

YALE UNIVERSITY : SCHOOL OF FORESTRY

BULLETIN No. 74



WOOD FORMATION AND THE CONCEPT  
OF WOOD QUALITY

By

PHILIP R. LARSON

*Principal Plant Physiologist,*

*Pioneering Unit in Physiology of Wood Formation,*

*North Central Forest Experiment Station,*

*U.S. Department of Agriculture,*

*Forest Service, Rhinelander, Wisconsin*

*1967-68 U.S. Plywood-Champion Papers, Inc. Lectureship*

Library

Northeastern Forest Experiment Station  
Forest Service-U.S. Dept. of Agriculture

NEW HAVEN : YALE UNIVERSITY

1969

BULLETINS PUBLISHED BY YALE UNIVERSITY SCHOOL OF FORESTRY\*

- 5.—The Den—A Preliminary Report, with Map, of a Tract of Woodland Given to the School by Mr. and Mrs. Winthrop Perry, by James W. Toumey and Ralph C. Hawley. 1920. (Free.)
- 13.—The Transportation of Logs on Sleds, by Alexander M. Koroleff and Ralph C. Bryant. 1924. Price 50 cents.
- 15.—Studies of Connecticut Hardwoods. The Treatment of Advance Growth Arising as a Result of Thinnings and Shelterwood Cuttings, by Louis J. Leffelman and Ralph C. Hawley. 1925. Price 50 cents.
- 17.—Studies of Connecticut Hardwoods. The Form of Hardwoods and Volume Tables on a Form Quotient Basis, by Ralph C. Hawley and Rodgers G. Wheaton. 1926. Price 50 cents.
- 30.—Trenched Plots under Forest Canopies, by James W. Toumey and Raymond Kienholz. 1931. Price 35 cents.
- 36.—Some Aspects of an Early Expression of Dominance in White Pine (*Pinus strobus* L.), by J. Lee Deen. 1933. Price 35 cents.
- 46.—*Asterolecanium varicosolum* Ratzeburg, A Gall-forming Coccid, and Its Effect upon the Host Trees, by Thaddeus Parr. 1940. Price 75 cents.
- 47.—Penetration of the Walls of Wood Cells by the Hyphae of Wood-Destroying Fungi, by Phimister Proctor, Jr. 1941. Price 50 cents.
- 49.—Management of Loblolly Pine in the Pine-Hardwood Region in Arkansas and in Louisiana West of the Mississippi River, by Herman H. Chapman. 1942. Price \$1.00.
- 50.—Decay of Western Hemlock in Western Oregon and Washington, by G. H. Englerth. 1942. Price 75 cents.
- 52.—White Pine Blister Rust in Western North America, by J. L. Mielke. 1943. Price \$1.00.
- 55.—The Yale Forest in Tolland and Windham Counties, Connecticut, by Walter H. Meyer and Basil A. Plusnin. 1945. Price \$1.00.
- 56.—Ecology and Silviculture of Whitecedar and Associated Hardwoods in Southern New Jersey, by Silas Little, Jr. 1950. Price \$1.50.
- 57.—Effect of Fire on Forest Soils in the Pine Barren Region of New Jersey, by Paul Y. Burns. 1952. Price \$1.00.
- 58.—Taxation and Other Factors Affecting Private Forestry in Connecticut, by Eugene V. Zumwalt. 1953. Price \$1.50.
- 59.—Drying Rates of Thin Sections of Wood at High Temperatures, by Herbert O. Fleischer. 1953. Price \$1.50.
- 60.—The Effect of Synthetic Resin Adhesives on the Strength and Physical Properties of Wood Veneer Laminates, by Stephen B. Preston. 1954. Price \$1.50.
- 61.—Properties of American Beech in Tension and Compression Perpendicular to the Grain and Their Relation to Drying, by Eric L. Ellwood. 1954. Price \$1.50.
- 62.—Amount and Chemical Composition of the Organic Matter Contributed by Overstory and Understory Vegetation to Forest Soil, by David Robert Main Scott. 1955. Price \$1.50.
- 63.—Effect of Environment on the Percentage of Summerwood and Specific Gravity of Slash Pine by Philip R. Larson. 1957. Price \$1.50.
- 64.—Variation in Tracheid Length and Wood Density in Geographic Races of Scotch Pine by Robert M. Echols. 1958. Price \$1.50.
- 65.—Aboriginal Man and White Man as Historical Causes of Fires in the Boreal Forest, with Particular Reference to Alaska, by Harold J. Lutz. 1959. Price \$1.00.
- 66.—Financial Management of Large Forest Ownerships. 1960. Price \$2.00.
- 67.—Investment Theory and Forest Management Planning, by Barney Dowdle. 1962. Price \$1.50.
- 68.—Private Nonindustrial Ownership of Forest Land, by Robert O. McMahon. 1964. Price \$1.75.
- 69.—Time Discounting by Certain Forest Landowners, by Donald F. Flora. 1966. Price \$1.50.
- 70.—Thermophysical Properties of Bark of Shortleaf, Longleaf, and Red Pine by William E. Reifsnnyder, Lee P. Herrington, and Karl W. Spalt. 1967. Price \$1.50.
- 71.—The Structure of Germination in *Pinus lambertiana* Dougl., by Graeme P. Berlyn. 1967. Price \$1.50.
- 72.—Optimal Forest Investment Decisions Through Dynamic Programming, by Gerard F. Schreuder. 1968. Price \$2.00.
- 73.—On Temperature and Heat Flow in Tree Stems, by Lee P. Herrington. 1969. Price \$2.00.
- 74.—Wood Formation and the Concept of Wood Quality, by Philip R. Larson. 1969. Price \$2.00.

The following bulletins are currently out of print: 1, 2, 3, 4, 6, 7, 8, 9, 10, 11, 12, 14, 16, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 31, 32, 33, 34, 35, 37, 38, 39, 40, 41, 42, 43, 44, 45, 48, 51, 53, 54.

\* For sale by Yale University School of Forestry, 205 Prospect Street, New Haven, Conn. 06511 USA.

YALE UNIVERSITY : SCHOOL OF FORESTRY

Bulletin No. 74

WOOD FORMATION AND THE CONCEPT  
OF WOOD QUALITY

BY

PHILIP R. LARSON

*Principal Plant Physiologist,  
Pioneering Unit in Physiology of Wood Formation,  
North Central Forest Experiment Station,  
U.S. Department of Agriculture,  
Forest Service, Rhinelander, Wisconsin*

New Haven: Yale University

1969



## FOREWORD

---

---

THE FOLLOWING paper is based on a series of three lectures delivered to the Yale School of Forestry during the week of April 22, 1968. The lecture series was made possible by a grant to the Yale School of Forestry by the U.S. Plywood-Champion Papers, Inc.

The purpose of these first lectures was to promote a greater understanding among forestry students of the processes of wood formation and the complexities of wood quality evaluation. My primary aim was therefore to be instructive and informative. The presentation represents a personal approach to the problems of wood formation and wood quality that I have developed over the past 15 years. This approach has evolved not only from the results of research in our laboratory, but also from a synthesis of the extensive world literature on the subject. However, since this paper deals largely with broad concepts and consists of a generalized approach to an extensive subject, few outside references have been cited. My own publications have been cited liberally, not because I consider them authoritative, but because when taken together they constitute a fairly comprehensive coverage of the pertinent literature on wood formation and quality. In addition, each of these papers contains a more detailed account of the particular point under discussion.

In appreciation of the cordial hospitality shown me at Yale University, I should like to express my gratitude to Professor François Mergen, Dean of the School of Forestry, and to Professor Graeme Berlyn, coordinator of the lecture series. I should also like to express my appreciation to my colleague, Dr. John Gordon, for the many helpful and stimulating discussions during preparation of the manuscript.



## TABLE OF CONTENTS

---

---

BASIC PATTERNS OF WOOD GROWTH AND DEVELOPMENT	i
Introduction	i
The Concept of Wood Quality	2
Bud and Shoot Development	3
Growth Patterns of a Young Tree	8
Long-Term and Short-Term Effects on Wood Formation	15
Concept of the Continuum	19
PHYSIOLOGY OF WOOD FORMATION	24
Developmental Studies of Wood Formation	25
The Hypothesis of Tracheid Diameter Regulation	27
The Hypothesis of Secondary Wall Thickness Regulation	29
Interactions During Tracheid Differentiation	32
APPLICATIONS OF THE CONCEPT OF WOOD QUALITY	35
The Concept of Earlywood and Latewood	35
Regulation of Stem Form	39
Silvicultural Control of Wood Quality	42
Some Potential Applications of Silviculture	47
LITERATURE CITED	53





# BASIC PATTERNS OF WOOD GROWTH AND DEVELOPMENT

---

---

## INTRODUCTION

WOOD HAS been the principal product of trees from the first hunting club or digging tool of ancient man to the rich variety of industrial and decorative uses of modern civilization. The universal practical value and aesthetic appeal of wood may be traced to the seemingly infinite variation in its characteristics. These variations arise from the structure and arrangement of the individual cells, which vary not only among tree species but also within individual trees. The variability in these wood characteristics is what I shall refer to as wood quality.

Even ancient man, through trial and error, gained some knowledge of wood quality, which served in judging the strength and weight of his hunting club. Through the ages, experience and research have taught us a great deal about wood quality, but it is still a timely and important subject in forestry today. We repeatedly hear predictions of the future wood requirements in our nation and throughout the world. And we frequently hear the controversy as to whether these requirements can best be satisfied by concentrating solely on quantity production, or whether both quantity and quality should be taken into consideration. In either case, forest managers must possess an awareness and a thorough understanding of the fundamental principles of tree growth and wood formation if they are to maximize production. An even greater understanding of these fundamental principles is required by researchers actively engaged in wood quality evaluation and improvement.

In the discussion that follows, a few of the basic principles of tree growth will be presented, and an attempt will be made to establish the concept whereby wood formation on the bole is regulated by the growth and development of the foliar organs of the crown. Although obvious, the significance of this crown-stem relationship is frequently overlooked in forestry practice. Nevertheless, with this knowledge the patterns of wood formation become clear and comprehensible, and the variations in these patterns due to environmental factors and silvicultural treatments can be interpreted and sometimes predicted. Of far greater importance, a thorough understanding of the crown-stem relationship and the fundamental principles of tree growth permits the imaginative researcher to develop new approaches to manipulating wood yield and quality in forest stands.

For the sake of brevity and simplicity the discussion here will be limited to the

## WOOD FORMATION AND QUALITY

---

genus *Pinus*, although with slight modifications most of the concepts presented could be applied to other conifers and to most hardwoods as well. The discussion of wood formation will be further confined to development of the annual growth ring and to the wood elements constituting the growth ring. Variations in these characteristics are the principal determinants of wood quality.

Frequently, wood quality is measured by arbitrary ratios or indices such as latewood percentage or specific gravity, which are, in turn, correlated with strength or yield properties of the wood. However, since quality is not a specific attribute of wood but an arbitrary set of values, we may think of wood quality in terms of a concept.

### THE CONCEPT OF WOOD QUALITY

Anatomically, wood is the xylem of a tree. It is a product of the cambium and it consists of cells or wood elements that have passed through various phases of development. All the developmental phases of cellular division, differentiation, and maturation taken together constitute wood formation. During wood formation, numerous factors both inside and outside the tree lead to variation in the type, number, size, shape, physical structure, and chemical composition of the wood elements. Wood quality is the arbitrary classification of these variations in the wood elements when they are counted, measured, weighed, analyzed or evaluated for some specific purpose. Wood quality is therefore a concept—an idea formulated by generalization from particulars, the particulars in this instance being the wood elements produced in wood formation.

Full appreciation of wood quality as a concept permits one to approach its evaluation and its regulation in a logical manner. Wood formation is a biological process occurring within the living tree, whereas wood quality is the arbitrary evaluation of an isolated piece of wood, tree part, or wood derivative. Wood formation is the process, wood quality is the result. Consequently, wood quality can only be altered via the processes of wood formation. A specific wood characteristic may be altered, but it cannot be altered independently, for the entire zone of developing wood will participate in the change. Similarly, a specific wood quality characteristic may be measured or evaluated, but its isolation is artificial and it cannot be completely divorced from the remaining wood. Wood quality encompasses the whole of the wood, and when certain characteristics are segregated for measurement or evaluation, it must be recognized that the evaluation is arbitrary and the segregation artificial.

When the numerous biological processes contributing to wood formation are considered, the potential magnitude of wood quality variation becomes evident.

## PATTERNS OF GROWTH AND DEVELOPMENT

---

Although all the biological causes of variability cannot be completely explained, many of them can be placed in perspective by considering the developmental process of wood formation as an integral part of tree growth. Since the xylem is part of the vascular system, the discussion will begin with the bud and developing shoot where the vascular system originates.

### BUD AND SHOOT DEVELOPMENT

It is sometimes difficult to visualize the developing xylem in a space-time relationship. Each cambial derivative differentiating into a xylem cell will vary in development according to its distance from the stem apex and its age, or distance, from the central pith. Consequently, at any one position on the tree stem, there will exist a space-time relationship in xylem development during the seasonal course of growth and also a space-time relationship resulting from the cumulative effect of previous seasons' growth. These space-time relationships should be fully comprehended if one is either to understand wood formation or evaluate wood quality.

The conceptual problems associated with the space-time development of xylem can be readily grasped if we recognize that the xylem is a part of the tree's vascular system. Even though most of the interior xylem of a large tree may be defunct and inactive in translocation, it was nonetheless active at one time. We must further recognize that the stem xylem is both developmentally and functionally related to the xylem in the vascular system of the needles. Discrete vascular bundles are evident in each needle, and the cambia in the basal meristems of these needles merge to produce the branch or stem cambium. The xylem then develops by sequential accretion of the cambial derivatives. Thus, the needle xylem and the stem xylem are simply parts of the same vascular system separated in space-time. A brief description of the vascular system as it develops may help to bring this relationship into proper perspective.

In *Pinus*, bud formation for the following season's growth begins at about the time shoot extension for the current season ends. During the remainder of the growing season, formation of the primordial organs within the developing bud occurs in an ontogenetic sequence (2, 27). The first organs formed are the sterile bracts (Figure 1A), a series of spirally arranged cataphylls that do not contain axillary buds. These are followed by a lengthy series of cataphylls bearing the dwarf shoots or needle primordia (Figure 1B) and the lateral buds (Figure 1C); we will disregard the floral primordia in this discussion. The final series of foliar structures formed at the end of the season are the terminal bud scales that will enclose the bud to be produced during the next season (Figure 1D). The winter

SHOOT APEX OF PINUS WINTER BUD

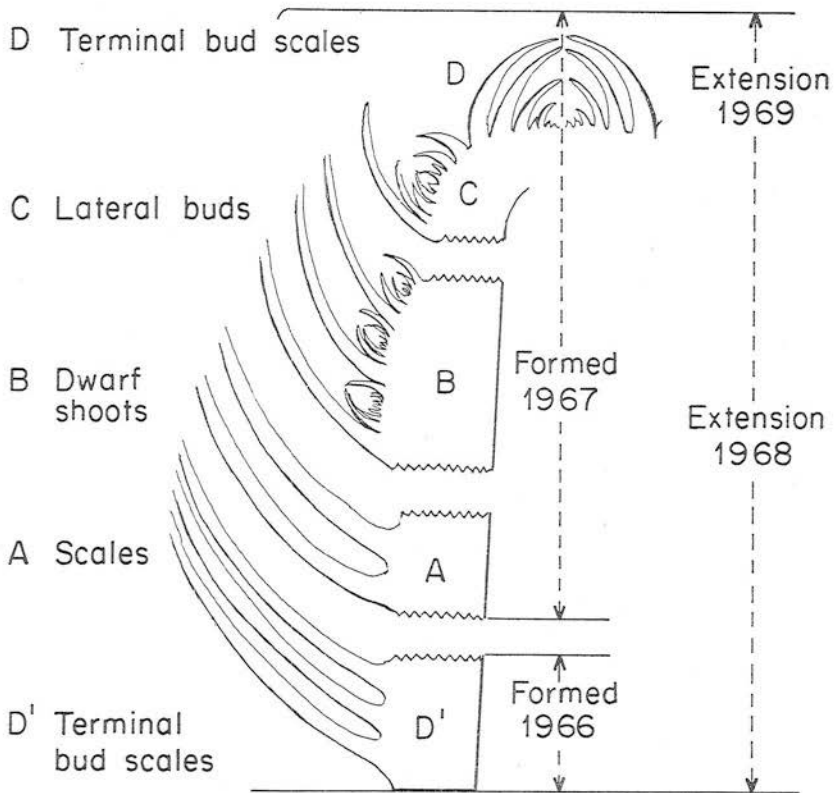


FIGURE 1. The winter bud of *Pinus* contains all the structures required for the following season's growth. The sequence of primordia formation is described in the text. (After Sacher 1954)

## PATTERNS OF GROWTH AND DEVELOPMENT

---

bud is therefore a telescoped shoot containing all the primordia for the following year. Bud and shoot elongation consist of extension growth of the internodal region between each of these primordia, with the exception of the terminal bud scales (Figure 1D').

Within the bud, procambial strands develop upward from existing vascular tissue in the stem to each foliar primordium as it is initiated (5) (Figure 2). These procambial strands are eventually transformed to vascular traces by the addition of primary phloem and xylem elements on the outer and inner procambial surfaces, respectively. Phloem elements usually differentiate upward along the procambial strands from their connection with the phloem of older leaf traces. Xylem differentiation, which follows that of phloem, is initiated near the base of the needle primordium and progresses from there upward into the needle and downward to unite with the primary xylem of older traces. It is evident that the vascular traces are intimately related to the origin and development of the foliar primordia, and that they form a closely interconnected network throughout the fully developed winter bud.

Growth and extension of the winter bud to produce a shoot proceeds by expansion of pre-existing cells in the bud and also by cell division. During the grand period of shoot extension, the bulk of the shoot consists of pith and protective cortex. Needle elongation is temporarily suppressed at this time, but development of the primary vascular system keeps pace with the expanding shoot. This period is critical in the formation of a new shoot, because the succulent tissue, although flexible, is relatively weak and has a low dry weight/volume ratio. Increases in both dry weight and strengthening tissue follow vigorous needle elongation, and it is during this period that the vascular system of the shoot develops rapidly. It is therefore evident that the distinction between stem and needle development within a shoot is somewhat arbitrary. Even though we may outwardly distinguish two quite distinct phases of shoot growth in pine, the development of the vascular system within the shoot proceeds continuously. The shoot is primarily a vascular system serving the needles and subtending structures, and stem and needles are developmentally and functionally united into a single organ. This relation is easily visualized in the new shoot and even in a young seedling, but it becomes increasingly difficult when extended to a mature tree. I have purposely emphasized this point because frequent reference will be made to the growth correlations between different phases of shoot development and wood formation on the stem. It is imperative that these be recognized as arbitrarily defined phases of a continuous developmental process.

The vascular system consists of a contiguous network of vascular traces ema-

## DEVELOPMENT OF PRIMARY VASCULAR SYSTEM IN CONIFER BUD

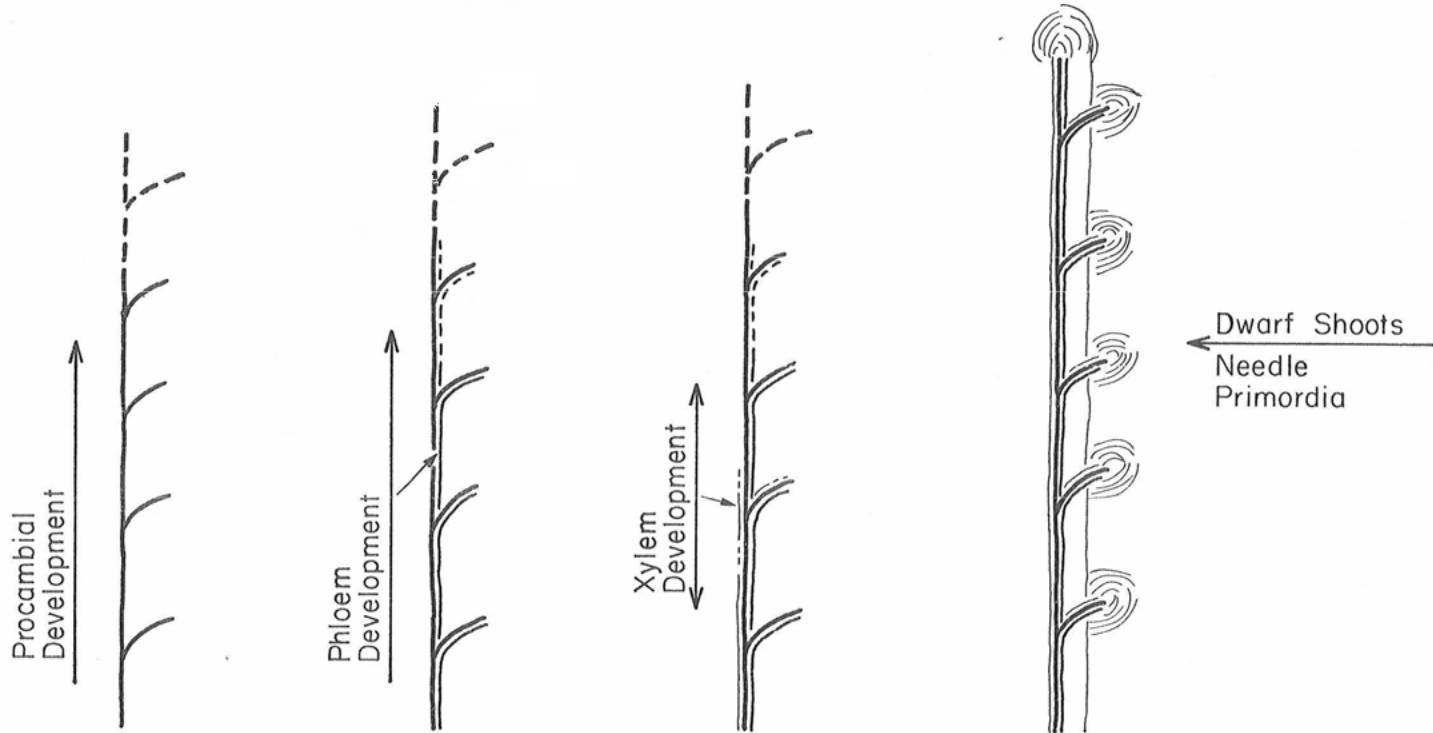


FIGURE 2. Procambial development proceeds upward from existing cambial tissue. The procambial strands are transformed to vascular traces by the addition of primary phloem and xylem elements on the outer and inner procambial surfaces, respectively.

## PATTERNS OF GROWTH AND DEVELOPMENT

---

nating from the needles during the early stages of bud growth and shoot extension. When the shoot is viewed in cross-section, this network appears as a series of isolated vascular strands or bundles. As the needles begin to elongate, an interfascicular cambium differentiates from parenchymatous cells and unites the vascular traces into a hollow cylinder, or sheath, which completely encircles the stem. This sheath, which is united at its base with the cambium of the main stem, develops upward as the shoot matures. At the termination of shoot extension, the stem cambium of the new shoot not only is continuous with that of the main axis but it also diverges into the needles. The newly formed needles are therefore directly connected with the cambium, and the xylem and phloem products of the cambium, throughout the entire crown and stem system.

Once formed, the cambium continues dividing, and by season's end a zone of xylem tracheids extends throughout the entire new shoot. Because both the number of contributing needles and the time available for xylem formation decrease progressively up the shoot, the growth ring will be wider at the base than at the apex. The stem of a fully developed new shoot will therefore consist of a xylem sheath that tapers upward.

Physiological processes associated with breaking of dormancy and initiation of bud growth in the spring also reactivate the cambium on the older stem parts. Under normal conditions of growth, cambial activity begins just beneath the buds and progresses downward toward the stem base as shown by the classical studies of Priestley (26). The exact timing of the initiation of cambial activity and rate of spread throughout the tree vary considerably among species and according to growth conditions. Although explicit proof is not available, cumulative evidence suggests that the stimulus for cambial reactivation is provided by a hormone originating in the buds (12, 30).

With bud growth and shoot extension, the nodal discontinuities between the new and old cambia also disappear. Thus, the stem cambium originating in the developing shoot and the cambium on the older stem unite to form a continuous sheath. This sheath encircles the main stem and all lateral appendages where secondary growth occurs. In the branch-free bole, the cambium and its derivatives gradually conceal all branch scars, and on the xylem surface there is no outward evidence of the annual height increments. The final product of the cambium is a vascular system that extends from the needles to all living cells in the tree with a minimum of discontinuities to interrupt the vital translocation streams.

Once the cambium has been activated, it continues producing xylem over most of the growing season as long as conditions remain favorable. There are, how-

## WOOD FORMATION AND QUALITY

---

ever, marked differences in the rate and duration of cambial activity among trees of different vigor classes and even among different parts of the stem of the same tree. Nevertheless, throughout these sustained periods of cambial activity and xylem production, continuity must be maintained between the vascular tissues of the stem and branches and needles of all ages. Little is known concerning these processes, but Elliott (4) has shown that as the xylem expands, vascular connections between the stem or branch and the firmly embedded needle are either constantly broken, or become nonfunctional and new ones established (Figure 3). These connections are vital to the complex translocation system of the tree, and physiological processes within the needle are responsible for maintaining the union.

The foregoing summary is brief, by necessity, and it must be appreciated that a highly complex subject has been greatly simplified to stress a point. Yet, it is clear that the initiation of foliar primordia within the buds and the progressive development of the cambium and vascular system on the stem are intimately related. As the foliar organs move upward with each new season's growth, this relation does not terminate on those internodes left behind. The xylem sheath, even though separated from the foliage, remains an integral part of the vascular system, intimately associated with the physiological processes of the needles. As a result, every change in the growth or development of the needles will be registered by a concomitant change in the cambium or its derivatives at some point on the stem. An awareness of these physiological growth correlations permits one to approach the study of wood formation and the effects of growth conditions on wood formation with greater insight.

The relation between foliar growth and wood development will now be pursued from another perspective by considering the growth patterns of a young tree.

### GROWTH PATTERNS OF A YOUNG TREE

The relation between foliage growth and wood formation is highly expressed in the young tree. A young tree is essentially all crown, and the crown structure exerts a pronounced influence on the type of wood produced. The current-year shoot at the apex of a tree several years of age still constitutes a sizeable proportion of the total tree, and consequently it dominates wood production on the stem. As the young tree grows older and larger, the lateral branches assume an increasingly larger role in the production and regulation of wood formation. Since it is known that earlywood formation is favored by close proximity to the foliage organs, it is not surprising that the stems of young trees contain an exceptionally high proportion of earlywood. In the current-year internode, the tracheids produced in close



Vascular connections to Needle are broken and reformed as Xylem expands.

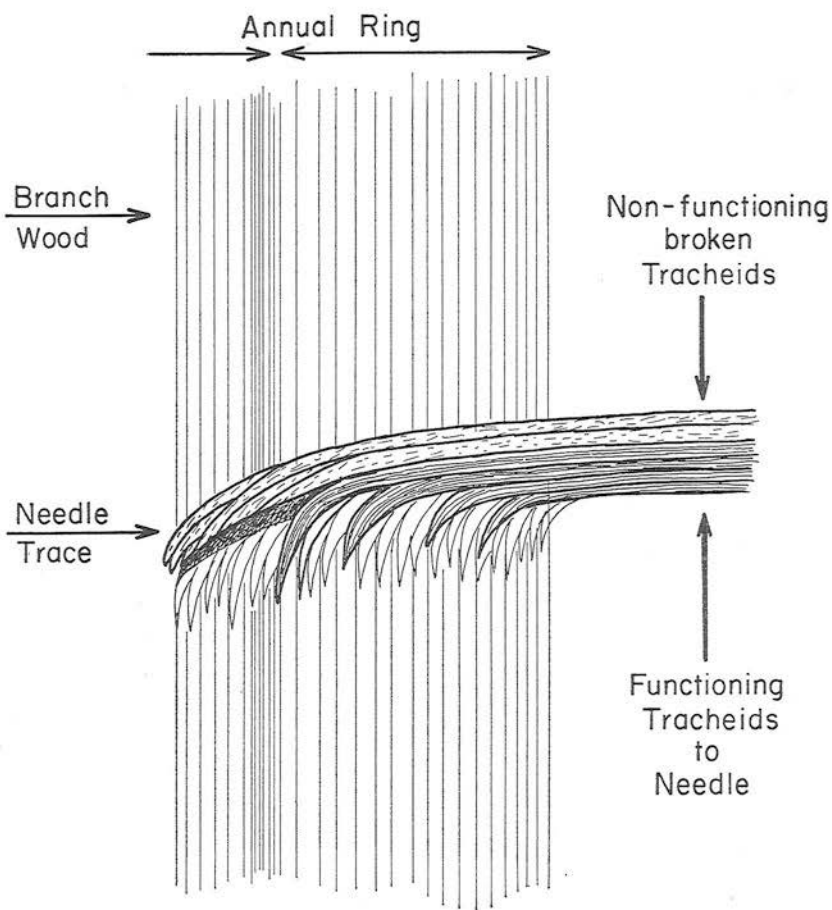


FIGURE 3. Physiological processes within the needle are responsible for maintaining the union between the vascular systems of the stem and needle throughout the course of seasonal growth and during subsequent seasons of growth. (After Elliott 1937)

## WOOD FORMATION AND QUALITY

---

proximity to the needles are almost exclusively of the earlywood type. However, even in the lower portion of this internode some narrow-diameter tracheids resembling latewood may be produced just prior to cambial dormancy. Downward in the stem, the percentage of latewood tracheids in the growth ring will gradually increase as the distance from the foliar organs increases. Earlywood tracheids will nevertheless predominate in the growth ring, because the branches of young trees are generally short and extremely vigorous.

Latewood is initiated at or near the stem base in trees of all ages, and it progresses upward as the season advances. The width of the zone of latewood therefore tapers upward in the stem reaching a point of extinction near the apex. This pattern of latewood development is a function of age and distance from the active crown, both of which increase simultaneously.

The characteristics of wood formed in close proximity to the foliage in a young tree introduce the concept of juvenile wood. The term juvenile wood is actually a misnomer; its recognition is based upon arbitrary criteria and there is no acceptable definition by which it may be identified. Although it aptly describes the type of wood produced in a young tree, the same or a very similar type of wood is also produced in the rings nearest the pith at all heights in the stem. It may therefore be more appropriately described positionally as core wood, or developmentally as crown-formed wood. Because of its widespread acceptance, the term juvenile wood will be adhered to in this paper. In general, juvenile wood is characterized by a high proportion of earlywood and a low proportion of transition-latewood tracheids, but juvenile traits are also expressed in certain physical and chemical properties of the tracheids. For example, transition-latewood tracheids may be slightly smaller in radial diameter and slightly thicker-walled than the earlywood tracheids in the same growth ring. The width of the zone of juvenile wood and its duration in age varies greatly with species and with prevailing growth conditions. In pines, juvenile wood is always produced by the uppermost crown, and some juvenile wood is formed by trees of all ages as height growth continues.

The growth of a young pine into the sapling stage and beyond brings about pronounced changes in growth ring structure. The upper crown of a vigorous sapling is comparable in many respects to the whole above-ground part of a young tree. Wood formation in the current-year shoot is similar, and in the outermost growth ring the percentage of latewood gradually increases as distance from the apex increases. Also, the transition latewood of juvenile wood gradually merges into true latewood with increasing distance from the apex and growth ring age from the pith. Thus, distance from the foliage and age from the pith

## PATTERNS OF GROWTH AND DEVELOPMENT

---

function together in overcoming the propensity for juvenile wood formation. To these we must also add crown vigor, which will be discussed later.

Height growth consists of the consecutive addition of shoot internodes to the terminal axis of a tree. It has just been pointed out, however, that regardless of the increase in total tree height, wood formed within the upper crown remains similar in structure. The major changes in wood formation and quality occur in the lower stem beneath the living crown or beneath the most active branches of the crown. In terms of wood formation, height growth can thus be viewed as the consecutive addition of internodes at the stem base (Figure 4). Theoretically, the stem base is the culmination point of the age and distance factors that regulate wood formation. The theoretical pattern is found under many, but not all, growth conditions. The physiological gradients regulating wood formation are frequently altered so that the culmination point in any one growth ring occurs somewhat higher up the stem, as we will discuss in a moment.

Trees in the sapling stage may retain crowns extending to the ground if open-grown. These long, vigorous crowns can promote and prolong the period of juvenile wood formation, but not indefinitely. Eventually, the foliar organs of the lower branches, although still vigorous, will become far removed from the main stem and their regulating influence will decline. Thus, like the terminal shoot, each lateral branch influences wood formation according to its position on the stem and its relative vigor. Although the crown structure of an open-grown sapling may be conducive to the formation of a high proportion of earlywood, latewood content will nevertheless increase toward the stem base. Further increases in height and age of an open-grown tree result in the appearance of mature wood at progressively higher levels in the stem. But even though considered mature, the growth rings of many large open-grown trees may still contain a broad, indistinct transition zone and a low percentage of latewood.

In contrast to an open-grown tree, a pine that has grown under competition in a closed stand exhibits a different pattern of development. Competition results in the progressive decline and death of the lowermost branches. The upper stem, in close proximity to the most vigorous branches, continues to produce juvenile wood. However, because of the rapid decline in vigor of the laterals as distance from the apex increases, the structure of the wood within the growth rings changes dramatically. For example, progressing down the stem in a stand-grown tree, the wood achieves mature characteristics in growth rings closer to the pith, the transition to latewood becomes more abrupt, and the percentage of latewood in the growth rings increases. Again, these latter characteristics generally culminate at or near the stem base. A stand-grown tree may therefore exhibit a much

Growth in height may be viewed as adding Internodes to stem base. Juvenile wood continues to form in upper stem.

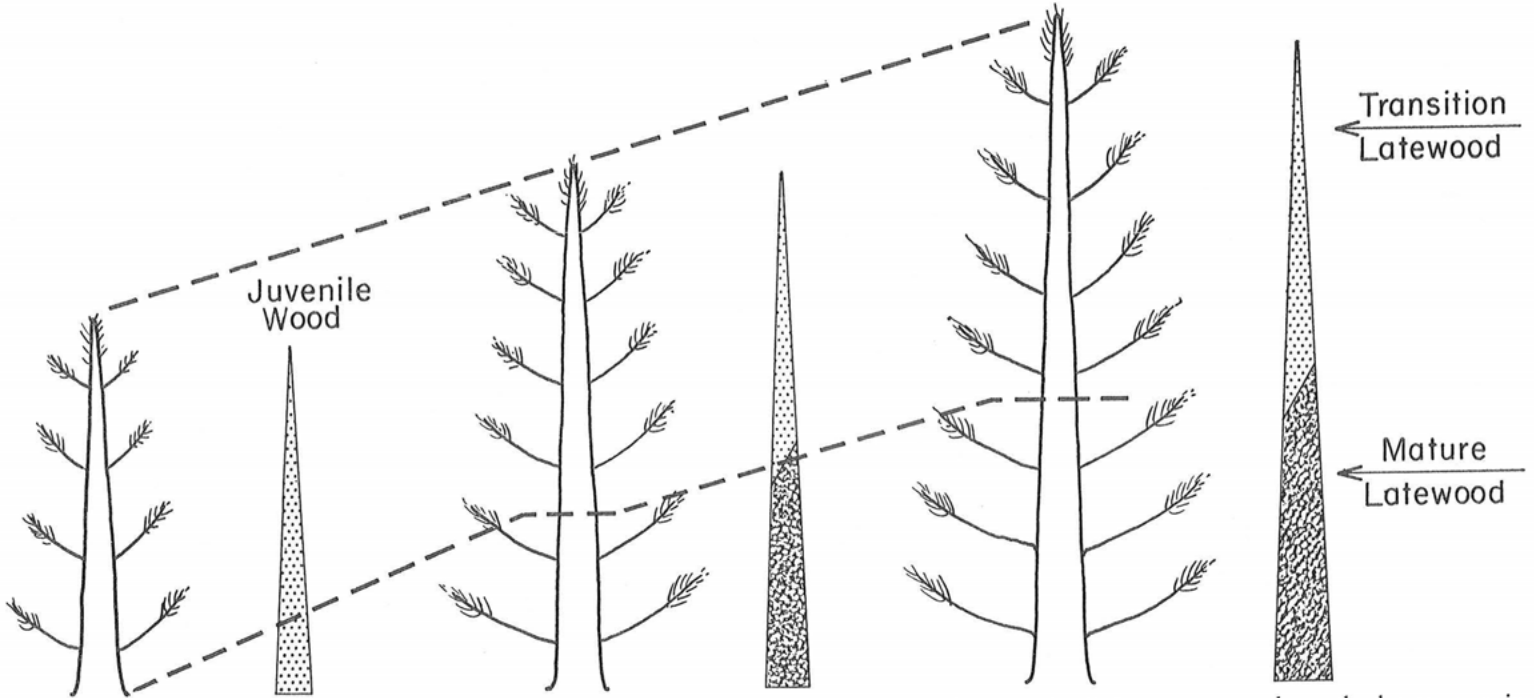


FIGURE 4. The major changes in wood formation and quality occur in the lower stem beneath the living crown, or beneath the most active branches of the crown.

## PATTERNS OF GROWTH AND DEVELOPMENT

---

greater range of wood quality variation throughout its bole than an open-grown tree of comparable age.

The role of the branches has been emphasized up to this point because accumulated evidence strongly suggests that the foliar organs regulate wood formation during the entire seasonal course of development. The developmental sequence of lateral branch growth in pine is interesting. In early spring, all lateral buds stand upright and remain upright as they elongate. These upright shoots produce the so-called "candles," and the upright position is presumably due to the high auxin production of the elongating shoot. As the needles begin to elongate, the angle of the new shoot gradually decreases as shoot weight increases and auxin production declines. By season's end, the shoot is either horizontal or almost parallel to the parent branch. Therefore, a graph of the year-to-year growth of the bud and shoot of a lower branch does not show a straight line, but a sinuous curve.

Senescence and death of a lower-crown branch in pine result from a series of predisposing events (Figure 5). A healthy, vigorous branch has good foliage, and contributes photosynthate to the remainder of the tree. A healthy branch also produces a complete growth ring along its entire length, which forms an active union with new growth of the main stem, and which assures the branch of a steady supply of water and nutrients.

Senescence is generally triggered by a decrease in light, due to shading, that severely limits photosynthesis (Figure 5). The decrease in photosynthesis is followed by a smaller bud the next season that further decreases the potential for photosynthesis and auxin production. These events lead, in turn, to a decrease in wood growth on the branch and to the formation of an incomplete growth ring. Since no growth ring is produced at the branch base, the branch is no longer able to maintain contact with the main translocation pathways in the tree. And, as contact with the main stem diminishes, the branch competes less favorably with healthier branches for water during times of stress, and it contributes little or nothing to stem growth. These growth-suppressing events, operating as a negative feedback system, continue until the branch tip is barely maintaining itself. Branch death soon follows. A similar series of events occurs during senescence and death of a suppressed tree.

Thus, it is unrealistic to measure crown size or crown length and expect to arrive at a statistical correlation between these measures and wood growth on the stem. Under ideal conditions, a high correlation may be obtained. However, unless one can accurately determine how much a branch is contributing to stem growth, the mere fact that it is still living is really of little importance.

It has been found in "average" pines that branches within the upper one-third

# SENESCENCE AND BRANCH DEATH

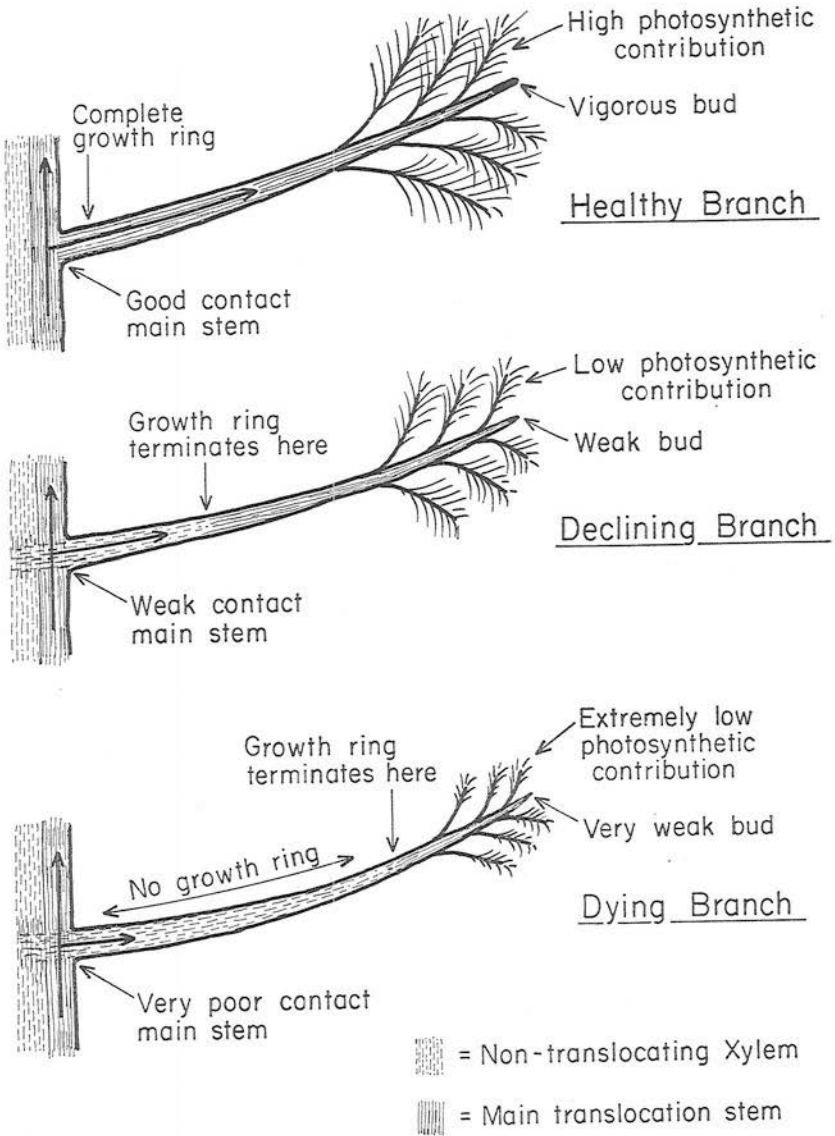


FIGURE 5. Branch senescence may be viewed as a series of growth-suppressing events, generally initiated by a decrease in light due to shading, that operate as a negative feedback system.

## PATTERNS OF GROWTH AND DEVELOPMENT

---

of the crown are the principal contributors to stem growth, and perhaps the primary regulators of wood formation (Figure 6). These are the most vigorous branches and they have the shortest translocation pathways to the main stem. The relative contribution of different branches will, of course, vary with growth conditions, particularly whether the tree is open-grown or stand-grown. For purposes of discussion, an analogy has been drawn between the development and wood formation of a young tree and that of the upper crown of an older tree. Retention of additional branches down the stem of the older tree, if open-grown, provides more foliage for wood production on the lower stem and also a greater regulatory influence on the wood produced. Conversely, removal of the lower branches through stand competition confines the sources for wood production and regulatory processes to branches of the upper stem. Since neither branch death nor the contribution of different branches to growth is uniform, it is difficult to quantify these relationships. Nevertheless, it is evident that there are long-term effects of tree development with short-term effects of seasonal development superimposed upon them, and together they determine the overall course of wood formation (18).

### LONG-TERM AND SHORT-TERM EFFECTS ON WOOD FORMATION

The long-term effects are those that develop gradually over a period of years (Figure 7), resulting in changes in the overall size and shape of the crown and in the distribution of the branches along the bole. The long-term effects determine the general shape of the growth curve. Aside from aging, the most notable long-term effect is stand closure. A young tree growing unhindered in a stand may gradually become crowded by its neighbors and, perhaps, eventually overtopped. Each increase in the degree of competition or suppression would decrease crown size and also decrease efficiency of the remaining branches. The changes in crown attributes would, in turn, be registered by a decline in wood growth, by alterations in the distribution of growth along the bole, and by changes in the percentage of latewood within the growth rings.

The short-term effects may be defined as those induced by fluctuations in growing conditions, primarily weather factors, that influence the seasonal development of the foliage organs (Figure 8). The short-term effects are superimposed on the long-term patterns and produce the saw-toothed growth curve. For example, if an environmental factor, such as soil moisture, is either severely limiting or in excess during much of the growing season, then the net production of tracheids will be influenced and growth ring width will vary considerably from the norm. On the other hand, if an unusual change in environment is limited to

## WOOD FORMATION AND QUALITY

Contribution of branches to wood formation declines with age and length of branches.

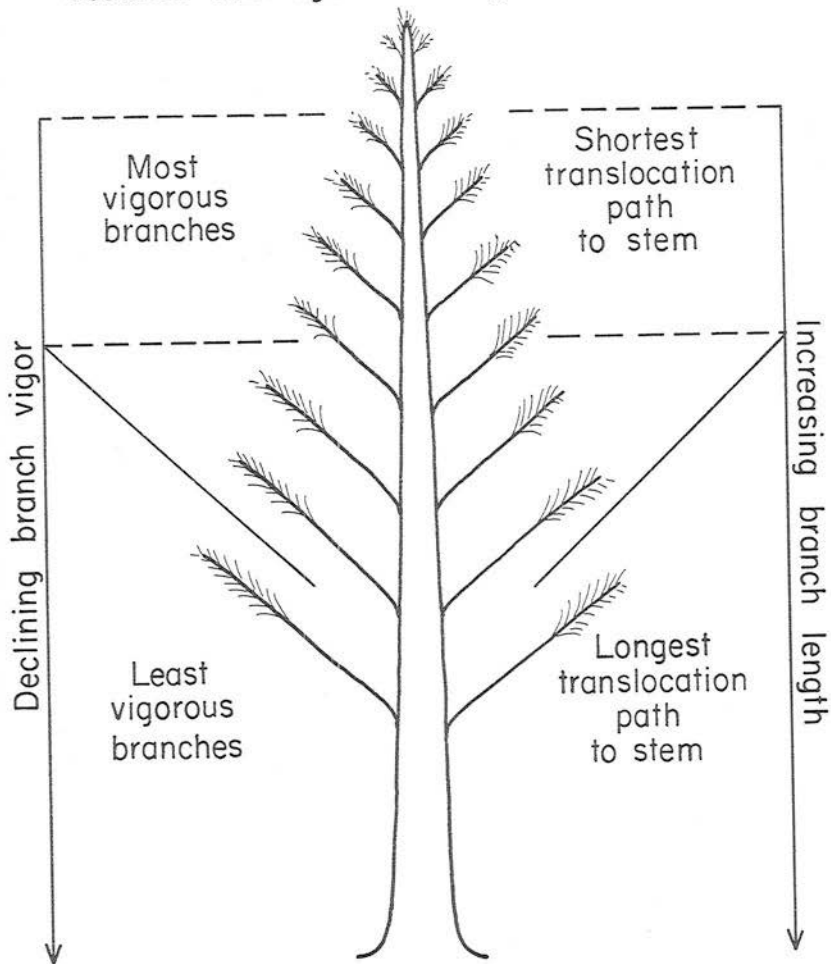
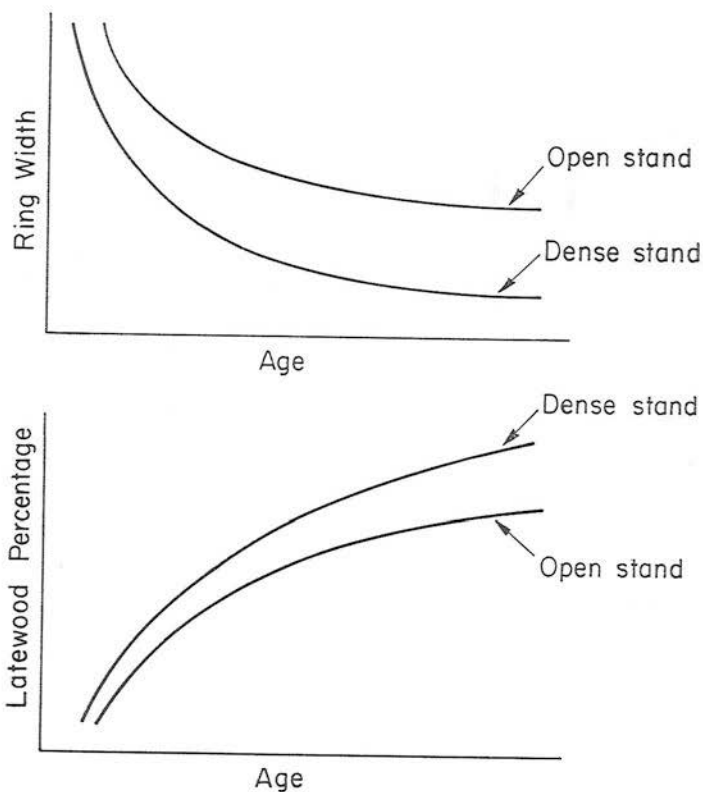


FIGURE 6. Branches within the upper one-third of the crown are the principal contributors to stem growth, and perhaps the primary regulators of wood formation, in trees growing under average stand conditions.



## LONG-TERM EFFECTS ON WOOD FORMATION

Cause: Age, stand density, local environment,  
determine long-term smooth growth curve.



### Effect On Crown:

Influence overall crown size, shape,  
distribution along stem, and branch vigor.

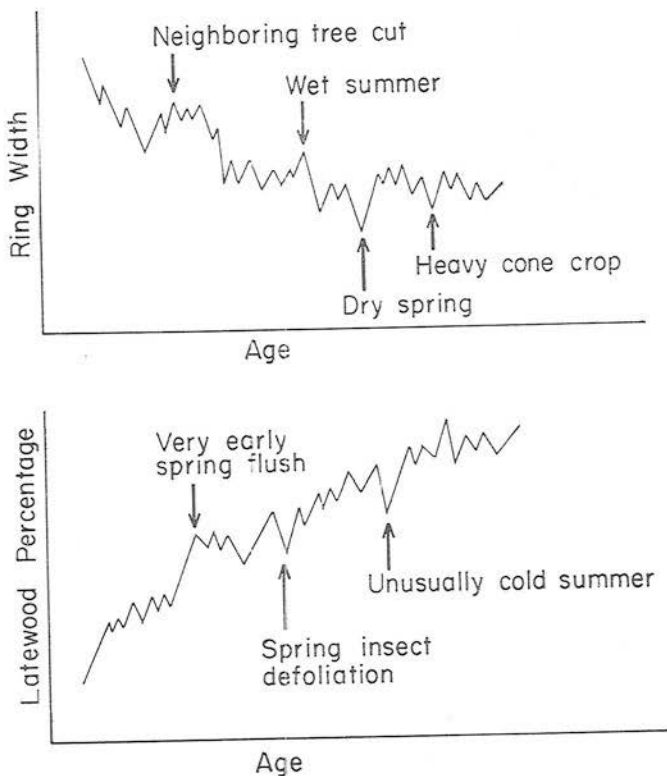
### Effect On Wood:

Determine general width of growth ring,  
distribution of growth ring along bole,  
percentage of latewood in growth ring,  
and early - latewood transition.

FIGURE 7. The long-term effects on tree growth are those that develop gradually over a period of years.

## SHORT-TERM EFFECTS ON WOOD FORMATION

Cause: Seasonal weather fluctuations, insect attacks, flower and cone crops produce saw-toothed growth curve.



### Effect On Crown:

Seasonal development of buds and needles.  
Variable environmental factors which alter  
seasonal course of development.

### Effect On Wood:

Superimposed on long-term effect causing  
minor fluctuations.

FIGURE 8. The short-term effects on tree growth are those induced by fluctuations in growing conditions (primarily weather conditions) that influence the seasonal development of the foliage organs.

## PATTERNS OF GROWTH AND DEVELOPMENT

---

a particular part of the growing season, then the variation may be confined to the width of either the earlywood or the latewood, and latewood percentage will be altered. Examples of the latter would be an early spring flush of growth that, in effect, extends the period of latewood formation by lengthening the growing season, or an unusually cold summer that reduces the period of latewood formation. We could cite numerous examples of these fluctuating and randomly occurring short-term effects, such as unseasonable temperatures, cloudy weather, insect depredations, and even periodic cone crops. Each of these factors would induce variation in either the net production of tracheids, or the characteristics of tracheids within one to several growth zones. Furthermore, these variations in wood formation may occur throughout the tree, or they may be confined to particular portions of the bole or growth increment. As will be shown later, each of these short-term effects exerts its influence directly on the foliage and only indirectly on the wood subsequently formed. Because of the many interactions, advance predictions concerning wood formation cannot be made with certainty, although the physiological basis for the observed results can be explained.

### CONCEPT OF THE CONTINUUM

Throughout this discussion the role of the crown in regulating wood formation on the stem has been stressed. It has been pointed out that the cambium and the vascular system developing from the cambium exist in an intimate relationship with the foliar organs, both developmentally and functionally. It has been further pointed out that the width of the xylem growth rings and the relative proportion of earlywood to latewood within the growth rings are determined by growing conditions that either directly or indirectly influence crown development. As a result of environmental conditions and the inevitable growth of the tree in size and age, the intimate relation between the crown and different cambial regions on the stem is being constantly altered. Yet, in spite of this, the crown continues to exert a regulatory influence on wood formation throughout the life of the tree. This persistent relation between crown and stem results in the creation of gradients in xylem development. These gradients, which occur in both the biochemical processes regulating xylem differentiation and the products of the differentiation processes, exhibit a series of continua extending from the apex to the base of the tree (Figure 9).

Briefly, the concept of the continuum states that the development of a tracheid will be determined by its distance from the crown (foliar organs), its age, or distance from the pith, and its time of formation within the growth ring. Therefore, as the age and distance factors increase, progressive changes in tracheid de-

## CONCEPT OF CONTINUUM

Development of tracheid determined by :

1. Distance from foliar organs of crown.
2. Age or distance from pith.
3. Time of formation in growth ring.

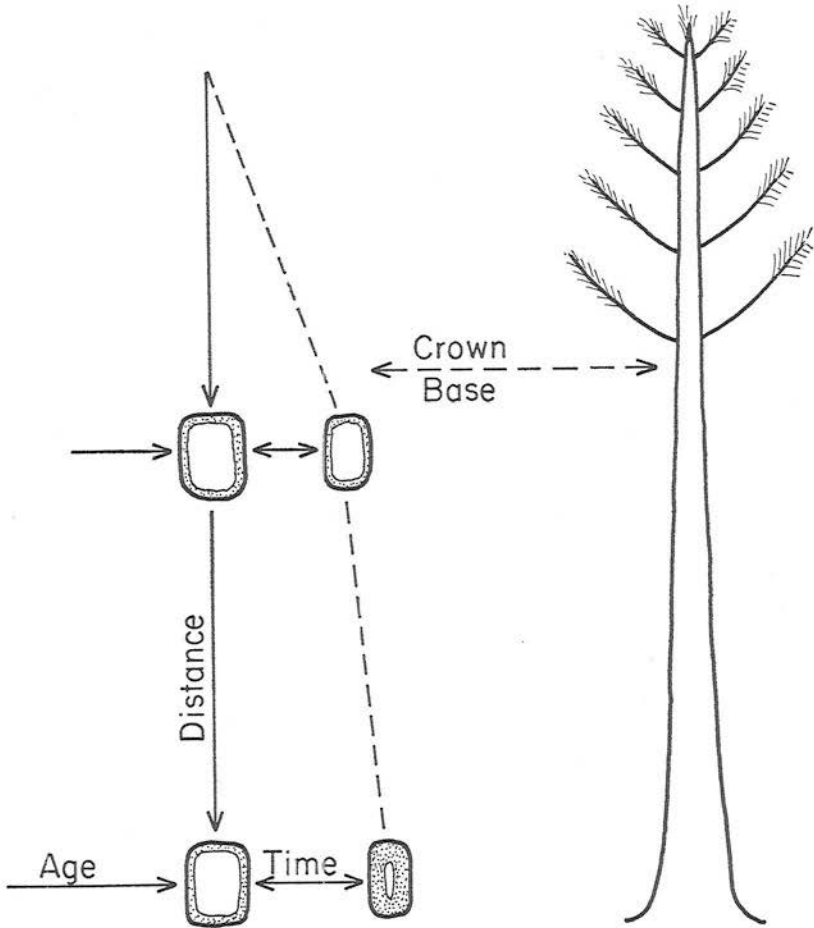


FIGURE 9. Both the biochemical processes regulating xylem differentiation and the products of differentiation exhibit continua extending from the apex to the base of the tree.

## PATTERNS OF GROWTH AND DEVELOPMENT

---

velopment will result in gradients in all tracheid characteristics. These continua are not immutable, since they can be altered by superimposing effects of other factors upon them.

In an ideal tree with a symmetrical, vigorous crown extending to the stem base, the growth rings would increase uniformly down the stem. And, within the growth rings, there might be perfect upward and downward taper for latewood and earlywood, respectively. However, the ideal is never realized, and at best is only roughly approximated in the current-year shoot of a vigorous pine or the stem of a young, open-grown tree. Actually the width of a growth ring, the percentage of latewood within a growth ring, and the individual characteristics of the tracheids constituting a growth ring all reach a culmination point at some position within each incremental sheath. The presence of these culmination points, and the constant fluctuations of the culmination point within and among growth increments, tends to obscure the ideal pattern.

Several factors operate against maintenance of an ideal continuum. The crown is not perfectly uniform in structure. Individual branches differ in size and vigor, and their contribution to wood formation is extremely variable. Furthermore, once the crown begins to recede, the branch-free bole is no longer a series of recognizable internodes with subtending branches, but a single, long internode totally dependent upon the remainder of the crown for its growth requirements. As the branch-free bole lengthens, the culmination point for many wood characteristics gradually shifts upward in accord with the receding crown base. Under these circumstances, the culmination point may broaden to a plateau or undulations may appear in the downward progression of a wood characteristic. Irregularities in a continuum may also be traced to growth stresses, caused primarily by the wind, which may stimulate growth at the stem base. Thus, the ideal continuum is never realized because the long-term effects are constantly changing the size, shape, and efficiency of the crown, and the short-term effects are constantly influencing the seasonal course of crown development.

The purpose of emphasizing the continuum concept is twofold. First, because it is an excellent demonstration of the crown-stem relationship in wood formation. And second, because it is an excellent portrayal of the extreme variability in wood quality within a stem. For simplicity, I have stressed only earlywood and latewood; but when we recognize that every tracheid characteristic that we might wish to measure is related to earlywood and latewood (17), then we can begin to appreciate the range of wood quality variation we are dealing with in a single tree. It has been pointed out on a number of occasions that there is more variability within a single tree than there is among trees in a stand.

## WOOD FORMATION AND QUALITY

---

This brings us to the problem of uniformity. One of the greatest problems facing wood-using industries is the lack of uniformity in wood quality both within and among trees. When we consider the continuum concept, we can begin to appreciate the magnitude of wood quality variation within trees, and when we consider the effects of environment, we can begin to appreciate the range of variation among trees. Increasing uniformity is one of the best methods of improving wood quality; this subject will be discussed in more detail in Part III.

The continuum concept also helps us understand the statistical relations with which we are dealing. The variability of wood formation results from physiological gradients down the stem from the crown. Therefore, the correlations between crown and stem are physiological growth correlations, and as such they are not necessarily mathematical correlations. With regard to wood quality, we must recognize that we are sampling a continuum and all statistical evaluations must take this source of variation into consideration. All wood quality evaluations are statistical, and failure to consider the biological sources of variation is one of the greatest causes of confusion in the wood quality literature.

In summation, it is evident that a multitude of conditions can influence crown development and determine the course of tracheid differentiation and wood formation. The long-term effects, which determine the age and distance factors, create the major patterns. Superimposed on these are the short-term effects, which create the minor fluctuations. Each of these patterns is produced tracheid by tracheid. Hence, each file of tracheids, in fact each tracheid, will develop in accordance with its position in the growth ring relative to the crown and relative to the developmental stage of the crown during the growing season. And, each foliar organ will contribute to wood growth and to the regulation of tracheid development in accordance with its position in the crown and its relative vigor. It is therefore readily apparent that minor continua within the growth ring will be superimposed on the major continua for each wood characteristic. These constantly shifting and fluctuating patterns of tracheid development in response to a constantly changing crown development are the principal sources of variation in wood quality. Wood quality can only be evaluated by appreciating the magnitude of variation, and it can only be controlled by understanding the source of variation.

Students of tree growth and wood formation will recognize the foregoing discussion as being generalized and as portraying ideal conditions. This simplified approach was selected not only for the sake of brevity, but also for stressing the fact that wood formation is an integral part of tree growth that cannot be studied independently. It must be recognized that these basic patterns of tree growth

## PATTERNS OF GROWTH AND DEVELOPMENT

---

vary not only with growth conditions, but also with species. Even within the genus *Pinus*, many variations will be found, particularly in the multinodal pines and in those growing either in semitropical or arid climates.

Up to this point, we have only considered the visible expressions of tree growth, the patterns which can be observed and frequently measured. In the next section, we will consider the causes of these patterns, the physiological processes involved in wood formation.

## PHYSIOLOGY OF WOOD FORMATION

---

RESEARCH on the physiology of wood formation began many years ago with workers such as Jost and Hartig in Germany. Their work has been built upon and expanded over the years by many investigators throughout the world. Although some of these researchers devoted their entire careers to the investigation of rather specific problems, much of the ensuing research was of short duration with no sustained exploration in depth. Yet, each new finding added to our fund of knowledge and advanced science one step farther.

In recent years there has been renewed and accelerated interest in the general subject of the physiology of wood formation, and research is now progressing rapidly on many fronts. We are still building upon the past, confirming previous findings and discovering new information. And like our predecessors, we are constantly re-interpreting hypotheses and developing concepts as ideas emerge from the blending of new knowledge with the old. The hypotheses help us define our immediate problem and serve as guides for further research, whereas the concepts aid us in reassembling seemingly isolated hypotheses and scattered bits of knowledge back into a whole.

In the following discussion, I will present hypotheses on several phases of wood formation and some of the evidence supporting them. I will also attempt to show how these hypotheses relate to the basic patterns of tree growth and to the general crown-stem concept of wood formation. For this discussion, I am going to rely almost exclusively on research conducted in our own laboratory because it relates directly to the crown-stem relationship. Please bear in mind that this is only one approach to the study of wood formation, and much excellent research has been and is being done in other laboratories that is also pertinent to the discussion.

Wood formation is an all-inclusive term for a series of biological processes that can be arbitrarily divided into four developmental phases: (1) Awakening of the cambium from dormancy, (2) cell division of cambial initials and mother cells, (3) differentiation of cambial derivatives, and (4) maturation. We will be concerned only with the final stages of differentiation and maturation. We will also restrict the discussion to conifers, primarily *Pinus resinosa*, or red pine. And, since red pine wood consists almost exclusively of tracheids, we will confine the discussion still further to the differentiation and maturation processes of tracheids. By differentiation and maturation of tracheids, I refer to the phases of radial ex-



## PHYSIOLOGY OF WOOD FORMATION

---

pansion, secondary wall thickening, and eventual cell death, which is maturity for a pine tracheid. Although most of the work to be discussed was conducted a number of years ago, it will provide background information for understanding the physiological processes relating foliar growth and development to wood formation.

### DEVELOPMENTAL STUDIES OF WOOD FORMATION

The most conspicuous features of coniferous wood from the North Temperate Region, and of pines in particular, are the growth rings. Under most circumstances, one growth ring is produced each year consisting of a zone of earlywood followed by a zone of latewood (Figure 10). Growth rings are not necessarily uniform in width from year to year, nor is the percentage of latewood within a growth ring uniform from year to year (Figure 11). Annual and seasonal changes cause considerable variability in wood quality and also raise some intriguing questions regarding wood formation.

The seasonal changes from earlywood to latewood are determined by the changes in dimensions of the individual tracheids constituting the growth ring. Normally, the transition to latewood is brought about by a decrease in tracheid radial diameter and by an increase in secondary wall thickness.

Our first studies verified previous findings that earlywood was produced during the period of active terminal growth (11). That is, most of the earlywood formed when the new shoot was actively elongating, and the transition to latewood occurred *about* the time terminal growth stopped and the bud set for the next season's growth. "About" has been emphasized because this relationship is physiological, and strong statistical correlations may or may not exist. As will be shown, many growth conditions can prolong the period of earlywood formation beyond bud set either throughout the entire tree or within the upper crown.

The relation between terminal growth and wood formation on the stem could be tested by environmental control. For example, it is known that short photoperiods suppress vegetative growth and long photoperiods promote vegetative growth. When young red pines were grown under a long-day:short-day:long-day regime they produced a false ring with narrow-diameter tracheids of the latewood type in the growth ring corresponding to the short photoperiod (Figure 12). In this case a growth correlation was evident, because needle elongation was suppressed by the short photoperiod and needle growth resumed when the trees were returned to long days.

By independently exposing the buds and the needles to different photoperiods and different light intensities, it was possible to separate the influence of each

## WOOD FORMATION AND QUALITY

---

of these organs on wood formation (13). During active extension growth of the shoot, for example, the bud exerts a decisive regulatory influence on tracheid diameter, but the needles become the principal regulating organs later in the season when extension growth has terminated. Since the needles of pines have an indeterminate basal meristem, their growth can continue late into the season if growing conditions permit. Needle activity is also extremely sensitive to external growth conditions and readily subject to environmental control. The nature of needle growth and activity and the sensitivity of needle growth to environmental conditions help to explain many of the anomalous patterns of tracheid diameter observed in trees from different growth environments. The role of the needles in regulating tracheid diameter also explains why a tree continues to produce earlywood in the upper crown while latewood formation is underway at the stem base, and why earlywood formation can be prolonged beyond bud set.

Results similar to those obtained by manipulating photoperiod were obtained by using drought as an environmental control (15). When two drought periods of moderate intensity were interposed during the growing season, two false rings composed of narrow-diameter tracheids were produced. Each band of narrow-diameter tracheids corresponded to a short period of artificial drought (Figure 13). Again, as with photoperiod, the effect of drought was found to be primarily on needle growth, and only indirectly on the wood. Therefore, when needle growth was suppressed by drought, narrow-diameter tracheids were produced, and when needle growth was stimulated by re-watering, large-diameter tracheids were again produced. The use of moderate drought conditions as an environmental control was merely to study the effect of temporary suppression of needle growth on tracheid diameter. That this was not simply a dehydration-rehydration effect on the cambium was demonstrated by placing drought trees under short-day photoperiods following re-watering. In this case, they continued to produce narrow-diameter tracheids because needle growth was still suppressed by the short-day conditions. The fact that severe drought conditions can cause xylem abnormalities was demonstrated by Glerum and Farrar (7).

In addition to photoperiod and artificial drought, controlled temperature experiments can also be used to demonstrate the relation between terminal growth and wood formation (22) (Figure 14). Each of these factors affects terminal growth in a somewhat different way, and complex physiological interactions exist. However, it appears that any environmental factor that causes a temporary suppression of terminal growth, particularly needle elongation, will result in a reduction of tracheid diameter in some part of the stem, and any factor that promotes vigorous terminal growth activity will result in an increase in tracheid di-

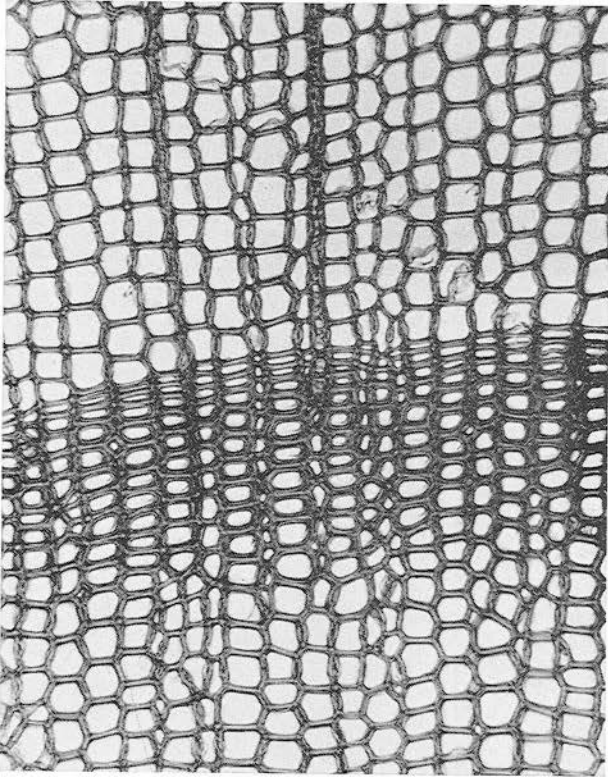


FIGURE 10. Coniferous trees of the North Temperate Region usually produce one growth ring each season. Each growth ring consists of a zone of large-diameter, thin-walled earlywood tracheids followed by a zone of narrow-diameter, thick-walled latewood tracheids.

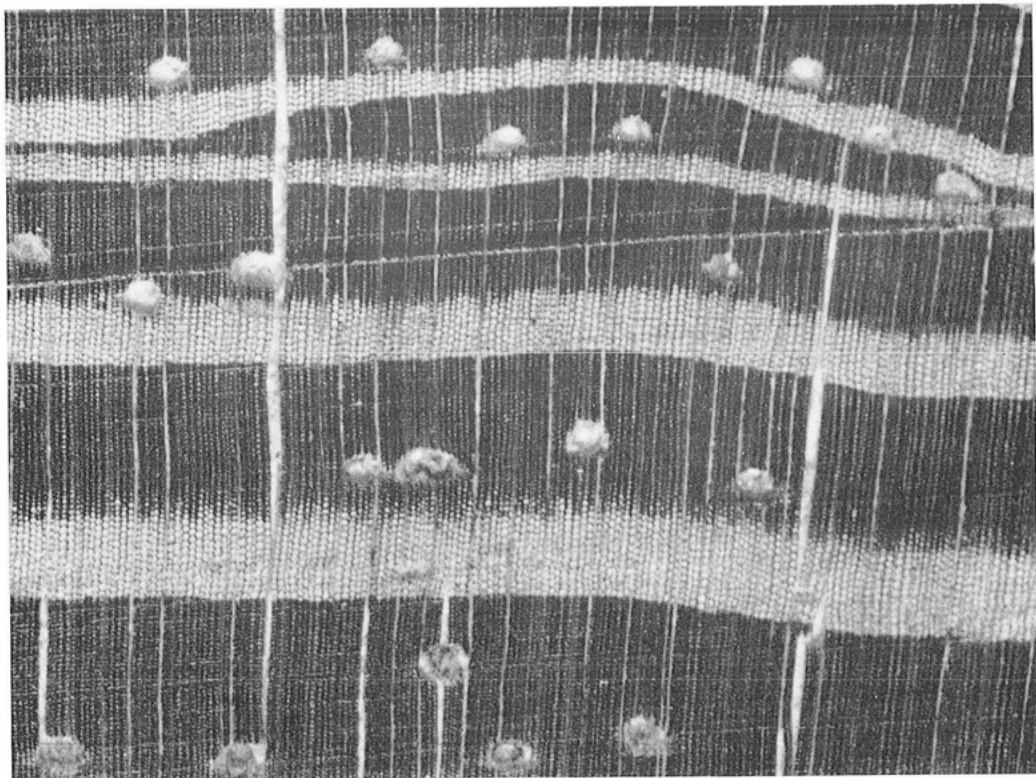


FIGURE 11. Growth rings are not necessarily uniform in width from year to year, nor is the percentage of latewood within a growth ring uniform from year to year. The growth ring in the upper part of this photomicrograph is an extreme example of irregularity, but it does illustrate the variability that can be found.

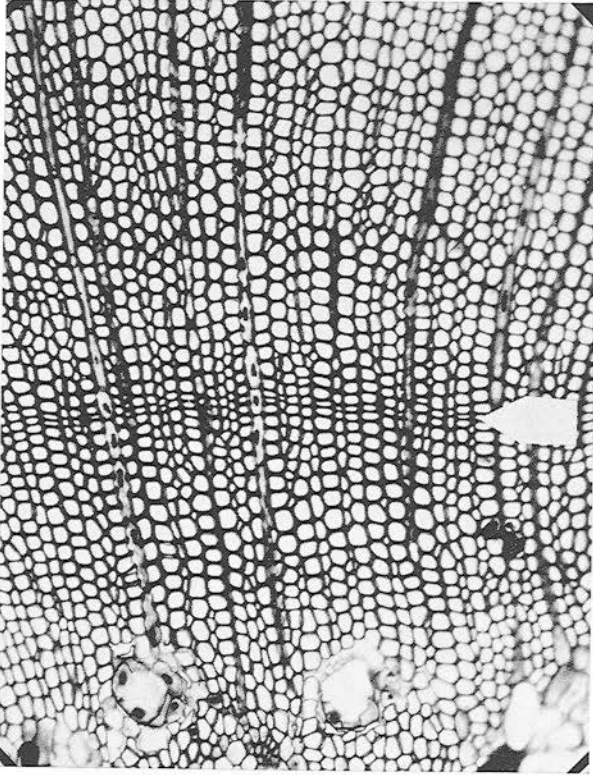


FIGURE 12. Young red pines grown under a long-day: short-day:long-day regime produced a false ring with narrow-diameter tracheids of the latewood-type in the growth ring (arrow) corresponding to the short photoperiod.

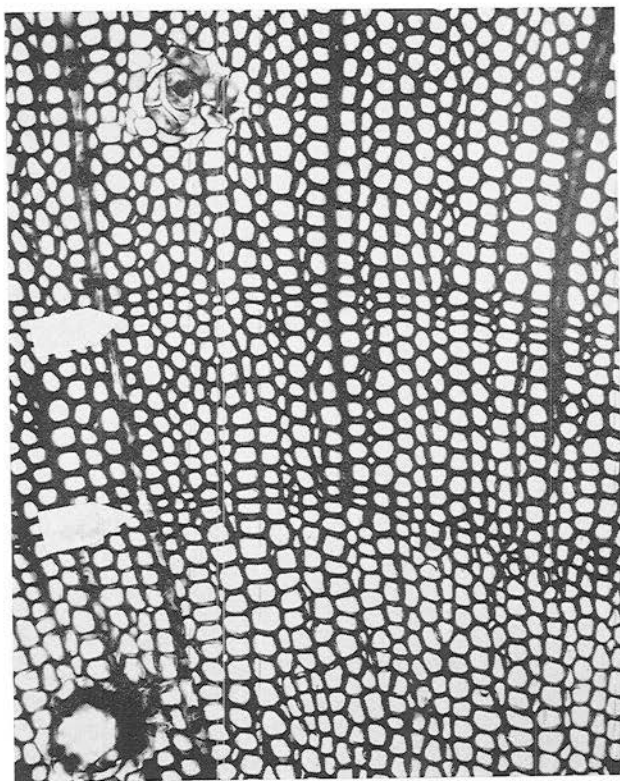


FIGURE 13. When two drought periods of moderate intensity were interposed during the growing season, two false rings (arrows) composed of narrow-diameter tracheids were produced. Each band of narrow-diameter tracheids corresponded to a short period of artificial drought.

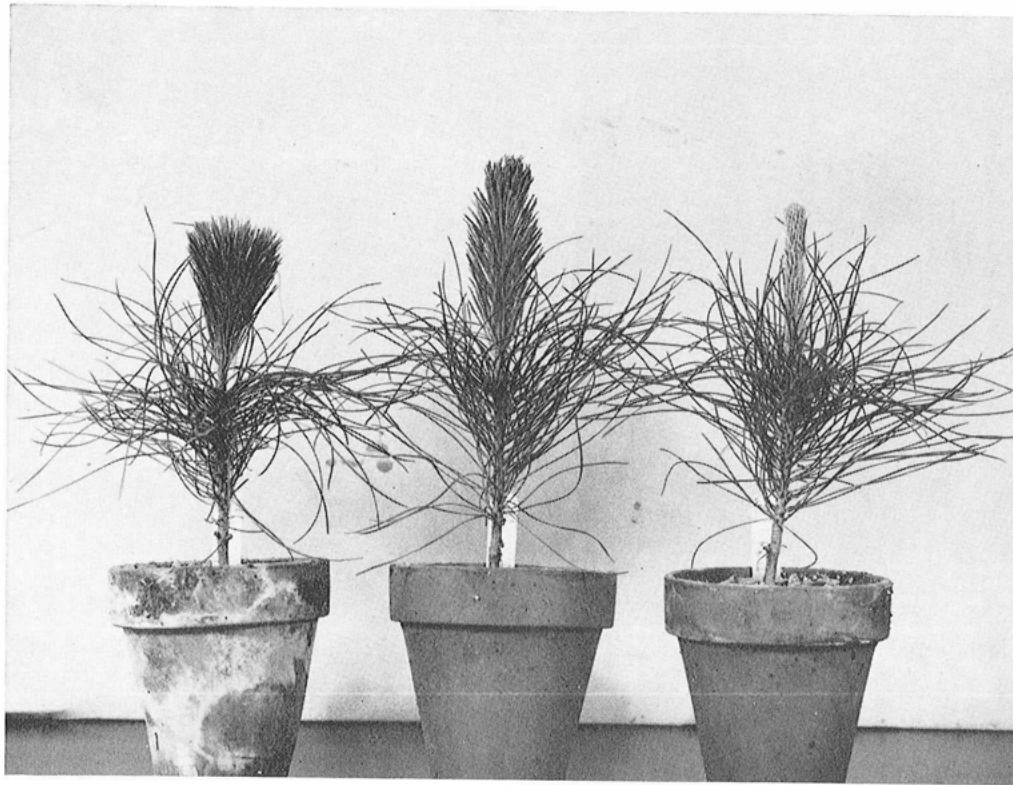


FIGURE 14. Growing season temperature can influence development of the terminal shoot in red pine. High temperatures ( $29^{\circ}$  C. day,  $18^{\circ}$  C. night) promoted precocious needle development at the expense of shoot extension (left), whereas low temperatures ( $18^{\circ}$  C. day,  $13^{\circ}$  C. night) suppressed needle elongation while height growth continued (right). Control trees grown at intermediate temperatures ( $24^{\circ}$  C. day,  $13^{\circ}$  C. night) developed normally (center).

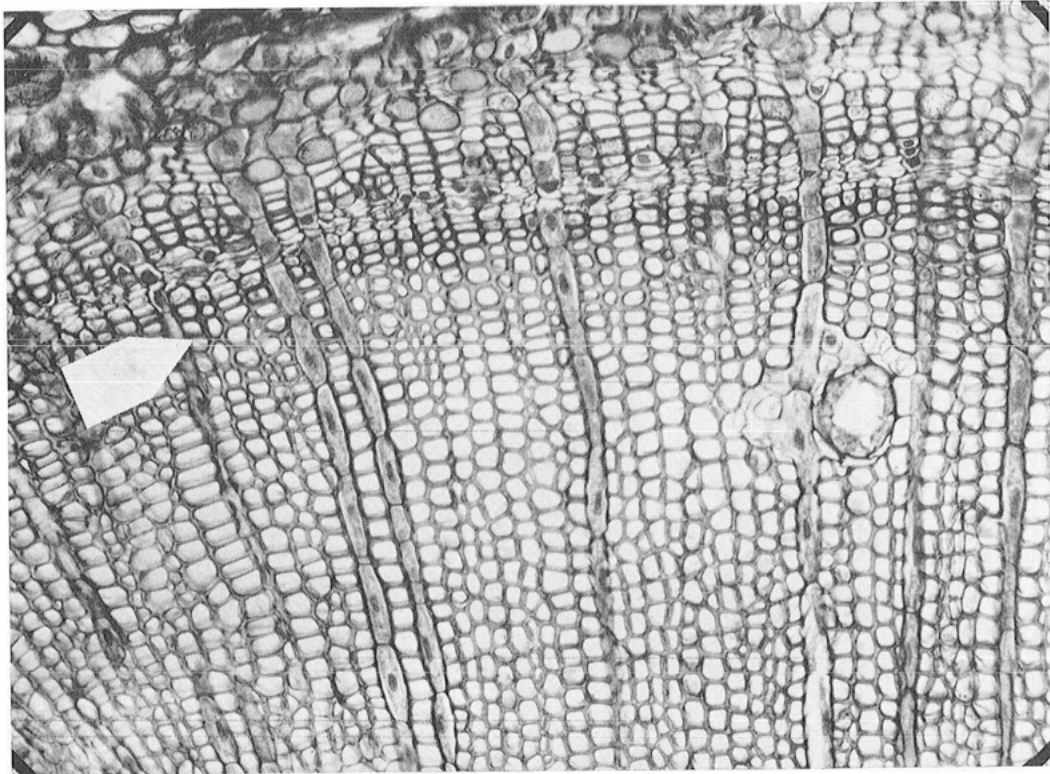


FIGURE 15. A false growth ring was produced by applying indole-3-acetic acid (IAA) to the decapitated tip of a young red pine growing on short-day photoperiods. The IAA induced formation of several rows of large diameter tracheids (arrow) within the zone of narrow-diameter tracheids produced during short-day exposure.



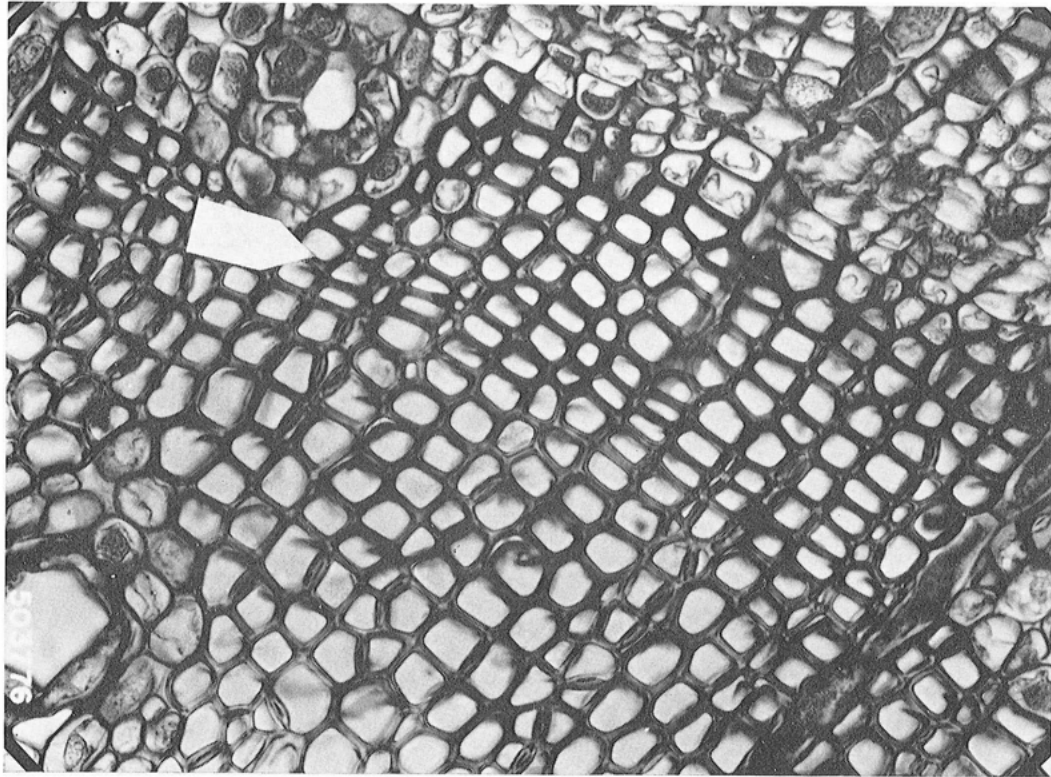


FIGURE 16. A false ring growth was produced by applying 2,3,5-tri-iodobenzoic acid (TIBA) to the decapitated stem tip of young red pine growing on long-day photoperiods. The TIBA induced the formation of several rows of narrow-diameter tracheids within the zone of large-diameter tracheids produced during long-day exposure.

THEORETICAL AUXIN GRADIENTS

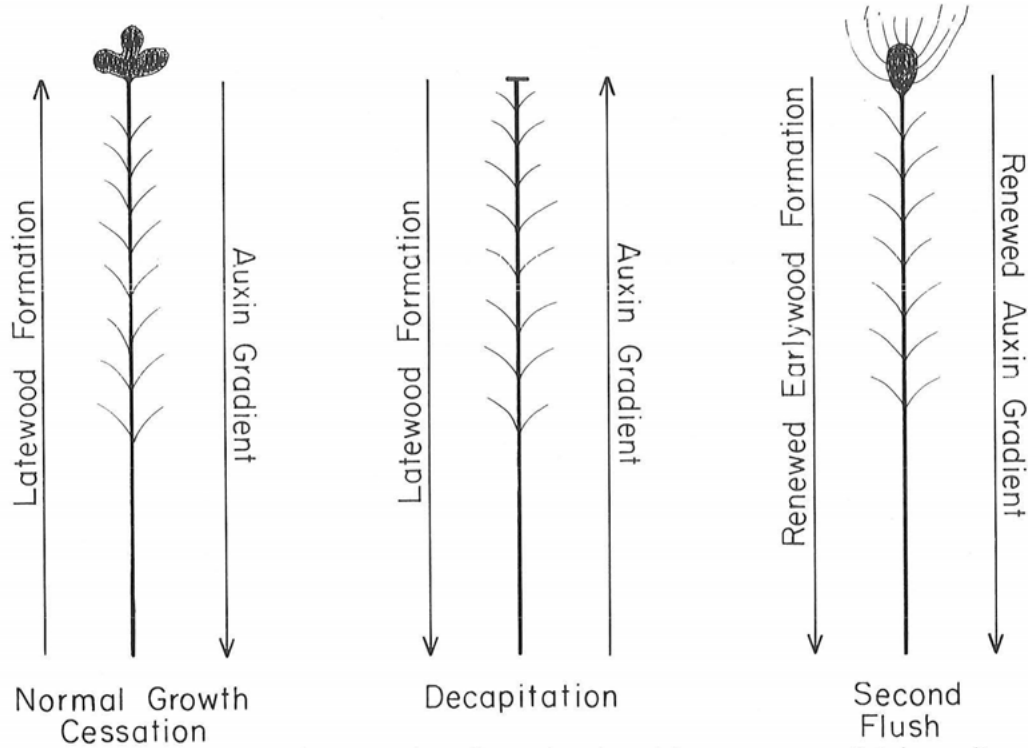


FIGURE 17. Theoretically, the seasonal gradients of auxin activity appear to parallel the gradients of tracheid diameter from apex to base within the stem.

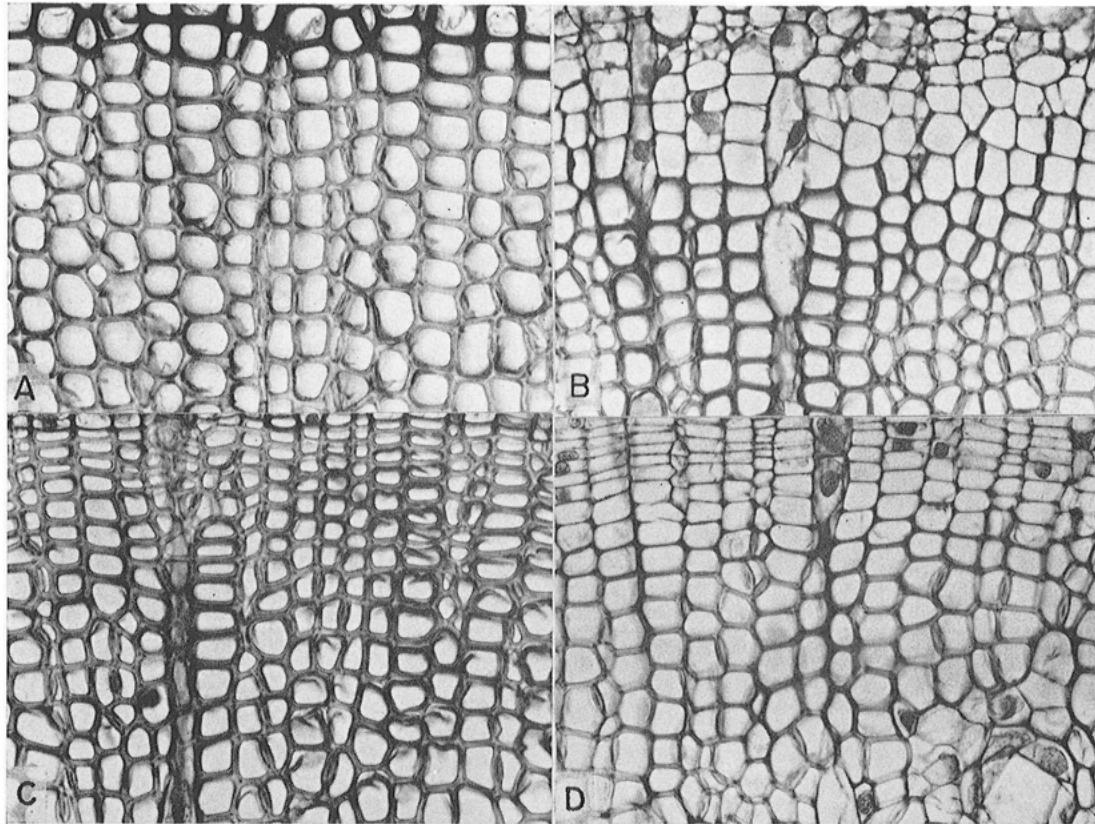


FIGURE 18. Tracheid diameter and wall thickness can be altered independently for limited periods by appropriate growth control. It was possible to produce tracheids with: (A) large diameters, thick walls by maintaining both auxin synthesis and photosynthesis; (B) large diameters, thin walls by maintaining auxin synthesis but restricting photosynthesis; (C) narrow diameters, thick walls by restricting auxin synthesis but maintaining photosynthesis; and (D) narrow diameters, thin walls by restricting both auxin synthesis and photosynthesis.

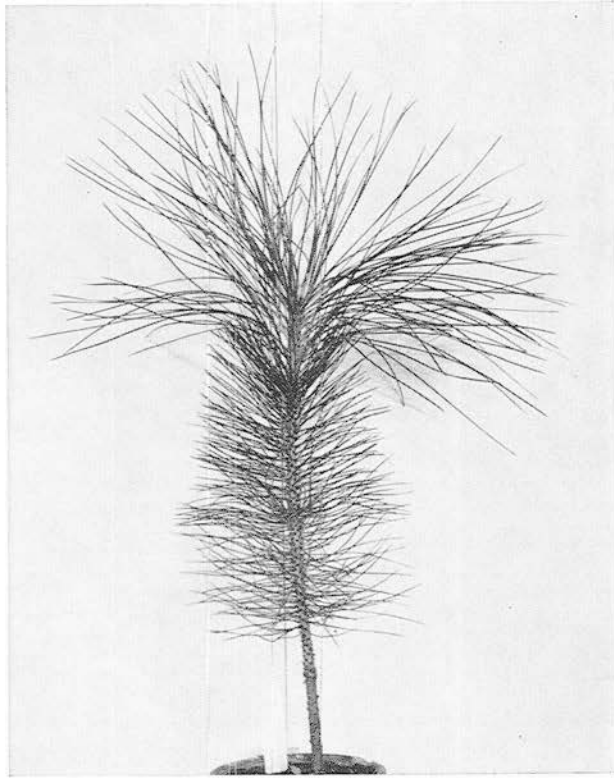


FIGURE 19. The needles of young red pines grow abnormally long when the trees are maintained for extended periods under favorable long-day conditions.

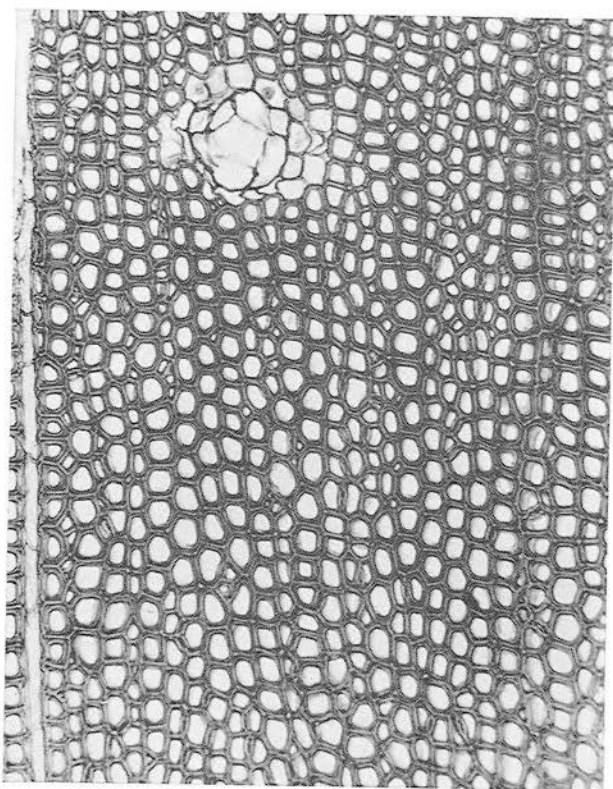


FIGURE 20. The wood produced by the tree shown in figure 19 is quite unusual and has been referred to as "long-day latewood." The continued needle elongation promoted formation of large-diameter tracheids, and the high late-season photosynthesis promoted formation of extremely thick cell walls.

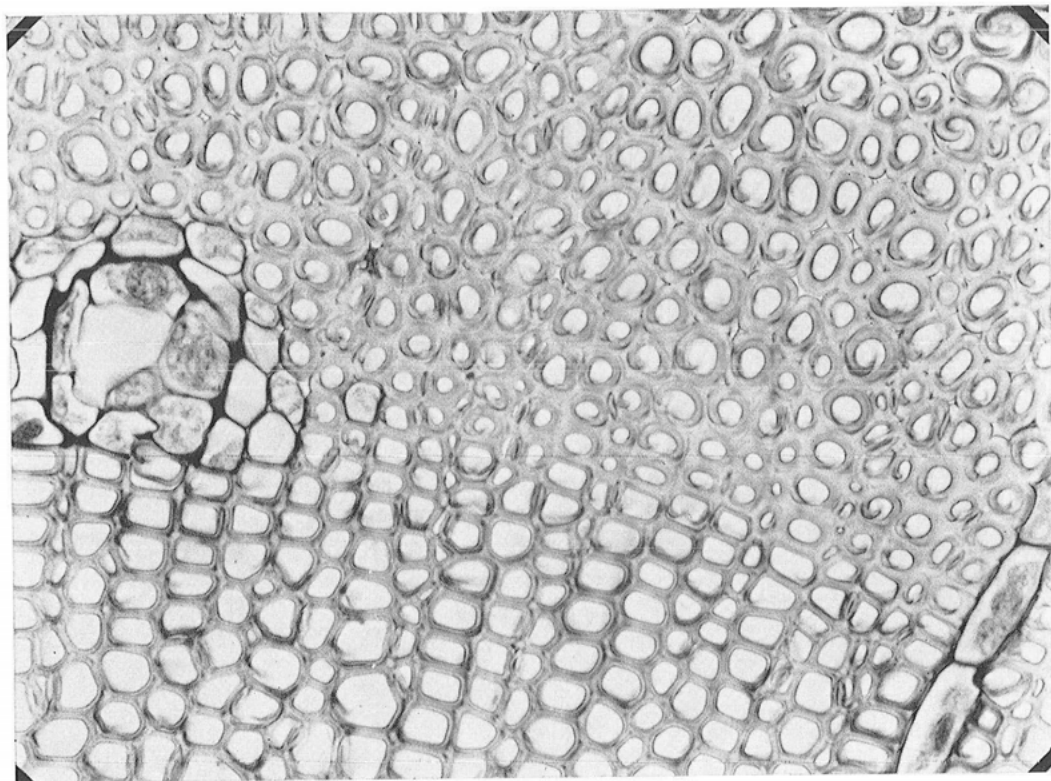


FIGURE 21. Compression wood can be produced artificially by applying high concentrations of IAA to red pine stems. This artificially produced compression wood is physically and chemically indistinguishable from natural compression wood.

## PHYSIOLOGY OF WOOD FORMATION

---

ameter. This is a general statement and the numerous exceptions that will most certainly occur must be interpreted on the basis of the growth correlations involved.

As mentioned earlier, the segregation of stem and needle growth into separate phases is convenient for study, but the distinction is somewhat artificial with regard to the continuous development of the internal vascular system. In a teleological sense, the "purpose" of the earlywood is translocation of water to the upper stem and transpiring needles. Actively growing needles embedded in an actively growing stem will require constant renewal of the vascular connections. Furthermore, the high water requirements of active needles can perhaps be best satisfied by large-diameter tracheids, which may be occasionally thick-walled. Although this may explain purpose, it in no way explains the physiological basis for large-diameter tracheid formation. The requirements for water alone cannot determine the extent and direction of tracheid differentiation. However, it can be shown that physiological processes associated with vascular development in the stem and needle complex of the shoot can regulate tracheid diameter. The translocation system thus created can serve as a water conduit.

### THE HYPOTHESIS OF TRACHEID DIAMETER REGULATION

Evidence from many sources has suggested that tracheid diameter is regulated by a hormonal stimulus produced by the vegetative organs and transmitted to the developing tracheids in the stem (12, 29, 30). Jost (9) anticipated the so-called "hormonal hypothesis" long before the discovery of auxin by suggesting that some form of stimulus was produced by the buds and shoots. It is also of interest that much of the early work with auxins, following their discovery by Went in 1928, was in the field of cambial activity. Nevertheless, in spite of the work done since that time, our knowledge of the production sites, translocation processes, and modes of action of the auxins involved in xylem differentiation is still fragmentary. Recent evidence suggests that the gibberellins and cytokinins may also be involved in the initiation of cambial activity and in maintaining the cambium in a dividing state, whereas growth inhibiting substances may be responsible for the cessation of cambial activity. Because of the many possible hormonal interactions, the discussion that follows will be confined exclusively to the regulation of tracheid diameter during differentiation.

In our experiments, we have used three approaches to test the hormonal hypothesis of tracheid diameter regulation (19). The first was direct applications of synthetic auxin, indole-3-acetic acid (IAA). When IAA was applied to the decapitated stem tip of a young red pine producing narrow-diameter tracheids on

## WOOD FORMATION AND QUALITY

---

a short-day photoperiod, large-diameter tracheids could be induced to form (Figure 15). When the decapitated tip was bisected by inserting a glass coverslip into an incision and IAA applied unilaterally to one of the halves, large-diameter cells were produced immediately beneath the point of application. With increasing distance around the periphery, however, cell diameter gradually decreased until normal latewood was encountered on the untreated half. Vertically, a similar gradient of cell size from true earlywood to true latewood could be observed beneath the point of application.

On the contrary, when the auxin-antagonist 2, 3, 5-tri-iodobenzoic acid (TIBA) was applied to young trees producing large-diameter tracheids on long-day photoperiods, narrow-diameter tracheids could be induced to form (Figure 16). Again, vertical gradients of cell size, and peripheral gradients in the case of unilateral applications, could be observed emanating from the point of application. Physiologically active concentrations of both IAA and TIBA that will evoke morphologically normal cell responses are relatively short-lived and tracheid diameter reverts rather soon to that produced prior to treatment.

The second approach to test the hormonal hypothesis was by means of bioassays of naturally occurring auxins. The shoots of trees exposed to long days showed a relatively high activity of growth-promoting hormone compared to those from trees exposed to short days. When a tree was exposed to long days, then to short days, and then back to long days, the auxin content again increased under the final long-day exposure. These patterns of auxin level under long days:short days:long days corresponded with the patterns of needle growth and false ring formation described earlier. An almost identical pattern of auxin activity, foliar growth, and tracheid diameter was obtained by the treatment sequence of water:drought:water. Although the auxin activity curves obtained by these procedures are strictly relative, they do provide corroborative evidence of an auxin-mediated link between apical growth and tracheid development.

The third test of the auxin hypothesis was by means of the naturally occurring auxin gradients within the tree stem (Figure 17). The most vigorous shoots with their developing needles appear to be the principal source of auxin for tracheid enlargement. Furthermore, the seasonal gradients of auxin activity appear to parallel the gradients of tracheid diameter not only temporally across the growth ring but spatially down the stem. For example, under normal conditions of terminal growth cessation, or the inhibition of foliar growth by manipulation of the environment, latewood will be initiated at the stem base and narrow-diameter cells will subsequently appear at progressively higher levels. This acropetal trend of latewood formation is presumably due to the waning auxin production



## PHYSIOLOGY OF WOOD FORMATION

---

of the terminal organs. With increasing proximity to the auxin source, however, the latewood becomes more transitional, and true earlywood production continues within the upper crown throughout most of the growing season. On the contrary, the abrupt removal of the auxin source by decapitation will reverse the auxin gradient, and narrow-diameter cells will first be apparent at the apex. Renewal of the auxin gradient by the flushing of a summer bud after latewood formation has been initiated throughout the stem will regenerate a new zone of earlywood. But the distance that this new band of earlywood is propagated down the stem will depend on the intensity of the apical growth stimuli; in many cases the resulting false ring will be evident only in the crown. These gradients are presumably responsible, at least in part, for the continua of tracheid characteristics in the stem that were discussed previously.

Evidence confirming the auxin hypothesis is gradually accumulating. Balatinez and Kennedy (1) have successfully produced earlywood cells in the stems of young larch that were previously producing latewood by applying the auxin extracted from active phloem tissue of mature larch trees. And, Shepherd and Rowan (28) have convincingly shown that the auxin in mature Monterey pine cambial tissue is authentic IAA. In both cases, the auxin concentration gradients appeared well correlated with the patterns of cambial activity and the gradients of cell diameter as predicted by the auxin hypothesis. It is not my intent at this time to critically review or appraise the literature relevant to the auxin hypothesis. Rather, my objective has been to demonstrate that physiological processes originating in the foliar organs of the crown can regulate the gradients in tracheid radial diameter throughout the stem. Even though the mode of auxin action has not been discussed and may not be thoroughly understood, an awareness of the processes involved helps one visualize the physiological growth correlations between foliar growth and wood formation.

### THE HYPOTHESIS OF SECONDARY WALL THICKNESS REGULATION

The auxin hypothesis is concerned almost exclusively with the regulation of tracheid diameter. However, we are also highly interested in the second measure of latewood formation, tracheid wall thickness. Our early studies showed that tracheid diameter and secondary wall thickening were to a large extent independent, and were regulated by somewhat different physiological processes. Whereas tracheid diameter was primarily determined by the amount of auxin reaching a developing tracheid, wall thickness appeared to be determined by the amount of sucrose, or photosynthate, reaching each tracheid. We were therefore able to produce tracheids with desired characteristics by controlling growth con-

## WOOD FORMATION AND QUALITY

---

ditions for limited periods of time (Figure 18). It was possible, for example, to produce tracheids with large diameters and thick walls by maintaining both auxin synthesis and photosynthesis at favorable levels; with large diameters and thin walls by maintaining auxin synthesis but restricting photosynthesis; with narrow diameters and thick walls by restricting auxin synthesis but maintaining photosynthesis; and, with narrow diameters and thin cell walls by restricting both auxin synthesis and photosynthesis.

Further evidence of the contribution of photosynthates to wall formation, and also of the relative independence of radial diameter and secondary wall thickening, could be obtained by again using long days. When young red pines were exposed to very favorable long-day conditions for extended periods, the needles grew to exaggerated lengths (Figure 19). The wood of such trees was quite unusual (Figure 20). The continued needle elongation promoted formation of large-diameter tracheids, and the high late-season photosynthetic production promoted formation of extremely thick-walled tracheids, called "long-day late-wood." In all of our early developmental studies, we noted that tracheid diameter could be altered more readily than wall thickness at any time during the growing season. Also, changes in wall thickness could be produced most easily during the normal period of latewood formation.

An explanation of how the distribution of photosynthates in the tree facilitates their participation in latewood formation was obtained in some recent investigations. In a preliminary study to test a hypothesis of latewood wall thickness (19), light was excluded from different-aged needles throughout a growing season by covering them with light-proof cloth bags (20). This work was extended in a more recent experiment (8), in which the contribution of different-aged needles to wood formation was studied over a season of growth by means of an infrared gas analyzer and radioactive  $^{14}\text{CO}_2$ . Results of both studies were similar, but the data of the latter experiment using  $^{14}\text{C}$  provided convincing evidence supporting the following hypothesis.

The distribution of photosynthates within a tree can be viewed as a system of competing metabolic sinks, or areas of rapid growth that are importing disproportionately large quantities of the tree's photosynthetic production. Early in the spring, prior to the initiation of shoot growth, the roots of conifers can be heavy importers of current photosynthates. However, when shoot extension begins, this newly developing growth center becomes a powerful metabolic sink that attracts not only a large proportion of the current photosynthetic production, but possibly a sizeable amount of the reserve food stored in older tree parts. Some of the imported photosynthate is lost through respiration, but the bulk of it is transformed

## PHYSIOLOGY OF WOOD FORMATION

---

and permanently fixed as cell wall substance and structural tissue. In red pines, needle elongation follows shoot extension, and, as the new needles begin to elongate, they too require photosynthate imported from the older needles. Eventually, however, the current-year needles reach a developmental state, which we call "new needle maturity," when they are self-sufficient photosynthetically. At this time, they are no longer importers, but exporters of photosynthate to other tree parts. This stage of new needle maturity marks the time when the increase in secondary wall thickness associated with latewood becomes noticeable in newly differentiated tracheids of the lower stem.

I have pointed out that the changes in tracheid radial diameter are physiologically correlated with changes occurring in the shoot and foliar organs. Auxin presumably provides the mediating stimulus correlating these events, but because of the numerous and complex intervening processes it is not yet possible to make meaningful quantitative or statistical studies of crown growth and wood formation. The same limitations apply to the relation between photosynthetic production and cell wall thickness, and it is for this reason that we adopted the term "new needle maturity."

New needle maturity, or the developmental stage at which the new needles begin exporting photosynthate, may or may not coincide with the cessation of needle elongation. Under normal growth conditions, it seems to occur just prior to the cessation of needle elongation, but because pine needles have indeterminate basal meristems, needle elongation can vary tremendously with environmental conditions. For example, it is difficult to induce production of thick-walled tracheids during normal earlywood formation in red pine because the spring surge of growth is sustained even under fairly adverse conditions, and the developing shoot continues to attract photosynthates. However, if the adverse condition (such as short-day photoperiod) is of a sufficient duration to suppress needle elongation, wall thickness will increase. On the contrary, during formation of "long-day latewood," export of photosynthates begins and new needle maturity is attained while the current-year needles are still actively elongating. Mutilations, such as partial defoliation, that seriously interfere with photosynthetic ability evoke almost immediate alterations in wall development, and cells with extremely tenuous walls can be produced. It is therefore evident that although new needle maturity can be readily correlated with latewood wall thickening under closely controlled conditions, it may be far more difficult to make similar correlations under the vagaries of natural environments unless the correct growth parameters can be measured.

Many observations under natural conditions do suggest, nonetheless, the strong

## WOOD FORMATION AND QUALITY

---

relation between current photosynthetic production and tracheid wall thickness. We have noted, for example, bands of tracheids with varying wall thickness in young red pines grown for prolonged periods in the greenhouse. The bands of thinner-walled tracheids appeared to be correlated with periods of cloudy weather when photosynthesis was curtailed, and the bands of thicker-walled tracheids with sunny weather. Also, pines growing in semitropical regions often possess thick-walled earlywood tracheids (6, 10). Presumably, under continuous, daily high-light conditions, the older needles are capable not only of meeting the demands of the new shoot, but also of exporting large quantities of photosynthate to the developing earlywood.

The differences in wall thickness between earlywood and latewood tracheids cannot be interpreted solely on the location of the predominating metabolic sinks, because the nature of these sinks must also be considered. The cambial region, a diffuse meristem, constitutes a relatively weak metabolic sink, and thus competes poorly with the mass meristems of the shoot and root. Yet, in the aggregate, the cambial region over an entire stem is a large consumer of photosynthates. During earlywood formation much of the photosynthetic production and stored food is converted to cell-wall substance in the woody stem, but this material must be rationed among a vast number of developing cells. Hence, each developing tracheid also constitutes a small-scale metabolic sink and competition within the zone of tracheid differentiation can be a major factor determining wall thickness.

### INTERACTIONS DURING TRACHEID DIFFERENTIATION

During this discussion, I have treated radial expansion and secondary wall thickening as separate phases of tracheid differentiation. It was shown that by subjecting trees to appropriate growth controls both tracheid dimensions could be altered independently, and that they appeared to be regulated by somewhat different physiological processes. At the level at which we distinguish earlywood from latewood this independence holds essentially true. But at the more fundamental level of tracheid development, radial expansion and wall formation are closely integrated and evidence indicates that auxin as a regulator and sucrose as a substrate interact during several phases of differentiation and secondary wall synthesis. An extreme product of this interaction is compression wood.

In nature, compression wood forms on the lower side of leaning stems and branches. It is believed to result from a high auxin gradient, which, in turn, brings about the mobilization of foods required for wood formation. Since the cambial zone is a relatively weak sink for assimilates, localized cambial regions cannot compete effectively with the mass meristems during active growth. However,

## PHYSIOLOGY OF WOOD FORMATION

---

bending induces a condition that commands the mobilization of assimilates at the expense of other tree parts. The result is compression wood formation and reorientation of the stem.

Compression wood can be produced artificially by applying high concentrations of IAA to red pine stems (Figure 21). The compression wood so formed is physically and chemically indistinguishable from naturally occurring compression wood. Types of compression wood ranging from severe to mild ones resembling normal earlywood can be found. Each of these types can be found in nature and each can also be produced artificially.

The interaction between auxin and sucrose in producing compression wood results in tracheids with large diameters and extremely thick cell walls. Physically, compression wood tracheids are somewhat similar to those of juvenile wood produced in the high auxin environment in close proximity to the crown. Chemically, the normal metabolic pathways appear to be altered during compression wood formation so that production of constituents normally confined to the outer wall layers is perpetuated across the wall. The close similarity in both physical and chemical characteristics between compression wood and juvenile wood suggest that juvenile wood may also perform a stem regulatory or reorientation function during the critical stages of leader and stem development. Although compression wood is an extreme example of the auxin-sucrose interaction, this interaction occurs to varying degrees during all wood formation, thus leading to some intriguing problems of wall biosynthesis (Figure 22).

It should be clear that the physiology of wood formation is much more complex than the relatively simple hypotheses presented might suggest, and that the challenging areas of current research have been left unmentioned. I deliberately adopted this simplified approach to emphasize the strong regulatory control exerted by the foliar organs on wood formation, particularly during the seasonal development of the foliar organs and xylem tracheids. My objective was twofold: (1) to demonstrate that the xylem, as a part of the vascular system, is intimately related both developmentally and functionally to the foliar organs, and (2) to show that physiological processes originating in the foliar organs, and which are dependent upon the developmental state of the foliar organs, are the primary regulators of wood formation on the stem. It is my sincere belief that if the significance of these two points is fully appreciated, the patterns of wood formation on the stem can be more easily comprehended and the basic physiological processes of wood formation more logically investigated.

In the course of research, we frequently find it convenient to test hypotheses by isolating various factors or components of a system for analysis. However, it is

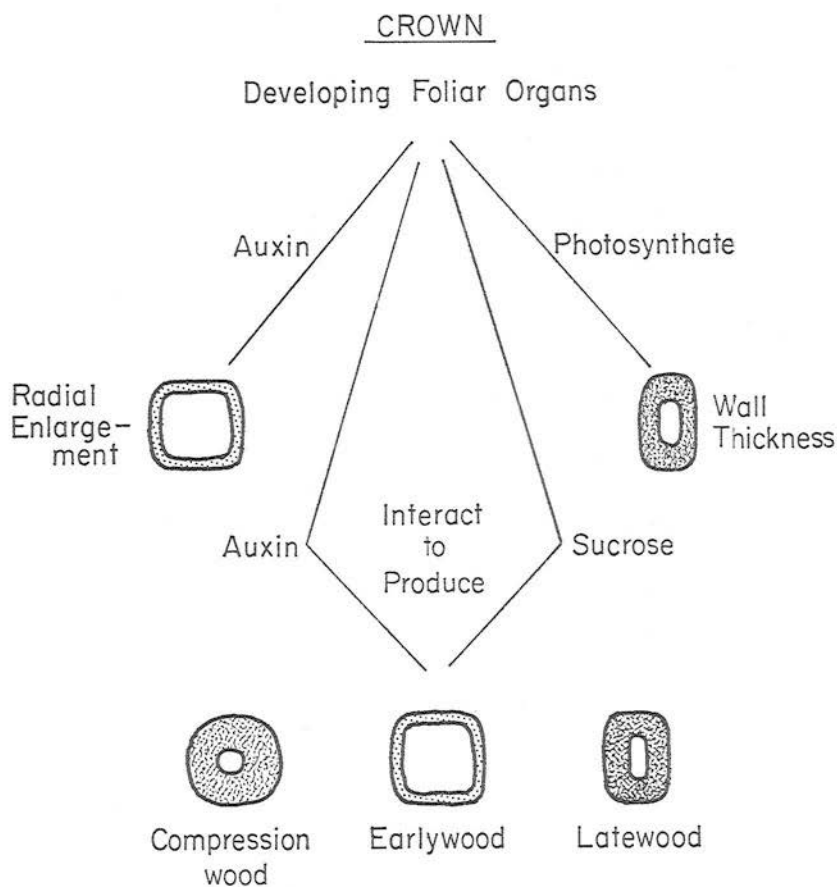


FIGURE 22. The two phases of tracheid differentiation, radial enlargement and wall thickening, may be separated for convenience of study and discussion. However, evidence suggests that the interaction between auxin and sucrose from the foliar organs during the differentiation process determines the type of tracheid produced.

essential that we resynthesize the isolated bits and pieces of the system we are studying if we wish to comprehend the whole. The two hypotheses regarding tracheid radial diameter and secondary wall thickening are simply components of the overall concept of wood formation, and it is necessary to somehow restore them in the biological system if we wish to understand tree growth. To do this, I will continue the discussion begun earlier on the patterns of wood formation and the continua of tracheid characteristics in the growing tree.

## APPLICATIONS OF THE CONCEPT OF WOOD QUALITY

---

---

### THE CONCEPT OF EARLYWOOD AND LATEWOOD

IT HAS BEEN pointed out that tracheid development during radial enlargement and secondary wall thickening are regulated by a complex of factors, and that metabolically these phases of development are closely interrelated. Yet, at the microscopic level at which we measure tracheid dimensions, a certain degree of independence can be seen to exist. For example, tracheid radial diameter and secondary wall thickening, which are the main characteristics distinguishing earlywood from latewood, can be altered independently. We will therefore perceive either earlywood or latewood when one phase of differentiation is favored over another. The term "favored" is admittedly an over-simplification of the physiological processes, but it does convey a meaning with regard to the type of tracheid produced.

Earlywood tracheids form when radial expansion is favored over secondary wall thickening. Normally, radial expansion of tracheids occurs throughout the tree during active shoot growth in spring and within the crown as long as the needles are actively elongating. According to the auxin hypothesis, tracheid radial diameter is determined by the distance from the auxin source, and the time of formation within the growth ring. A continuum in radial diameter of the earlywood tracheids therefore exists down the stem from the apex in early summer. As the season advances, the reduction in tracheid diameter occurs first at the stem base, and then progresses upward in the stem and outward in the growth ring, presumably as auxin availability declines. This progression continues until narrow-diameter tracheids are produced throughout the stem length just prior to cambial dormancy.

Latewood tracheids form when secondary wall thickening is favored over radial expansion. Normally, the increase in secondary wall thickening associated with latewood tracheids begins when the requirements of the major metabolic sinks within the crown have been met and the current-year needles begin exporting photosynthates to other parts of the tree, primarily the stem. This phase of wall thickening begins at the stem base and progresses upward and outward in a manner similar to that of the decrease in radial diameter (Figure 23). Consequently, a continuum of increasing tracheid wall thickness also exists from the apex downward.

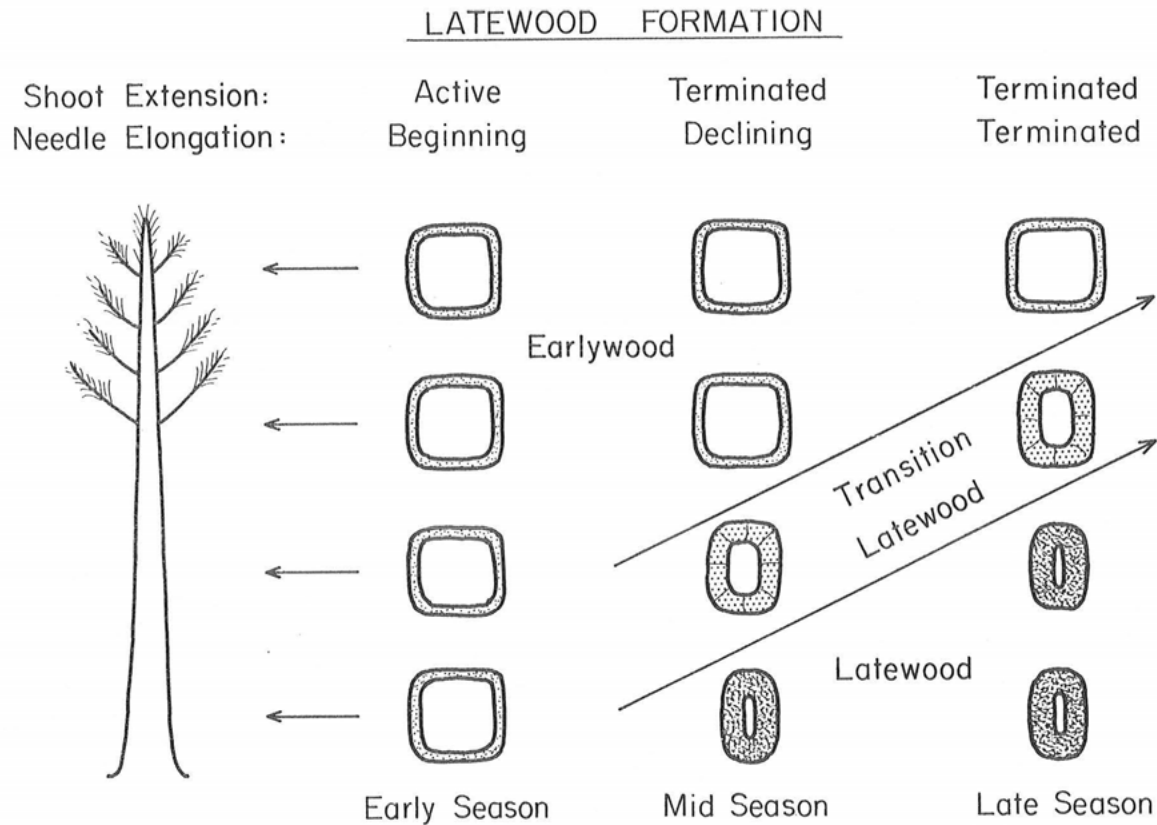


FIGURE 23. The decrease in radial diameter and the increase in secondary wall thickening that characterize latewood usually begin near the stem base and progress upward as the season advances.



## APPLICATIONS OF QUALITY CONCEPT

---

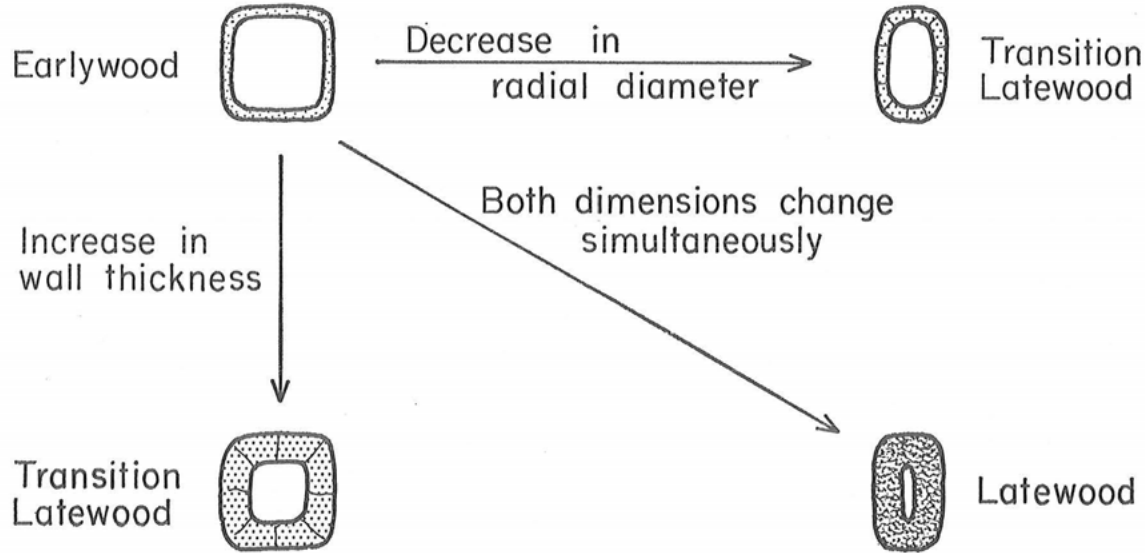
In the lower bole of a mature pine, when the decrease in radial diameter and the increase in wall thickness occur simultaneously, we can recognize true latewood tracheids. Frequently, latewood begins abruptly in the lower stem and a sharp transition can be observed between the last earlywood and the first latewood tracheids. Higher in the stem, as the crown is approached, the transition becomes less distinct. At first this may be traced to more gradual changes in both tracheid dimensions, but farther upward within the crown either dimension may change independently.

The most commonly used definition of latewood is that of Mork (25), who defined a latewood tracheid as one in which the width of the common cell wall between two adjacent tracheids, multiplied by two, was equal to or greater than the width of the lumen. This definition, formulated for mature spruce wood, tacitly assumes a simultaneous change in both radial diameter and wall thickness. Although extremely useful, Mork's definition fails in juvenile wood and in growth rings with diffuse transition zones, where its application was never intended.

Since radial diameter and secondary wall thickness do vary independently, no definition of latewood tracheids will satisfy all conditions (Figure 24). Some tracheids may qualify as latewood simply because of the decrease in radial diameter with no change in wall thickness, whereas others may qualify because of an increase in wall thickness with no change in radial diameter. As mentioned, both dimensions will exhibit continua from the apex downward and at some lower level in the stem they will coincide and true latewood can be recognized. However, at higher levels in the stem and within the crown, transition latewood will form and in many cases it is difficult to assign tracheids to either earlywood or latewood. Earlywood and latewood are therefore arbitrary concepts. They are extremely useful in wood quality evaluation, but they are only useful when their development is understood and their limitations appreciated.

In understanding earlywood and latewood development, it is important to remember that events within the crown determine the course of wood formation on the stem. It is immaterial whether or not one accepts the hypotheses regarding auxin and photosynthates in regulating wood formation, as long as the crown-stem relation is recognized. However, it is my belief that the production of growth regulators and photosynthates will vary with growth and development of the crown organs, and these crown-formed products will in turn dictate the rate of cambial division and the degree of differentiation of the cambial derivatives. Thus, a given quantity of photosynthate available for stem growth may be deposited as wood consisting of either a large volume of large-diameter, thin-walled

## DEVELOPMENT OF TRANSITION LATEWOOD



Transition latewood, in which only one dimension changes, can qualify as latewood by Mork's definition.

FIGURE 24. Since radial diameter and wall thickness vary independently, no definition of latewood will satisfy all conditions. Transition latewood, which occurs frequently, is intermediate between true earlywood and true latewood.

## APPLICATIONS OF QUALITY CONCEPT

---

tracheids, or a smaller volume of narrow-diameter, thick-walled tracheids (Figure 25). It is evident that whether or not a cambial derivative develops into an earlywood or a latewood tracheid will depend upon a host of conditions both within the tree and within the tree's environment. It is also evident that, within the inherent potential of the tree, there is a relatively wide latitude for tracheid development both with height in the tree and with position in the growth ring. Trees of the same species also show large variations, and occasionally the latewood tracheids in one tree may be as large in radial diameter as the earlywood tracheids in another. This again illustrates the arbitrariness of the commonly used definitions for latewood.

### REGULATION OF STEM FORM

Among the conditions that cause variations in the earlywood-latewood transition are those that influence stem form. We have mentioned how the ideal continua of tracheid characteristics from stem apex to base are seldom realized. Peaks frequently appear near the stem base or within the branch-free bole. These peaks may arise either from the irregular distribution of branches, or from external growth stresses. It has been pointed out how the branches of the crown can vary in their contribution to stem growth, and how the length and vigor of the crown can determine the amount and type of wood produced on the stem. The crown largely controls the distribution of growth on the stem and determines the type of wood to be deposited. However, the regulatory influence of the crown on the branch-free portion of the bole diminishes as the active crown recedes upward.

Stresses created by the weight of the tree and by the bending force of the wind on a tree can cause a pronounced redistribution of growth along the bole (16) (Figure 26). The auxin hypothesis also helps to interpret this phenomenon. For example, we noted that the cambium is normally a relatively weak sink for assimilates. But, under the influence of wind sway or bending stress, a steeper gradient of auxin may be induced down the stem (21). The greater supply of auxin would in turn create a more concentrated metabolic sink and attract assimilates to the region of stress. Duffield (3) recently pointed out that the major missing link in this hypothesis is a biological feedback mechanism or communication pathway between the region of stress and the source of auxin in the crown. As an intriguing extension of the auxin hypothesis, piezoelectric effects, which are produced in response to stress stimuli in crystalline materials, may provide this missing link. Wood cellulose is a highly crystalline material and its piezoelectric properties have been studied in detail. Furthermore, there is much information

A given quantity of Photosynthate  
may be deposited as

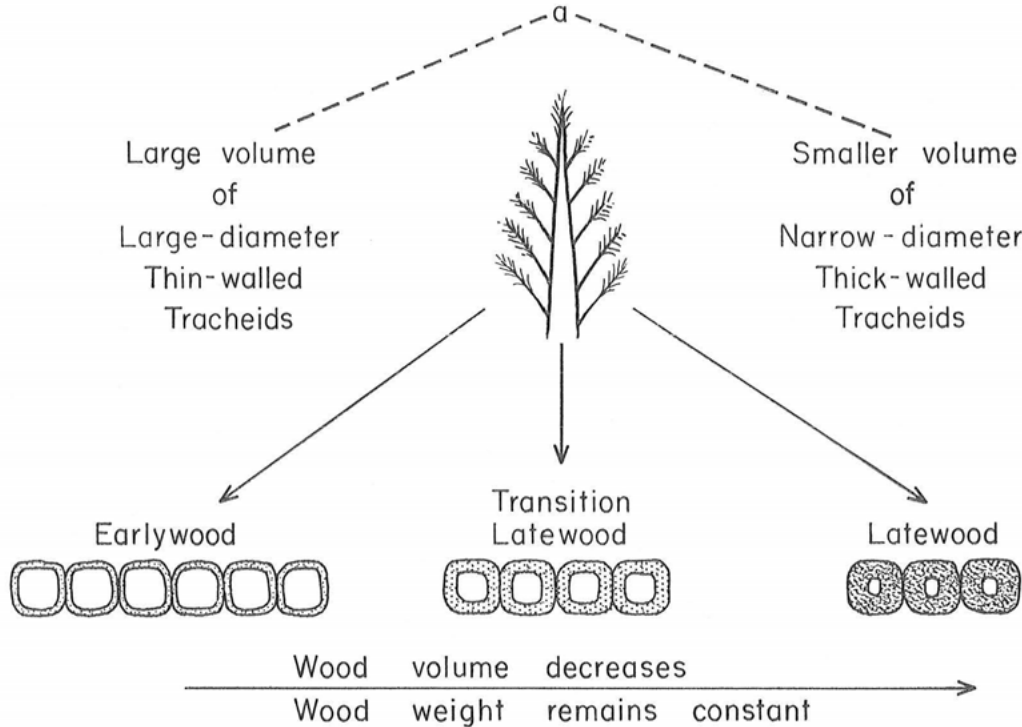


FIGURE 25.

Stresses created by the wind are effective in causing redistribution of assimilates to lower stem.

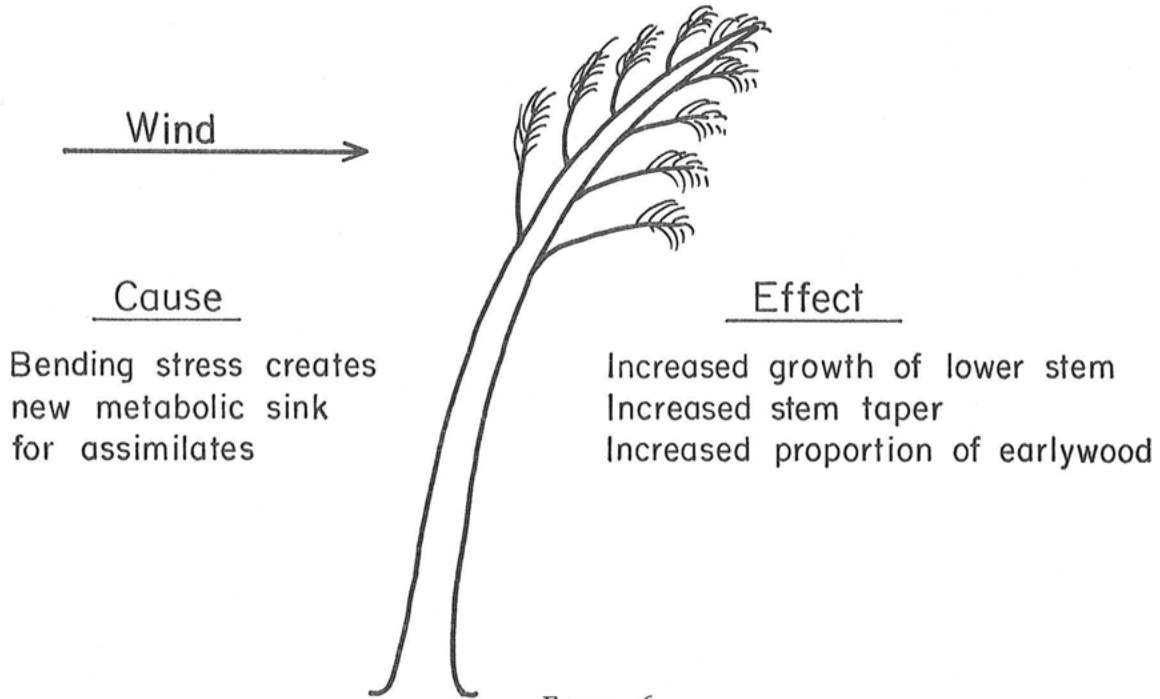


FIGURE 26.

## WOOD FORMATION AND QUALITY

---

regarding electrical potentials in plants, and attempts have been made to relate these potentials to the movement of growth hormones. It is entirely possible that stress stimuli, such as wind, can induce piezoelectric effects in the crystalline cellulose of the developing wood cell walls. Although the hypothesis has not been tested experimentally, such piezoelectric gradients could conceivably function as the line of communication between the region of stress on the stem and the source of auxin in the crown.

The result of bending stress is not only a redistribution of growth favoring the region of stress, but also an alteration in the continua of tracheid characteristics down the stem. Under normal conditions of tree growth, these changes due to wind sway are gradual, but over a period of years they exert an effective influence on the quality of the wood produced as well as on the form or taper of the bole.

With the background information presented on the growth patterns and their causes, it is now possible to interpret and in some cases predict the variability in wood quality that might be encountered under most growth conditions. At this time, I would like to briefly discuss a few of the probable ways in which wood quality of pines can be regulated by silvicultural practices.

### SILVICULTURAL CONTROL OF WOOD QUALITY

Manipulation of stand density is the most powerful method available to the silviculturist for regulating both total wood yield and wood quality. We have discussed the role of branches in wood formation and the growth patterns in open-grown versus stand-grown trees. As a general rule, the open-grown tree will have a long crown and short clear bole, whereas the stand-grown tree will have a short crown and long clear bole. From our knowledge of stem form, we also know that the open-grown tree will possess a more tapered stem consisting of a large volume of low density wood, whereas the stand-grown tree will possess a more cylindrical stem composed of a smaller volume of high-density wood. With regard to wood quality, the open-grown tree will have a high proportion of juvenile wood in the upper crown, a low percentage of latewood in the lower bole, and a gradual latewood transition zone throughout its length. In contrast, the stand-grown tree will have a more restricted zone of juvenile wood in the upper crown, a high percentage of latewood in the lower bole, and a more abrupt latewood transition. These are extreme cases and all gradations may be found. The important point to remember is that stand density has a tremendous influence on the quality of wood formed. These effects are brought about by gradual changes in crown size, structure, and efficiency. And, through these changes we can interpret a large amount of the variability in wood quality (14).

## APPLICATIONS OF QUALITY CONCEPT

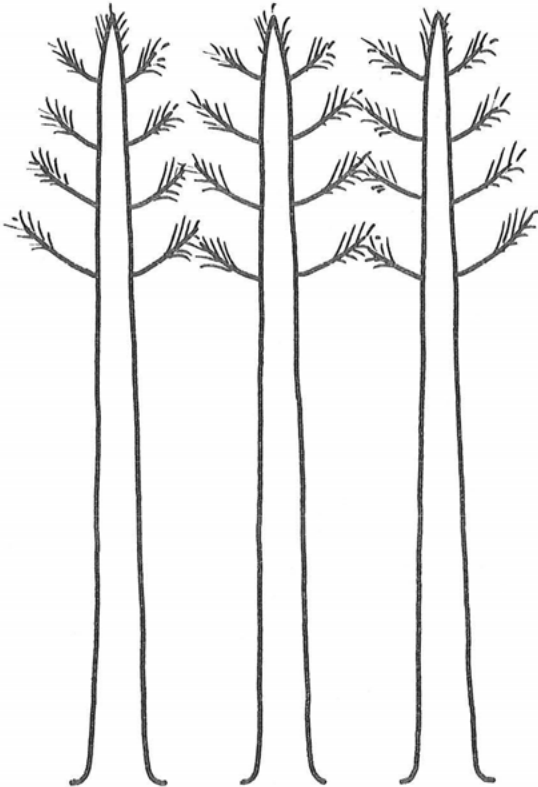
---

The crowns of trees within a developing stand gradually recede upward with age and stand closure, and the rate and extent to which the crown recedes will determine the type of wood formed on the stem. The silviculturist can control initial stocking by planting and in some situations by control of natural regeneration. Once regeneration is established, he can regulate stand density by thinning or other cutting procedures. The purpose of thinning is to provide more growing space for both roots and crown (Figure 27). Following a heavy thinning, the upward crown recession slows, the crown broadens, individual branch size increases, and more branch wood is produced. In many cases, foliage throughout the crown thickens and efficiency of the crown as a whole increases. These effects on the crown result in an overall increase in wood production, but, because of a relatively greater growth promotion in the lower stem, stem taper may increase. Measurable changes in wood quality may also be found, such as an increase in the proportion of juvenile wood within the crown, a more gradual latewood transition down the stem, and a decrease in the percentage of latewood in the lower stem. We can immediately see that these effects are contrary to those produced by extreme stand closure, and thinning simply delays or slows the trend in that direction. The intensity of the thinning, of course, determines the degree of response. Since a thinned pine can never regain its lost lower branches, it will never revert to the form of an open-grown tree. Consequently, a tree with a fairly long, clear bole, or a mature tree, will continue to form high-quality wood in spite of a relative increase in earlywood production following a heavy thinning. Exceptions to this general pattern occur frequently, however, because the response to thinning will depend upon the particular limiting factor that is alleviated. For example, where late season soil moisture availability is critical, thinning may result in an increase in latewood.

Judicious thinning schedules provide the silviculturist with a powerful means of regulating both wood yield and quality. Early thinnings in young stands will provide quite different patterns of wood production than delayed thinnings in older stands, and the effects of each thinning or cutting must be assessed separately. Although I am not in favor of rules of thumb, one general statement holds quite well. In most situations, silvicultural practices striving for optimum wood yield will also produce optimum wood quality. As stressed repeatedly throughout this discussion, however, every general rule or statement will have a host of exceptions and must be interpreted with prudence.

Pruning is analogous to artificially creating a stand-grown tree from an open-grown one (Figure 28). The purpose of pruning is to produce more clear wood by removal of the lower branches, but the resulting change in crown size also

## HEAVY THINNING



Upward crown recession slows  
Crown broadens  
Branch size increases  
Foliage thickens  
Foliage efficiency increases

Wood production increases  
Relative length of clear bole decreases  
Stem taper increases  
Percentage of latewood decreases  
Latewood transition becomes more gradual

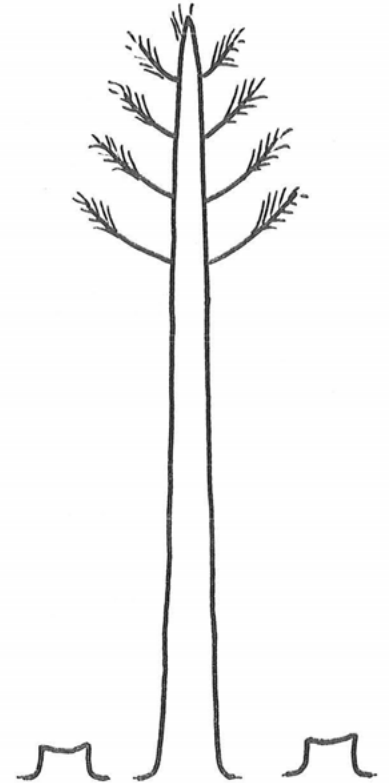


FIGURE 27. The growth response following thinning is generally in the direction of an open-grown tree. However, the growth factor most limited by high stand density will be the first to respond following release.



## HEAVY GREEN PRUNING

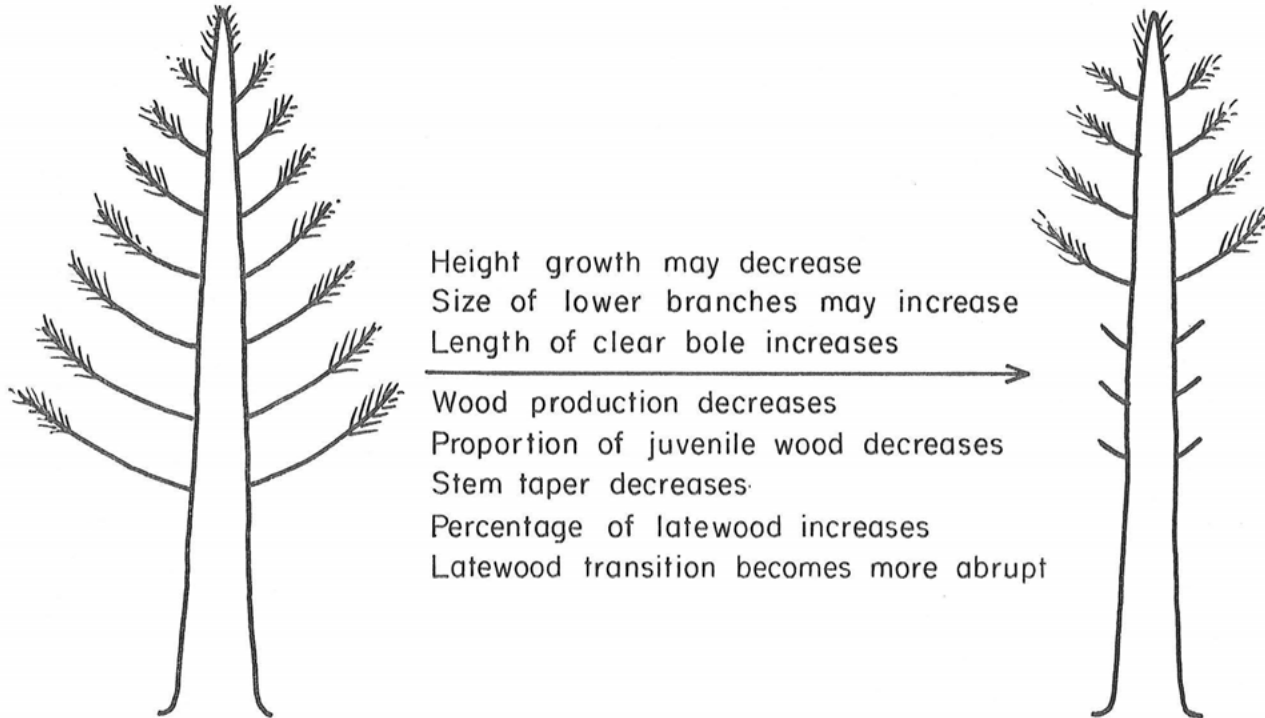


FIGURE 28. The growth response following pruning is generally in the direction of a stand-grown tree. However, a range of responses may be obtained, depending upon the intensity of the silvicultural measure and the crown response.

alters wood quality. Following heavy pruning, height growth may decrease, and the lower branches may increase in size by compensatory growth. The length of the clear bole quite naturally increases and overall wood production decreases. However, the greatest decrease occurs at the stem base; stem taper therefore decreases and the stem becomes more cylindrical. Because of the smaller crown in a heavily pruned tree, the proportion of juvenile wood within the stem decreases, the latewood transition down the stem becomes more abrupt, and the percentage of latewood in the lower stem increases. These are extreme effects that may be observed in heavily pruned trees, but, as with stand density and thinning, a whole range of responses may be obtained depending upon the intensity of the treatment and the crown response.

You have perhaps noted throughout the discussion of stand density, thinning, and pruning, that each change in crown size results in a change in growth rate as well as in wood quality. This relation has led to a heated controversy over the years regarding the effect of growth rate on wood quality. The controversy can be easily settled by considering the role of the crown in wood formation. We know that there is an inherent increase in latewood percentage with age that is related to the changing development and structure of the lower and upper crown. Under most conditions, there is also a simultaneous decrease in ring width with age. Hence, a young, wide growth ring will contain a lower percentage of latewood than an older, narrow growth ring. Almost every investigator who has demonstrated an effect of growth rate on latewood percentage has confounded this relation. When age is taken into consideration, the relation between ring width and latewood percentage is either very weak or nonexistent. As an example, it is frequently possible to find trees with growth rings of the same age and of the same width possessing either a very low or a very high percentage of latewood.

The argument often used to illustrate an effect of growth rate on wood quality rests on the change in wood quality following a sudden change in growth rate. For example, a sudden increase in growth rate is frequently accompanied by an increase in earlywood production and a consequent decrease in latewood percentage. Admittedly, this is an effect of growth rate, but an effect of limited circumstances and it is well to recognize the limitations. It is by far simpler and much more realistic to interpret the changes in terms of crown response.

The relations among growth rate, wood quality, and crown development are also strongly influenced by site conditions. The effects of site, however, are extremely complex and not easily evaluated. Nevertheless, I do want to mention site because of the current interest in fertilization, which is perhaps the most effec-

## APPLICATIONS OF QUALITY CONCEPT

---

tive silvicultural practice for site improvement. The primary effect of fertilization is on crown and root development. The effect on wood formation is secondary, and is the result of crown development (23). Fertilization influences crown development by increasing the photosynthesizing surface and possibly by increasing the photosynthetic efficiency of the foliage.

Invariably, the increases in crown development following fertilization promote earlywood formation on the stem. And so, we can make two general statements: First, heavy fertilization in young stands can be most deleterious to wood quality because it increases crown and branch size and delays natural pruning. Young trees are in the stage of juvenile wood formation and fertilization not only enlarges the core of juvenile wood but also delays the transition to mature wood. Second, fertilization is much more effective in pole stands and those approaching maturity. In pole stands, the crowns have generally closed and the base of the live crown has receded up the stem. Because of this crown-stem relation, moderate fertilization in pole stands generally results in increased growth of both earlywood and latewood with relatively little change in wood quality.

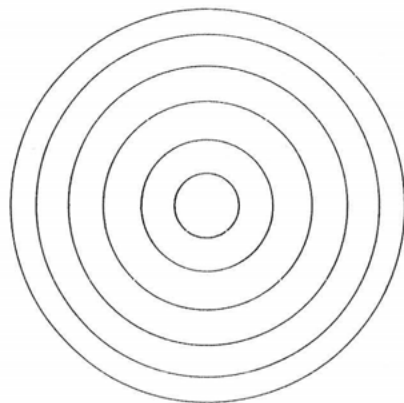
### SOME POTENTIAL APPLICATIONS OF SILVICULTURE

Several silvicultural practices that may be used to control wood quality have now been considered. With these practices, what can we expect to achieve in the way of wood quality improvement? I made the general statement that good silvicultural practices that produce optimum wood yield will also usually produce optimum wood quality. Perhaps I should start by explaining this generalization in further detail.

One of the greatest wood quality problems facing all wood-using industries is lack of uniformity (24). Lack of uniformity is a natural consequence of tree growth. It is due to the change from juvenile to mature wood both on a cross-section and down the bole. We cannot eliminate nonuniform wood in our trees, but we can minimize its presence. For example, the more erratic the growth conditions, the greater the nonuniformity of the wood produced (Figure 29). Failure to thin a fast-growing stand that has closed in, or radical thinning of a dense stand, can both produce nonuniform wood. These are simple examples, but it is obvious that the silvicultural goals for volume production are often compatible with those for wood quality. Therefore, we might broaden the rule of thumb and say that good silviculture striving for optimum wood yield *and* uniformity of growth will usually produce optimum wood quality. In fact, if we could increase uniformity through better silvicultural practices, we could significantly improve wood quality and also increase the volume of usable wood.

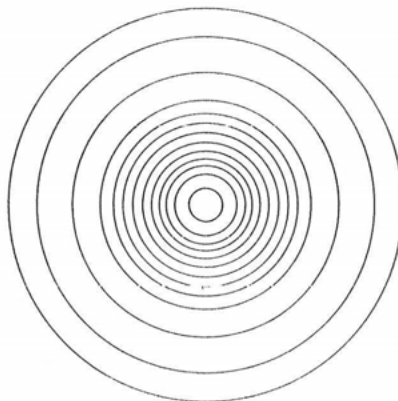
## UNIFORMITY OF RING STRUCTURE

Uniform

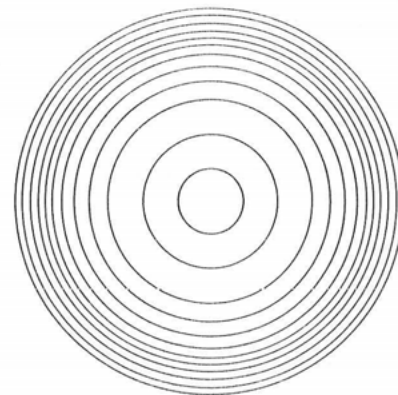


Even growth-rings  
or  
growth-rings decrease  
gradually in width

Non-Uniform



Dense stand  
thinned  
too heavily  
too quickly



Fast growing stand  
closed in  
unthinned

In each tree, latewood percentage will normally increase with age, but at different rates.

FIGURE 29. Uniformity of wood can be achieved in a number of ways. One of the most widely recognized silvicultural goals is uniformity of growth ring structure.

## APPLICATIONS OF QUALITY CONCEPT

---

In addition to the traditional silvicultural measures just discussed, other methods can further improve wood quality by raising the genetic potential. Genetic improvement by selection is the easiest and most efficient from the standpoint of the silviculturist. High-quality trees may be left standing as seed trees, or seed may be collected from selected trees or seed production areas. In either case, the progeny from these selected trees should produce wood of higher quality, and there should be greater uniformity in wood characteristics among trees in the stand. However, selection by itself is of little value. The full potential of selection can only be realized if the genetically superior stock is grown under fairly intensive silvicultural care. It is unrealistic to consider planting genetically superior stock on wild land to be managed under extensive forestry practices. In fact, the silvicultural goals should be taken into consideration prior to or during the selection process. In my opinion, selection without considering the silvicultural system of management to be used is also unrealistic. On the contrary, genetically superior stock combined with good silviculture could conceivably produce significant gains in wood yield, quality, and uniformity.

As I have pointed out just now and on several previous occasions, we, as a scientific community, have a tremendous wealth of information on tree growth and development at our disposal. We have the collective knowledge, but perhaps not the acquired experience, to produce sizeable gains in both yield and quality over much of our forest land by means of intensive silvicultural practice. As I see it, two main deterrents stand in the way of our utilizing this knowledge. The first is the failure of many practicing foresters to avail themselves of the opportunities which this knowledge provides. Silviculture is too often viewed as a mechanical series of operations, rather than as a manipulation of tree growth. If there was a better appreciation of how environmental conditions and silvicultural treatments influence the crown-stem relationship, the potentials of silviculture could be more realistically achieved.

The second deterrent is economics. Every silvicultural operation must be weighed against cost and return. In present-day forestry, most silvicultural operations to improve wood quality do not stand up well under economic scrutiny. Nevertheless, although economic arguments can be a deterrent, they can also be a stimulant and a driving force behind progressive silviculture. Perhaps what is needed is a completely new, creative approach to silviculture in which our vast knowledge of tree growth can be utilized by adapting it within an economic framework.

When we consider silvicultural control of wood quality, we must not think in terms of extensive areas of wild forest land. Even though we may know how to

## WOOD FORMATION AND QUALITY

---

improve or how to control wood quality, about the best we can hope to do is increase yield and uniformity on those limited areas where intensive silviculture can be practiced. In recent years, however, there has been an increasing trend toward more intensive management on the better forest sites. It is on these areas, where trees will be grown on short rotations like farm crops, that both economic and biological silviculture can be practiced.

We know that traditional silvicultural measures, ranging from planting to the final harvesting, have the potential for increasing both yield and quality. And we know that mass selection, as accomplished through seed production areas, also has the potential for improving yield and quality. The changes in wood formation following mass selection, however, are by no means specific, and all wood characteristics are altered simultaneously. This means that although some wood characteristics may improve following selection, others may be affected negatively. Mass selection may be considered an interim improvement measure for application to extensive forestry. But the real breakthrough in new forestry ventures will only come through intensive selection or by controlled breeding for highly selective growth traits. Currently, most tree improvement programs have long-range goals that do not go much beyond mass selection; that is, a general, overall improvement in growth and quality. Few tree improvement programs are directed at the real problems of intensive forestry.

The hesitancy with which action programs in intensive forestry are initiated can be traced to many causes. One cause may be a reluctance to go beyond traditional silvicultural and forest management procedures, whereas another may be the frequent failure to adapt the ultimate goal of a tree improvement program to the requirements of intensive forestry. The latter criticism is due, in part, to the fact that the essential criteria for establishing imaginative programs are either largely lacking or unappreciated, which further suggests that tree physiologists and silviculturists have often failed to adequately define their goals. And so, we again return to the basic problem—it is necessary to know how trees grow before their growth can be manipulated by any type of improvement program.

Just for purposes of discussion, what type of improvement goal might we strive for? First, let's consider a simple hypothetical goal that might be confined to the better sites within a region: It would consist of a species capable of improvement through manipulation, a short rotation, an intensive silvicultural system striving for maximum yield of usable fiber, and mechanized harvesting. With these few criteria, which are by no means new, the geneticist, physiologist, silviculturist, pathologist, entomologist, and economist all have limits within which to concentrate their efforts and, working together, each can maximize his contribution.

## APPLICATIONS OF QUALITY CONCEPT

---

This may sound like a systems analysis approach to forestry. Perhaps it is. But if it is, the system and the entire forestry venture must be based on sound biological principles. The greatest challenge is in asking the right questions, and if the system is to function, each discipline must seek its answers in concert with the others.

The reasons for specifying a species capable of improvement through manipulation are obvious. All species are not readily adaptable to either rapid genetic improvement or short rotation silviculture. There are, however, a number of species that would be appropriate for such an improvement goal and undoubtedly others could be found that are now considered noncommercial.

In addition to economics, the purpose of including a short rotation in the goal is to make it possible to concentrate improvement on the juvenile traits, which are most amenable to manipulation. The juvenile traits, referring here to those of a young tree as well as those of a seedling, are most easily studied by the physiologist. In fact, the bulk of our basic knowledge of tree growth relates to the juvenile stages and we actually know very little about the physiology of mature trees. Similarly, the geneticist's problems are simplified by limiting the rotation age. Heritability estimates of selected traits are frequently high in the juvenile stages, but they rapidly diminish with age as the inherent and environmental interactions become more complex. By concentrating on the juvenile stages of tree development, the physiologist and the geneticist will find much in common, and it is here that the contributions of physiology and genetics can be brought together.

It is frequently argued that such an approach attempts to predict future uses of wood and leads to narrow genetic specialization. However, a pulpwood or wood fiber economy already prevails over much of our forest area. As research foresters we should not only recognize this as a current reality, but we should also look to the future, toward further improvement of our most promising fiber-producing species. Silviculturists and forest managers have been relatively successful in reducing rotation age in many forest types, but the real contributions from the coordinated efforts of physiologists and geneticists are long overdue.

What type of information do we need to implement such an improvement goal? What we urgently need are developmental life histories through short-rotation age of the commercial species we wish to manage. Agronomists and horticulturists have long been familiar with their crops, but we do not have an adequate life history on a single tree species. Although data are accumulating, there is as yet no concentrated effort to obtain such information, and only a few attempts have been made to collate the information we already have.

If we knew how trees grow, we could manipulate their growth. For example, if we knew the growth requirements of a species and how it responded to the

## WOOD FORMATION AND QUALITY

---

environment, and if we had more information on the growth correlations between different tree parts and their physiology during the seasonal course of development, then geneticists could select the most promising characters for improvement. Our greatest current need in this respect is information on yield. I am not referring simply to merchantable yield of the tree, but to the so-called energy budget, the physiological processes involved in the production, distribution, and utilization of the tree's photosynthate that ultimately ends up as wood.

During this discussion I have mentioned a few crown attributes that determine both yield and quality, but our information on the subject is still somewhat meager. We need a better knowledge of how the crown functions, which branches contribute most to growth, and how the efficiency of foliage in different parts of the crown changes during the season and in response to external influences. With more information of this nature, perhaps we could reshape the crown to make it more efficient. Perhaps we could also reshape the root system for better utilization of fertilizers and for greater efficiency in intensively managed areas. With regard to wood quality, we know that the juvenile wood in the core is generally of low quality. On the other hand, we also know something about how and why juvenile wood is formed. Furthermore, we know that the quality of the juvenile wood core can be improved to some extent by selection and breeding. These are all simple examples from an almost infinite array of possibilities. I do not pretend to know the "correct" approach we should take in formulating an improvement goal. But I do believe that if we are to make progress, we must adopt a more creative approach and look at a tree as a biological organism that might be manipulated more to the needs of man.

Ancient man no doubt carefully selected his hunting club, for his very survival depended on the stoutness of his weapon. We too should carefully define the criteria for our future forestry ventures, since today's decisions determine tomorrow's abundance. As a scientific forestry community, we are quite knowledgeable. However, we don't know how to reach agreement on what we want, or how to go about getting it. One of the biggest problems facing us today is not our lack of knowledge of tree growth, but how to use what knowledge we already have. It is my sincere opinion that if we were to carefully define our goals, capitalize on our collective knowledge, and cooperate in our research endeavors, we could soon revolutionize American forestry.



## LITERATURE CITED

---

1. BALATINECZ, J. J., and R. W. KENNEDY. 1967. Mechanism of earlywood-latewood differentiation in *Larix decidua*. TAPPI Fourth Forest Biol. Conf. Proc., Pointe Claire, Quebec, Oct. 12-13, 1967:36-55.
2. DOAK, C. C. 1935. Evolution of foliar types, dwarf shoots, and cone scales of *Pinus*. Univ. Ill. Bull. 32(49):1-106.
3. DUFFIELD, J. W. 1968. An evolutionary view of wood. J. Forest. 66:354-357.
4. ELLIOTT, J. H. 1937. The development of the vascular system in evergreen leaves more than one year old. Ann. Bot. 1:107-127.
5. ESAU, K. 1965. Vascular differentiation in plants. 160 p. Holt, Rinehart & Winston.
6. FRY, G., and L. CHALK. 1957. Variation of density in the wood of *Pinus patula* grown in Kenya. Forestry 30:29-45.
7. GLERUM, C., and J. L. FARRAR. 1966. Frost rings in the stems of some coniferous species. Can. J. Bot. 44:879-886.
8. GORDON, J. C., and P. R. LARSON. 1968. The seasonal course of photosynthesis, respiration, and distribution of  $^{14}\text{C}$  in young *Pinus resinosa* trees as related to wood formation. Plant Physiol. 43:1617-1624.
9. JOST, L. 1891. Ueber Dickenwachstum und Jahresringbildung. Bot. Zeit. 485-496; 501-510; 525-531; 541-547; 557-563; 573-579; 589-596; 605-611; 625-630.
10. LARSON, P. R. 1957. Effect of environment on the percentage of summerwood and specific gravity of slash pine. Yale Univ. School Forest. Bull. 63, 78 p.
11. ———. 1960. A physiological consideration of the springwood-summerwood transition in red pine. Forest. Sci. 6:110-122.
12. ———. 1962a. Auxin gradients and the regulation of cambial activity. In Tree Growth. T. T. Kozlowski, ed. p. 97-117. New York: Ronald Press.
13. ———. 1962b. The indirect effect of photoperiod on tracheid diameter in *Pinus resinosa*. Amer. J. Bot. 49:132-137.
14. ———. 1962c. A biological approach to wood quality. TAPPI 45:443-448.
15. ———. 1963a. The indirect effect of drought on tracheid diameter in red pine. Forest. Sci. 9:52-62.
16. ———. 1963b. Stem form development of forest trees. Forest Sci. Monogr. 5, 42 p.
17. ———. 1963c. Microscopic wood characteristics and their variation with tree growth. IUFRO Forest Prod. Sect. 41 Madison, Wis., Sept. 11-13, 1963: 24 p.
18. ———. 1963d. Evaluating the environment for studies of the inheritance of wood properties. In World Consultation Forest Genet. Tree Improvement Proc., Stockholm, Sweden, Aug. 1963, II(7/1):1-6.
19. ———. 1964a. Some indirect effects of environment on wood formation. In The formation of wood in forest trees. M. H. Zimmermann, ed. p. 345-365. New York: Academic Press.
20. ———. 1964b. Contribution of different-aged needles to growth and wood formation of young red pines. Forest. Sci. 10:224-238.
21. ———. 1965. Stem form of young *Larix* as influenced by wind and pruning. Forest. Sci. 11:412-424.
22. ———. 1967a. Effects of temperature on the growth and wood formation of ten *Pinus resinosa* sources. Silvae Genet. 16:58-65.
23. ———. 1967b. Assessing wood quality of fertilized coniferous trees. Forest Fertilization Symp., Gainesville, Fla., Apr. 18-21, 1967:275-280.

## WOOD FORMATION AND QUALITY

---

24. ———. 1967c. Silvicultural control of the characteristics of wood used for furnish. TAPPI Fourth Forest Biol. Conf. Proc., Pointe Claire, Quebec, Oct. 12-13, 1967:143-151.
25. MORK, E. 1928. Die Qualität des Fichtenholzes unter besonderer Rücksichtnahme auf Schleif- und Papierholz. Papier Fabrikant 26:741-747.
26. PRIESTLEY, J. H. 1932. The growing tree. Forestry 6:105-112.
27. SACHER, J. A. 1954. Structure and seasonal activity of the shoot apices of *Pinus lambertiana* and *Pinus ponderosa*. Amer. J. Bot. 41:749-759.
28. SHEPHERD, K. R., and K. S. ROWAN. 1967. Indoleacetic acid in cambial tissue of radiata pine. Austral. J. Biol. Sci. 20:637-646.
29. WAREING, P. F. 1958. The physiology of cambial activity. J. Inst. Wood Sci. 1:34-42.
30. WILCOX, H. 1962. Cambial growth characteristics. In Tree Growth, T. T. Kozlowski, ed. p. 57-88. New York: Ronald Press.

Additional copies  
of this Bulletin may be procured  
from the Yale University School of Forestry  
New Haven, Connecticut,  
at \$2.00 per copy.