **173**, 593–594.
- Hart, J. H. (1965). Formation of discolored sapwood in three species of hardwoods. *Mich. Agr. Exp. Sta., Quart. Bull.* **48**, 101–116.
- Hart, J. H. (1968). Morphological and chemical differences between sapwood, discolored sapwood, and heartwood in black locust and osage orange. *Forest Sci.* **14**, 334–338.
- Hasegawa, M., and Shiroya, M. (1967). Translocation and transformation of sucrose in the wood of *Prunus yedoensis*. *IUFRO Meet. 1967*, Sec. 41.
- Hatano, K. (1963). Respiration of germinating pine seeds. *Plant Cell Physiol.* **4**, 129–134.
- Hatano, K. (1967). Detection of coumarin and o-coumaric acid in the seed coats of *Pinus densiflora*. *J. Jap. Forest Soc.* **49**, 205–207.
- Hatano, K., and Asakawa, S. (1964). Physiological processes in forest tree seeds during maturation, storage, and germination. *Int. Rev. Forest Res.* **1**, 279–323.

- Hatano, K., and Nakamura, Y. (1967). Detection of coumarin and phenolic compounds in the seed coats of *Pinus* spp. and *Sciadopitys verticillata* Sieb. et Zucc. *J. Jap. Forest Soc.* **49**, 231–233.
- Hatcher, E. S. J. (1959). Auxin relations of the woody shoot. *Ann. Bot. (London)* [N.S.] **23**, 409–423.
- Hatert, J. (1958). Premières observations sur le système radiculaire du caïeiro robusta. *Bull. Agr. Congo Belge* **49**, 461–482.
- Head, G. C. (1966). Estimating seasonal changes in the quantity of white unshrubberized root on fruit trees. *J. Hort. Sci.* **41**, 197–206.
- Head, G. C. (1968). Seasonal changes in the diameter of secondarily thickened roots of fruit trees in relation to growth of other parts of the tree. *J. Hort. Sci.* **43**, 275–282.
- Hedlund, A. (1964). Epicormic branching in north Louisiana delta. *U.S. Forest Serv., Res. Note SO-8*.
- Heiberg, S. O., and White, D. P. (1951). Potassium deficiency of reforested pine and spruce stands in northern New York. *Soil Sci. Soc. Amer., Proc.* **15**, 369–376.
- Heinicke, A. J., and Childers, N. F. (1937). The daily rate of photosynthesis, during the growing season of 1935, of a young apple tree of bearing age. *Cornell Univ., Agr. Exp. Sta., Mem.* **201**.
- Heit, C. E. (1961). Abnormal germination during laboratory testing in coniferous tree seeds. *Proc. Int. Seed Test. Assoc.* **26**, 419–427.
- Hellmers, H., and Bonner, J. (1960). Photosynthetic limits of forest tree yields. *Proc. Soc. Amer. Forest.* 1959 pp. 32–35.
- Hemberg, T. (1949). Growth-inhibiting substances in terminal buds of *Fraxinus*. *Physiol. Plant.* **2**, 37–44.
- Hemberg, T. (1961). Biogenous inhibitors. *Encycl. Plant Physiol.* **14**, 1162–1184.
- Hendershott, C. H., and Bailey, L. F. (1955). Growth inhibiting substances in dormant flower buds of peach. *Proc. Amer. Soc. Hort. Sci.* **65**, 85–92.
- Hendershott, C. H., and Walker, D. R. (1959a). Identification of a growth inhibitor from extracts of dormant peach flower buds. *Science* **130**, 798–900.
- Hendershott, C. H., and Walker, D. R. (1959b). Seasonal fluctuation in quantity of growth substances in resting peach flower buds. *Proc. Amer. Soc. Hort. Sci.* **74**, 121–129.
- Herman, F. R. (1956). Growth and phenological observations of Arizona junipers. *Ecology* **37**, 193–195.
- Higdon, R. J. (1950). The effects of insufficient chilling on peach varieties in South Carolina in the winter of 1948–49. *Proc. Amer. Soc. Hort. Sci.* **55**, 236–238.
- Higuchi, T., and Fukazawa, K. (1966). Study on the mechanism of heartwood formation. III. On the role of phenylalanine deaminase. *J. Jap. Wood Res. Soc.* **12**, 135–139.
- Hilgeman, R. H., Dunlap, J. A., and Sharples, G. C. (1967). Effect of time of harvest on Valencia oranges, leaf carbohydrate content and subsequent set of fruit. *Proc. Amer. Soc. Hort. Sci.* **90**, 110–115.
- Hillis, W. E. (1956). Leucoanthocyanins as the possible precursors of extractives in woody tissues. *Aust. J. Biol. Sci.* **9**, 263–280.
- Hillis, W. E., ed. (1962). "Wood Extractives and their Significance to the Pulp and Paper Industries." Academic Press, New York.
- Hillis, W. E. (1965). Biological aspects of heartwood formation. I.U.F.R.O. Meet 1965. Sect. 41.
- Hillis, W. E. (1968). Chemical aspects of heartwood formation. *Wood Sci. Technol.* **2**, 241–259.
- Hillis, W. E., and Carle, A. (1962). The origin of the wood and bark polyphenols of *Eucalyptus* species. *Biochem. J.* **82**, 435–439.

- Hillis, W. E., and Hasegawa, M. (1963). The formation of polyphenols in trees. I. The administration of ^{14}C glucose and subsequent distribution of radioactivity. *Phytochemistry* **2**, 195–199.
- Hillis, W. E., Humphreys, F. H., Bamber, R. K., and Carle, A. (1962). Factors influencing the formation of phloem and heartwood phenols. *Holzforschung* **16**, 114–121.
- Hobbs, C. H. (1944). Studies on mineral deficiency in pine. *Plant Physiol.* **19**, 590–602.
- Holdsworth, M. (1963). Intermittent growth of the mango tree. *J. West Afr. Sci. Assoc.* **7**, 163–171.
- Holman, R. M., and Robbins, W. W. (1934). "A Textbook of General Botany." Wiley, New York.
- Holst, M. H., and Yeatman, C. W. (1961). A provenance study in *Pinus banksiana* Lamb. *Recent Advan. Bot.* Part 2, 1612–1616.
- Holtum, R. E. (1931). On periodic leaf-change and flowering of trees in Singapore. *Gard. Bull. Singapore* **5**, 173–206.
- Holtum, R. E. (1940). On periodic leaf changes and flowering of trees at Singapore. II. *Gard. Bull. Singapore* **11**, 119–175.
- Hopping, G. R. (1951). Forest entomology in relation to silviculture in Canada. Part V. The mountain pine beetle. *Forest Chron.* **27**, 26–29.
- Hopping, G. R., and Beall, G. (1948). The relation of diameter of lodgepole pine to incidence of attack by the bark beetle *Dendroctonus monticolae* Hopkins. *Forest. Chron.* **24**, 141–145.
- Hopping, G. R., and Mather, W. G. (1945). Observations on outbreaks and control of mountain pine beetle in the lodgepole pine stands of western Canada. *Forest. Chron.* **21**, 98–108.
- Horton, J. S., Mounts, F. C., and Kraft, J. M. (1960). Seed germination and seedling establishment of phreatophyte species. U.S. Forest Serv. Rocky Mt. For. Range Exp. Sta. Sta. Pap. 48.
- Horton, K. W. (1958a). Rooting habits of lodgepole pine. *Can., Forest Res. Div., Tech. Note* **67**.
- Horton, K. W. (1958b). Seasonal leader growth of lodgepole pine in the subalpine forest of Alberta. *Forest. Chron.* **34**, 382–386.
- Hoshaw, R. W., and Guard, A. T. (1949). Abscission of marcescent leaves of *Quercus palustris* and *Q. coccinea*. *Bot. Gaz.* **110**, 587–593.
- Hosner, J. (1957). Effects of water upon the seed germination of bottomland trees. *Forest Sci.* **3**, 67–70.
- Huberman, M. A. (1940). Normal growth and development of southern pine seedlings in the nursery. *Ecology* **21**, 323–334.
- Humphries, E. C., and Wheeler, A. W. (1963). The physiology of leaf growth. *Annu. Rev. Plant Physiol.* **14**, 385–410.
- Illick, J. (1928). Pennsylvania trees. *Pa., Dep. Forests Waters, Bull.* **11**.
- Ingestad, T. (1959). Studies on the nutrition of forest tree seedlings. II. *Physiol. Plant.* **12**, 568–593.
- Irgens-Moller, H. (1960). Localized genotypic variation in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). *Bull. Ecol. Soc. Amer.* **41**, 48.
- Iroshnikov, A. I., Lebkov, V. F., and Cherednikova, Y. S. (1966). Fruit bearing of stone pine forests of the Lena-Ilion interfluvial area. *Tr. Inst. Lesa Drev. Akad. Nauk SSSR, Sib. Otd.* **62**, 35–71 (Engl. Transl.)
- Irving, R. M. (1969). Characterization and role of an endogenous inhibitor in the induction of cold hardiness in *Acer negundo*. *Plant Physiol.* **44**, 801–805.
- Irving, R. M., and Lanphear, F. O. (1967a). Environmental control of cold hardiness in woody plants. *Plant Physiol.* **42**, 1191–1196.

- Irving, R. M., and Lanphear, F. O. (1967b). The long day leaf as a source of cold hardiness inhibitors. *Plant Physiol.* **42**, 1384–1388.
- Irving, R. M., and Lanphear, F. O. (1968). Regulation of cold hardiness in *Acer negundo*. *Plant Physiol.* **43**, 9–13.
- Isonogle, I. T. (1944). Effects of controlled shading upon the development of leaf structure in two deciduous species. *Ecology* **25**, 404–413.
- Jackson, G. A. D., and Blundell, J. B. (1963). Germination in *Rosa*. *J. Hort. Sci.* **38**, 310–320.
- Jackson, L. W. R. (1959). Relation of pine overstory opening diameter to growth of pine reproduction. *Ecology* **40**, 478–480.
- Jackson, L. W. R. (1967). Effect of shade on leaf structure of deciduous tree species. *Ecology* **48**, 498–499.
- Jacobs, M. R. (1938). Notes on pruning *Pinus radiata*. I. Observations on features which influence pruning. *Aust., Commonw. Forest Bur., Bull.* **23**, 88–91.
- Jacobs, M. R. (1955). Growth habits of the eucalypts. *Aust., Forest Timber Bur.*, 1–262.
- Jacquot, C. (1955). Action du meso-insositol et des l'adenine sur la formation de bourgeons par le tissu cambial d'*Ulmus campestris* cultive *in vitro*. *C. R. Acad. Sci.* **233**, 815–817.
- Jane, F. W. (1956). "The Structure of Wood." Black, London.
- Jane, F. W. (1963). Botanical aspects of wood science. *Vistas Bot.* **2**, 1–35.
- Janisevskii, D. E., and Pervuhina, N. V. (1941). Prolonging the life of seed which lose their viability quickly. *Sov. Bot.* **3**, 80–86; *Biol. Abstr.* **21**, 25989 (1947).
- Jarvis, P. G., and Jarvis, M. S. (1963). The water relations of tree seedlings. I. Growth and water use in relation to soil water potential. *Physiol. Plant.* **16**, 215–235.
- Johnson, E. D. (1926). A comparison of the juvenile and adult leaves of *Eucalyptus globulus*. *New Phytol.* **25**, 202–212.
- Johnson, M. A. (1951). The shoot apex in gymnosperms. *Phytomorphology* **1**, 188–204.
- Jones, H. A. (1920). Physiological study of maple seeds. *Bot. Gaz.* **69**, 127–152.
- Jones, L., and Havel, K. (1968). Effect of methyl bromide treatments on several species of coniferous seed. *J. Forest.* **66**, 859–860.
- Jones, L., Barber, J. C., and Mabry, J. E. (1964). Effect of methyl bromide fumigation on germination of longleaf, slash and loblolly pine seed. *J. Forest.* **62**, 737–739.
- Jones, L. (1961). Effect of light on germination of forest tree seeds. *Proc. Int. Seed Test. Assoc.* **26**, 437–452.
- Jorgensen, E. (1961). The formation of pinosylvin and its monomethyl ether in the sapwood of *Pinus resinosa* Ait. *Can. J. Bot.* **39**, 1765–1772.
- Jorgensen, E. (1962). Observations on the formation of protection wood. *Forest. Chron.* **38**, 292–294.
- Jump, J. A. (1938). A study of forking in red pine. *Phytopathology* **28**, 798–811.
- Jurasek, L. (1956). Vznik thyl v bukovem dreve. *Drev. Vysk.* **1**, 7–15.
- Jurasek, L. (1958). Pusobeni teploty a vlhkosti dreva na tvorbu thyl u buku. *Drev. Vysk.* **3**, 5–13.
- Jurasek, L. (1960). Studium osmotickych tlaku v bukovem dreve a moznost ochrany proti vzniku thyl. *Drev. Vysk.* **5**, 129–135.
- Kalela, E. K. (1950). Männikoiden fa kuusikoiden juurisuhteista it. *Acta. Forest. Fenn.* **57**, 1–68.
- Kaszkurewicz, A., and Fogg, P. J. (1967). Growing seasons of cottonwood and sycamore as related to geographic and environmental factors. *Ecology* **48**, 785–793.
- Kaufmann, M. R. (1968). Water relations of pine seedlings in relation to root and shoot growth. *Plant Physiol.* **43**, 281–288.
- Kawase, M. (1961). Growth substances related to dormancy in *Betula*. *Proc. Amer. Soc. Hort. Sci.* **78**, 532–544.

- Keen, F. P. (1936). Relative susceptibility of ponderosa pines to bark beetle attack. *J. Forest.* **34**, 919–927.
- Keen, F. P. (1943). Ponderosa pine tree classes redefined. *J. Forest.* **41**, 249–253.
- Kefford, N. P. (1955). The growth substances separated from plant extracts by chromatography. I. *J. Exp. Bot.* **6**, 129–151.
- Kefford, N. P., and Goldacre, P. L. (1961). The changing concept of auxin. *Am. J. Bot.* **48**, 643–650.
- Kemmer, E. (1962). Stadienversuche bei Kernobstsämlingen. *Erwerbostbach* **4**, 161–174.
- Kessler, B., Bak, R., and Cohen, A. (1959). Flowering in fruit trees and annual plants as affected by purines, pyrimidines, and triiodobenzoic acid. *Plant Physiol.* **12**, 1–7.
- Kienholz, R. (1934). Leader, needle, cambial, and root growth of certain conifers and their relationships. *Bot. Gaz.* **96**, 73–92.
- Kienholz, R. (1941). Seasonal course of height growth in some hardwoods in Connecticut. *Ecology* **22**, 249–258.
- Knowles, R. H., and Zalic, S. (1958). Effect of temperature treatment and of a native inhibitor on seed dormancy and of cotyledon removal on epicotyl growth in *Viburnum trilobum*. *Can. J. Bot.* **35**, 561–566.
- Koch, W., and Keller, T. (1961). Der Einfluss von Alterung und Abschneiden auf den CO₂-Gaswechsel von Pappelblättern. *Ber. Deut. Bot. Ges.* **74**, 64–74.
- Koller, D., Mayer, A. M., Poljakoff-Mayber A., and Klein, S. (1962). Seed germination. *Annu. Rev. Plant Physiol.* **13**, 437–464.
- Kondo, T. (1964). On the wood enzyme. *J. Jap. Wood Res. Soc.* **10**, 43–48.
- Kondo, Y., and Ogasawara, R. (1962). Studies on auxins in the buds of *Pinus densiflora*. *Hokkaido Exp. Forest Res. Bull.* **21**, 317–322.
- Koran, Z., and Coté, W. A. (1965). The ultrastructure of tyloses. In "Cellular Ultrastructure of Woody Plants" (W. A. Coté, Jr., ed.), pp. 319–333. Syracuse Univ. Press, Syracuse, New York.
- Koriba, K. (1958). On the periodicity of tree growth in the tropics, with reference to the mode of branching, the leaf fall, and the formation of the resting bud. *Gard. Bull.* **17**, 11–81.
- Kormanik, P. P., and Brown, C. L. (1964). Origin of secondary dormant buds in sweetgum. *U.S. Forest Serv. Res. Note SE-36*.
- Kormanik, P. P., and Brown, C. L. (1967). Root buds and the development of root suckers in sweetgum. *Forest Sci.* **13**, 338–345.
- Korodý, E. (1937). Studien am Spross-Vegetationspunkt von *Abies concolor*, *Picea excelsa*, und *Pinus montana*. *Beitr. Biol. Pflanz.* **25**, 23–59.
- Kosceev, A. L. (1952). Lesovodstvennoe znacenie pridatocnyh kornei drevesnyh porod. *Lesn. Hoz.* **5**, 48–50; *Forestry Abstr.* **16**, 3886 (1955).
- Kosceev, A. L. (1953). The silvicultural significance of adventitious roots on tree species in waterlogged clear-felled areas. *Dep. Forest. Ottawa*; transl. from *Tr. Inst. Les.* No. 13, 116–129.
- Kovalenko, M. P. (1960). Mnogohvojnost vtoricnyh (letnih) pogebov *Pinus silvestris* L. i *Pinus pallasiana* Lamb. na Wiznedneprovskih poskah. *Z. Bot.* **45**, 152–153.
- Kozłowski, T. T. (1949). Light and water in relation to growth and competition of Piedmont forest tree species. *Ecol. Monogr.* **19**, 207–231.
- Kozłowski, T. T. (1955). Tree growth, action and interaction of soil and other factors. *J. Forest.* **53**, 508–512.
- Kozłowski, T. T. (1958). Water relations and growth of trees. *J. Forest.* **56**, 498–502.
- Kozłowski, T. T. (1960). Some problems in the use of herbicides in forestry. *Proc. North Centr. Weed Contr. Conf.* **17**, 1–10.
- Kozłowski, T. T. (1961). The movement of water in trees. *Forest Sci.* **7**, 177–192.

- Kozlowski, T. T. (1962a). Photosynthesis, climate and growth of trees. In "Tree Growth" (T. T. Kozlowski, ed.), Chapter 8. Ronald Press, New York.
- Kozlowski, T. T., ed. (1962b). "Tree Growth." Ronald Press, New York.
- Kozlowski, T. T. (1963a). Characteristics and improvement of forest growth. *Advan. Front. Plant Sci.* **2**, 73-136.
- Kozlowski, T. T. (1963b). Growth characteristics of forest trees. *J. Forest.* **61**, 655-662.
- Kozlowski, T. T. (1964a). Shoot growth in woody plants. *Bot. Rev.* **30**, 335-392.
- Kozlowski, T. T. (1964b). "Water Metabolism in Plants." Harper, New York.
- Kozlowski, T. T. (1965). Variable toxicity of triazine herbicides. *Nature (London)* **205**, 104-105.
- Kozlowski, T. T. (1967). Growth and development of *Pinus resinosa* seedlings under controlled temperatures. *Advan. Front. Plant Sci.* **19**, 17-27.
- Kozlowski, T. T. (1968a). Water balance in shade trees. *Proc. 44th Int. Shade Tree Conf.* 1968, pp. 29-42.
- Kozlowski, T. T. (1968b). Soil water and tree growth. In "The Ecology of Southern Forests" (N. E. Linnartz, ed.), pp. 30-57. Louisiana State Univ. Press, Baton Rouge, Louisiana.
- Kozlowski, T. T., ed. (1968c). "Water Deficits and Plant Growth." Vol. I. Development, Control, and Measurement. Academic Press, New York.
- Kozlowski, T. T., ed. (1968d). "Water Deficits and Plant Growth." Vol. II. Plant Water Consumption and Response. Academic Press, New York.
- Kozlowski, T. T. (1969). Tree physiology and forest pests. *J. Forest.* **69**, 118-122.
- Kozlowski, T. T. (1970). Physiological implications in afforestation. *Proc. Sixth World Forestry Congress, (Madrid) 1966*, **2**, 1304-1316.
- Kozlowski, T. T., and Clausen, J. J. (1965). Changes in moisture contents and dry weights of buds and leaves of forest trees. *Bot. Gaz.* **126**, 20-26.
- Kozlowski, T. T., and Clausen, J. J. (1966). Shoot growth characteristics of heterophyllous woody plants. *Can. J. Bot.* **44**, 827-843.
- Kozlowski, T. T., and Gentile, A. C. (1958). Respiration of white pine buds in relation to oxygen availability and moisture content. *Forest Sci.* **4**, 147-152.
- Kozlowski, T. T., and Gentile, A. C. (1959). Influence of the seed coat on germination, water absorption and oxygen uptake of eastern white pine seed. *Forest Sci.* **5**, 389-395.
- Kozlowski, T. T., and Greathouse, T. E. (1970). Shoot growth characteristics of tropical pines. *Unasylva* (in press).
- Kozlowski, T. T., and Keller, T. (1966). Food relations of woody plants. *Bot. Rev.* **32**, 293-382.
- Kozlowski, T. T., and Kuntz, J. E. (1963). Effect of simazine, atrazine, propazine, and eptam on growth of pine seedlings. *Soil Sci.* **95**, 164-174.
- Kozlowski, T. T., and Sasaki, S. (1968a). Effects of direct contact of pine seeds or young seedlings with commercial formulations, active ingredients, or inert ingredients of triazine herbicides. *Can. J. Plant Sci.* **48**, 1-7.
- Kozlowski, T. T., and Sasaki, S. (1968b). Germination and morphology of red pine seeds and seedlings in contact with EPTC, CDEC, CDAA, 2,4-D and picloram. *Proc. Amer. Soc. Hort. Sci.* **93**, 655-662.
- Kozlowski, T. T., and Sasaki, S. (1970). Effects of herbicides on seed germination and development of young pine seedlings. In "Proc. Int. Symp. on Seed Physiology of Woody Plants," Poznan, Poland (1968), pp. 19-24.
- Kozlowski, T. T., and Scholtes, W. H. (1948). Growth of roots and root hairs of pine and hardwood seedlings in the Piedmont. *J. Forest.* **46**, 750-754.
- Kozlowski, T. T., and Torrie, J. H. (1964). Effects of hydrogen peroxide on germination of eastern white pine seed. *Advan. Front. Plant Sci.* **9**, 131-144.

- Kozlowski, T. T., and Torrie, J. H. (1965). Effect of soil incorporation of herbicides on seed germination and growth of pine seedlings. *Soil Sci.* **100**, 139-146.
- Kozlowski, T. T., and Ward, R. C. (1957a). Seasonal height growth of conifers. *Forest Sci.* **3**, 61-66.
- Kozlowski, T. T., and Ward, R. C. (1957b). Seasonal height growth of deciduous trees. *Forest Sci.* **3**, 168-174.
- Kozlowski, T. T., and Ward, R. C. (1961). Shoot elongation characteristics of forest trees. *Forest Sci.* **7**, 357-368.
- Kozlowski, T. T., and Winget, C. H. (1964). The role of reserves in leaves, branches, stems, and roots on shoot growth of red pine. *Amer. J. Bot.* **51**, 522-529.
- Kozlowski, T. T., Hughes, J. F., and Leyton, L. (1966). Patterns of water movement in dormant gymnosperm seedlings. *Biorheology* **3**, 77-85.
- Kozlowski, T. T., Sasaki, S., and Torrie, J. H. (1967a). Influence of temperature on phytotoxicity of triazine herbicides to pine seedlings. *Amer. J. Bot.* **54**, 790-796.
- Kozlowski, T. T., Sasaki, S., and Torrie, J. H. (1967b). Effects of temperature on phytotoxicity of monuron, picloram, CDEC, EPTC, CDAA, and sesone to young pine seedlings. *Silva Fenn.* **3.2**, 13-28.
- Krahmer, R. L., and Coté, W. A., Jr. (1963). Changes in coniferous wood cells associated with heartwood formation. *Tappi* **46**, 42-49.
- Krajicek, J. E. (1959). Epicormic branching in even-aged, undisturbed white oak stands. *J. Forest.* **57**, 372-373.
- Kramer, P. J. (1936). Effect of variation in length of day on growth and dormancy of trees. *Plant Physiol.* **11**, 127-137.
- Kramer, P. J. (1943). Amount and duration of growth of various species of tree seedlings. *Plant Physiol.* **18**, 239-251.
- Kramer, P. J. (1946). Absorption of water through suberized roots of trees. *Plant Physiol.* **21**, 37-41.
- Kramer, P. J. (1957). Some effects of various combinations of day and night temperatures and photoperiod on the height growth of loblolly pine seedlings. *Forest Sci.* **3**, 45-55.
- Kramer, P. J. (1958a). Photosynthesis of trees as affected by their environment. In "The Physiology of Forest Trees" (K. V. Thimann, ed.), Chapter 8. Ronald Press, New York.
- Kramer, P. J. (1958b). Thermoperiodism in trees. In "The Physiology of Forest Trees" (K. V. Thimann, ed.), Chapter 30. Ronald Press, New York.
- Kramer, P. J., and Bullock, H. C. (1966). Seasonal variations in the proportions of suberized and unsuberized roots of trees in relation to the absorption of water. *Amer. J. Bot.* **53**, 200-204.
- Kramer, P. J., and Decker, J. P. (1944). Relation between light intensity and rate of photosynthesis of loblolly pine and certain hardwoods. *Plant Physiol.* **19**, 350-358.
- Kramer, P. J., and Kozlowski, T. T. (1960). "Physiology of Trees." McGraw-Hill, New York.
- Krasilnikov, P. K. (1960). Adventitious roots and the root system of *Pinus sibirica* in the central Sayan Mountains. *Can., Forest Prod., Lab.* No. 12, transl. by H. Bernard from *Bot. Z.* **41**, 1194-1206 (1956).
- Kraybill, H. R., Sullivan, J. T., and Miller, L. P. (1931). Seasonal changes in the composition of Stayman apple trees. I. Carbohydrates. *Proc. Amer. Soc. Hort. Sci.* **27**, 206.
- Kriebel, H. B. (1957). Patterns of genetic variation in sugar maple. *Ohio, Agr. Exp. Sta., Res. Bull.* **791**, 1-56.
- Kriedemann, P. E. (1969). ^{14}C translocation in orange plants. *Aust. J. Agr. Res.* **20**, 291-300.

- Krueger, K. W. (1967). Nitrogen, phosphorus and carbohydrate in expanding and year-old Douglas-fir shoots. *Forest Sci.* **13**, 352-356.
- Kuroiwa, S. (1960). Ecological and physiological studies on the vegetation of Mt. Shimagare. IV. Some physiological functions concerning matter production in young *Abies* trees. *Bot. Mag. (Tokyo)* **73**, 133-141.
- Kuse, G. (1954). Bud inhibition and correlative growth of petiole in sweet potato stem. *Mem. Coll. Sci., Univ. Kyoto, Ser. B* **21**, 1/15.107.
- Lairand, D. E. (1963). About the cytochemistry of wood elements. *Drev. Vysk.* **1**, 1-11.
- Lang, A. (1965). Physiology of flower initiation. *Encycl. Plant Physiol.* **15**, Part 1, 1380-1536.
- Langlet, O. (1959a). A cline or not a cline—a question of Scots pine. *Silvae Genet.* **8**, 13-22.
- Langlet, O. (1959b). Norrlandstallens praktiska och systematiska avgränsning. *Sv. Skogs-vardsfoeren. Tidskr.* **57**, 425-436.
- Langlet, O. (1962). Ecological variability and taxonomy of forest trees. In "Tree Growth" (T. T. Kozlowski, ed.), Chapter 23. Ronald Press, New York.
- Langner, W. (1964). The origins of so-called juvenile forms in *Chamaecyparis*. *Silvae Genet.* **12**, 57-63.
- Lanner, R. M. (1964). Temperature and the diurnal rhythm of height growth in pines. *J. Forest.* **62**, 493-495.
- Lanner, R. M. (1966). The phenology and growth habits of pines in Hawaii. *U.S., Forest Serv., Res. Pap. PSW-29*.
- Larson, P. R. (1964). Contribution of different-aged needles to growth and wood formation of young red pines. *Forest Sci.* **10**, 224-238.
- Larson, P. R. (1969). Wood formation and the concept of wood quality. *Yale Univ. Sch. Forest. Bull.* **74**.
- Larson, P. R., and Gordon, J. C. (1969). Leaf development, photosynthesis, and ¹⁴C distribution in *Populus deltoides* seedlings. *Amer. J. Bot.* **56**, 1058-1066.
- Lasheen, A. M., and Blackhurst, H. T. (1956). Biochemical changes associated with dormancy and after-ripening of blackberry seeds. *Proc. Amer. Soc. Hort. Sci.* **67**, 331-340.
- Lawrence, W. H., and Rediske, J. H. (1962). Fate of sown Douglas-fir seed. *Forest Sci.* **8**, 210-218.
- Lentz, A. N. (1965). Unique culture of christmas trees. *J. Forest.* **63**, 841-844.
- Leopold, A. C. (1961). Senescence in plant development. *Science* **134**, 1727-1732.
- Leopold, A. C. (1964). "Plant Growth and Development." McGraw-Hill, New York.
- Leopold, A. C. (1967). The mechanism of foliar abscission. *Symp. Soc. Exp. Biol.* **21**, 507-516.
- Lerner, R. H., and Evenari, M. (1961). The nature of the germination inhibitor present in leaves of *Eucalyptus rostrata*. *Physiol. Plant.* **14**, 221-229.
- Leshem, B. (1965). The annual activity of intermediary roots of the Aleppo pine. *Forest Sci.* **11**, 291-298.
- Liashenko, N. I. (1958). Branching of dormant buds of shrubs. *Proc. Acad. Sci. USSR, Bot.* **120**, 139-140.
- Libbert, E. (1954a). Zur Frage nach der Natur der korrelativen Hemmung. *Flora (Jena)* **141**, 271-297.
- Libbert, E. (1954b). Das Zusammenwirken von Wuchs und Hemmstoffen bei der korrelativen Knospenhemmung. I. Mitt. *Planta* **44**, 286-318.
- Libbert, E. (1955a). Das Zusammenwirkung von Wuchs und Hemmstoffen bei der korrelativen Knospenhemmung. II. Mitt. *Planta* **45**, 68-81.

- Libbert, E. (1955b). Nachweis und chemische Trennung des Korrelationshemmstoffes und seiner Hemmstoffvorstufe. *Planta* **45**, 405–425.
- Libbert, E. (1955c). Die Hydrolyse des "Korrelationshemmstoffes" zu auxin. *Planta* **46**, 256–271.
- Lines, R., and Mitchell, A. F. (1966). Differences in phenology of Sitka spruce provenances. *Forest Bur. (London). Rep. Forest Res.* pp. 173–184.
- Lipe, W. N., and Crane, J. C. (1966). Dormancy regulation in peach seeds. *Science* **153**, 541–542.
- Lister, G. R., Slankis, V., Krotkov, G., and Nelson, C. D. (1967). Physiology of *Pinus strobus* L. seedlings grown under high or low soil moisture conditions. *Ann. Bot. (London)* [N.S.] **31**, 121–132.
- Little, C. H. A. (1970). Apical dominance in long shoots of white pine (*Pinus strobus*). *Can. J. Bot.* **48**, 239–253.
- Little, S., and Somes, H. A. (1956). Buds enable pitch and shortleaf pine to recover from injury. U.S. Forest Serv., Northeastern Forest Exp. Sta. Sta. Pap. 81.
- Little, S., and Somes, H. A. (1960). Sprouting of loblolly pine. *J. Forest.* **58**, 195–197.
- Littlefield, E. W. (1956). More on late-seasonal growth of red pine. *J. Forest.* **54**, 533.
- Lodewick, J. E. (1931). Some effects of irrigation and fertilization on the size of longleaf pine needles. *Forest Worker* **7**, 12–13.
- Logan, K. T. (1965). Growth of tree seedlings as affected by light intensity. I. White birch, yellow birch, sugar maple, and silver maple. *Can. Dep. Forest., Publ.* **1121**.
- Logan, K. T. (1966a). Growth of tree seedlings as affected by light intensity. II. Red pine, white pine, jack pine, and eastern larch. *Can., Dep. Forest., Publ.* **1160**.
- Logan, K. T. (1966b). Growth of tree seedlings as affected by light intensity. III. Basswood and white elm. *Can. Dep. Forest., Publ.* **1176**.
- Longman, K. A., and Wareing, P. F. (1958). Effect of gravity on flowering and shoot growth in Japanese larch (*Larix leptolepis* Murray). *Nature (London)* **182**, 379–381.
- Lotan, J. E., and Zahner, R. (1963). Shoot and needle responses of 20-year-old red pine to current soil moisture regimes. *Forest Sci.* **9**, 497–506.
- Lubbock, J. (1892). "Seedlings." Appleton, New York.
- Lückhoff, H. A. (1964). The natural distribution, growth, and botanical variation of *Pinus caribaea* Mor. and its cultivation in South Africa. *Ann. Univ. Stellenbosch* **39**, 1–160.
- Luckwill, L. C. (1952). Growth inhibiting and growth promoting substances in relation to the dormancy and afterripening of apple seeds. *J. Hort. Sci.* **27**, 53–67.
- Luckwill, L. C. (1959). The physiological relationships of root and shoot. *Sci. Hort.* **14**, 22–26.
- Lyford, W. H., and Wilson, B. F. (1964). Development of the root system of *Acer rubrum* L. *Harvard Forest Pap.* **10**.
- Lyr, H., and Hoffman, G. (1967). Growth rates and growth periodicity of tree roots. *Int. Rev. Forest. Res.* **2**, 181–206.
- Lyr, H., Polster, H., and Fiedler, H. J. (1967). "Gehölzphysiologie." Fischer, Jena.
- McCabe, R. A., and Labisky, R. F. (1959). Leader forking of red and white pines in plantations. *J. Forest.* **57**, 94–97.
- MacDaniels, L. H. (1953). Anatomical basis of socalled adventitious buds in apple. *N. Y. Agr. Exp. Sta., Mem.* **325**.
- MacDaniels, L. H., and Cowart, F. F. (1944). The development and structure of the apple leaf. *Cornell Univ., Agr. Exp. Sta., Mem.* **258**.

- MacDougall, D. T. (1938). "Tree Growth." *Chronica Botanica*, Waltham, Massachusetts.
- McGregor, W. H. D., and Kramer, P. J. (1963). Seasonal trends in rates of photosynthesis and respiration of loblolly pine. *Amer. J. Bot.* **50**, 760-765.
- MacHattie, L. B., and Horton, K. W. (1963). Influence of microclimates on mortality and growth of planted white spruce, jack pine and white pine. *Forest. Chron.* **39**, 301-312.
- McLaughlin, S. B., and Madgwick, H. A. I. (1968). The effects of position in crown on the morphology of needles of loblolly pine (*Pinus taeda* L.). *Amer. Midl. Natur.* **80**, 547-550.
- McNaughton, S. J. (1967). Genetic control of bud bursting in altitudinally diverse Cascade forest community samples. *Amer. Midl. Natur.* **77**, 528-532.
- Maini, J. S. (1966a). Apical growth of *Populus* spp. I. Sequential pattern of internode, bud and branch length of young individuals. *Can. J. Bot.* **44**, 615-622.
- Maini, J. S. (1966b). Apical growth of *Populus* spp. II. Relative growth potential of apical and lateral buds. *Can. J. Bot.* **44**, 1581-1590.
- Majid, A. (1954). Root systems of ash and sycamore (*Acer pseudoplatanus*) seedlings. *J. Oxford Univ. Forest Soc. Ser. 4* No. 2, 18-21.
- Maki, T. E. (1961). Some effects of fertilizers on loblolly pine. *Trans. 7th Int. Congr. Soil Sci.* 1960, Vol. 3, pp. 363-375.
- Marcus, A., and Feeley, J. (1964). Activation of protein synthesis in the imbibition phase of seed germination. *Proc. Nat. Acad. Sci. U.S.* **51**, 1075-1079.
- Marquis, D. A., Bjorkbom, J. C., and Yelenosky, G. (1964). Effect of seedbed condition and light exposure on paper birch regeneration. *J. Forest.* **62**, 876-881.
- Marrero, J. (1943). A seed storage study of some tropical hardwoods *Carib. Forest.* **4**, 99-106.
- Marth, P. C., Audia, W. V., and Mitchell, J. W. (1956). Effects of gibberellic acid on growth and development of plants of various genera and species. *Bot. Gaz.* **118**, 106-111.
- Martin, J. T. (1966). The cuticles of plants. *NAAS Quart. Rev.* **72**, 139-144.
- Mattoon, W. R. (1908). The sprouting of shortleaf pine in the Arkansas National Forest. *Forest. Quart.* **6**, 158-159.
- Mayer, A. M., and Poljakoff-Mayber, A. (1963). "The Germination of Seeds." Macmillan, New York.
- Mergen, F., and Koerting, L. E. (1957). Initiation and development of flower primordia in slash pine. *Forest Sci.* **3**, 145-155.
- Merrill, S., and Kilby, W. W. (1952). Effect of cultivation, irrigation, fertilization and other cultural treatments on growth of newly planted tung trees. *Proc. Amer. Soc. Hort. Sci.* **59**, 69-81.
- Metcalf, W. (1924). Artificial reproduction of redwood. *J. Forest.* **22**, 873-893.
- Meyer, B. S., and Anderson, D. B. (1952). "Plant Physiology." Van Nostrand, Princeton, New Jersey.
- Meyer, M. M., and Tukey, H. B., Jr. (1965). Nitrogen, phosphorus, and potassium plant reserves and the spring growth of *Taxus* and *Forsythia*. *Proc. Amer. Soc. Hort. Sci.* **87**, 537-544.
- Migita, K., Kawana, A., and Takahashi, M. (1956). Absorption of water by the seeds of Japanese red pine (*Pinus densiflora*) in the aqueous media with various concentrations of oxygen. *J. Jap. Forest. Soc.* **38**, 465-466.
- Mikola, P. (1950). Puiden kasvun vaihteluista ja niden merkityksestä kasvututkimuksissa. *Comm. Inst. Forest. Fenn.* **385**, 1-131.
- Mikola, P. (1951). Kasvun luonnollinen kehitys. *Eripainos Metsät. Aikakauslehdestä* **2**, 1-4.

- Mikola, P. (1962). Temperature and tree growth near the northern timber line. In "Tree Growth" (T. T. Kozlowski, ed.), Chapter 16. Ronald Press, New York.
- Mikulka, B. (1955). Spät- und frühreibende Buchen im Sihlwald. *Schweiz. Fortsw.* **106**, 666-670.
- Millington, W. F. (1963). Shoot tip abortion in *Ulmus americana*. *Amer. J. Bot.* **50**, 371-378.
- Milthorpe, F. L., ed. (1956). "The Growth of Leaves." Butterworth, London and Washington, D.C.
- Minckler, L. S., and Woerheide, J. D. (1968). Weekly height growth of cottonwood. *Forest Sci.* **14**, 212-222.
- Mirov, N. T. (1943). Storage and germination of California cork oak acorns. *Calif. Forest Range Exp. Sta., Res. Note* **36**.
- Mirov, N. T. (1944). Possible relation of linolenic acid to the longevity and germination of pine seed. *Nature (London)* **154**, 218-219.
- Mirov, N. T., Duffield, J. W., and Liddicote, A. R. (1952). Altitudinal races of *Pinus ponderosa*—a 12-year progress report. *J. Forest.* **50**, 825-831.
- Mochizuki, T., and Hanada, S. (1957). The anisophily on the lateral shoots of apple trees and the effect of soil moisture. *Bull Fac. Agr., Hirosaki Univ.* **3**, 1-8.
- Mochizuki, T., and Hanada, S. (1958). The effect of nitrogen on the formation of the anisophily on the terminal shoots of apple trees. *Soil Plant Food (Tokyo)* **4**, 68-74.
- Molisch, H. (1922). "Pflanzenphysiologie als Theorie der Gärtnerie Ed." 5 Fischer, Jena.
- Molisch, H. (1938). "The Longevity of Plants." Science Press, Lancaster, Pennsylvania.
- Möller, C. M., Müller, D., and Nielsen, J. (1954). Graphic representation of dry matter production of European beech. *Det. Forstl. Forsøgsrv. Danmark.* **21**, 327-335.
- Monselise, S. P. (1951). Light distribution in citrus trees. *Bull. Res. Council Isr.* **1**, 36-53.
- Moorby, J., and Wareing, P. F. (1963). Aging in woody plants. *Ann. Bot. (London)* [N.S.] **27**, 291-308.
- Moore, K. G. (1965). Senescence in leaves of *Acer pseudoplatanus* L. and *Parthenocissus tricuspidata* Planch. I. Changes in some leaf constituents during maturity and senescence. *Ann. Bot. (London)* [N.S.] **29**, 433-444.
- Moore, K. G. (1966). Senescence in leaves of *Acer pseudoplatanus* L. and *Parthenocissus tricuspidata* Planch. II. Changes in potassium and sodium content in leaves and leaf discs of *Acer*. *Ann. Bot. (London)* [N.S.] **30**, 683-699.
- Morel, G. (1946). Action de l'acide parthothénique sur la croissance des tissus d'Aubepine. *C.R. Acad. Sci.* **223**, 166-168.
- Mork, E. (1941). Om sambandet mellom temperatur og Nekst. *Medd. Nor. Skogforsoksv.* **8**, 1-89.
- Motley, J. A. (1949). Correlation of elongation in white and red pine with rainfall. *Butler Univ. Bot. Stud.* **9**, 1-8.
- Mounts, B. T. (1932). The development of foliage leaves. *Stud. Nat. Hist. Univ. Iowa* **14**, 1-19.
- Muelder, D. W., and Schaeffer, R. (1962). On the correlation between weather and annual growth layers in trees, a contribution to the theory. *Proc. 13th Int. Union Forest Res. Organ., 1961*, Vol. 1, Part 2, pp. 21-24.
- Murashige, T. (1966). The deciduous behavior of a tropical plant, *Plumeria acuminata*. *Physiol. Plant.* **19**, 348-355.
- Nanda, K. K., and Purohit, A. N. (1964a). Effect of gibberellin on forest plants. I. Rate of extension growth in seedlings of *Salmania malabarica*. Schott. and Endl. *Indian J. Plant Physiol.* **7**, 35-47.
- Nanda, K. K., and Purohit, A. N. (1964b). Effect of gibberellin on forest plants. II. Internodal growth in seedlings of *Salmania malabarica* Schott. and Endl. *Indian J. Plant Physiol.* **7**, 57-70.

- Nanda, K. K., and Purohit, A. N. (1965). Effect of gibberellin on mobilization of reserve food and its correlation with extension growth. *Planta* **66**, 121-125.
- Neuwirth, G. (1959). Der CO₂-Stoffwechsel einiger Koniferen während des Knospen-austriebes. *Biol. Zentralbl.* **78**, 559-584.
- Newman, I. V. (1961). Pattern in the meristems of vascular plants. II. A review of shoot apical meristems of gymnosperms, with comments on apical biology and taxonomy and a statement of some fundamental concepts. *Proc. Linn. Soc. N.S.W.* **86**, 9-59.
- Nienstaedt, H., and Olson, J. S. (1961). Effects of photoperiod and seed source on seedling growth of eastern hemlock. *Forest Sci.* **7**, 81-96.
- Nitsch, J. P. (1957a). Growth responses of woody plants to photoperiodic stimuli. *Proc. Amer. Soc. Hort. Sci.* **70**, 512-525.
- Nitsch, J. P. (1957b). Photoperiodism in woody plants. *Proc. Amer. Soc. Hort. Sci.* **70**, 526-544.
- Nixon, R. W., and Wedding, R. T. (1956). Age of date leaves in relation to efficiency of photosynthesis. *Proc. Amer. Soc. Hort. Sci.* **67**, 265-269.
- Njoku, E. (1963). Seasonal periodicity in the growth and development of some forest trees in Nigeria. *J. Ecol.* **59**, 617-624.
- Njoku, E. (1964). Seasonal periodicity in the growth and development of some forest trees in Nigeria. II. Observations on seedlings. *J. Ecol.* **52**, 19-26.
- Noelle, W. (1910). Studien zur vergleichenden Anatomie und Morphologie der Konifernwurzeln mit Rücksicht auf die Systematik. *Bot. Z.* **68**, 169-266.
- Nyman, B. (1961). Effect of red and far red irradiation on the germination process in seeds of *Pinus sylvestris* L. *Nature (London)* **191**, 1219-1220.
- Ogasawara, R. (1960). Physiological studies of adventitious roots formation in *Pinus densiflora*. I. Changes in concentrations of growth substances with the growth of the tree. *J. Jap. Forest. Soc.* **42**, 356-358.
- Ogasawara, R. (1961a). Studies on auxins and inhibitors in *Pinus thunbergii*. *J. Jap. Forest. Soc.* **43**, 50-54.
- Ogasawara, R. (1961b). Studies on auxins and inhibitors in the buds of *Pinus strobus*. *J. Jap. Forest. Soc.* **43**, 307-310.
- Oland, K. (1963). Changes in the content of dry matter and major nutrient elements of apple foliage during senescence and abscission. *Physiol. Plant.* **16**, 682-694.
- Olofinboba, M. O. (1969). Seasonal variations in the carbohydrates in the xylem of *Antiaris africana*. *Ann. Bot. (London)* [N.S.] **33**, 339-349.
- Olson, J. S., Stearns, F., and Nienstaedt, A. (1959). Eastern hemlock seeds and seedlings. Response to photoperiod and temperature. *Conn., Agr. Exp. Sta., New Haven, Bull.* **620**.
- Ooyama, N. (1954). The growth inhibiting substances contained in the leaf-litter of the trees. I. The inhibiting effect on germination of the coniferous seeds. *J. Jap. Forest. Soc.* **36**, 38-41.
- Ordin, L. (1958). The effect of water stress on the cell wall metabolism of plant tissue. *Radioisotopes Sci. Res. Proc. Int. Conf.*, 1957 Vol. IV, pp. 553-564.
- Ordin, L. (1960). Effect of water stress on cell wall metabolism of *Avena coleoptile* tissue. *Plant Physiol.* **35**, 443-450.
- Osborne, D. J. (1955). Acceleration of abscission by a factor produced in senescent leaves. *Nature (London)* **176**, 1161-1163.
- Osborne, D. J. (1958). The role of 2,4,5-T butyl ester in the control of leaf abscission in some tropical woody species. *Trop. Agr. (London)* **35**, 145-158.
- Osborne, D. J. (1959). Control of leaf senescence by auxins. *Nature (London)* **183**, 1459-1460.
- Osborne, D. J. (1962). Effect of kinetin on protein and nucleic acid metabolism in *Xanthium* leaves during senescence. *Plant Physiol.* **37**, 595-602.

- Osborne, D. J. (1965). Interactions of hormonal substances in the growth and development of plants. *J. Sci. Food Agr.* **16**, 1-13.
- Osborne, D. J. (1968). Defoliation and defoliants. *Nature (London)* **219**, 564-567.
- Osborne, D. J., and Hallaway, M. (1960a). Auxin control of protein levels in detached autumn leaves. *Nature (London)* **188**, 240-241.
- Osborne, D. J., and Hallaway, M. (1960b). The role of auxins in the control of leaf senescence. Some effects of local applications of 2,4-dichlorophenoxyacetic acid on carbon and nitrogen metabolism. In "Plant Growth Regulation" (W. Klein, ed.), pp. 329-340. Iowa State Univ. Press, Ames, Iowa.
- Osborne, D. J., and Hallaway, M. (1964). The auxin, 2,4-dichlorophenoxyacetic acid as a regulator of protein synthesis and senescence in detached leaves of *Prunus*. *New Phytol.* **63**, 334-347.
- Ostretkov, M. Y. (1957). The rate of photosynthesis in pine needles. Vsesoyuz. konf. pofotozintezu. *Prob. Photosyn. 2nd Rep. All-Union Conf. Photosyn. 1957* V2 915-920 45/v965 Ae; transl. from *Probl. Fotosin., Dokl. Vses. 2nd Konf. Fotosin.*, 1957.
- Ovington, J. D. (1957). Dry matter production by *Pinus sylvestris* L. *Ann. Bot. (London) [N.S.]* **21**, 287-314.
- Ovington, J. D. (1958). Some biological considerations of forest production. In "The Biological Productivity of Britain," pp. 1-18. Inst. Biol., London.
- Ovington, J. D., and Madgwick, H. A. I. (1959). The growth and composition of mature stands of birch. I. Dry matter production. *Plant Soil* **10**, 271-283.
- Ovington, J. D., and Pearsall, W. H., (1956). Production ecology 2. Estimates of average production by trees. *Oikos* **7**, 202-205.
- Ovington, J. D., Heitkamp, D., and Lawrence, D. B. (1963). Plant biomass and productivity of prairie, savanna, oakwood, and maize ecosystems. *Ecology* **44**, 52-63.
- Owens, J. N. (1968). Initiation and development of leaves in Douglas fir. *Can. J. Bot.* **46**, 271-278.
- Owston, P. W. (1968). Multiple flushing in eastern white pine. *Forest Sci.* **14**, 66-67.
- Owston, P. W. (1969). The shoot apex in eastern white pine: Its structure, seasonal development, and variation within the crown. *Can. J. Bot.* **47**, 1181-1188.
- Panshin, A. J., De Zeeuw, C., and Brown, H. P. (1964). "Textbook of Wood Technology." Vol. I. McGraw-Hill, New York.
- Parke, R. V. (1959). Growth periodicity and the shoot tip of *Abies concolor*. *Amer. J. Bot.* **46**, 110-118.
- Parke, R. V. (1963). Initial vascularization of the vegetative shoot of *Abies concolor*. *Amer. J. Bot.* **50**, 464-469.
- Parker, J. (1954). Available water in stems of some Rocky Mountain conifers. *Bot. Gaz.* **115**, 380-385.
- Parker, J. (1963). Cold resistance in woody plants. *Bot. Rev.* **29**, 123-201.
- Parker, J. (1965). Mineral deficiencies. *Advan. Front. Plant Sci.* **12**, 181-222.
- Parker, J. (1969). Further studies of drought resistance in woody plants. *Bot. Rev.* **35**, 317-371.
- Passecker, F. (1952). Geschlechtsreife, Blühwilligkeit und Senilität bei holzigen Gewächsen. *Zuechter* **22**, 26-33.
- Patton, R. F. (1961). The effect of age upon susceptibility of eastern white pine to infection by *Cronartium ribicola*. *Phytopathology* **51**, 429-434.
- Patton, R. F. (1962). Prospect of disease problems in plantations. *Proc. Soc. Amer. Forest.* **1961**, 27-33.
- Patton, R. F., and Riker, A. J. (1958). Rooting cuttings of white pine. *Forest Sci.* **4**, 116-126.

- Pauley, S. S., and Perry, T. O. (1954). Ecotypic variation of the photoperiodic response in *Populus*. *J. Arnold Arboretum Harvard Univ.* **35**, 167-188.
- Pauley, S. S., Spurr, S. H., and Whitmore, F. H. (1955). Seed source trials of eastern white pine. *Forest Sci.* **1**, 244-256.
- Pearson, G. A. (1918). The relation between spring precipitation and height growth of western yellow pine saplings in Arizona. *J. Forest.* **16**, 677-689.
- Penfold, A. R., and Willis, J. L. (1961). "The Eucalypts." Wiley (Interscience), New York.
- Perry, T. O. (1962). Racial variation in the day and night temperature requirements of red maple and loblolly pine. *Forest Sci.* **8**, 336-344.
- Perry, T. O., and Simons, R. W. (1967). Growth of bud scales and leaves during the winter. *Forest Sci.* **13**, 400-401.
- Perry, T. O., and C. W. Wang (1960). Genetic variation in the winter chilling requirement for date of dormancy break for *Acer rubrum*. *Ecology* **41**, 785-790.
- Perry, T. O., Wang, C. W., and Schmitt, D. (1966). Height growth for loblolly pine provenances in relation to photoperiod and growing season. *Silvae Genet.* **15**, 61-64.
- Phares, R. E., and Crosby, J. S. (1962). Basal sprouting of fire-injured shortleaf pine trees. *J. Forest.* **60**, 204-205.
- Pharis, R. P., and Morf, W. (1967). Experiments on the precocious flowering of western red cedar and four species of Cupressus with gibberellins A₃ and A₄/A₇ mixture. *Can. J. Bot.* **45**, 1519-1524.
- Pharis, R. P., and Morf, W. (1968). Physiology of gibberellin-induced flowering in conifers. In "Biochemistry and Physiology of Plant Growth Substances" (F. Wightman, and G. Setterfield, eds.), pp. 1341-1356. Runge Press, Ottawa.
- Pharis, R. P., Ruddat, M., Phillips, C., and Heftmann, E. (1965). Precocious flowering of Arizona cypress with gibberellin. *Can. J. Bot.* **43**, 923-927.
- Phelps, V. H. (1948). White spruce reproduction in Manitoba and Saskatchewan. *Can., Dep. Mines Resour., Silv. Res. Note* **86**.
- Philipson, W. R. (1964). Changes in the structure of the cambium and its derivatives in heteroblastic trees. *Abstr. 10th Int. Bot. Congr.*, 1964, p. 307.
- Phillips, I. D. J., and Wareing, P. F. (1958a). Studies in the dormancy of sycamore. I, Seasonal changes in the growth substances content of the shoot. *J. Exp. Bot.* **9**, 350-364.
- Phillips, I. D. J., and Wareing, P. F. (1958b). Effect of photoperiodic condition on the level of growth inhibitors in *Acer pseudoplatanus*. *Naturwissenschaften* **45**, 317.
- Pieniazek, J. (1964). Kinetin induced breaking of dormancy in 8-month old apple seedlings of "Antonovka" variety. *Act. Agrobot.* **16**, 297-306.
- Pinfield, N. J. (1968). The promotion of isocitrate lyase activity in hazel cotyledons by exogenous gibberellin. *Planta* **82**, 337-341.
- Pisek, A., and Tranquillini, W. (1954). Assimilation und Kohlenstoffhaushalt in der Krone von Fichten (*Picea excelsa* Link) und Rotbuchenbäumen (*Fagus silvatica* L.) Flora (Jena) **141**, 237-270.
- Place, I. C. M. (1950). Comparative moisture regimes of humus and rotten wood. *Can., Dep. Resour. Develop. Silv., Leafl.* **37**.
- Place, I. C. M. (1955). The influence of seed-bed conditions on the regeneration of spruce and fir. *Can., Forest. Br., Bull.* **117**.
- Plaisted, P. H. (1958). Some biochemical changes during development and aging of *Acer platanoides* L. leaves. *Contrib. Boyce Thompson Inst.* **19**, 245-254.
- Plaut, Z., and Ordin, L. (1961). Effect of soil moisture content on the cell wall metabolism of sunflower and almond leaves. *Physiol. Plant.* **14**, 646-658.
- Plymale, E. L., and Wylie, R. B. (1944). The major veins of mesomorphic leaves. *Amer. J. Bot.* **31**, 99-106.

- Polhamus, L. G. (1962). "Rubber." Wiley (Interscience), New York.
- Pollock, B. M., and Olney, H. O. (1959). Studies of the rest period. I. Growth, translocation, and respiratory changes in the embryonic organs of the after-ripening cherry seed. *Plant Physiol.* **34**, 131-142.
- Pomeroy, M. K., Siminovitch, D., and Wightman, F. (1970). Seasonal biochemical changes in the living bark and needles of red pine (*Pinus resinosa*) in relation to adaptation to freezing. *Can. J. Bot.* **48**, 953-967.
- Popham, R. A. (1951). Principal types of vegetative shoot apex organization in vascular plants. *Ohio J. Sci.* **51**, 249-270.
- Popham, R. A. (1960). Variability among vegetative shoot apices. *Bull. Torrey Bot. Club* **87**, 139-150.
- Priestley, C. A. (1962a). Carbohydrate resources within the perennial plant. *Commonw. Bur. Hort. Plant. Crops (Gt. Brit.), Tech. Commun.* **27**.
- Priestley, C. A. (1962b). The location of carbohydrate resources within the apple tree. *Proc. 16th Int. Hort. Congr.* 1961, pp. 319-327.
- Priestley, J. H. (1932). The growing tree. *Forestry* **6**, 105-112.
- Purohit, A. N., and Nanda, K. K. (1966). Seasonal variation in ascorbic acid content of shoot apex and its relationship with extension growth of *Collistemon viminalis*. *Plant Cell Physiol.* **7**, 499-501.
- Quinlan, J. D. (1969). Mobilization of ^{14}C in the spring following autumn assimilation of $^{14}\text{CO}_2$ by an apple rootstock. *J. Hort. Sci.* **44**, 107-110.
- Redmond, D. R., and Robinson, R. C. (1954). Viability and germination in yellow birch. *Forest. Chron.* **30**, 79-87.
- Reed, J. F. (1939). Root and shoot growth of shortleaf and loblolly pines in relation to certain environmental conditions. *Duke Univ. Sch. Forest., Bull.* **4**.
- Rees, A. R. (1963a). Some factors affecting the germination of oil palm seeds under natural conditions. *J. West Afr. Inst. Oil Palm Res.* **4**, 201-207.
- Rees, A. R. (1963b). A note on the fate of oil palm seed in a number of habitats. *J. West Afr. Inst. Oil Palm Res.* **4**, 208-211.
- Rehfeldt, G. E., and Lester, D. T. (1966). Variation in shoot elongation of *Pinus resinosa* Ait. *Can. J. Bot.* **44**, 1457-1469.
- Reid, R. W. (1961). Moisture changes in lodgepole pine before and after attack by the mountain pine beetle. *Forest. Chron.* **37**, 368-375.
- Rendle, B. J. (1960). Juvenile and adult wood. *J. Inst. Wood Sci.* **5**, 58-61.
- Resende, F. (1964). Senescence induced by flowering. *Port. Acta Biol., Ser. A.* **8**, 248-266.
- Rhandawa, G. S., and Dinsa, H. S. (1947). Relation of growth to fruiting in citrus. *Proc. Amer. Soc. Hort. Sci.* **50**, 151-160.
- Rhoads, W. A., and Wedding, R. T. (1953). Leaf drop in citrus. *Calif. Agr.* **7**, 9.
- Richards, P. W. (1964). "Tropical Rain Forest." Cambridge Univ. Press, London and New York.
- Richardson, S. D. (1957). The effect of leaf age on the rate of photosynthesis in detached, leaves of tree seedlings. *Acta Bot. Neer.* **6**, 445-457.
- Riding, R. T. (1967). Early ontogeny of jack pine and red pine seedlings. M.S. Thesis University of Wisconsin, Madison, Wisconsin.
- Righter, F. I. (1939). Early flower production among the pines. *J. Forest.* **37**, 935-938.
- Robbins, W. J. (1957). Physiological aspects of aging in plants. *Amer. J. Bot.* **44**, 289-294.
- Robbins, W. J. (1960). Further observations on juvenile and adult *Hedera*. *Amer. J. Bot.* **47**, 485-491.
- Roberts, B. R., Kramer, P. J., and Karl, C. M., Jr. (1963). Long-term effects of gibberellin on the growth of loblolly pine seedlings. *Forest Sci.* **9**, 202-205.
- Roberts, R. H. (1920). Off-year apple bearing. *Wisc., Agr. Exp. Sta., Bull.* **317**.

- Robinson, L. W., and Wareing, P. F. (1969). Experiments on the juvenile-adult phase change in some woody plants. *New Phytol.* **68**, 67-78.
- Roe, E. I. (1941). Effect of temperature in seed germination. *J. Forest.* **39**, 413-414.
- Romberger, J. A. (1963). Meristems, growth and development in woody plants. *U.S., Dep. Agr. Tech. Bull.* **1293**.
- Rose, A. H. (1958). The effect of defoliation on foliage production and radial growth of quaking aspen. *Forest Sci.* **4**, 335-342.
- Rothacher, J. S., Blow, F. E., and Potts, S. M. (1954). Estimating the quantity of the foliage in oak stands in the Tennessee Valley. *J. Forest.* **52**, 169-173.
- Rowe, J. S. (1964). Environmental preconditioning with special reference to Forestry. *Ecology* **45**, 399-403.
- Rudinsky, J. A. (1962). Ecology of Scolytidae. *Annu. Rev. Entomol.* **7**, 327-348.
- Rudman, P. R. (1966). Heartwood formation in trees. *Nature (London)* **210**, 608-610.
- Rudolph, T. D. (1962). Lammas growth and prolepsis in jack pine in the Lake States. *Diss. Abstr.* **22**, 2156-2157.
- Rudolph, T. D. (1964). Lammas growth and prolepsis in jack pine in the Lake States. *Forest Sci. Monogr.* **6**.
- Rumball, W. (1963). Wood structure and heteroblastism. *Phytomorphology* **13**, 206-214.
- Rutter, A. J. (1957). Studies in the growth of young plants of *Pinus sylvestris* L. I. The annual cycle of assimilation and growth. *Ann. Bot. (London) [N.S.]* **21**, 399-426.
- Sacher, J. A. (1954). Structure and seasonal activity of the shoot apices of *Pinus lambertiana* and *Pinus ponderosa*. *Amer. J. Bot.* **41**, 749-759.
- Sacher, J. A. (1955). Dwarf shoot ontogeny in *Pinus lambertiana*. *Am. J. Bot.* **42**, 784-792.
- Sacher, J. A. (1957). Relationship between auxin and membrane-integrity in tissue senescence and abscission. *Science* **125**, 1199-1200.
- Sachs, T., and Thimann, K. V. (1967). The role of auxins and cytokinins in the release of buds from dominance. *Amer. J. Bot.* **54**, 136-144.
- Sakai, A. (1962). Studies in the frost hardiness of woody plants. I. The causal relation between sugar content and frost hardiness. *Contrib. Inst. Low Temp. Sci., Hokkaido Univ., Ser. B* **11**, 1-40.
- Sakai, A. (1968). Mechanism of desiccation damage of forest trees in winter. *Contrib. Inst. Low Temp. Res., Hokkaido Univ., Ser. B* **15**, 15-35.
- Saks, A. (1956). O formah jasenja obyknovennogo (*Fraxinus excelsior* L.). *Tr. Inst. Lesokhoz Probl. Riga* **11**, 113-120.
- Samish, R. M. (1954). Dormancy in woody plants. *Annu. Rev. Plant Physiol.* **5**, 183-204.
- Sands, K., and Rutter, A. J. (1959). Studies in the growth of young plants of *Pinus sylvestris* L. II. The relation of growth to soil moisture tension. *Ann. Bot. (London) [N.S.]* **23**, 269-284.
- Sargent, C. S. (1926). "Manual of the Trees of North America." Houghton, Boston, Massachusetts.
- Sasaki, S., and Kozlowski, T. T. (1967). Effects of herbicides on carbon dioxide uptake of pine seedlings. *Can. J. Bot.* **45**, 961-971.
- Sasaki, S., and Kozlowski, T. T. (1968a). The role of cotyledons in early development of pine seedlings. *Can. J. Bot.* **46**, 1173-1183.
- Sasaki, S., and Kozlowski, T. T. (1968b). Effects of herbicides on seed germination and early seedling development of *Pinus resinosa*. *Bot. Gaz.* **129**, 238-246.
- Sasaki, S., and Kozlowski, T. T. (1968c). Effects of herbicides on respiration of red pine (*Pinus resinosa* Ait.) seedlings. I. s-triazine and chlorophenoxy acid herbicides. *Advan. Front. Plant Sci.* **22**, 187-202.

- Sasaki, S., and Kozlowski, T. T. (1968d). Effects of herbicides on respiration of red pine (*Pinus resinosa* Ait.) seedlings. II. Monuron, diuron, DCPA, dalapon, CDEC, CDAA, EPTC, and NPA. *Bot. Gaz.* **129**, 286-293.
- Sasaki, S., and Kozlowski, T. T. (1969). Utilization of seed reserves and currently produced photosynthates of embryonic tissues of pine seedlings. *Ann. Bot. (London)* [N.S.] **33**, 472-482.
- Sasaki, S., and Kozlowski, T. T. (1970). Effects of cotyledon and hypocotyl photosynthesis on growth of young pine seedlings. *New Phytol.* **69**, 493-500.
- Sasaki, S., Kozlowski, T. T., and Torrie, J. H. (1968). Effect of pretreatment of pine seeds with herbicides on seed germination and growth of young seedlings. *Can. J. Bot.* **46**, 255-262.
- Sato, K. (1963). Some physiological actions of gibberellins on forest trees. *Proc. World Consultation Forest Genet. Tree Improvement, FAO*, 1963, Vol. II, 5-2.
- Satoo, T. (1966). Variation in response of conifer seed germination to soil moisture conditions. *Misc. Info. Tokyo Univ. Forests* **16**, 17-20.
- Sauer, M. R. (1951). Growth of orange shoots. *Aust. J. Agr. Res.* **2**, 105-117.
- Sax, K. (1962). Aspects of aging in plants. *Annu. Rev. Plant Physiol.* **13**, 489-506.
- Schaffalitzky de Muckadell, M. (1954). Juvenile stages in woody plants. *Physiol. Plant.* **7**, 782-796.
- Schaffalitzky de Muckadell, M. (1959). Investigations on aging of apical meristems in woody plants and its importance in silviculture. *Det. Forstl. Forsøgsy. Danmark* **25**, 309-455.
- Schaffalitzky de Muckadell, M. (1962). Environmental factors in development stages of trees. In "Tree Growth" (T. T. Kozlowski, ed.), Chapter 18. Ronald Press, New York.
- Schier, G. A. (1970). Seasonal pathways of ^{14}C -photosynthate in red pine labeled in May, July, and October. *Forest Sci.* **16**, 2-13.
- Schimper, A. F. W. (1903). "Plant Geography upon a Physiological Basis" (English translation). Oxford Univ. Press (Clarendon), London and New York.
- Schmidt, A. (1924). Histologische Studien an Phanerogamen Vegetationspunkten. *Bot. Arch.* **8**, 345-404.
- Scholtes, W. H. (1953). The concentration of forest tree roots in the surface zone of some Piedmont soils. *Proc. Iowa Acad. Sci.* **60**, 243-259.
- Schomaker, C. E., and Rudolph, V. J. (1964). Nutritional relationships affecting height growth of planted yellow-poplar in southwestern Michigan. *Forest Sci.* **10**, 66-76.
- Schramm, R. (1912). Über die anatomischen Jugendformen der Blätter einheimischer Holzpflanzen. *Flora (Jena)* **104**, 225-295.
- Schroeder, C. A. (1951). Shoot growth in citrus. *Calif. Citrogr.* **37**, 16, 19, and 20.
- Schulman, E. (1958). Bristlecone pine, oldest known living thing. *Nat. Geogr. Mag.* **113**, 355-372.
- Scott, F. M., Schroeder, M. R., and Turrell, F. M. (1948). Development, cell shape, suberization of internal surface, and abscission in the leaf of the Valencia orange, *Citrus sinensis*. *Bot. Gaz.* **109**, 381-411.
- Scurfield, G., and Moore, G. W. E. (1958). Effects of gibberellic acid on species of *Eucalyptus*. *Nature (London)* **181**, 1276-1277.
- Shalucha, B. (1946). Auxin and nitrogen content of developing peach shoots. *Amer. J. Bot.* **33**, 838.
- Sharples, G. C., and Burkhardt, L. (1954). Seasonal changes in carbohydrates in Marsh grapefruit in Arizona. *Proc. Amer. Soc. Hort. Sci.* **63**, 74-80.
- Shearer, R. C. (1961). A method of overcoming seed dormancy in subalpine larch. *J. Forest.* **59**, 513-514.

- Shearer, R. C., and Tackle, D. (1960). Effect of hydrogen peroxide on germination in three western conifers. *U.S., Forest. Serv., Interm. Forest Range Exp. Sta., Res. Note* **80**.
- Shigo, A. L. (1965a). Decays and discolorations in northern hardwoods in the northeastern United States: A consideration of microorganisms and external signs. *IUFRO Meet.*, 1961, Sect. 41.
- Shigo, A. L. (1965b). The pattern of decays and discolorations in northern hardwoods. *Phytopathology* **55**, 648-652.
- Shigo, A. L. (1966). Decay and discoloration following logging wounds on northern hardwoods. *U.S., Forest Serv., Res. Pap.* **NE-47**.
- Shigo, A. L. (1967a). The early stages of discoloration and decay in living hardwoods in northeastern United States: A consideration of wound-initiated discoloration and heartwood. *Proc. 14th Int. Union Forest. Res. Organ.* 1967, pp. 117-133.
- Shigo, A. L. (1967b). Successions of organisms in discoloration and decay of wood. *Int. Rev. Forest. Res.* **2**, 237-299.
- Sifton, H. B. (1966). On the abscission region in leaves of the blue spruce. *Can. J. Bot.* **43**, 985-993.
- Silver, G. T. (1956). Some growth characteristics of eastern white cedar *Thuja occidentalis* L. *Bimonth. Prog. Rep., Div. Forest Biol., Dep. Agr., Can.* **12**, No. 6, 1.
- Siminovitch, D., Wilson, C. M., and Briggs, D. R. (1953). Studies on the chemistry of the living bark of the black locust in relation to frost hardiness. V. Seasonal transformation and variations in the carbohydrates: starch-sucrose interconversions. *Plant Physiol.* **28**, 383-400.
- Simkover, H. G., and Shenefelt, R. D. (1952). Phytotoxicity of some insecticides to coniferous seedlings with particular reference to benzene hexachloride. *J. Econ. Entomol.* **45**, 11-15.
- Simon, S. V. (1914). Studien über die Periodizität der Lebensprozesse der in dauernd feuchten Tropengebieten heimischen Bäume. *Jahr. Wiss. Bot.* **54**, 71-187.
- Sinnott, F. W. (1960). "Plant Morphogenesis." McGraw-Hill, New York.
- Skoog, F. (1955). Growth factors, polarity, and morphogenesis. *Int. Union Biol. Sci., Colloq.* **20**, 1-13.
- Skoog, F., and Miller, C. O. (1957). Chemical regulation of growth and organ function in plant tissues cultured *in vitro*. *Symp. Soc. Exp. Biol.* **11**, 118-131.
- Skoog, F., and Tsui, C. (1951). Growth substances and the formation of buds in plant tissues. In "Plant Growth Substances" (F. Skoog, ed.), pp. 263-285. Univ. of Wisconsin Press, Madison, Wisconsin.
- Slee, M. U., and Nikles, D. G. (1968). Variability of *Pinus caribaea* (Mor.) in young Queensland plantations. *Proc. 9th Commonw. Forest. Conf.*, 1968, p. 1-50.
- Smith, D. L. (1959). The effect of juvenility on rooting of cuttings from apple seedlings. *J. Arnold Arboretum* **40**, Harvard Univ. 172-175.
- Smith, D. M. (1951). The influence of seedbed conditions in the regeneration of eastern white pine. *Conn., Agr. Exp. Sta., New Haven, Bull.* **545**.
- Smith, D. M. (1962). "The Practice of Silviculture." Wiley, New York.
- Smith, H., and Kefford, N. P. (1964). The chemical regulation of the dormancy phases of bud development. *Amer. J. Bot.* **51**, 1002-1012.
- Smith, M. E. (1943). Micronutrients essential for the growth of *Pinus radiata*. *Aust. Forest.* **7**, 22-27.
- Smith, P. F. (1944). Inhibition of growth in guayule as affected by tapping and defoliation. *Amer. J. Bot.* **31**, 328-336.
- Smith, P. F., Reuther, W., and Specht, A. W. (1952). Seasonal changes in Valencia orange leaves. II. Changes in micro-elements, sodium, and carbohydrates in leaves. *Proc. Amer. Soc. Hort. Sci.* **59**, 31-35.

- Smith, R. F. (1967). The leaf dimorphism of *Liquidambar styraciflua*. *Amer. Midl. Natur.* **77**, 42-50.
- Smyth, E. M. (1934). The seasonal cycles of nitrogenous and carbohydrate materials in fruit trees. *J. Pomol. Hort. Sci.* **12**, 249-292.
- Soegaard, B. (1956). Leaf blight resistance in *Thuja*. Experiments on resistance to attack by *Didymascella thujina* (Dur.) Maire (*Keithia thujina*) on *Thuja plicata*. *Roy. Vet. Agr. Coll. Yearb. Copenhagen*, pp. 30-48.
- Sokolev, S. Y., and Artyushenko, Z. T. (1957). Ivanov (Lammas) shoots in the pine. *Bor. Z.* **42**, 741-745.
- Sondheimer, E., Tzou, D. S., and Galson, E. C. (1968). Abscisic acid levels and seed dormancy. *Plant Physiol.* **43**, 1443-1447.
- Späth, H. L. (1912). "Der Johannistriebe." Parey, Berlin.
- Squillace, A. E. (1966). Geographic variation in slash pine. *Forest Sci. Monogr.* **10**.
- Squillace, A. E., and Bingham, R. T. (1958). Localized ecotypic variation in western white pine. *Forest Sci.* **4**, 20-34.
- Squillace, A. E., and Silen, R. R. (1962). Racial variation in ponderosa pine. *Forest Sci. Monogr.* **2**.
- Stamm, A. J. (1964). "Wood and Cellulose Science." Ronald Press, New York.
- Stanley, R. G. (1957). Krebs cycle activity of mitochondria from endosperm of sugar pine seed (*Pinus lambertiana* Dougl.). *Plant Physiol.* **32**, 409-412.
- Stanley, R. G. (1958). Gross respiratory and water uptake patterns in germinating sugar pine seed. *Physiol. Plant.* **11**, 503-515.
- Stanley, R. G., and Conn, E. E. (1957). Enzyme activity of mitochondria from germinating seedlings of sugar pine (*Pinus lambertiana* Dougl.). *Plant Physiol.* **32**, 412-418.
- Steinhart, C., Anderson, L., and Skoog, F. (1962). Growth promoting effect of cyclitols on spruce tissue cultures. *Plant Physiol.* **37**, 60-66.
- Stephenson, G. K., Goodrum, P. D., and Packard, R. L. (1963). Small rodents as consumers of pine seed in east Texas uplands. *J. Forest.* **61**, 523-526.
- Sterling, C. (1945). Growth and vascular development in the shoot apex of *Sequoia sempervirens* (Lamb.) Endl. I. Structure and growth of the shoot apex. *Amer. J. Bot.* **32**, 118-126.
- Sterling, C. (1946). Growth and vascular development in the shoot apex of *Sequoia sempervirens* (Lamb.) Endl. III. Cytological aspects of vascularization. *Amer. J. Bot.* **33**, 35-45.
- Sterling, C. (1947). Organization of the shoot of *Pseudotsuga taxifolia* (Lamb.) Britt. II. Vascularization. *Amer. J. Bot.* **34**, 272-280.
- Stewart, C. M. (1966). The chemistry of secondary growth in trees. *CSIRO, Div. Forest Prod., Tech. Pap.* **43**.
- Stiell, W. M. (1962). Crown structure in plantation red pine. *Can., Forest Prod. Res. Br., Tech. Note* **122**.
- Stiles, W. (1950). "An Introduction to the Principles of Plant Physiology." Methuen, London.
- Stillwell, M. A. (1956). Pathological aspects of spruce budworm attack. *Forest Sci.* **2**, 174-180.
- Stoate, T. N. (1950). Nutrition of the pine. *Aust. Forest. Timber Bur., Bull* **30**.
- Stoeckeler, J. H. (1960). Soil factors affecting the growth of quaking aspen forests in the Lake States. *Minn. Agr. Exp. Sta., Tech. Bull.* **233**.
- Stoeckeler, J. H., and Mason, J. W. (1956). Regeneration of aspen cutover areas in northern Wisconsin. *J. Forest.* **54**, 13-16.

- Stone, E. C. (1957). Embryo dormancy and embryo vigor of sugar pine as affected by length of storage and storage temperatures. *Forest Sci.* **3**, 357-371.
- Stone, E. L. (1953a). Magnesium deficiency of some northeastern pines. *Soil Sci. Soc. Amer., Proc.* **17**, 297-300.
- Stone, E. L. (1953b). The origin of epicormic branches in fir. *J. Forest.* **51**, 366.
- Stone, E. L. (1968). Microelement nutrition of forest trees: A review. In "Forest Fertilization-Theory and Practice," pp. 132-175. T.V.A., Muscle Shoals, Alabama.
- Stone, E. L., and Stone, M. H. (1943a). "Dormant" versus "adventitious" buds. *Science* **98**, 62.
- Stone, E. L., and Stone, M. H. (1943b). Dormant buds in certain species of *Pinus*. *Amer. J. Bot.* **30**, 346-351.
- Stone, E. L., and Will, G. M. (1965). Boron deficiency in *Pinus radiata* and *P. pinaster*. *Forest Sci.* **11**, 425-433.
- Stone, E. L., Jr., and Stone, M. H. (1954). Root collar sprouts in pine. *J. Forest.* **52**, 487-491.
- Stout, A. B. (1916). The intermittent annual growth of woody plants. *J. N.Y. Bot. Gard.* **17**, 147-152.
- Stoutemyer, V. T., Britt, O. K., and Goodin, J. R. (1961). The influence of chemical treatments, understocks and environment on growth phase changes and propagation of *Hedera canariensis*. *Proc. Amer. Soc. Hort. Sci.* **77**, 552-557.
- Stover, E. L. (1944). Varying structure of conifer leaves in different habitats. *Bot. Gaz.* **106**, 12-25.
- Stransky, J. J., and Wilson, D. R. (1964). Terminal elongation of loblolly and shortleaf pine seedlings under soil moisture stress. *Soil Sci. Soc. Amer., Proc.* **28**, 439-440.
- Strasburger, E., Jost, L., Schenck, H., and Karsten, G. (1912). "A Textbook of Botany." MacMillan, London.
- Strelis, I., and Green, H. V. (1962). Tyloses and their detection. *Pulp Paper Mag. Can.* **63**, 307-310 and 330.
- Swan, H. S. D. (1965). Reviewing the scientific use of fertilizers in forestry. *J. Forest.* **63**, 501-508.
- Szymanski, S., and Szczerbinski, W. (1955), Paczki jako wskaznik potencjalu zyciowego mlodej sosny. *Roczn. Sekcji Dendrol. Pol. Tow. Bot.* **10**, 275-304.
- Tadaki, Y., and Shidei, T. (1960). Studies on productive structure of forest. I. The seasonal variation of leaf amount and the dry matter production of deciduous sapling stand (*Ulmus parviflora*). *J. Jap. Forest. Soc.* **42**, 427-434.
- Tadros, T. M. (1957). Evidence of the presence of an edapho-biotic factor in the problem of serpentine tolerance. *Ecology* **38**, 284-307.
- Talbert, C. M., and Holch, A. E. (1957). A study of the lobing of sun and shade leaves. *Ecology* **38**, 655-658.
- Tamari, C. (1962). Variation in moisture content and reducing sugar concentration in hardening process of Todomatsu (*Abies sachalinensis* Most.) seedling with lammas shoot. *Hokkaido Univ. For. Res. Bull.* **21**, 409-414.
- Tamm, C. O. (1951). Seasonal variation in composition of birch leaves. *Physiol. Plant.* **4**, 461-469.
- Tarrant, R. F. (1949). Douglas fir site quality and soil fertility. *J. Forest.* **47**, 716-720.
- Taylor, B. K. (1967). The nitrogen nutrition of the peach tree. I. Seasonal changes in nitrogenous constituents in mature trees. *Aust. J. Biol. Sci.* **20**, 379-387.
- Taylor, B. K., and May, L. H. (1967). The nitrogen nutrition of the peach tree. II. Storage and mobilization of nitrogen in young trees. *Aust. J. Biol. Sci.* **20**, 389-411.

- Tepper, H. B. (1963a). Leader growth of young pitch and shortleaf pines. *Forest Sci.* **9**, 344-353.
- Tepper, H. B. (1963b). Dimensional and zonational variation in dormant shoot apices of *Pinus ponderosa*. *Amer. J. Bot.* **50**, 589-596.
- Tepper, H. B. (1964). Ontogeny of the shoot apex of seedlings of *Pinus ponderosa*. *Amer. J. Bot.* **51**, 859-865.
- Tepper, H. B. (1966). Comparative study of the long-shoot apex in the genus *Pinus*. *Phyto-morphology* **16**, 469-474.
- Tetley, U. (1932). The development and cytology of the leaves of healthy and "silvered" Victoria plum trees. *Ann. Bot. (London)* **46**, 633-652.
- Tetley, U. (1936). Tissue differentiation in some foliage leaves. *Ann. Bot. (London)* **50**, 523-557.
- Thimann, K. V., ed. (1952). "The Action of Hormones in Plants and Invertebrates." Academic Press, New York.
- Thimann, K. V., ed. (1958). "The Physiology of Forest Trees." Ronald Press, New York.
- Thimann, K. V. (1959). Correlative aspects of the shoot. *Proc. 9th Int. Bot. Congr.*, 1959, Vol. 2, pp. 396-397.
- Thomas, J. B. (1958). The production of lammas shoots on jack pine in Ontario. *Forest Chron.* **34**, 307-309.
- Thomas, T. H., Wareing, P. F., and Robinson, P. M. (1965). Action of the sycamore 'dormin' as a gibberellin antagonist. *Nature* **205**, 1270-1272.
- Titman, P. W., and Wetmore, R. H. (1955). The growth of long and short shoots in *Cercidiphyllum*. *Amer. J. Bot.* **42**, 364-372.
- Tolsky, A. P. (1914). Mensuration, finance and management. *Forest. Quart.* **12**, 277-278.
- Toole, E. H., Hendricks, S. B., Borthwick, H. A., and Toole, V. K. (1956). Physiology of seed germination. *Annu. Rev. Plant Physiol.* **7**, 299-324.
- Toole, V. K., Toole, E. H., Hendricks, S. B., Borthwick, H. S., and Snow, A. G., Jr. (1961). Responses of seeds of *Pinus virginiana* to light. *Plant Physiol.* **36**, 285-290.
- Tranquillini, W. (1954). Die Lichtabhängigkeit der Assimilation von Sonnen und Schattenblättern einer Buche unter ökologischen Bedingungen. *Proc. 8th Int. Bot. Congr.*, 1954, Sect. 13, pp. 100-102.
- Tranquillini, W., and Unterholzer, R. (1968). Das Wachstum Zweijähriger Lärchen einheitlicher Herkunft in verschiedener Seehöhe. *Centralbl. Gesamte Forstw.* **85**, 43-49.
- Trappe, J. M. (1961). Strong hydrogen peroxide for sterilizing coats of tree seed and stimulating germination. *J. Forest.* **59**, 828-829.
- Trippi, V. S. (1963a). Studies on ontogeny and senility in plants. I. Changes of growth vigor during the juvenile and adult phases of ontogeny in *Tilia parviflora* and growth in juvenile and adult zones of *Tilia*, *Ilex aquifolium*, and *Robinia pseudoacacia*. *Phyton (Buenos Aires)* **20**, 137-145.
- Trippi, V. S. (1963b). Studies on ontogeny and senility in plants. V. Leaf-fall in plants of different age and the effect of gibberellic acid on *R. pseudoacacia* and *Morus nigra*. *Phyton (Buenos Aires)* **20**, 167-171.
- Trippi, V. S. (1963c). Studies on ontogeny and senility in plants. VI. Reversion in *Acacia melanoxylon* and morphogenetic changes in *Gaillardia pulchella*. *Phyton (Buenos Aires)* **20**, 172-174.
- Turner, R. M. (1956). A study of some features of growth and reproduction of *Pinus ponderosa* in northern Idaho. *Ecology* **37**, 742-753.
- Turrell, F. M. (1934). Leaf surface of a twenty-one-year-old catalpa tree. *Proc. Iowa Acad. Sci.* **41**, 80-84.

- Turrell, F. M. (1936). The area of the internal exposed surface of dicotyledon leaves. *Amer. J. Bot.* **23**, 255–264.
- Turrell, F. M. (1944). Correlation between internal surface and transpiration rate in mesomorphic and xeromorphic leaves grown under artificial light. *Bot. Gaz.* **105**, 413–425.
- Turrell, F. M., and Turrell, M. E. (1943). The effect of the great drought of 1934 on the leaf structure of certain Iowa plants. *Proc. Iowa Acad. Sci.* **50**, 185–192.
- Ursino, D. J., Nelson, C. D., and Krotkov, G. (1968). Seasonal changes in the distribution of photo-assimilated ^{14}C in young pine plants. *Plant Physiol.* **43**, 845–852.
- Vaartaja, O. (1954). Photoperiodic ecotypes of trees. *Can. J. Bot.* **32**, 392–399.
- Vaartaja, O. (1957). Experimental evidence of photoperiodic ecotypes in several tree species. *Ecol. Soc. Amer. Bull.* **38**, 76.
- Vaartaja, O. (1959). Evidence of photoperiodic ecotypes in trees. *Ecol. Monogr.* **29**, 91–111.
- Vaartaja, O. (1960). Ecotypic variation of photoperiodic responses in trees, especially in two *Populus* species. *Forest Sci.* **6**, 200–206.
- Vaartaja, O. (1961). Demonstration of photoperiodic ecotypes in *Liriodendron* and *Quercus*. *Can. J. Bot.* **39**, 649–654.
- Van der Pijl, L. (1952). Absciss-joints in the stems and leaves of tropical plants. *Proc. Kon. Ned. Akad. Wetensch.* **55**, 574–586.
- van Overbeek, J. (1938). Auxin distribution in seedlings and its bearing on the problem of bud inhibition. *Bot. Gaz.* **100**, 133–166.
- van Overbeek, J. (1962). Endogenous regulators of fruit growth. In "Proceedings Plant Science Symposium," pp. 37–58. Campbell Soup Co., Camden, New Jersey.
- van Overbeek, J. (1966). Plant hormones and regulators. *Science* **152**, 721–731.
- Vardar, Y. (1955). A study on the apical inhibition upon the lateral branches. *Rev. Fac. Sci. Univ. Istanbul, Ser. B* **20**, 245–256.
- Varner, J. E. (1961). Biochemistry of senescence. *Annu. Rev. Plant Physiol.* **12**, 245–264.
- Vasilevskaya, V. K., and Kondratjeva, E. A. (1955). Obrazovanie pocek na kornjab dreves-nokustornikovyh rastenii. *Dokl. Akad. Nauk SSSR* **101**, 951–954.
- Vegis, A. (1964). Dormancy in higher plants. *Annu. Rev. Plant Physiol.* **15**, 185–224.
- Vezina, P. E., and Boulter, D. W. K. (1966). The spectral composition of near ultraviolet and visible radiation beneath forest canopies. *Can. J. Bot.* **44**, 1267–1284.
- Vidal Suarez, M. (1955). Transcurso de la brotacion foliar en cacao durante un ano. *Cacao Colomb.* **4**, 121–158.
- Villiers, T. A. (1961). Dormancy in tree seeds. A brief review of recent work. *Proc. Int. Seed Test. Assoc.* **26**, 516–536.
- Villiers, T. A. (1968). An autoradiographic study of the effect of the plant hormone abscisic acid on nucleic acid and protein metabolism. *Planta* **82**, 342–354.
- Villiers, T. A., and Wareing, P. F. (1965). The possible role of low temperature in breaking the dormancy of seeds of *Fraxinus excelsior* L. *J. Exp. Bot.* **16**, 519–531.
- Viro, P. J. (1965). Estimation of the effect of forest fertilization. *Commun. Inst. Forest. Fenn.* **59.3**, 5–42.
- Visser, T. (1964). Juvenile phase and growth of apple and pear seedlings. *Euphytica* **13**, 119–129.
- Vité, J. P. (1961). The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa*. *Contrib. Boyce Thompson Inst.* **21**, 37–66.
- Vité, J. P., and Wood, D. L. (1960). A study on the applicability of the measurement of oleoresin exudation pressure in determining susceptibility of second growth ponderosa pine to bark beetle infestation. *Contrib. Boyce Thompson Inst.* **21**, 67–78.

- Voigt, G. K., Stoeckeler, J. H., and Wilde, S. A. (1958). Response of coniferous seedlings to soil applications of calcium and magnesium fertilizers. *Soil Sci. Soc. Amer., Proc.* **22**, 343-345.
- Vomperskij, S. E. (1959). Osobennosti stroenija korneych sistem *Pinus silvestris* L. na osusennyh torfjanyh pocvah. *Bot. Z.* **44**, 79-87.
- Wadleigh, C. H., and Gauch, H. G. (1948). Rate of leaf elongation as affected by the intensity of the total soil moisture stress. *Plant Physiol.* **23**, 485-495.
- Wakeley, P. C. (1954). Planting the southern pines. U.S. Forest Service, Agr. Monograph No. 18.
- Wakeley, P. C. (1961). Results of the southwide pine seed source study through 1960-61. *Proc. 6th S. Conf. Forest Tree Improvement*, 1961.
- Wakeley, P. C., and Marrero, J. (1958). Five-year intercept as site index in southern pine plantations. *J. Forest.* **56**, 332-336.
- Walker, L. C. (1956). Foliage symptoms as indicators of potassium deficient soils. *Forest Sci.* **2**, 113-120.
- Walker, R. B., Gessel, S. P., and Haddock, P. G. (1955). Greenhouse studies in mineral requirements of conifers: Western red cedar. *Forest Sci.* **1**, 51-60.
- Walters, J., and Soos, J. (1961). Some observations on the relationship of lammas shoots to the form and growth of Douglas-fir seedlings. *Res. Pap. Fac. Forest. Univ. B. C.* No. 40.
- Walters, J., and Soos, J. (1963). Shoot growth patterns of some British Columbia conifers. *Forest Sci.* **9**, 73-85.
- Ward, R. T. (1961). Some aspects of the regeneration habits of the American beech. *Ecology* **42**, 828-832.
- Ward, W. W. (1964). Bud distribution and branching in red oak. *Bot. Gaz.* **125**, 217-220.
- Ward, W. W. (1966). Epicormic branching of black and white oaks. *Forest Sci.* **12**, 290-296.
- Wardlaw, C. W. (1965). "Organization and Evolution in Plants." Longmans, Green, New York.
- Wardrop, A. B. (1962). Cell wall organization in higher plants. I. The primary wall. *Bot. Rev.* **28**, 241-285.
- Wardrop, A. B., and Cronshaw, J. (1962). Formation of phenolic substances in the ray parenchyma of angiosperms. *Nature (London)* **193**, 90-92.
- Wareing, P. F. (1953). Growth studies in woody species. V. Photoperiodism in dormant buds of *Fagus sylvatica* L. *Physiol. Plant.* **6**, 692-706.
- Wareing, P. F. (1954). Growth studies in woody species. VI. The locus of photoperiodic perception in relation to dormancy. *Physiol. Plant.* **7**, 261-277.
- Wareing, P. F. (1956). Photoperiodism in woody plants. *Annu. Rev. Plant Physiol.* **7**, 191-214.
- Wareing, P. F. (1958). Reproductive development in *Pinus sylvestris* In "The Physiology of Forest Trees" (K. V. Thimann, ed.), Chapter 35. Ronald Press, New York.
- Wareing, P. F. (1959). Problems of juvenility and flowering in trees. *J. Linn. Soc. London, Bot.* **56**, 282-289.
- Wareing, P. F. (1961). Dormancy of woody plants. *Recent Advan. Bot.* pp. 1216-1219.
- Wareing, P. F. (1963). The germination of seeds. *Vistas Bot.* **3**, 195-227.
- Wareing, P. F. (1964a). Tree physiology in relation to genetics and breeding. *Unasylva* **18**, 1-10.
- Wareing, P. F. (1964b). Phase change in woody plants. *Abstr. 10th Int. Bot. Congr.*, 1964, pp. 308-309.
- Wareing, P. F. (1965a). Endogenous inhibitors in seed germination and dormancy. *Encycl. Plant Physiol.* **15**, No. 2, 909-924.

- Wareing, P. F. (1965b). Dormancy in plants. *Sci. Progr.* **53**, 529–537 (*London*).
- Wareing, P. F. (1966). The physiologist's approach to tree growth. *Forestry* **39**, *Suppl.*, 7–18.
- Wareing, P. F., and Nasr, T. A. A. (1958). Gravimorphism in trees. Effects of gravity on growth, apical dominance and flowering in fruit trees. *Nature (London)* **182**, 379–381.
- Wareing, P. F., and Nasr, T. A. A. (1961). Gravimorphism in trees. I. Effects of gravity on growth and apical dominance in fruit trees. *Ann. Bot. (London)* [N.S.] **25**, 321–340.
- Wareing, P. F., and Robinson, L. W. (1963). Juvenility problems in woody plants. *Rep. Forest. Res.* pp. 125–127.
- Wareing, P. F., and Seth, A. K. (1967). Aging and senescence in the whole plant. *Symp. Soc. Exp. Biol.* **21**, 543–558.
- Weaver, R. J. (1963). Use of kinin in breaking rest in buds of *Vitis vinifera*. *Nature (London)* **198**, 207–208.
- Webber, H. J., and Batchelor, L. D., eds. (1943). "The Citrus Industry." Univ. of California Press, Berkeley, California.
- Weinberger, J. H. (1950). Prolonged dormancy of peaches. *Proc. Amer. Soc. Hort. Sci.* **56**, 129–133.
- Wellwood, R. W. (1955). Sapwood-heartwood relationships in second growth Douglas fir. *Forest Prod. J.* **5**, 108–111.
- Went, F. W. (1942). Some physiological factors in the aging of a tree. *Proc. 18th Nat. Shade Tree Conf.* 1942, pp. 330–334.
- Went, F. W. (1951). The development of stems and leaves. In "Plant Growth Substances" (F. Skoog, ed.), p. 287–298. Univ. of Wisconsin Press: Madison, Wisconsin.
- Westing, A. H. (1959). Effect of gibberellin in conifers. Generally negative. *J. Forest.* **57**, 120–122.
- Westing, A. H. (1964). The longevity and aging of trees. *Gerontologist* **4**, 10–15.
- Wetmore, R. H., and Garrison, R. (1959). The growth and organization of internodes. *Proc. 9th Int. Bot. Congr.*, 1959 Vol. 2, pp. 427–428.
- White, D. J. B. (1955). The architecture of the stem apex and the origin and development of the axillary buds in seedlings of *Acer pseudoplatanus*. *Ann. Bot. (London)* [N.S.] **19**, 437–449.
- Wickson, M., and Thimann, K. V. (1958). The antagonism of auxin and kinetin in apical dominance. *Physiol. Plant.* **11**, 62–74.
- Wieckowski, S. (1958). Studies on the autumnal breakdown of chlorophyll *Acta Biol. Cracov.*, Ser. Bot. **1**, 131–135.
- Wiersum, L. K. (1955). Observations on the rooting of *Hevea* cuttings. *Arch. Rubb. Cult.* **32**, 213–243.
- Wiggans, S. C., and Martin, L. W. (1961). The effect of gibberellic acid on germination and seedling growth of pecans. *Proc. Amer. Soc. Hort. Sci.* **77**, 295–300.
- Wight, W. (1930). Secondary elongation growth in oaks, 1929. *Naturalist* No. 877, pp. 65–70.
- Wight, W., and Barua, D. N. (1955). The nature of dormancy in the tea plant. *J. Exptl. Bot.* **6**, 1–5.
- Wilcox, H. (1962). Growth studies of the root of incense cedar, *Libocedrus decurrens*. II. Morphological features of the root system and growth behavior. *Amer. J. Bot.* **49**, 237–245.
- Wilcox, H. (1964). Xylem in roots of *Pinus resinosa* Ait. in relation to heterorhizy and growth activity. In "The Formation of Wood in Forest Trees" (M. H. Zimmermann, ed.), pp. 459–478. Academic Press, New York.
- Wilcox, H. E. (1968). Morphological studies of the root of red pine, *Pinus resinosa*. I. Growth characteristics and patterns of branching. *Amer. J. Bot.* **55**, 247–254.

- Wilde, S. A. (1964). Relationship between the height growth, the 5-year intercept, and site conditions of red pine plantations. *J. Forest.* **62**, 245–248.
- Wilde, S. A., and Voigt, G. K. (1952). Determination of color of nursery stock foliage by means of Munsell color charts. *J. Forest.* **50**, 622–623.
- Wilson, B. F. (1966). Development of the shoot system of *Acer rubrum*. *Harvard Forest Pap.* **14**.
- Wilson, B. F. (1968). Red maple stump sprouts: Development the first year. *Harvard Forest Pap.* **18**.
- Winget, C. H., and Kozlowski, T. T. (1965a). Yellow birch germination and seedling growth. *Forest Sci.* **11**, 386–392.
- Winget, C. H., and Kozlowski, T. T. (1965b). Seasonal basal area growth as an expression of competition in northern hardwoods. *Ecology* **46**, 786–793.
- Winget, C. H., Kozlowski, T. T., and Kuntz, J. E. (1963). Effects of herbicides on red pine nursery stock. *Weeds* **11**, 87–90.
- Wolf, F. T. (1956). Changes in chlorophyll a and b in autumn leaves. *Amer. J. Bot.* **43**, 714–718.
- Wolter, K. E., and Skoog, F. (1966). Nutritional requirements of *Fraxinus* callus cultures. *Amer. J. Bot.* **53**, 263–269.
- Woods, F. W., Harris, H. C., and Caldwell, R. E. (1959). Monthly variations of carbohydrates and nitrogen in roots of sandhill oaks and wiregrass. *Ecology* **40**, 292–295.
- Woodwell, G. M. (1958). Factors controlling growth of ponderosa pine seedlings in organic soils of the Carolinas. *Ecol. Monogr.* **28**, 219–236.
- Wright, J. W. (1944a). Genotypic variation in white ash. *J. Forest.* **42**, 489–495.
- Wright, J. W. (1944b). Ecotypic differentiation in red ash. *J. Forest.* **42**, 591–597.
- Wright, J. W. (1954). Preliminary report on a study of races in black walnut. *J. Forest.* **52**, 673–675.
- Wright, J. W. (1962). Genetics of forest tree improvement. *FAO Forest. Forest Prod. Study* **16**.
- Wright, J. W., and Baldwin, H. I. (1957). The 1938 International Union Scotch pine provenances test in New Hampshire. *Silvae Genet.* **6**, 2–14.
- Wright, J. W., and Bull, W. I. (1962). Geographic variations in European black pine—two year results. *Forest Sci.* **8**, 32–42.
- Wylie, R. B. (1949). Differences in foliar organization among leaves from four locations in the crown of an isolated tree (*Acer platanoides*). *Proc. Iowa Acad. Sci. Sci.* **56**, 189–198.
- Wylie, R. B. (1951). Principles of foliar organization shown by sun-shade leaves from ten species of deciduous dicotyledon trees. *Amer. J. Bot.* **38**, 355–361.
- Yager, R. E. (1960). Possible role of pectic enzymes in abscission. *Plant Physiol.* **35**, 157–162.
- Yanagisawa, T. (1954). Some phenological observations on forest trees at various altitudes on Mt. Muine in Hokkaido. *Bull. For. Exp. Sta. Meguro, Tokyo* **70**, 71–92.
- Yardeni, D., and Evenari, M. (1952). The germination inhibiting, growth inhibiting, and phytocidal effect of certain leaves and leaf extracts. *Phyton (Buenos Aires)* **2**, 11–16.
- Yazawa, K., and Ishida, S. (1965). On the wet heartwood of some broadleaved trees grown in Japan. II. Seasonal moisture content of Yachi-damo and Haru-nire by months. *J. Fac. Agr., Hokkaido Univ.* **54**, Part 2, 123–136.
- Young, H. E., and Kramer, P. J. (1952). The effect of pruning on the height and diameter growth of loblolly pine. *J. Forest.* **50**, 474–479.
- Zahner, R. (1962). Terminal growth and wood formation by juvenile loblolly pine under two soil moisture regimes. *Forest Sci.* **8**, 345–352.
- Zahner, R. (1968). Water deficits and growth of trees. In "Water Deficits and Plant Growth" (T. T. Kozlowski, ed.), Vol. II. Chapter 5. Academic Press, New York.

- Zahner, R., and Stage, A. R. (1966). A procedure for calculating daily moisture stress and its utility in regressions of tree growth on weather. *Ecology* **47**, 64-74.
- Zak, B. (1964). Role of mycorrhizae in root disease. *Annu. Rev. Phytopathol.* **2**, 377-392.
- Zeevart, J. A. D. (1962). Physiology of flowering. *Science* **137**, 723-731.
- Zimmer, W. J., and Grosse, R. J. (1958). Root systems and root-shoot ratios of seedlings of some Victorian Eucalypts. *Aust. Forest.* **22**, 13-18.
- Zimmermann, M. H., ed. (1964). "The Formation of Wood in Forest Trees." Academic Press, New York.
- Zimmermann, W. A. (1936). Untersuchungen über die räumliche und Zeitliche Verteilung des Wuchsstoffes bei Bäumen. *Bot. Z.* **30**, 209-252.
- Zucker, M. (1963). Experimental morphology of stomata. *Conn., Agr. Exp. Sta., New Haven, Bull.* **664**, 1-17.

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