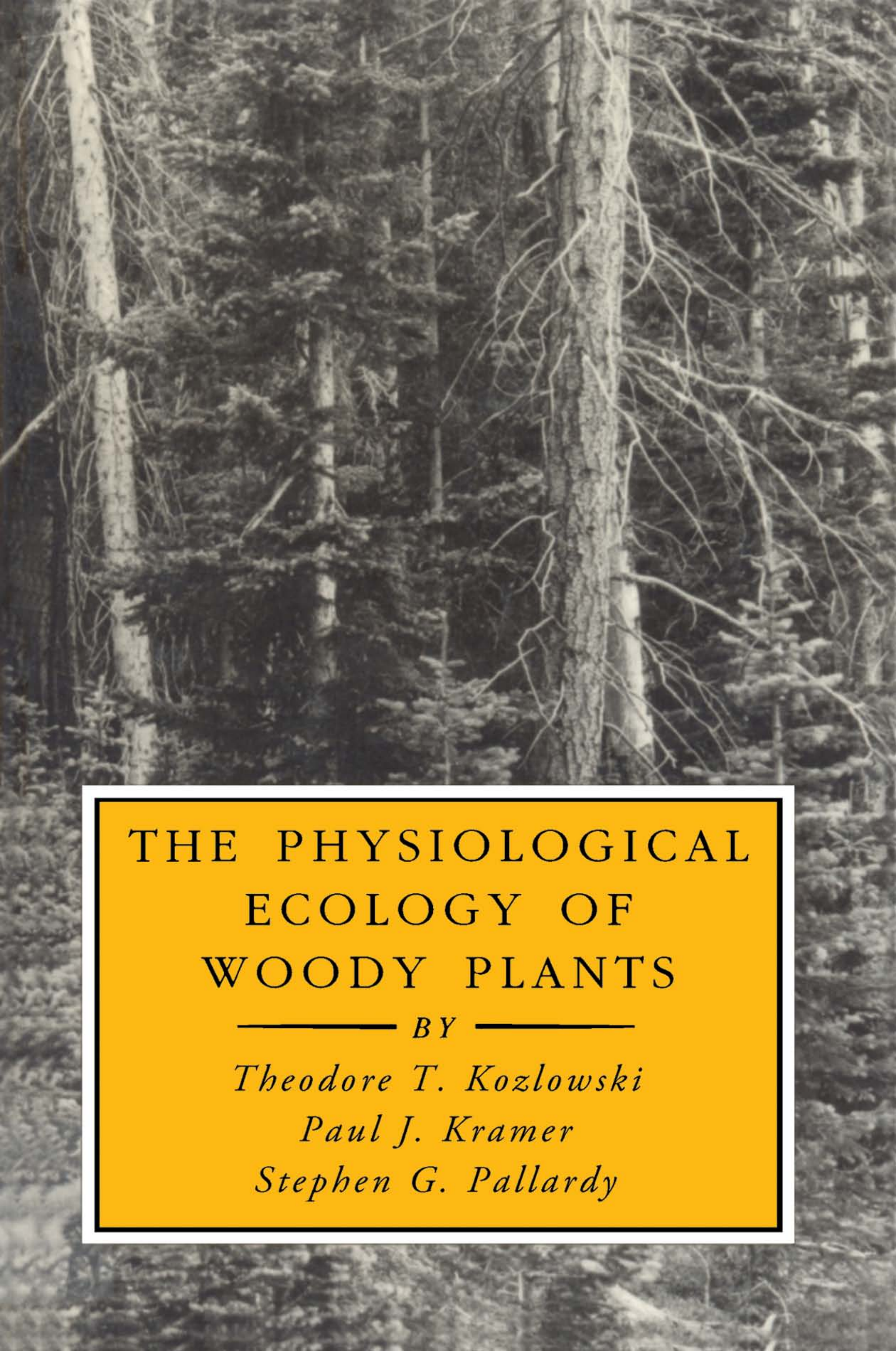

THE PHYSIOLOGICAL ECOLOGY OF WOODY PLANTS

BY

Theodore T. Kozlowski
Paul J. Kramer
Stephen G. Pallardy

The Physiological Ecology of Woody Plants

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Preface

This book was written for use as a text by students and teachers and as a reference for investigators and growers who desire a better understanding of how woody plants grow and communities of woody plants are established and develop. Because of its interdisciplinary scope, the book will be useful to a wide range of plant scientists including agronomists, arborists, plant ecologists, foresters, horticulturists, geneticists, plant breeders, plant physiologists, soil scientists, and landscape architects.

The book is based on the premise that efficient management of growth of shade, orchard, and forest trees and other woody plants depends on our understanding of the physiological processes that control growth, the environmental complex that controls those processes, and our ability to modify the environment to maintain conditions that will be conducive to favorable rates of physiological processes. Accordingly this book:

1. emphasizes the interactions of heredity and environment in influencing growth of woody plants, and points out the importance of various environmental factors and the interactions among them on growth;
2. outlines differences in responses of individual trees and of communities of trees to environmental stresses. The primary emphasis is on the impact of environmental stress factors (alone and in combination) on growth and development of communities of woody plants; and
3. provides information about various cultural practices useful for efficient management of shade, forest, and fruit trees as well as shrubs and woody vines.

The first chapter describes growth characteristics of woody plants, emphasizes the importance of the physiological processes that are the critical intermediaries through which heredity and environment interact to influence growth, and introduces the complexity of environmental control of woody plants. The second chapter describes the compounds essential for plant growth, including foods (carbohydrates, proteins, lipids), water, mineral nutrients, and hormonal growth regulators. Separate sections are devoted to sources and functions of these compounds.

The third chapter deals with stand regeneration, seedling establishment, and subsequent growth and development of stands of trees. Considerable attention is given to competition among canopy trees and between canopy trees and subordinate vegetation for resources (light, water, mineral nutrients). Also included are sections on plant succession and accumulation and partitioning of biomass.

Chapters 4 to 12 deal with effects of important environmental factors on physiological processes and on vegetative and reproductive growth of communities of woody plants. Separate chapters are devoted to radiation (light intensity, light quality, and duration of exposure); temperature; soil physical properties and mineral nutrition; water deficits; soil aeration, compaction, and flooding; air pollution; carbon dioxide; fire; and wind. Special attention is given to environmental preconditioning and interactive effects of various environmental stress factors on growth.

The final chapter describes a variety of cultural practices that can be employed to improve propagation and production of planting stock in the nursery and growth of established landscape trees, fruit trees, and forest trees in plantations and natural forests. The cultural practices discussed include site preparation treatments (slash disposal, prescribed burning, harrowing, disking, bedding, use of herbicides, and drainage), fertilizer application, irrigation, thinning of forest stands, pruning of branches and roots, use of chemical growth retardants and pesticides, and integrated pest management. A final section on planting for high yield discusses short-rotation forestry, agroforestry, and high density fruit and nut orchards.

A summary list of general references has been included at the end of each chapter and papers cited in the text are listed in the Bibliography at the end of the book. We have selected significant references from a voluminous world literature in order to make the work authoritative, well-documented, and up-to-date. Where appropriate, we have presented contrasting views and often have given our personal conclusions, on the basis of the weight of evidence, on controversial issues. As new research data become available, some conclusions will require revision, and we hope that readers will join us in modifying their views when changes are appropriate.

In the text we have used common names for most well-known species of plants. Scientific names are used for a few unusual plants that do not have widely used names. Separate lists of common and scientific names, and scientific and common names, are given following the text. Names of North American forest trees are largely based on E. L. Little's *Check List of Native and Naturalized Trees of the United States* (1979), Agriculture Handbook No. 41, U.S. Forest Service, Washington, D.C. However, to facilitate use of the common name index for a wide audience, we chose not to employ the rules of compounding and hyphenating recommended by Little (1979). These rules, while reducing taxonomic ambiguity in common names, often result in awkward construction and unusual placement within an alphabetical index. Names of other species are from various sources.

We express our appreciation for the contributions of the many people who assisted directly and indirectly in the preparation of this book. Much information and stimulation came from our graduate students, research collaborators, and from arborists, foresters, plant ecologists, horticulturists, and plant physiologists all over the world with whom we have worked and discussed problems.

Various chapters were read by C. E. Ahlgren, N. L. Christensen, R. Oren, P. B. Reich, W. H. Schlesinger, and W. E. Winner. However, the text has been revised since they read and commented on individual chapters, and they should not be held responsible for errors that may occur. W. Ferren, R. Haller, R. Miller, C. H. Muller,

J. L. Rhoads, and R. M. Wilbur assisted with preparation of the list of scientific names of species.

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Chapter 1

How Woody Plants Grow

Introduction

The objective of this book is to explain how individual trees and shrubs grow, how they develop into communities, and how environmental factors and cultural practices affect the quantity and quality of growth. Ecologists, arborists, foresters, horticulturists, and gardeners know that some kinds of trees and shrubs grow better than others on dry sites; that only a few thrive in wet soil; and that cultural practices such as thinning, pruning, fertilization, irrigation, and drainage, used properly, often improve growth. However, they seldom know why plants respond as they do to environmental stresses and cultural treatments. Over a century ago Johnson (1868) wrote that in order to grow plants efficiently it is necessary to understand how plants grow. Such an understanding is even more important today because of the increasing complexity of the environment caused by industrial air pollution and by the increasing concentration of atmospheric CO_2 and associated changes in climatic conditions. Also, forest trees are being treated more as crop plants (Cannell and Jackson, 1985). Furthermore, modern biotechnology is increasing the possibility of producing superior genotypes if the desirable attributes can be linked to specific genes. Thus there are increasing pressures from several directions for a better understanding of the interaction between the physiological processes of woody plants and their environment (Osmond *et al.*, 1987).

Particularly important to ecologists and foresters is an understanding of the factors involved in successful competition. For example, why are plants such as birch and white or loblolly pine, which are successful pioneers on recently disturbed land, unable to perpetuate themselves and therefore are succeeded by other species? Will the increasing concentration of atmospheric CO_2 and associated climatic changes affect the competitive capacity of competing species differently and change natural succession or the choice of species for planting? Will shorter rotations increase the severity of mineral deficiencies and the need for fertilization? Why do some tree seedlings and shrubs thrive in the shade where others fail? Answers to such questions require an understanding of how plant growth is affected by environmental factors, and in this book we attempt to provide physiological explanations for those effects.

Heredity and Environment

The growth of woody plants, like that of all other organisms, is controlled by their heredity and environment, operating through their physiological processes as shown in Fig. 1.1. Although all trees exhibit some common growth characteristics, such as increase in height and stem diameter, they also show considerable variability in growth because of their hereditary differences. Genetic variations in size, crown form, straightness of stems, wood density, leaf retention, and longevity are particularly well known. Less obvious but often equally important are hereditary differences in rates of growth, winterhardiness, drought tolerance, flooding tolerance, and disease and insect resistance. Genetic variations in physiological and growth characteristics are responsible for the differences between tropical and temperate zone trees and evergreen and deciduous trees, as well as differences among and within species (e.g., differences in growth among clones, ecotypes, and seed sources). For example, Arizona–New Mexico sources of white fir grew 50 to 100% faster than Utah–Colorado sources when planted in the eastern United States (Wright, 1976). Such differences are important in establishing plantations of Christmas trees or trees for pulp and timber because trees from some sources can be harvested at half the age of trees from other seed sources. Important differences have been found in growth, cold and drought tolerance, length of growing period, and other characteristics of seedlings grown from seed of the same species obtained from various geographic regions or provenances (e.g., Lester, 1970; Scholz and Stephan, 1982).

Experience also shows that trees and other plants sometimes grow much better in a new and different environment than in their native environment (Jones, in Cannell and Jackson, 1985, p. 69). Monterey pine from California and several species of

Hereditary potentialities
The field of genetics
Selection and breeding programs
Potential rate of growth, size, and longevity of trees
Type of xylem, depth and extent of root systems

Environmental factors
The fields of ecology, soil science, climatology, meteorology, etc.
Radiation, temperature, minerals, competition, pests, silvicultural practices, etc.

↓

Physiological processes and conditions
The field of plant physiology
Photosynthesis, carbohydrate and nitrogen metabolism
Respiration, translocation
Plant water balance and its effects on growth and metabolism
Growth regulators, etc.

Quantity and quality of growth
The field of arboriculture, forestry, and horticulture
Amount and quality of wood, fruit, or seed produced
Vegetative versus reproductive growth
Root versus shoot growth

Figure 1.1 Diagram showing how the hereditary potentialities of plants and the environment operate through physiological processes and conditions to determine the quantity and quality of plant growth. (From Kramer and Kozlowski, 1979, by permission of Academic Press.)

pine from the southeastern United States grow better in New Zealand than in their native habitats (Jackson, 1965). In contrast, Rehfeldt (1986) claimed that in central Idaho, ponderosa pine should not be planted more than 290 km from the seed source, and Lowe *et al.* (1977) reported that balsam fir from local seed grows best in northern New England. However, several North American tree species grow well in other parts of the world, such as Sitka spruce in Scotland and Germany and bald cypress in China. The early history of successes and failures in the introduction of exotic trees was reviewed by Moulds (1957), and Zobel *et al.* (1987) published an interesting book on exotic trees.

The environment determines the extent to which the hereditary potentialities of plants are attained, as shown by the differences in size of trees of the same species growing in moist fertile soil and in dry infertile soil. An extreme effect of environmental and cultural conditions on growth is seen in the dwarf trees (bonsai) of China and Japan, which have been so dwarfed by cultural treatments that they are less than a meter high after a century or more, although their normal height may be 15 or 20 m (Fig. 1.2). Another example is the short life expectancy for urban trees (10 years

Figure 1.2 A bonsai of eastern red cedar dwarfed by a restricted root system. In nature, eastern red cedar grows to heights of 50 to 75 ft or more (15–23 m). (Photo courtesy of Arnold H. Webster.)

for streetside trees) compared to that of the same kinds of trees growing in the forest (Foster and Blaine, 1978).

The physiological processes of plants comprise the machinery through which cultural treatments—such as thinning, fertilization, and irrigation—and environmental stresses—such as drought, flooding, abnormally high or low temperatures, air pollution, insect pests, and diseases—influence growth. If a tree breeding program or a cultural treatment increases growth, it does so by improving the functioning of the physiological machinery. The environmental changes that alter growth do so through their influence on rates and balances among such processes as photosynthesis, respiration, hormone synthesis, absorption of water and minerals, and translocation of substances needed for growth (including carbohydrates, nitrogen compounds, hormones, water, and mineral nutrients). Furthermore, reduction of growth or death of trees is preceded by a series of abnormal physiological events. Hence, some understanding of the physiological processes involved in growth and the manner in which such processes respond to variations in environmental factors is essential to formulation of management programs for growing trees and shrubs efficiently.

The importance of the role of physiological processes in the response of plants to changes in environmental factors and to cultural practices can be illustrated by a few examples:

1. Defoliating insects damage plants by reducing the amount of foliage available for photosynthesis. See Chapter 2.
2. Fungal pathogens damage leaves and cause their premature shedding (abscission), sometimes block the movement of water in the xylem or carbohydrates in the phloem, and produce toxins that adversely affect physiological processes. See Chapter 2.
3. Abnormally short nights caused by artificial lighting retard development of dormancy in some trees and shrubs, resulting in winter injury. See Chapter 4.
4. Fertilization supplies the mineral nutrients associated with enzymes and the formation of new protoplasm and cell walls. Such nutrients also have an important role as buffers and as solutes that maintain osmotic pressure in cells. See Chapter 6.
5. Irrigation prevents water deficits that inhibit cell expansion, induce stomatal closure, and reduce photosynthesis. See Chapter 7.
6. Compaction or flooding of soil reduces availability of soil oxygen and inhibits root respiration, thus decreasing root growth and absorption of water and mineral nutrients and affecting the production of certain hormones. Anaerobic soil conditions also favor activity of fungi that cause death of roots and suppress development of mycorrhizae, further decreasing uptake of mineral nutrients and water. See Chapter 8.
7. Thinning of tree stands reduces competition for water and minerals among the remaining trees and postpones the reduction in growth that is characteristic of aging overstocked stands. See Chapters 3 and 13.

Growth Characteristics

Before going into a detailed discussion of the physiological processes and environmental conditions controlling the growth of woody plants, we will discuss some characteristics of growth and yield itself. Foresters are interested primarily in yield of wood, whereas horticulturists and gardeners are interested in fruit, flowers, or aesthetically pleasing plants. In any event, yield is the result of growth, which involves a complex series of processes beginning with the formation of new cells and progressing through the differentiation of cells into tissues, and finally integration of the tissues into the organs of a plant. Growth usually is measured as increase in height, stem diameter, or dry or fresh weight, and yield in terms of the commercially valuable product such as volume of wood, fruit, or nuts, number and quality of flowers, or the aesthetic success of ornamental shrubs and trees. Growth and high-quality yield are not necessarily closely correlated. More rapid tree growth can be obtained by wider spacing, but at the cost of reduction in yield per acre and possibly in quality of wood.

Growth of a shrub or tree can be considered analogous to a complex biochemical factory that builds itself from its own products, following a pattern provided by its heredity. The chloroplasts represent the machines that produce the primary carbohydrates in photosynthesis. Carbon dioxide and water are the raw materials, and sunlight supplies the energy. The products of photosynthesis go through intermediate processes, including fat and protein synthesis, and eventually some are transformed into new tissues.

At the cellular level, growth involves cell division, enlargement, and maturation into the various tissues constituting a plant. At the whole-plant level, it involves integration of tissues into the various organs of the plant; the roots, stems, and leaves, and eventually flowers, fruits, and seeds. Cell differentiation and maturation seem to be regulated by organizing factors that influence form and function by controlling relative rates of growth and degrees of differentiation. As all cells in a tree have the same genome, new cells formed in a meristematic region might develop into any kind of tissue. However, cell differentiation is so controlled that cells in various parts of plants develop quite differently, resulting in the diverse tissues of roots, stems, and leaves. The formless masses of cells often found in tissue cultures show what occurs in the absence of control by the proper hormonal growth regulators. Usually such masses of undifferentiated cells can be induced to differentiate into plantlets only by applying the proper combination of growth regulators in the appropriate sequence (Henke *et al.*, 1985; Durzan, in Kossuth and Ross, 1987). This situation supports de Bary's aphorism: "The plant forms cells, not cells the plant" (Barlow, 1982). At the physiological level, growth processes are dependent on a supply of food provided by photosynthesis, followed by a complex series of biochemical processes ending in the production of new protoplasm and its products. As stated earlier, all of this is under control of growth regulators and biochemical and physical equilibria that tend to keep various processes and structures in balance. This will be discussed in more detail in Chapter 2, but the complex constellation of processes involved in growth and development presents many puzzling problems.

Location of Growing Regions

In plants, unlike in animals, growth is localized in apical and lateral meristems, tissues that contain cells with a capacity to divide. In woody plants, apical meristems are localized in stem and root tips. Height growth of trees and elongation of branches result from activity of apical meristems contained in buds. Growth in diameter of stems, branches, and major roots results from activity of the vascular cambium, a thin sheath of meristematic tissue located between the wood and bark. Cambial cells divide and the daughter cells on the inside become xylem (wood), whereas those on the outside become phloem (bark). In this manner new layers of wood are inserted each year between the previous year's layers of wood and bark, causing an increase in diameter of stems and branches. Because of this mode of growth, a tree stem consists of annual increments of wood, the annual rings, each new one being added outside of that of the preceding year. A longitudinal section of a tree stem shows annual increments of wood as a series of overlapping cones (Fig. 1.3). A small amount of increase in stem diameter is traceable to the activity of a cork cambium (phellogen), but the outer bark tends to be shed so, with a few exceptions such as in redwood, the bark usually remains relatively thin.

The annual rings of wood in a stem cross section can be distinguished because of differences in size of the cells produced early and late in the growing season. The wood formed early in the season (earlywood or springwood) has larger cells with thinner walls and a lower density than the wood formed later in the season (latewood or summerwood). Thus annual rings often are prominent in stem cross sections because of differences in cell diameter and density of the earlywood of one year, which is next to the smaller, last-formed latewood cells of the previous year (Fig. 1.4). Although trees of the temperate zone generally produce one ring of wood each year, they sometimes produce more than one. In the tropics, however, trees may grow continuously throughout the year and may not produce distinct annual rings of wood (Fig. 1.5).

Growth follows the same sequence of processes in apical and lateral regions, beginning with cell division and followed by cell enlargement and differentiation into the tissues characteristic of each organ. An important difference between apical and lateral growth is that cell division in apical meristems occurs chiefly in a plane perpendicular to the long axis of roots and stems, thus adding to their length, whereas division in lateral meristems occurs primarily in a plane parallel to their length, which adds to stem diameter. Other meristems develop at various locations in roots and stems, giving rise to branches. The meristems that produce branch roots originate in the pericycle, a ring of cells lying just outside the vascular tissue. In seed plants, stem branches usually arise from meristematic regions in axillary buds that originate in the axils of leaves. In addition, meristems arise in various regions

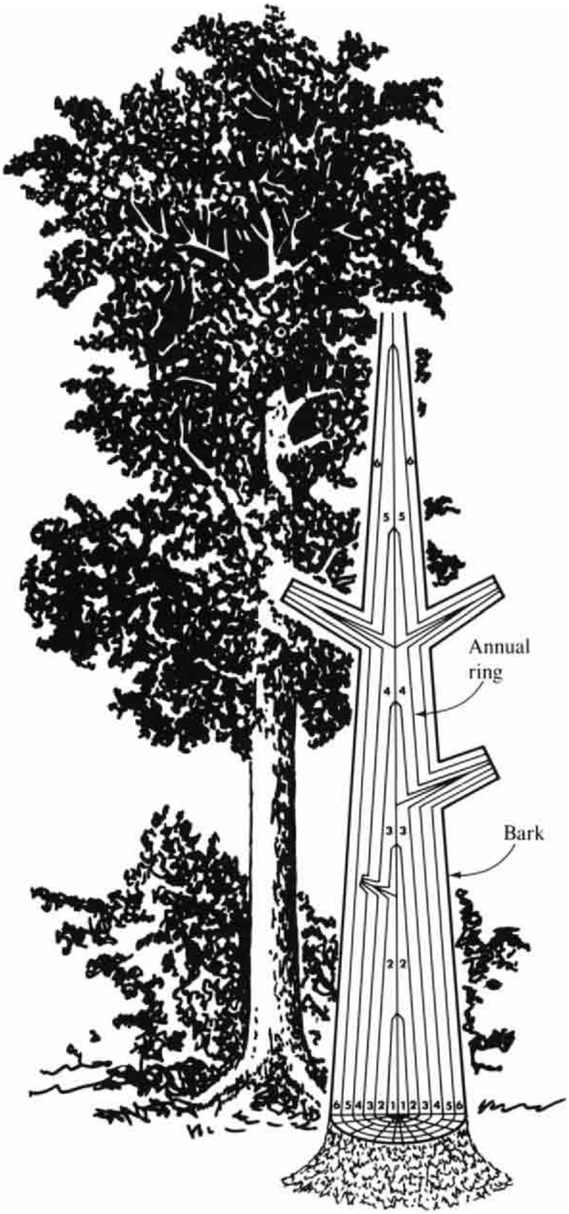

Figure 1.3 Diagrammatic median longitudinal section of a tree showing the pattern of annual xylem increments or "rings" in the stem and major branches. (From Kramer and Kozlowski, 1979, by permission of Academic Press.)

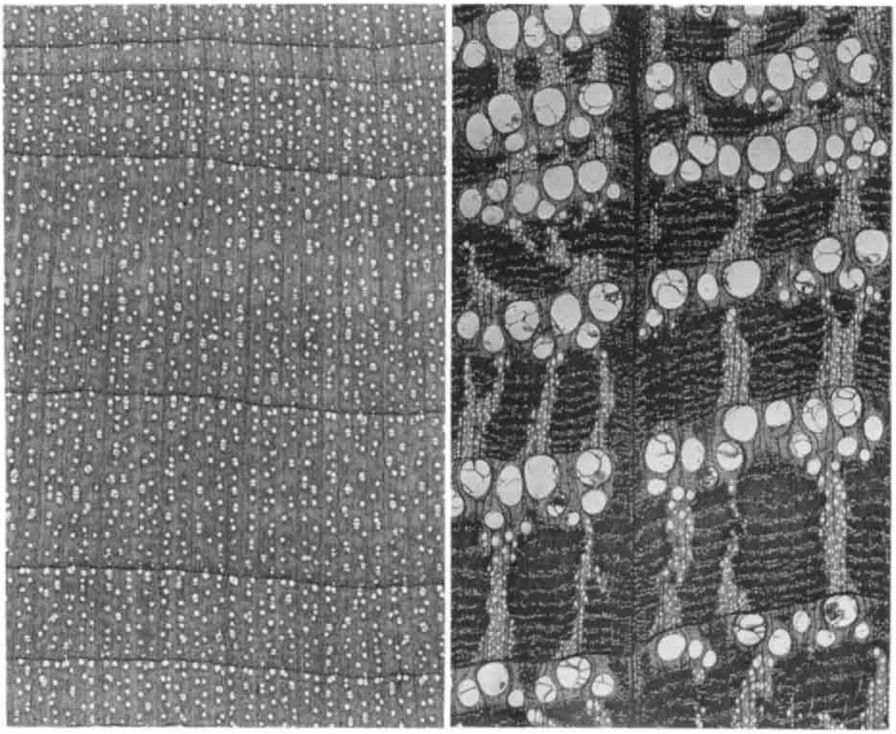

Figure 1.4 Cross sections of stems of a diffuse porous species, silver maple (*left*), and a ring porous species, white oak (*right*), showing differences in diameter and distribution of vessels in springwood and summerwood. (U.S. Forest Service photograph from Kramer and Kozlowski, 1979, by permission of Academic Press.)

of trees and shrubs as a result of wounding, flooding of soil, and other stimuli that produce adventitious roots and stems. The rooting of cuttings is an important example of adventitious root development. Most stump sprouts and epicormic branches (water sprouts) develop from dormant buds that were produced during primary growth but did not develop into visible branches until subjected to a special stimulus such as severe pruning, removal of the treetop, or increased exposure of the stem to light by thinning a stand. Tree growth is discussed in detail in the two-volume monograph by Kozlowski (1971a,b).

Variations in Rates of Growth and Apical Dominance

The relative rates of growth of the various stem tips of a tree or shrub control its shape. For example, in most conifers the apical meristems (buds) of terminal shoots grow more rapidly than those of lateral branches, resulting in their typically conical shape. Occasionally, apical dominance is lost with increasing tree age, resulting in

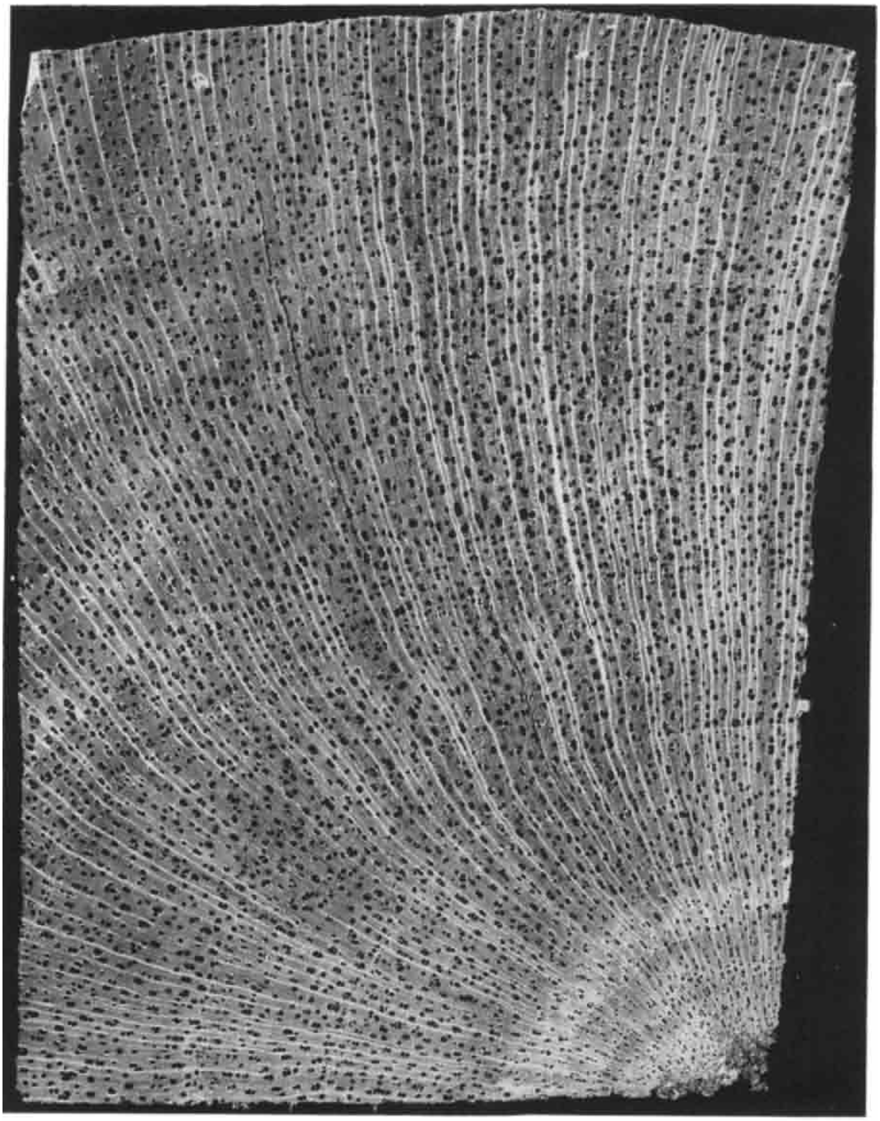

Figure 1.5 Cross section of stem of *Boswellia serrata,* a tropical tree, showing indistinct growth rings. (From Kozlowski, 1971b, p. 75, by permission of Academic Press.)

flat-topped trees such as stone pine. In most angiosperms there is less difference in the rate of growth among various shoot meristems, resulting in more rounded treetops. American elm, for example, is notable for its deliquescent form, characterized by a broad, spreading top. Its characteristic crown form develops because the terminal buds of elm die and numerous axillary buds develop into branches. Occasionally, upright or conical forms of angiosperms are found, such as Lombardy poplar and some selections of English oak and linden, which are useful in ornamental plantings. Some examples of tree form are shown in Fig. 1.6, and apical regulation of shoot growth is discussed by Kozlowski (1971a, pp. 282–295).

Differences in apical dominance and growth form are important to arborists and landscape designers because they enable them to create various visual effects. Differences in tree form must also be taken into account by horticulturists with regard to pruning, spraying, exposure of fruit to sun, and fruit picking. Apical dominance is very important to foresters, who desire strong, upright stems, because loss of the terminal bud of the main stem by insect or other injury results in undesirable stem forking. In contrast, growers of Christmas trees shear young trees

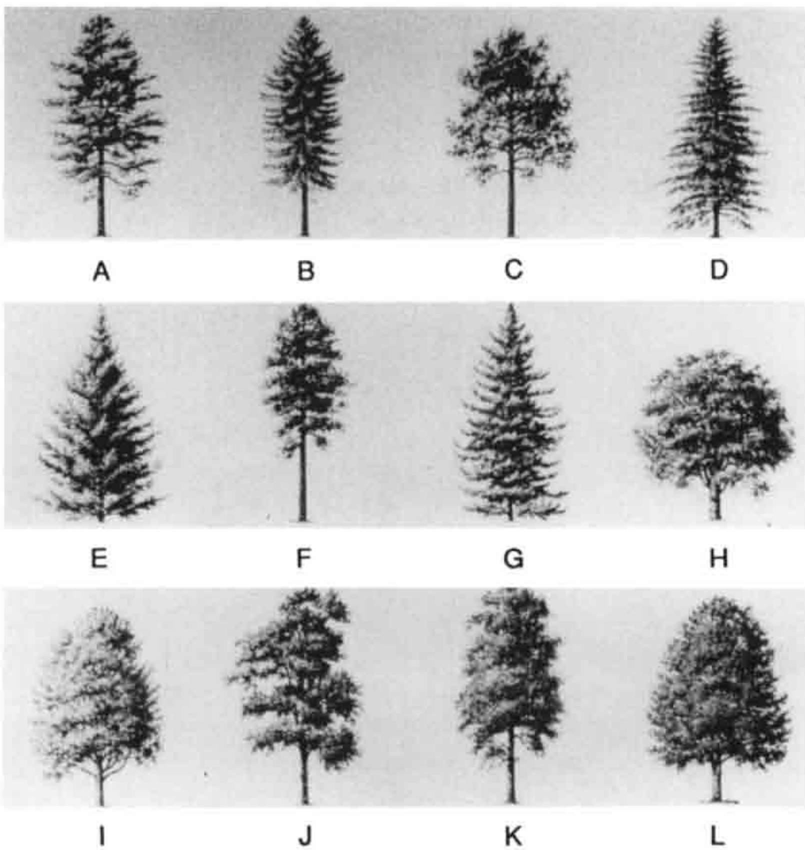

Figure 1.6 Variation in form among 12 species of open grown trees. (A) Eastern white pine; (B) Douglas-fir; (C) longleaf pine; (D) eastern hemlock; (E) balsam fir; (F) ponderosa pine; (G) white spruce; (H) white oak; (I) sweet gum; (J) shagbark hickory; (K) tulip tree; (L) sugar maple. (Courtesy of St. Regis Paper Co.)

to discourage apical dominance and encourage development of lateral buds and dense branching (Fig. 13.12). Heavy pruning of apical branches is also used to stimulate dense branching of ornamental shrubs, especially those used for hedges. Growth of trees in dense stands tends to suppress lateral branches by shading and encourages apical dominance. However, by careful pruning, a row of closely planted trees can be trained into a dense hedge that retains its lower branches (Fig. 1.7). There is currently a trend toward growing fruit trees in rows and pruning them into hedgelike arrangements that can be shaped and sprayed more efficiently than trees standing alone (Jackson, 1985) (see Chapter 13).

Duration of Growth

The duration of growth refers both to the length of the annual growing season and to the length of life of a tree or shrub. While plants are classified as annuals, biennials, or perennials on the basis of length of life, in this book we are interested only in woody perennials.

Life Span

There is a wide difference in the life span of various species of woody plants, ranging from a few decades to a few thousand years. Peach trees are old at 20 to 30 years, oaks often live to be several hundred years old, bald cypress may reach 1600,

Figure 1.7 An apple orchard with trees trained as a hedge. (From Westwood *et al.*, 1976.)

coast redwoods 3000, and bristlecone pine at least 5000 years. Some data on tree life spans are given by Harcombe (1987). Aging forest trees have some common characteristics such as reduced rates of growth, slow wound healing, decreased ratio of photosynthetic to nonphotosynthetic tissue, and increase in top dieback. However, it is not clear why apple trees typically live longer than peach trees and oak trees live longer than apple trees.

Good opportunities exist for some interesting and useful research on plant aging. Among the interesting problems is the fact that individual trees such as Lombardy poplar and peach are shortlived although the cultivars have been propagated vegetatively for many decades or even centuries. Lombardy poplar is said to have originated as a mutation in northern Italy between 1700 and 1720, and the genotype has been propagated successfully by cuttings for nearly three centuries even though individual trees are rather short-lived. Perhaps short-lived trees are more susceptible to injury from environmental and biotic stresses than long-lived trees. Loehle (1988a) suggested that slowly growing trees probably live longer than rapidly growing trees because they allocate more photosynthate to protective characteristics such as thick bark and decay-inhibiting chemicals. Some of the changes associated with aging were discussed by Kozlowski (1971a, Chapter 4) and plant senescence was discussed in detail by Thimann (1980).

Seasonal Span of Growth

Although the length of the growing season of woody plants in the temperate zones is controlled in general by temperature, photoperiod, and rainfall patterns, other factors seem to be involved. Shoot growth of most woody plants begins in the spring before the danger of frost is past, and this results in occasional damage to leaves and flowers from late frost. However, there are wide differences among species in the proportion of the potential growing season actually used and shoot growth ceases in some species long before temperatures are low enough to be the cause (Fig. 1.8). This suggests that length of growing season is also affected by internal factors. In North Carolina, red pine and eastern white pine seedlings imported from New York State and planted out-of-doors made most of their height growth in one flush in April and ceased growth by midsummer, whereas loblolly, slash, and shortleaf pine seedlings made approximately the same amount of shoot growth in several flushes over a period of more than 4 months. Likewise, white ash and various species of oaks make most of their height growth in one flush early in the season, whereas tulip poplar grows most of the summer. In general, shoot growth is said to occur over a longer season in young trees than in older trees (Kozlowski, 1971a, pp. 117–163), but Reich *et al.* (1980) observed a shorter growing season for white oak seedlings than for canopy trees in Missouri.

In the lowland tropics, where temperature is never limiting, the length of the growing season often is restricted by the occurrence of dry seasons during which water becomes limiting. Even where growth is not limited by a dry season, tropical trees and shrubs usually show marked periodicity in alternating between growth and dormancy in a manner that is not easily explained (Kozlowski, 1971a,