RADIAL GROWTH IN CONIFERS AND DECIDUOUS TREES A COMPARISON

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ABSTRACT

Cambial activity, leading to a variety of cell types composing the xylem and phloem, is responsible for amassing the majority of biomass produced by woody plants. Owing to the economic and ecological significance of such productivity, the radial growth process in conifer and hardwood trees has been the long-time subject of intense study by forest scientists. This paper viewsthis work by examining the radial growth phenomenon and its interrelationship with other tree physiological processes.

The patterns of growth will be presented for ring-porous, diffuse-porous, and tracheid tree types at various stages of development and will be developed in relationship to various phenological events. In order to present a comparison of radial growth in conifers and hardwoods, growth patterns will be discussed in terms of four principal functions of the xylem and phloem: (1) transport, (2) storage, (3) support and (4) protection. The environmental and tree factors which affect cambial growth will also be reviewed. Two relatively new concepts involving the xylem are its role

in water and food storage and its allometric and physiological connections to the foliage. The "pipe" theory of water transport originially proposed by Shinozaki and others will be examined in light of present ecological and physiological knowledge concerning the storage and transport functions of cambial derivatives.

Introduction

Radial growth in trees, leading to a variety of cell types comprising the xylem and phloem, is responsible for amassing the majority of standing biomass which characterizes temperate hardwood and conifer ecosystems (Grier and Logan 1977, Bartos and Johnston 1978, Harris et al. 1978) Owing to the economic, social, and ecological significance of such productivity, the radial growth process has been the longtime subject of study by mensurationists, silviculturalists, physiologists, and ecologists.

Tree stems have long been separated into four major morphological categories: bark, cambium, sapwood xylem, and heartwood xylem. Theophrastus in the third century B.C., first described the wood and bark of Abies alba as being composed of "...layers, like an onion." The Royal Society of Great Britain commissioned Evelyn to study forest trees and he wrote in 1664: "These rings or spaces appearing upon transverse section are no other than the extremities of so many integuments, investing the whole tree, and, perhaps, all boughs that are of the same age with any of them, or older. ... The growth and augmentation of trees, in all dimensions, is acquired by accession of new integuments yearly." Clearly, the importance of annual growth rings in forest trees has been recognized for a long time.

The development of the tree stem is made possible through the secondary thickening of the primary stem body by means of a secondary meristem or cambium. The secondary meristem is longitudinally, as well as peripherally, continuous. Thus, each annual increment of wood can be viewed as a layer covering the pre-existing woody portion of the stem, roots, and branches (Figure 1). Due to its importance, the dynamics and morphology of the cambium have been reviewed by many authors (e.g., Kozlowski 1971, Philipson et al. 1971, Zimmermann and Brown 1971, Berlyn 1980).

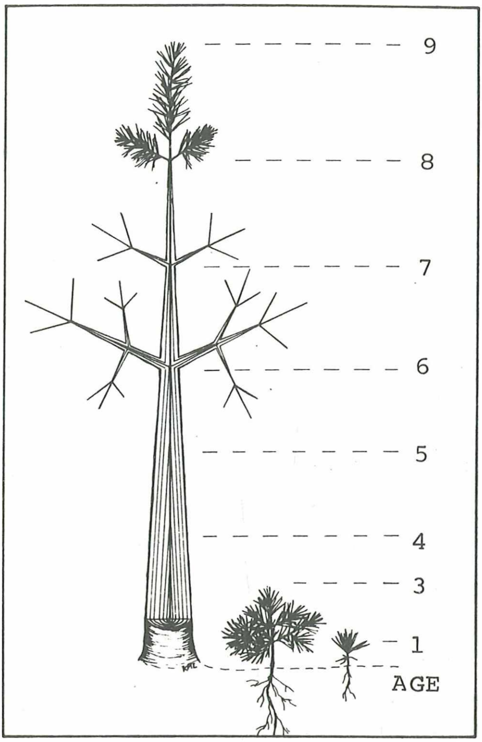


Figure 1. Schematic of a 9-year-old Pinus tree illustrating the addition of both elongation increments (apical meristems) and radial increments (cambial meristems).

The purpose of this review is to examine certain physiological aspects of cambial growth, activity, and function in forest trees. This will be accomplished by briefly outlining the location of the cambium, its general anatomy, and its growth activity; then by describing the function of the cambial derivatives, including aspects of transport, storage, and support. Cambial growth patterns and dynamics in conifers and hardwoods will be compared and contrasted whenever possible. In addition, examples will be presented illustrating various silvicultural implications related to growth and function of the cambium.

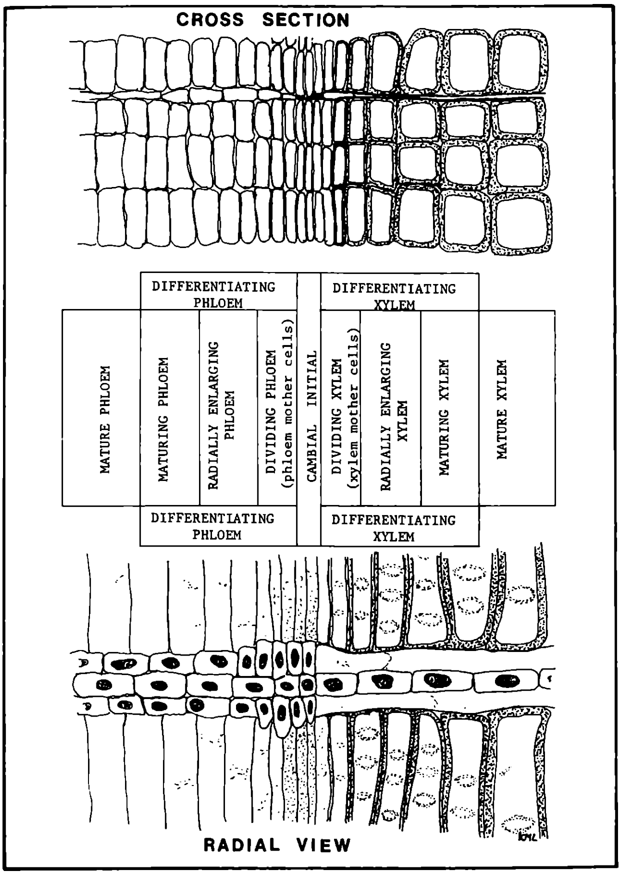
This discussion will concentrate on the aboveground xylem stem portions of forest trees common to temperate ecosystems. This restricted view of radial growth is necessary in order to limit the scope of this review. As will be shown later, roots, stem, and branches (foliage) are interrelated to the extent that a holistic approach to discussing tree growth and development is warranted. Those desiring more detailed information of root growth than will be presented in this paper are directed to the texts of Fayle (1968), Kozlowski (1971), and Marshall (1977).

The cambium
Location Anatomy and Activity

The vascular cambium is initially derived from procambial cells near the apex of the primary shoot. Following maturation of the primary xylem and phloem, the central portion of the vascular bundle remains meristematical active and functions as the vascular cambium. The cambium becomes a continuous circular sheath in the maturing portion of the elongating woody shoot by the tangential differentiation of new initials.

The term cambium actually denotes a zone of cells between the secondary xylem and phloem that undergo periclinal cell divisions; these cells include cambial initials and zones of undifferentiated or dividing xylem and phloem mother cells (Figur 2). During the dormant season the cambial zone is normally quite narrow, usually consisting of four to six layers of cells (Grillos and Smith 1959). During periods of high cambial activity, this zone may be composed of from 15 to 20 layers of cells, any of which may periclinally divide.

The cambial zone is composed of two major types of initiating cells producing an assortment of derivatives (Figure 2; Wodziki and Brown 1973). Fusiform initials give rise to tracheids (conifers) or vessels (hardwoods),libriform and tracheid fibers, and various axial parenchyma cells



igure 2. Diagram and associated terminology for the various ell types and tissues of the cambium and its derivatives for a conifer).

towards the inside, and sieve cells albuminous cells (conifers) or companion cells (hardwoods), and axial storage parenchyma cells to the outside. Sieve cells of the phloem are responsible for the conduction of photosynthates throughout the tree; while companion or albuminous cells are involved in the functioning of the sieve elements (Zimmermann and Brown 1971). In the xylem, tracheids or vessels are chiefly involved in the transport of water and nutrients from the soil reservoir, support, and, as will be discussed later, water storage. Tracheids and vessels differ considerably in both length and diameter (Figures 3 and 4). Fibers are primarily involved in storage and support.

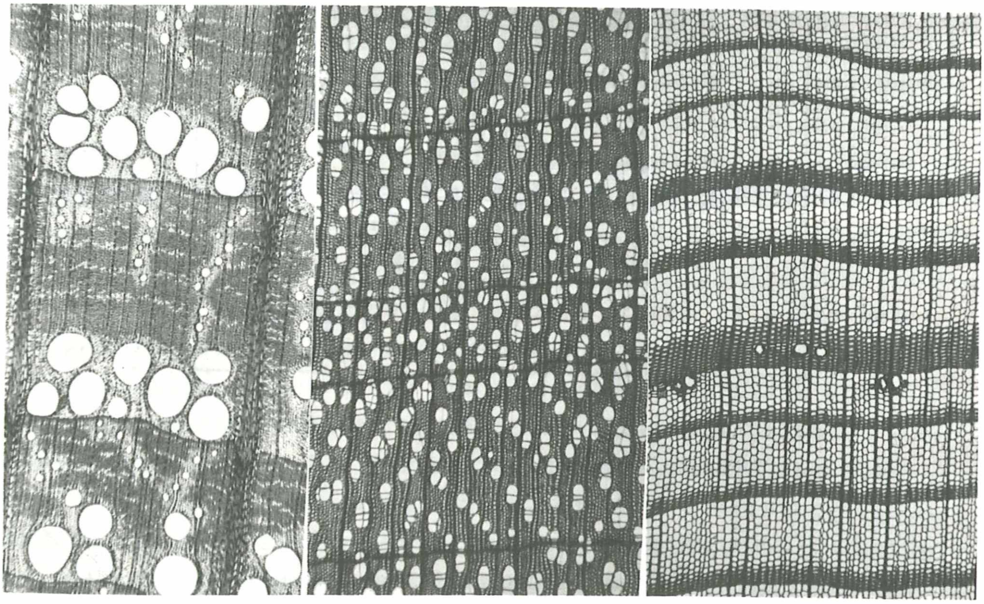


Figure 3. Cross section through the stems of (A) Quercus rubra (ring porous), (B) Betula spp. (diffuse porous) and (C) Pseudotsuga menziesii.
Photographs provided by Dr. L. Leney, University of Washington.

Ray initials give rise to ray parenchyma cells which represent an important radial communication network by which the phloem and xylem are inter-connected. Furthermore, ray parenchyma, like all axial parenchyma, are major sites of storage for carbohydrates.

After their production by xylem mother cells, daughter cells go through three distinct development phases before becoming functional elements (Figure 2; Wodzicki 1971). First is the radial enlargement phase characterized by the uptake of water into the vacuole, increases in turgor pressure, and cell expansion made possible by thin and elastic primary cell walls (Kozlowski 1971). Following enlargement, the maturation phase, involving secondary cell wall synthesis and lignification, is initiated. The synthesis of cellulose and other cell wall constituents begins during the expansion phase and lignification is underway by the time enlargement ceases. Both processes take place while the protoplasm is living, though death occurs shortly after completion (Brown et al. 1949), resulting in the final, mature xylem phase.

The primary factors that affect xylem differentiation are given in Table 1. Obviously, these categories overlap making the determination of control mechanisms quite difficult to quantitatively investigate. Readers interested in xylem and phloem differentiation, earlywood/latewood formation and transition, and cell growth are directed to the reviews and works of Nix and Wodzicki (1974), Kramer and Kozlowski (1979), Berlyn (1979), and Wodzicki and Wodzicki (1980).

Typically, sieve production and differentiation in the phloem begin early in the spring and continue until fall. Sieve cells abutt end-to-end, forming sieve tubes each separated by sieve plate pores with diameters between 1 and 2μ. Sieve cells cease to function during the fall due to the progressive accumulation of callose and slime plugs on the sieve areas (Crafts and Crisp 1971). During the growing season, the conducting phloem of conifers contains sieve cells produced during two consecutive seasons. When the phloem cells mature and die, becoming nonfunctional, they eventually collapse and are crushed as the treestem enlarges in diameter. As sieve

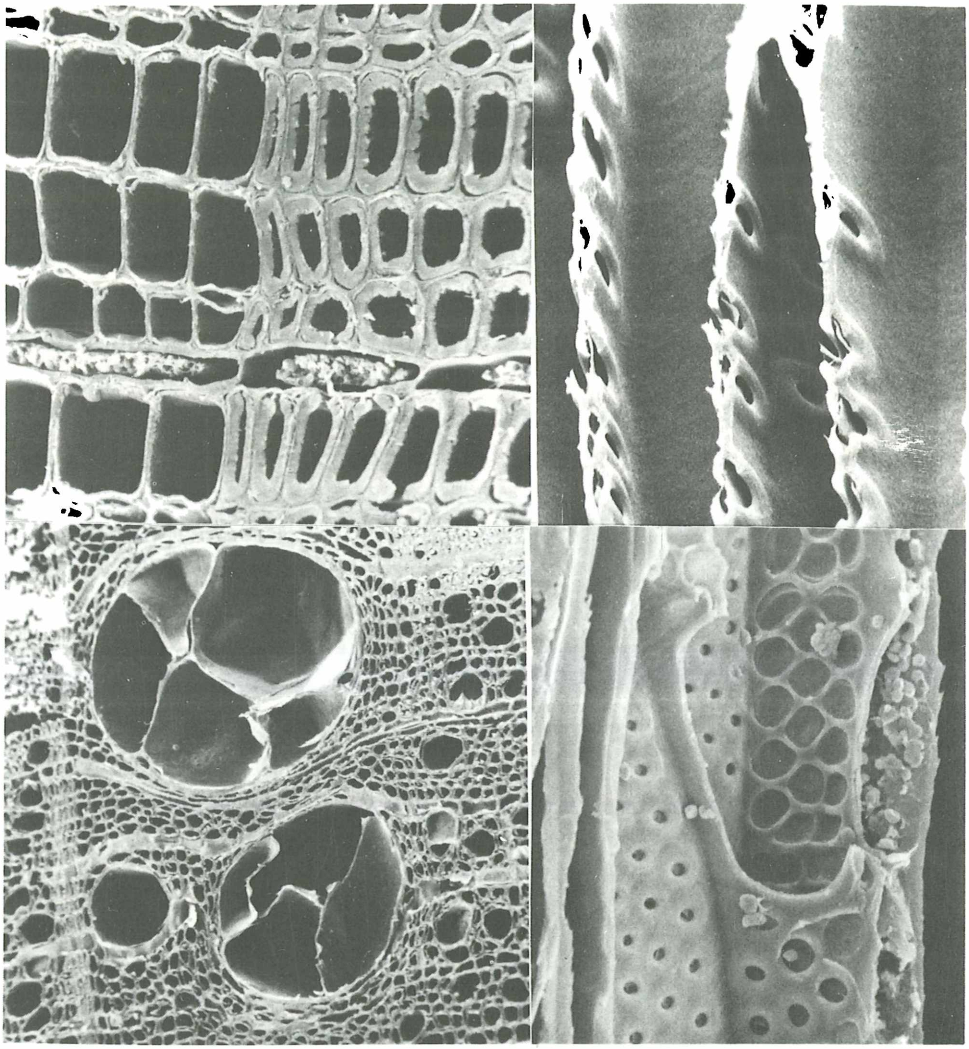


Figure 4. Cross (I) and radial (II) sections through the stems of (IA) Thuja occidentalis (1000x), (IIB) Pinus sylvestris (1000x), (IC) Quercus alba (150x) and (IID) Salix fragilis. One can see early- and latewood tracheids (IA) and vessels (IC). The earlywood vessels are plugged with tyloses. Photographs provided by Dr. J.E. Phelps, U.S. Forest Service, Rhinelander,

cells approach permanent cessation of function, massive amounts of calloses accumulate on the sieve areas; this is followed by loss of protoplasm and eventually partial collapse (Alfieri and Evert 1973).

Table 1. Factors in xylem cell differentiation (from Berlyn 1979).

I. PHYSICAL:	Water, light, temperature, wind, gravity, pressure, stress.
II. MINERAL:	Structural, stabilizing, and catalytic effects; Nutrientcarbohydrate.
III. HORMONES:	Types: auxins, cytokinins, gibberellins, ethylene, abscisic acid; Effects: cell size, number and qualitiy.
IV. INTRA-PLANT INTERACTIONS:	Types: organs, meristems; Effects: energy distribution and production, water relations, and hormones.
V. STRESS:	Mechanical, physiological; Elastic, plastic.
VI. GENETICS AND METABOLISM:	Genome: nuclear and cytoplasmic components; Regulator and feed-back systems; Environmental sensing apparatus.

Function of the Cambial Derivatives

Transport

The two principle tissues produced by the cambium, the xylem and phloem, provide a network for the transport of water, nutrients, photosynthates, and hormones from sites production (primarily the foliage and growing tips) or uptake (the soil) to sites of utilization within the tree. The xylem is primarily involved in water and nutrient transport from the roots to the foliage, while the phloem transports stored or currently produced photosynthates to active growing sites. The phloem is also invovled in the redistribution of nutrients and the transport of hormones throughout the tree.

Water transport through the xylem is by mass flow and is governed by the water potential gradient and resistance to flow along the pathway (Figure 5). Vertical water flow within a tree stem is driven by foliar water loss establishing a potential gradient throughout the xylary system to the soil. The diameter and specific type of xylem element will determine the resistance to flow. Tracheids with bordered pits tend to have higher resistances to flow than vessels. Groups of species have certain ranges of element diameters which depend on whether the species is ring- or diffuse-porous or tracheid (Figures 3,4, and 5), and by the rate of cambial

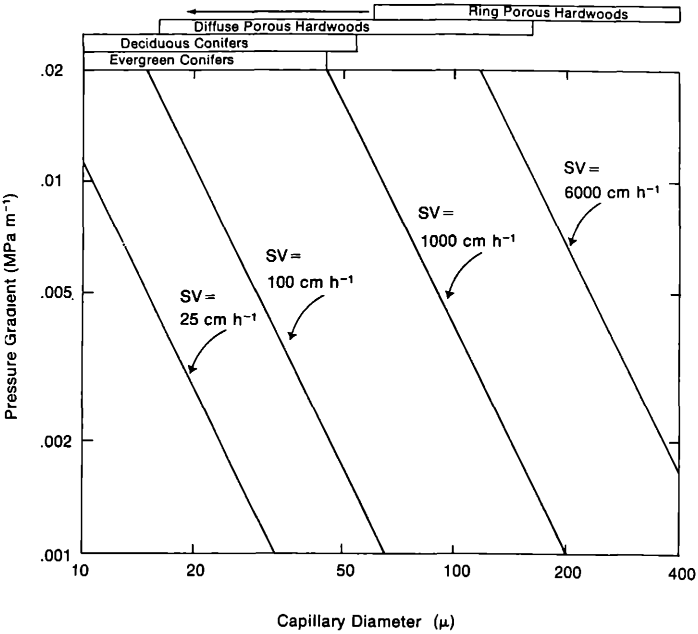


Figure 5. Relationship between pressure gradient, capillary diameter and peak sap velocities based on the Hagen-Poiseuille equation. Ranges of earlywood tracheid and vessel diameters are from Grosser (1977). The line with arrow indicates that diameters of latewood vessels can be small in ring porous hardwoods.

growth. Large elements can carry great quantities of water, but during drought periods cavitation of water columns can easily occur. Under such conditions, flow is restricted and the total xylem resistance to water flow increases. Small elements and, especially tracheids, have high resistances but most of the xylem remains functional under conditions of high water deficit.

The type of xylem element is important in determining cappillary diameter and hence the amount of water transported per unit time per xylem element (Figure 5). However, the total amount of water moved from the soil to the transpiring crown is also dependent upon cross-sectional area of the sapwood which is actively transporting water (Figure 6).

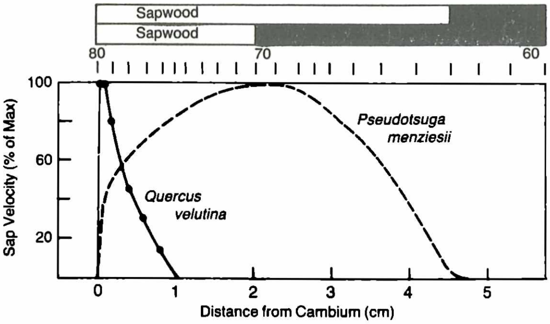


Figure 6. Sap flow velocity as a function of location in the xylem of a conifer and a ring porous hardwood (after Miller et al. 1980, Lassoie et al. 1977, Swanson 1972, Miller, unpubl. results).

Horizontal water transport also occurs in the stem, but very high resistances are encountered as water must move through and between xylem elements. Where present, ray parenchymes and resin canals can serve as pathways for lateral water movement (Erickson and Balatinecz 1964). The lateral movement of water, within the sapwood and from living tissues around the cambium to the sapwood, is important to the water storage function of the stem.

Translocation of carbohydrates occurs by mass flow in the sieve elements of the phloem along a source-sink gradient of increasing osmotic potentials (i.e., less negative) (Zimmermann and Brown 1971). Flow through the sieve elements may be bi-directional depending upon the relationship between source and sink strengths within the tree. Source strengths are primarily dependent upon the rate of net photosynthesis, while sink strengths vary seasonally with meristematic growth activities.

Flow of photosynthates is generally restricted to sieve tubes produced during the current growing season and is less than 100 cm hr^{-1} (e.g., Fraxinus americana; Zimmermann 1969). Sieve tubes are very long cells, laterally semipermeable, and permeable longitudinally through the sieve plates. Flow theoretically occurs along a gradient of decreasing osmotic and turgor pressure from the source to the sink. Most investigators have found osmotic gradients between 0.02 and 0.04 MPa m^{-1} (Huber et al. 1937, Zimmermann 1957, Kaufmann and Kramer 1967, Hammel 1968). Although the water potential of the phloem follows the daily and seasonal patterns exhibited by the xylem water potential, the relative change in phloem water potentials remains small (Kaufmann and Kramer 1967). Even when leaves are wilting or senescing, turgor pressures greater than zero occur in sieve tubes (Hammel 1968, Zimmermann 1971). In fact, turgor pressures remain positive until the first autumn freeze (Hammel 1968).

Storage

The consequence of transpirational water loss at the foliage-atmosphere interface is a localized decrease in foliar water content and water potential which eventually is transmitted to tissues throughout the tree. Contrary to strict adherence to the caternary theory of water transport, water required for transpiration can come from a number of internal sources in addition to the soil reservoir. All tree tissues can be regarded as potential sources of water; including living and dead portions of the stem, roots, leaves, and reproductive tissues. However, the relative importance of these internal storage areas in relation to the soil will depend upon (1) the size of the water potential gradient, (2) the resistances to flow between the transpiring foliage and the soil, (3) the resistances to flow between the foliage and the internal storage tissues and size and morphological characteristics of the storage tissue (Figure 7).

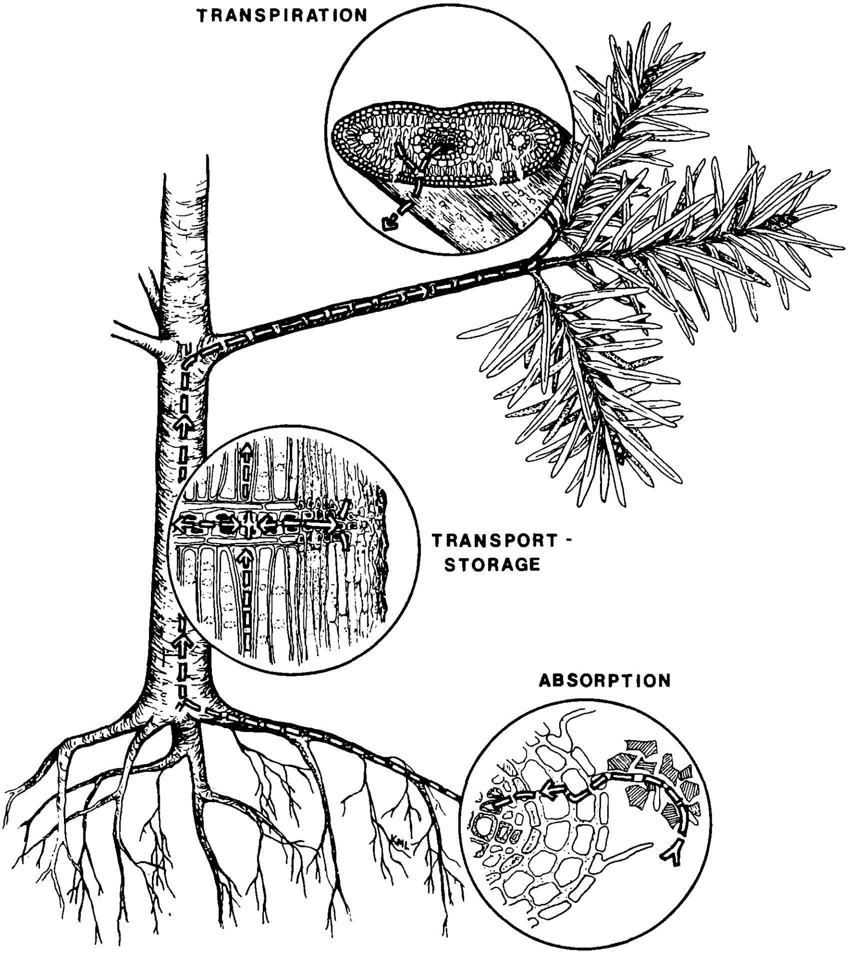


Figure 7. The water transport continuum in a tree.

There are two categories of internal sources of water in forest trees:
(1) elastic tissues which undergo dimensional changes when water is exchanged with the transpirational stream (e.g., foliage, fruits, buds, and phloem-cambium-immature xylem) and inelastic tissues that do not (e.g., mature lignified sapwood).

The majority of literature on stored water has dealt with examinations of elastic phloem-cambium-immature xylem tissue owing to the ease at which dimensional fluctuations may be monitored in tree stems (Lassoie 1975) (Figure 8). In general, diurnal fluctuations result from the development of daily tree water deficits while seasonal fluctuations (Figure 8) are indicative of seasonal changes in soil moisture (Lassoie 1973, Hinckley and Bruckerhoff 1975, Lassoie 1979). The magnitudes of both diurnal and seasonal shrinkages are closely related to the size and morphological condition of the storage zone involved, which vary with the season, tree vigor, and height along the stem; as well as with internal water relations of the trees (Lassoie 1979). The actual amount of water stored near the cambium of a large Pseudotsuga menziesii has been shown to account only for a minimal amount of the water lost during the summer but up to 5 % of the water transpired daily (Lassoie 1979).

Far less work has been done to examine storage in inelastic stemwood even though the conducting sapwood and the nonconducting sapwood may be significant storage areas (Jarvis 1975, Waring and Running 1978, Running 1980). Water content changes in the sapwood and heartwood (see Hinckley et al. 1978) and the cavitation of water columns in the sapwood (Waring and Running 1978) are known to occur in response to tree water loss; but, the importance of these phenomena have yet to be illustrated for different tree species.

There have been enough preliminary investigations with conifers to illustrate that considerable quantities of stored water may be involved in inelastic stem tissues. Richards(1973) estimated that between sunrise and solar noon as much as 80 % of the water lost from Picea sitchensis trees came from stored reserves and not the soil. Waring and Running (1978) estimated

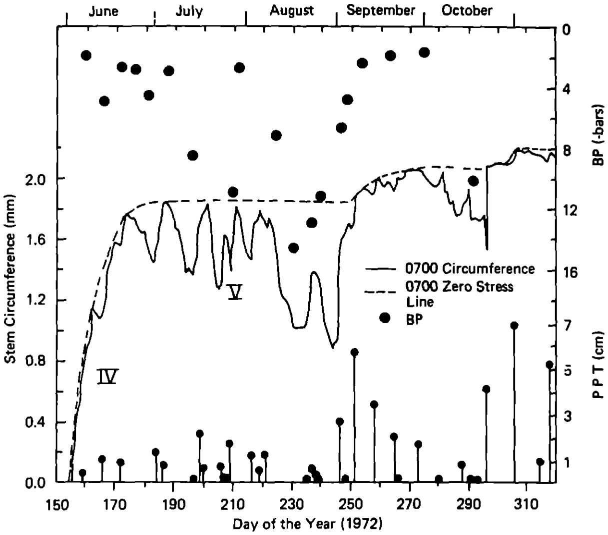


Figure 8. Seasonal pattern of base xylem pressure potential (BP), 0700-h stem circumference (beginning of day 154 is defined as 0.0 mm), 0700 zero stress line and precipitation (PPT) between day 150 (20 May) and 315 (10 Nov. 1972) in a Quercus alba tree from mid-Missouri.

that the total storage capacity of an old-growth Pseudotsuga menziesii forest was 267 m^3 of water per hectare (26.7 mm), 75 % of which was stored in the stemwood. In a recent study by Running (1980a), readily available water from internal storage was calculated to be capable of providing 0.6 hours of maximum transpiration in Pinus contorta. Needle water content contributed only 4 % of the total storage.

Water storage serves principally as a buffer during periods of high potential transpiration or low soil moisture. Food storage, or carbohydrate reserves, are also an important buffer in woody plants because of the seasonality of growth in temperature trees. Cycles of rapid growth and intense utilization of photosynthates are matched with cycles of no growth and storage. Reserves are obviously critical for deciduous species in order to meet maintenance respirational and root growth needs when there are no leaves present and the demands of the spring growth flush. However, reserves are also important in evergreen species (Gordon and Larson

1970, Ross 1972, Emmingham and Waring 1977, Schulze et al. 1977). In addition, hardwood species such as Liriodendron tulipifera and conifers such as Abies amabilis are known to have extensive production and turnover in fine root biomass and below ground production may equal or exceed that above ground (Harris et al. 1978, Grier et al. 1980). Much of this growth occurs during periods of low above ground activity and, therefore, depends on reserve material.

In contrast to fluctuations in stem water content, reserve material fluctuates less in conifers than in hardwoods (Waring and Franklin 1979, McLaughlin et al. 1980). The high concentrations of reserve material are found in the needles, the roots and phloem. However, the greatest amount, at least in trees, is found in the stem because of its large volume. In addition to providing a path of lateral water and food transport, ray parenchyma cells of the phloem and xylem are the major site for carbohydrate storage in the roots and stems of forest trees (Figure 9). The biochemical form of the storage compound differs amongst broad species groups with fats being the major form in most diffuse porous, starch in most ring porous and both in a third group (Kramer and Kozlowski 1979). Hemicelluloses of the cell wall may also represent an important source of reserve material (McLaughlin et al. 1980.

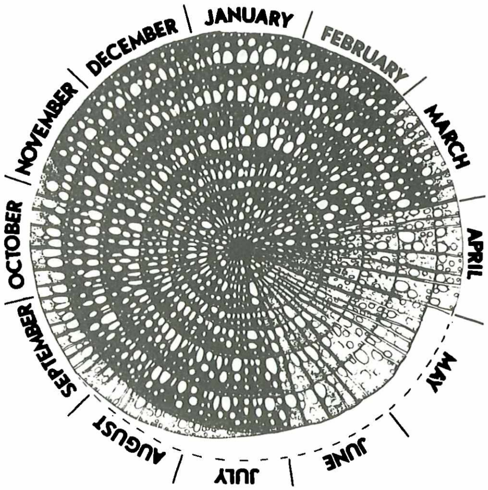


Figure 9. Cross section of the xylem of an Acer saccharum root showing the seasonal distribution of starch (after Wargo, 1979).

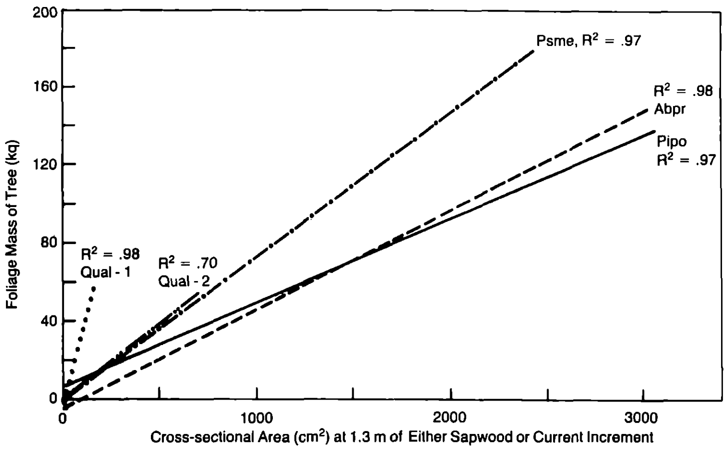


Figure 10. Relation between sapwood area and total biomass for Quercus alba (Qual), Pseudotsuga menziesii (Psme), Abies procera (Abpr) and Pinus ponderosa (Pipo) (after Grier and Waring, 1974; Rogers and Hinckley 1979) Qual - 1: for current increment.

Support

The support function of the stem is an obvious role when one considers the massive aboveground structures that forest trees develop. For example, aboveground total biomass of old-growth Pseudotsuga menziesii may exceed 10,000 kg (Grier and Logan 1977). A stem's ability to support this tremendous weight is derived primarily from the strength of the xylem elements. The following discussion will not deal with such physical considerations, but will instead examine the relationship between stem structure and function.

As a consequence of transport and storage properties of the xylem previously discussed, one might anticipate a high degree of correlation between the functional xylem and the tree's foliage area. Shinozaki et al. (1964) presented a model for viewing the stem as a system of pipes for transporting water and nutrients to the crown. A given cross- section of the "pipes" are required to support water and nutrient demands from a specific amount of foliage. By implication, a change in the quantity of foliage will require a change in the number of "pipes." Water in a tree can be described as a linear, donor-controlled, chain-like system where on a day-to-day basis the sum of water being absorbed by the roots must equal the sum of water being transported in the xylem, which in turn must be equal to the sum of water being lost from the foliage (Richter 1973).

Morikawa (1974) and Kline et al. (1976) have noted that the absolute amount of water transported in a conifer is linearly related to sapwood cross-sectional area. Recent work with Pinus sylvestris using radioactive phosphorus to estimate xylem water movement has shown a 1:1 relationship on a daily basis between water transport in the sapwood and water loss from the needles (Waring et al. 1979). When water transport in the xylem was compared to water loss on a less-than-daily basis, a hystersis loop developed due to the contribution of stored water to the transpiring stream (Morikawa 1974, Hinckley et al. 1978, Running 1980). Thus, on a daily basis a close relationship between transport area and foliage area or mass is suggested.

In 1974, Grier and Waring reported a sensitive linear relationship between sapwood cross-sectional area and either foliage biomass or area for three conifer species (Figure 10). Though the linear relationships did not change with stand density or age, a slight bias was introduced in leaf-sapwood area relations due to site influences on specific leaf areas. In contrast, tree leaf area versus sapwood area is not biased by changes in site quality (Grier and Running 1977). Whitehead (1978) reported that the relationship between leaf area and sapwood area in Pinus sylvestris was independent of tree spacing, but was dependent on site quality.

Recent investigations have built upon the "pipe-theory" and the work of Grier and Waring (1974). Since water is confined to the outer annual ring of ring-porous trees (Figure 6), Rogers and Hinckley (1979) found a better relationship between the area of the current annual ring and foliar biomass and area in Quercus alba and Q.velutina than when either stem diameter at breast height (1.3 m) or sapwood cross-sectional area was used (Figure 10).

Long et al. (1980) hypothesized that sapwood cross-sectional area at any location along a conifer stem should predict the foliar biomass above that point. They expanded on the "pipe-model" analysis of tree form originally used by Shinozaki et al. (1964) to differentiate structural and water conduction features of the stem (Figure 11). Sapwood cross-sectional area was shown to be linearly related to foliage biomass above the cross-section examined at any point along the stem. In large trees, an adequate structure is provided by the total stem for support of the crown; however, the entire cross-sectional area of the stem is not needed for water conduction. Therefore, heartwood formation occurs as transport functions decrease and xylary elements become non-functional. Similar results have been noted earlier by Morikawa (1974) in Chamaecyparis obtusa. However, Morikawa found that cross-sectional area increased below the live crown as xylem conductivity to water flow decreased. Therefore, a greater cross-sectional area of the stem was necessary to transport the same quantity of water.

Waring and co-workers have proposed a measure of the photosynthetic efficiency, or vigor, of a tree's crown (Waring and Pitman 1980, Waring et al. 1980). They reasoned that if sapwood cross-sectional area provides an estimate of the size of a tree's crown, then the area of the last ring or growth increment should be related to the efficiency of that crown. A tree vigor index was then defined as being equal to basal area increment divided by sapwood cross-sectional area. Individual tree vigor indices can be related to insect and pathogen susceptibility (see later discussion) and have been used to determine mean tree vigor and its relation to stand growth.

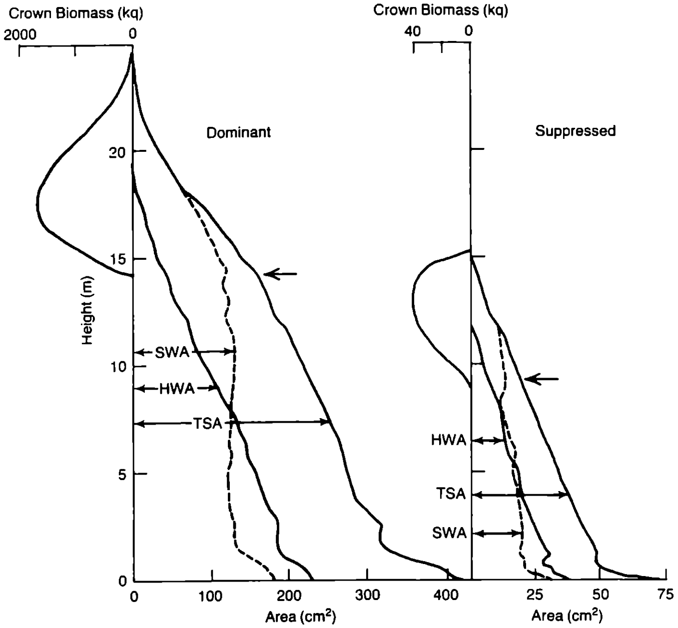


Figure 11. Vertical distribution of crown biomass, heatwood, sapwood and total cross-sectional area for a dominant and a suppressed Pseudotsuga menziesii (after Long, Smith and Scott, 1980).

FACTORS CONTROLLING STEM GROWTH

This section will deal with the factors controlling variation in stem growth of deciduous hardwoods and evergreen conifers. Several factors can be identified as having a major impact on stem growth: (1) time of year, (2) position along the stem, (3) crown class, (4) temperature, (5) water status, (6) nutrient status, and (7) pathogens and insects.

Phenology and stem growth

The phenology of stem growth as it is related to growth processes in other parts of the tree and time of year is shown in Figure 12 for three different types of forest trees. In all three types, root growth preceeds all aboveground growth activities. The initiation of Phase I of stem growth (rehydration of the cambial zone) is associated with bud swell. In the ring-porous hardwood, approximately 30 % of the total stem increment is added before bud burst (Phase II). Following bud burst in both ring- and diffuse-porous hardwoods, Phase III of stem growth begins and is slower than in either PhasesII or IV. There appears to be no real Phase III in the evergreen conifer. In all types, root growth is greatly reduced during the period of foliar expansion and during flower production. Phase IV is the fastest growth phase except for Phase II in the ring-porous tree. In Quercus alba, the rate of growth during Phase II is faster than Phase IV because there is no foliage on the tree at that time. Therefore, midday stem shrinkages due to internal dehydration during transpirational water loss periods do not occur. Phase V is characterized by either no growth or net stem size decreases due to low soil moisture. With recharge of the soil, growth can resume during Phase V.

Relatively little work has been done on root growth activity due in part to the difficulties involved in such investigations. In the most comprehensive study to date, Wargo (1979) studied root growth and the role of the root as a storage tissue in Acer saccharum (Figur 9). During mid-Juli, root cambial growth was initiated. Cambial growth of the root occurred when starch reserves were completely refilled and soil moisture levels were adequate. Since the entire sapwood of the root is used to transport water and nutrients while only the outer ring in ring porous and only several outer rings in diffuse porous species are functional, cambial growth of roots is a low priority. Hence, it is greatly reduced during years of drought of periods marked by defoliation (Wargo 1979).

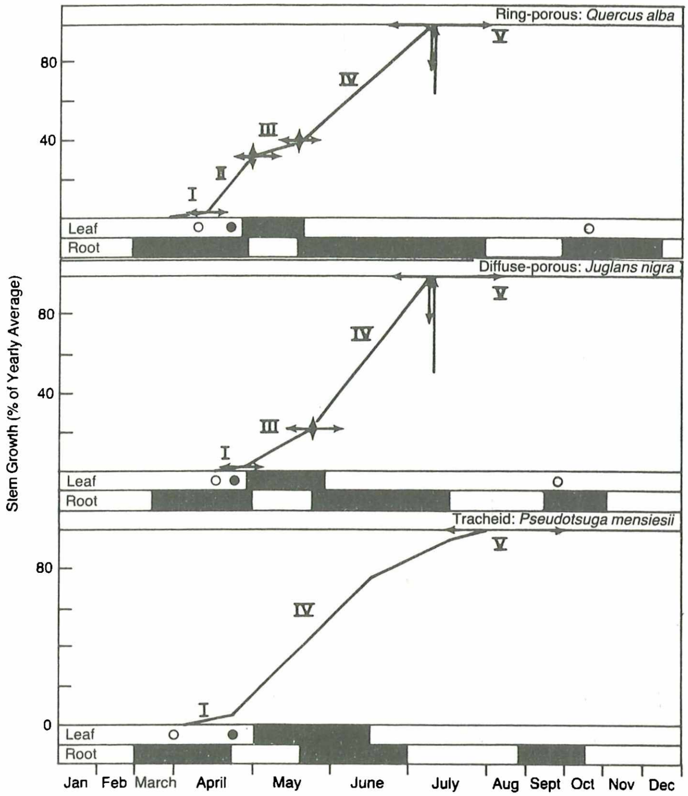


Figure 12. Seasonal progression of stem growth (as well as leaf and root growth) for the three broad types of forest trees. Roman numerals refer to phases of stem growth. Arrows about a given point represent possible deviation about the average due to environmental stresses. ○ - bud swell, ● - bud burst, ⊙ - leaf fall, ■ - active period of growth.

Position within the crown

Tree stem taper and form suggest a differential growth response related to the height position along the bole. Obviosly, cambial growth rates cannot be equal along the bole's length without resulting in an oddly formed stem. The greatest ring widths consistently observed along that section of the bole which is somewhat above the bulk of the crown (Figur 13). However, because of the exponential relationship between cross-sectional area and radius, smaller ring width below the point of maximum width actually represent a greater investment of biomass (energy) than wider rings in the upper portion of the stem.

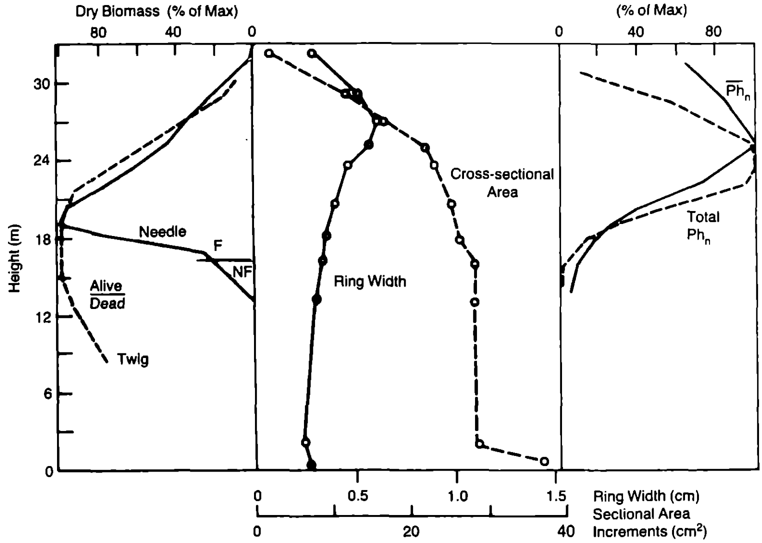


Figure 13. Vertical distribution of needle and twig biomass, ring-width, sectional area increments ($= [r_{80}^2 - r_{79}^2] * \pi$), average daily net photosynthesis (Ph_n) in a dominant Pseudotsuga menziesii (after Dobbs 1966, Dice 1968, Woodman 1970, Jensen 1976). F/NF refers to whether a branch is functional or non-functional. Branches which have the same number of rings as the whorl to which they are attached are defined as functional.

In a 32.8 m dominant Pseudotsuga menziesii (Figure 13), the widest ring was observed at 26.8 m; the area of the greatest total net photosynthetic rate was between 22 and 24 m; and the area of greatest needle biomass was near 19 m; and except for the root collar location, cross-sectional areas of growth rings increased steadily from the stem tip to about 16.4 and then remained farily constant. The greatest needle biomass was in the lower third of the functional crown and the nonfunctional crown was between 13.0 and 16.4 m. The nonfunctional crown in Pseudotsuga menziesii has been physiologically defined as the portion of the living crown which exports few photosynthates to other parts of the tree. This portion of the crown was once believed to be a metabolic drain on the tree, but recent translocation studies have indicated that a near-neutral influence exists (Ross 1972). Branches within the nonfunctional crown eventually die as their assimilarity capabilities fail to fully meet maintenance requirements. Recent nutrient cycling work has suggested that branches within the nonfunctional crown may be important in redistributing nutrients to other parts of the tree; especially in climates where decomposition and mineralization rates are slow (Long 1976).

From the previous discussion, a logical question might be what happens to the amount and distribution of stem growth when branches are removed? Pruning experiments with Pseudotsuga menziesii by Underwood (1967) suggested that removal of the nonfunctional crown had no immediate impact on stem growth (Figure 14). In contrast, the removal of functional branches appreciably reduced lower stem growth.

Positional differences occur along tree stems with regard to the amount of stem shrinkage experienced during the day or during the summer (Dobbs and Scott 1971, Lassoie 1973, 1979). Such contraction patterns are related to the interaction between water loss from the crown and the size of the stem tissues potential capable of internally exchanging water. Stem shrinkage commences in the morning at upper stem locations and then progressively moves downward in response to the propagation of internal water deficits through-

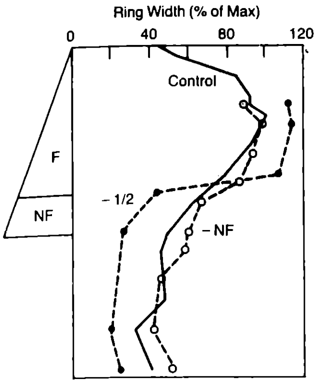


Figure 14. Vertical distribution of ring width in control and pruned dominant Pseudotsuga menziesii trees (after Dobbs 1966, Underwood 1967, Jensen 1976). In one case, all non-functional branches were removed while in the other case, 50 % of the live crown (non-functional plus functional branches) was removed.

out the stem. The reverse is true during the evening recharge period.

Based on the literature (e.g., Kramer and Kozlowski 1979) and Figure 13, the following conclusions concerning positional differences along tree stems are possible. These conclusions are somewhat obvious but are important to subsequent discussions.

(1) Cambial growth depends upon the functional crown to supply photosynthates and certain growth hormones (e.g., auxins) and is, therefore, interrelated with foliar production and maintenance. Likewise, water and other hormones are supplied by the roots and are related to root growth and activity.

(2) Ring width alone is not a clear indicator of biomass distribution and energy allocation along tree stems. Ring cross-sectional area is a better indicator of positional differences.

(3) The nonfunctional crown probably provides no net photosynthates to the main bole.

(4) The highest net photosynthetic rates occur in foliage above the point of maximum foliar biomass accumulation due to the higher light levels at

this position and mutual shading which occurs in lower portions of the functional crown.

(5) Water loss from the crown will dehydrate tissue in and around the cambium and can affect growth activity along the stem.

Crown class

As discussed, the functional crown provides the energy and carbohydrates necessary for cambial growth. Hence, there should be a close relationship between the size of the crown and ring widths. This relationship has been examined for Pseudotsuga menziesii (Figure 15). In general, dominant trees experience much better growing conditions (e.g., light, water, nutrients)

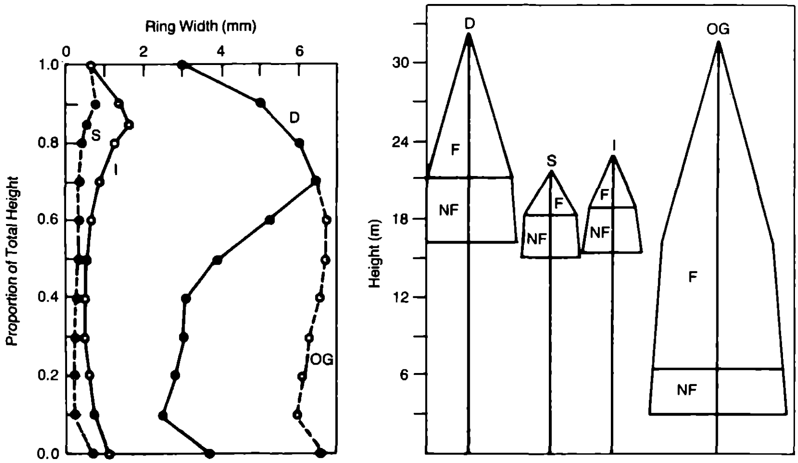


Figure 15. The influence of crown class on ring-width in Pseudotsuga menziesii trees from a 43-year-old stand (Hinckley and Scott, unpubl.).

than either intermediate or suppressed trees, and hence are able to accumulate greater amounts of biomass. In a close-canopy stand, low light levels will reduce net photosynthetic rates in lower branches of dominants and all branches of intermediate and suppressed trees (Woodman 1971, Schulze et al. 1977, Aubuchon et al. 1978), thereby limiting the maximum size of the functional crowns. In contrast, light levels to open-grown trees are only limited by mutual shading by branches, and thus develop and maintain much larger functional crowns than similar sized trees growing in a stand (Figure 15). This larger crown produces wider rings along the stem and greatly affects stem form.

Large, rapidly growing trees will maintain a large number of activity dividing and differentiating cells within and near the cambium. These tissues represent a potentially large area for internal water exchange. Thus dominants will experience greater diurnal and seasonal fluctuations in stem size than smaller trees. The importance of this is relationship to internal water storage has been examined for Pseudotsuga menziesii of different crown classes by Lassoie (1979).

Temperature

Temperature affects all metabolic processes and hence has numerous interrelated influences on radial growth. For example, as average temperature increases in the spring, root growth is initiated, stem tissues rehydrate, buds swell, and above-ground growth commences (Figure 12). Temperatures above freezing have a physical affect on stem size but resulting changes in stem size are insignificant compared to those due to diurnal changes in hydration (Lassoie 1975). Below freezing, however, large contractions in size occur (Lassoie 1975). Assuming sufficient quantities of water, the number of degree days (i.e., the duration of days above a certain threshold temperature) combine to determine the amount of growth possible (both growth rate and duration) in both hardwoods and conifers (Leikola 1969, Lassoie 1975, Hinckley et al. 1976).

Of course, temperature, particularly leaf temperature, directly controls net photosynthetic rates thereby influencing the amount of photosynthates available for the cambial growth process.

Air temperature similarly has a direct influence on cell growth activity within the cambium. Measurement of bark respiration has indicated two specific components: (1) the maintenance of respiration ($Q_{10} \cong 1.0$) and (2) respiration associated with the growth process ($Q_{10} \cong 2.0$) A plot of the relationship between bark respiration and bark temperature during the period of active cambial growth illustrates an exponential relationship with both hardwoods and conifers (Figure 16). However, during periods of active transpiration, the development of internal water deficits at the cambium can effectively stop or greatly reduce cell division as indicated by a decrease in respiration (Edwards and McLaughlin 1978).

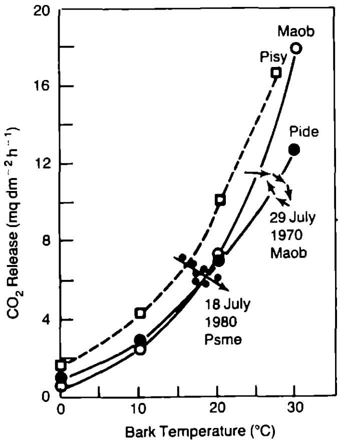


Figure 16. Relationship between bark temperature and CO_2 released from the bark in Magnolia obovata (Maob), Pinus densiflora (Pide) and Pinus sylvestris (Pisy) (after Negisi 1972, 1975, Linder and Troeng 1980). Two diurnal loops are given for Magnolia obovata (Maob) and Pseudotsuga menziesii (Psme) (after Negisi 1972, Morikawa, unpubl. data).

Water Status

Probably more work has been done describing the influence of tree water status on stem growth and stem shrinkage than on any other subject discussed in this review (e.g., Kozlowski 1972, Hinckley et al. 1978). The internal development of tree water deficits has direct and indirect influences on nearly all tree physiological processes and thus seasonal and diurnal fluctuations in tree water balance are intimately involved in regulating the stem growth process. Indirect effects include the production of carbohydrates which are greatly limited by hydroactive stomatal closure in the afternoon and late in the summer (Dougherty and Hinckley 1980, Lassoie and Salo 1980). Direct effects primarily involve the reduction of turgor pressure in the cambium and its derivatives.

Concerning the direct effect of internal water status on cambial growth, four possible conditions exist (Figure 17). Condition 1: This condition exists in ring-porous hardwoods early in the spring before the leaves emerge (Figure 12, Phase II) and in all species under extremely moist conditions associated with fog or mist (Figure 17A). During this time, cambial growth is primarily controlled by air temperature and the availability of photosynthates; which may either be from internal storage areas or directly from actively photosynthizing foliage. Condition 2: This condition can occur in any species when soil moisture levels are high but rapid transpiration rates during the day develop large internal water deficits (Figure 17B; Lassoie et al. 1977). Such conditions promote stomatal closure and reduced gas exchange rates during the afternoon as well as decreases in stem size. Positive increases in stem size primarily occur during the evening and night recharge period. Such increases are probably the result of cell expansion as cell division is not affected until greater water deficits are developed. The result is a net daily increases in stem size. This condition most frequently exists during the active cambial growth phase in the spring (Figure 12; Phase IV).

Condition 3: This condition can exist in all species and is usually associated with the summer drought period (Figure 12; Phase V). When soil moisture levels drop sufficiently so that evening recharge is incomplete, no stem growth occurs and a net day-to-day contraction in the stem is noted (Figure 17C). Both cell division and cell expansion are probably

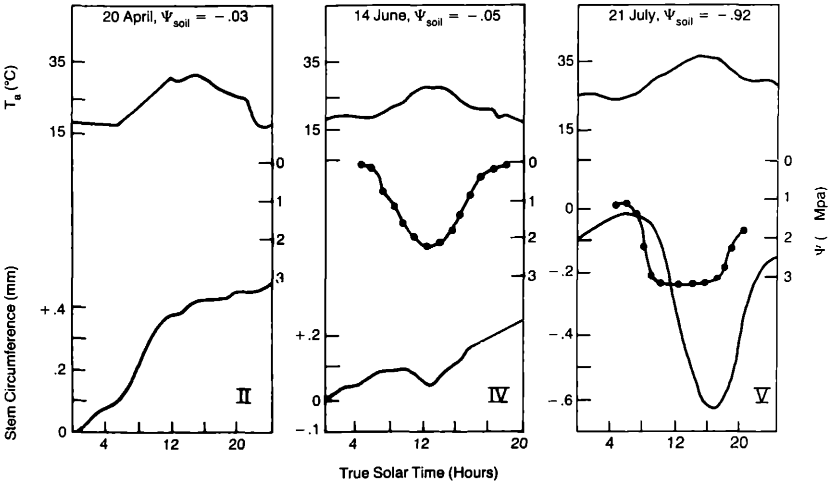


Figure 17. Diurnal patterns of air temperature (T_a), leaf water potential (ψ), and stem circumference in Quercus alba (after Hinckley et al 1976). On 20 April, there were no leaves on the tree.

affected during such periods.

Condition 4: This condition can also occur in all species and is associated with a rapid and major expansion of the stem (data not shown; see Hinckley and Bruckerhoff 1975, Lassoie et al. 1977, Lassoie 1979, Lassoie and Salo 1980). Such increases in stem size are associated with the hydration of the cambium which preceeds cell division in the spring and with the rehydration of cambial-associated cells following heavy rainfall at the end of a drought period. Cell division is probably not involved at such times.

Nutrients

Nutrients from the soil or those internally redistributed are necessary for all tree growth processes. At this time it is not absolutely clear if the level of nutrition directly affects the cambial growth process or indirectly controls it through its influence on foliage and fine root growth.

Regardless, trees growing in nutrient deficient soils will show reduced cambial growth and a positive response to fertilization (Figure 18; Miller and Cooper 1973, Lea et al. 1979). Hardwood and conifer trees growing on poor sites will allocate more energy (carbohydrates to their root systems thereby developing greater root biomasses than trees growing on good sites (Yen et al. 1978, Keyes and Grier 1980, Grier et al. 1980).

The initial response to the improvement of soil nutrient status by fertilization seems to be an increase in root growth which in turn improves the uptake of both water and additional nutrients (Brix and Mitchell 1980).
The response of the crown will depend not only on the fertilization application but also on the amount of light it receives. Hence, the greatest responses to the addition of nutrients to the soil occurs when trees are fertilized following the thinning of the stand; thinned trees cannot be left standing. This allows both the root and foliage systems to expand to their maximum amounts. A feedback loop occurs as trees with larger root and shoot systems are able to obtain greater amounts of necessary materials which enables faster growth rates and larger sapwood cross-sectional areas which in turn can support larger photosynthetic areas. In addition, the photosynthetic efficiency of the foliage may increase.

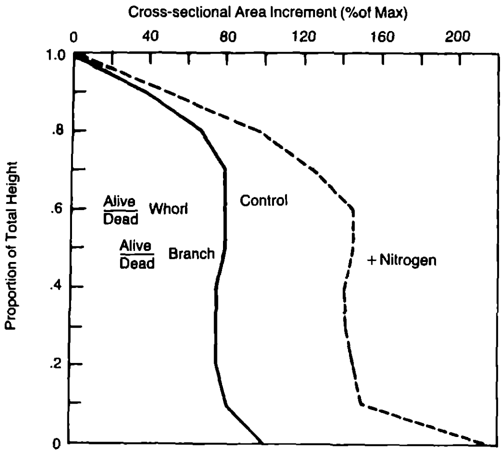


Figure 18. The influence of an addition of 168 kg/ha of nitrogen in May 1965 and May 1966 on stem cross-sectional area increment in 1966 of Pinus nigra var. maritima. There was no difference in increment in 1965 between treated and control trees (after Miller and Cooper 1973).

Since a tree's current root and crown system will greatly affect its ability to utilize added nutrients, different stands may respond quite differently to fertilization. In young stands, nutrient additions will accelerate stand differentiation into crown classes. In older stands, larger trees will disproportionately accumulate more nutrients thereby accelerating their growth rates over smaller trees. Regardless, lower crown classes are more quickly lost from the stand while the stand's overall leaf area and sapwood cross-sectional area remains the same (Jarvis 1975).

Pathogens and insects

Biological organisms injurious to trees can directly and indirectly affect cambial growth rates by either adversely affecting the roots and leaves or by directly attacking the stem. As previously discussed, roots, stem, and leaves are in balance with each other and any reduction in function of one component will in turn affect the other two.

A major outbreak of Orgyia pseudotsuga in 1946 and 1947 and the subsequent examination of its effect on stem growth of susceptible and nonsusceptible tree species in 1975 (Smith 1977) allows several observations regarding the impact of defoliation on stem growth (Figure 19). First, stem growth increased in Larix occidentalis following the outbreak and crown defoliation. This increase was especially noted at lower locations along the bole (Figure 19). It is interesting to note that L. occidentalis is a deciduous conifer and is not considered to be a preferred species of O. pseudotsuga. The importance of these two features to the response to partial defoliation has not been determined.

The second observation involved the impact of O.pseudotsuga on different crown classes of its preferred host, Pseudotsuga menziesii (Figure 19). Partial defoliation had a sever impact on the growth of all crown classes. In spite of the improved light levels in the lower canopy because of defoliation, intermediate and suppressed trees showed a greater impact than dominant trees. It seems possible that larger trees, possessing larger initial foliar area, were better able to maintain larger net photosynthetic balances, and were thus able to maintain larger cambial growth rates than smaller trees. The inability of a suppressed Pseudotsuga menziesii to maintain a positive net photosynthetic balance following partial defoliation has been suggested to be the cause of reduced cambial growth and the tree's eventual death by Lassoie (1979).

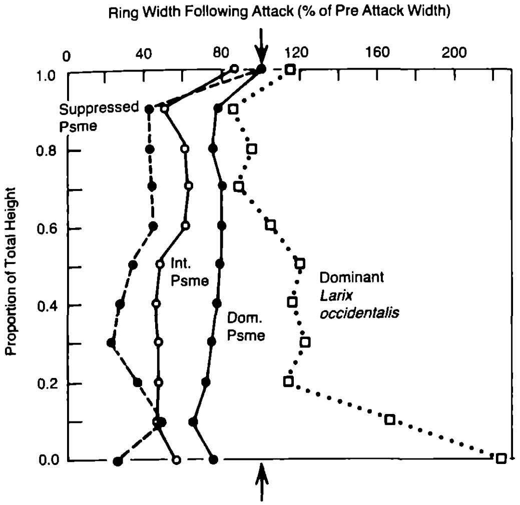


Figure 19. The influence of an outbreak of the Tussock moth (Orgyia pseudotsuga) on three different crown classes of Pseudotsuga menziesii (Psme) and dominant Larix occidentalis (after Smith 1977). Five years of ring growth after are compared to the five years before the outbreak.

The differential response of different crown classes to defoliation probably involves a variety of cause and effect relationships. Waring and his colleagues have developed a tree vigor index which integrates these relationships and have used it to explain why certain trees are severely affected by insects and pathogens while others are not. For example, Waring and Pitman (1980) found that tree vigor index could be used effectively to relate mortality of Pinus contorta to the intensity of attack by Dendroctonus ponderosae. They observed that trees with a low index (i.e., an inefficient crown) had low oleoresin exudation, low carbohydrate reserves which could be used to form terpenes, and a poor capacity to produce new carbohydrates. Waring (personal communication) has found similar results in Pseudotsuga menziesii susceptible to Phellinus (Poria) wierii root rot.

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