TREE
PHYSIOLOGY COLLOQUIUM

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PREFACE

These papers provide a broad coverage of growth characteristics and growth requirements of forest trees. They deal with vegetative and reproductive growth as well as the importance of carbohydrates, minerals, water, and hormones in growth. There are strong overtones throughout these papers of the role of silvicultural practices and environment on growth through the intermediation of internal physiological processes and conditions in trees. These papers should be of value to practicing foresters in helping them understand the basis for success or failure of forest trees when subjected to various silvicultural treatments or when exposed to different environmental regimes.

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INTRODUCTION

Many foresters have expressed the need for a sound foundation of basic information about tree growth on which to build a rational system of silviculture. As Kramer (1948) pointed out, foresters often have learned that certain silvicultural practices are successful under a given set of conditions, but often they do not know why. Their explanations are based on local observations. Until it is known why a given practice is successful in terms of sequential physiological responses in trees, foresters will have difficulty in generalizing about the usefulness of a given practice beyond the specific conditions under which they have tested it.

Kramer (1956) suggested that foresters can learn how to grow trees by learning how trees grow. By this he meant that the potential contribution of physiology to forestry lies in identifying and characterizing the fundamental internal processes of trees which influence their growth and for demonstrating how these processes are affected by heredity and environment.

One central consideration cannot be emphasized too strongly: that physiological processes are the critical intermediaries through which heredity and environment interact to influence tree growth (Kramer, 1956; Richardson, 1960; Kozlowski, 1961, 1963; Wareing, 1964). This is shown by the following diagram:

Hereditary Potentialities of Trees (Genetics and Tree Breeding) ↘

Environmental Factors (Ecology, soil science, meteorology entomology, pathology, etc.) ↙

Internal Physiological Processes and Conditions (Tree Physiology)

↓

Tree Growth (Forestry)

Environmental changes and silvicultural treatments which alter growth do not do so directly but rather indirectly through their influence on such physiological processes as photosynthesis, respiration, assimilation, hormone synthesis, absorption of water and minerals, translocation of growth requirements (e.g. carbohydrates, hormones, water, minerals), and other processes and internal physicochemical conditions. The overall control of tree growth involves many interactions among internal factors (Kozlowski, 1971a, 1971b). Thus, the important forestry problems of seed production, seed germination, wood production, wood quality, seed and bud dormancy, flowering, seed production, and drought resistance, for example, all involve a critical physiological base. Furthermore, growth inhibition or death of trees following catastrophic environmental events, insect attack, or disease inevitably is preceded by abnormal and sequential physiological events. The changes in internal processes and physicochemical conditions of trees are close to the event, growth, and they alter it. By contrast, environmental changes and silvicultural treatments do not really alter growth except through the sequential physiological-change pathway.
We might illustrate, with a few specific examples, the paramount importance of physiological processes, as influenced by changes in environment or silvicultural practices, in controlling tree growth. For example, soil moisture changes may or may not affect growth depending on whether or not they really affect cell turgor which is close to and causal to growth change in a tree. This may seem like an academic point because high soil moisture contents are assumed to reflect high turgor in plant tissues. Yet this correlation does not always exist for there are many times when high

internal water deficits develop in trees even when the soil is highly charged with water. This occurs whenever there is a steep vapor pressure gradient from the shoots to the surrounding atmosphere. This point was dramatically brought home to me in the hot and wet climate of Malaysia when I noted that, although it rained daily and the soil was very wet, some trees were wilted within a few hours after the rain stopped. Also when the soil is quite dry, leaf turgor may be high under conditions of low evaporative demand (e.g., high air relative humidity). We also know that, although cessation of shoot growth often has been linked to the shortening days of autumn, the short days do not directly promote shoot dormancy. We do know, however, that leaves perceive the change from long to short days and transmit some sort of a stimulus up the stem to the growing points which brings about the cessation of growth and formation of a resting bud. How can a leaf do this? The simplest hypothesis is that it is producing a growth inhibitor under short-day conditions which is transmitted from the leaf to the growing point and it is this inhibiting substance which stops extension growth of shoots. Thus we must recognize that environmental changes are really very remote from the final growth response.

Foresters may rightly ask why it should not be enough to relate changes in growth to trees to environmental changes and regimes. Why be concerned with the sequential internal physiological events in a tree that are triggered by an environmental change?

For our purposes we will consider the environment to be the sum of all external forces and substances affecting tree growth. Since growth of trees represents an integrated response to a complex of many fluctuating and interacting environmental factors it is difficult to evaluate the actual contribution of single external factors to growth and productivity. The environment varies not only in space but also in time. Some of the constant change in environment of a given tree during its lifetime is cumulative and some is cyclic. Furthermore, in a given environment, growth characteristics vary between tropical and temperate-zone species, angiosperms and gymnosperms, and ring- and diffuse-porous species, as well as in different parts of the same tree. A late-season environmental stress may be expected to affect differently the growth of species with shoots fully predetermined in the winter bud, heterophyllous species, and recurrently flushing species. Whereas shoot growth in the first group is completed early in the season, that of the latter two groups continues much longer and is more responsive to late-season environmental stresses. Another complication is that growth of internodes and leaves, as well as variously located shoots in the same tree, are affected differently by environmental changes.

The importance of internal growth control is emphasized by time-lag responses of trees to environmental regimes. For example, in some species there often is closer correlation between the amount of shoot growth and environment of the year of bud formation than with environment of the year of expansion of the bud into a shoot. This strong carryover effect of environment pertains primarily to species whose shoots expand rapidly and which have a full complement of unexpanded foliar organs of shoots already predetermined in the unopened bud (e.g. *Pinus resinosa*). Yet even in these species severe environmental stresses during the year of shoot expansion may limit shoot elongation. The importance of environment during the year of bud formation is emphasized by high correlations between the size of the bud developed in a given climatic regime and the length of the shoot that expands from it, usually in the subsequent year.

Lag responses of trees to environmental regimes are well illustrated by effects of stand thinning on cambial growth. After thinning, the released trees respond to more favorable environmental conditions by slowing down upward crown recession and increasing crown width and leaf volume. These changes lead to increased production and basipetal flow of carbohydrates and hormonal growth regulators (Kozlowski, 1971b). Eventually a more tapered stem is produced by greater stimulation of xylem production toward the stem base than at upper stem levels or by redistributing xylem increment to favor the lower stem. Often, however, a significant increase in cambial growth may not be evident in the lower stem until a few years after the thinning is made.

Another difficulty in dealing with effects of environment alone on growth responses of trees is that different combinations of environmental factors can bring about a critical internal balance of factors that triggers a growth response. For example, both chilling and long days can induce hormonal changes which break bud dormancy. But all species are not equally responsive to each of these factors. For example bud dormancy in _Fagus grandifolia_ seedlings can be readily broken by continuous light. In other species, long days are ineffective in breaking dormancy. When dormancy was induced by short days in _Acer pseudoplatanus_ and _Robinia pseudoacacia_ the plants could not then be induced to grow even after 10 weeks of continuous light (Wareing, 1954).

Bud dormancy can be induced by changing temperature, day length light quality, mineral supply or water supply. However, the environmental factors which accelerate dormancy vary for different species. Such variations often indicate differences among species in adaptation to climates in which the unfavorable season represents different environmental combinations. Some species become adapted to survive in cold winters; others to hot dry summers, and still others to both cold winters and hot, dry summers (Kozlowski, 1971a).

Interpretation of environmental conditions on tree growth is also complicated by environmental preconditioning. Rowe (1964) emphasized that, in the morphogenesis of a plant, early ecological influences can carry through to expression in later stages of development and behavior. Sensitive periods for preconditioning seem to be at the time of initiation and formation of buds and seeds as well as at the time when growth begins following a dormant or resting stage. Rowe concluded that it sometimes is difficult to separate "heritable" from environmentally induced effects because of the probability of preconditioning before the seed was collected.

Because of the complexity of the total environmental impact on tree growth it is suggested that a physiological-ecological approach be followed to try to explain why a given species or tree grows as it does in a particular environment and why it fails or succeeds in a competitive situation. This approach involves modeling of environmental regimes and changes as well as subsequent physiological and biochemical changes which are close to (in time) and causal to growth changes. In this regard we can learn much from the fields of medicine and horticulture. Medicine made its greatest progress when it began to concentrate on physiology and biochemistry. Horticulturists also learned early that basic research in the physiology of tree growth led to widespread application in handling their crop trees.

PHYSIOLOGICAL IMPLICATIONS IN FORESTRY PROBLEMS

A few examples will be given to show how a knowledge of tree physiology, or at least communication with a tree physiologist, can help foresters to better understand and deal with some important practical problems.

Interpretation of Data

A good basic knowledge of tree physiology can prevent certain important errors in growth measurement. For example, the forestry literature has many observations on alleged cambial growth increment which may be questioned because of failure to account for all factors which contribute to changes in stem diameter.

The physiologist recognizes that changes in stem diameter involve 2 major components: (1) cambial growth, including addition, enlargement, and maturation of cambial derivatives (xylem and phloem) and (2) reversible changes in stem size resulting from hydration and thermal effects. Thus, tree diameter sometimes changes appreciably because shrinking and swelling are superimposed on cambial growth increment. Sometimes such reversible changes are small; at other times very large. Hence, estimates of cambial growth from measurement in diameter increase sometimes are very misleading.

Recurrent shrinking and swelling of stems as a result of direct thermal effects are very large. However, these occur mostly during the winter and in much of the temperate zone they only seldom seriously complicate growth measurements during the growing season (Winget and Kozlowski, 1964; McCracken and Kozlowski, 1965). By contrast, the hydration changes often cause considerable error in growth measurement.

Foresters have often tried to determine the precise duration of seasonal cambial growth by measuring radial increase of stems with dendrometers and dendrographs. This task is not easily accomplished because, when cambial growth slows down toward the end of the growing season, reversible swelling and shrinking of stems continue as a result of hydration changes. In fact, it is possible for cambial growth (xylem increment) to occur while the tree is actually decreasing in diameter. This happens when stem shrinkage due to dehydration exceeds stem expansion caused by cambial growth. Fielding and Millett (1941) concluded that because of continuous shrinking and swelling of Pinus radiata stems they could not determine with dendrometers when seasonal cambial growth began or ended. Kozlowski (1967a, 1967b) observed that, during soil-drying cycles, stem diameters of Acer negundo seedlings decreased, at first gradually and then more abruptly as soil dried. Irrigation following a drought caused rapid stem rehydration and swelling. The seedling stems often shrank so much during a soil drying cycle that reliable estimates could not be made of cambial growth over short periods of time.

Investigators who attempt to estimate cambial growth from radial changes over short-time periods should be constantly aware of the fact that radial changes of stems due to hydration often exceed those resulting from cambial growth. For example, at certain times of the season, shrinkage of Pinus resinosa stems during one day was greater than a week's increment due to cambial growth (Kozlowski and Winget, 1964). Similar results have been found for Picea (Kern, 1961) and Pinus canariensis (Holmes and Shim, 1968). In fast-growing trees the trend of cambial growth increment can be estimated over a several-day period by connecting daily peaks or valleys of dendrograph traces if the amplitude of daily shrinkage and expansion does not change much. However, if weather conditions vary greatly from day to day, the ratio of stem hydration change to total radial change may also vary, rendering difficult the estimation of cambial growth from dendrograph traces. Stem shrinkage in response to severe drought often makes it impossible to use dendrographs or dendrometers to obtain useful measurements of cambial growth. In New Jersey, for example, Buell et al (1961) showed that tree stems shrank so much during a mid-August drought that their diameters were less than they were before the growing season started (even though xylem increment in these trees during the summer up to mid-August was appreciable). Thus, the whole amount of irreversible xylem increment up to mid-August was masked by stem shrinkage. The trees remained in a shrunken condition and did not increase in diameter until soil moisture was replenished in December. At that time the stems swelled rapidly.

The physiologist knows that the hydration component of diameter change in tree stems is greater over short periods of time than over long ones. Whereas total diameter change over a 5-year-period may largely reflect irreversible increment due to xylem deposition, diameter change over a few-day period often reflects reversible hydration changes almost entirely. Thus, the possible errors cited above should not detract from the usefulness of diameter changes over long periods of time for mensurational purposes such as volume changes in forest stands. They do, however, render suspect many measurements of radial change which have been made in an attempt to characterize certain fundamental aspects of cambial growth which are of interest to forest biologists.

Another error in growth measurement is that resulting from determination of radial increment at the traditional "breast height" or at a single radial position around the stem circumference. One cannot argue with the value of breast height measurements made in many trees for mensurational purposes such as increase of usable wood volume in forest stands. However, such measurements have been extended too often in attempts to answer such important biological questions as when seasonal cambial growth begins and ends in a tree. For this purpose such determinations often are questionable because, in a number of species, appreciable xylem production and diameter increase begin in the upper stem first, and diameter increase in the lower stem (e.g., breast height) may not be measurable until considerably later. Furthermore, in severely suppressed trees there may not be any seasonal xylem increment in the lower stem and an appreciable amount in the upper stem. Yet another common source of error in determination of cambial growth is failure to appreciate the eccentricity of cambial growth around the stem circumference (Kozlowski, 1971b).

Still another example of how a knowledge of tree physiology is useful involves the internal water balance of trees. Many investigators have erroneously used tissue moisture content as a measure of degree of internal water stress in trees. Although it is well-known that protoplasmic hydration greatly influences physiological activity and tree growth, physiological processes often have been unaffected over a fairly wide range of moisture contents of tissues. Thus, questions have been raised, from time to time, about using moisture content as a reliable measure of internal water stress in plants.

The physiologist knows that since dry weight changes often are not proportional to changes in the actual amount of water in tissues, the variations in moisture content do not necessarily reflect changes in protoplasmic hydration. Photosynthesis, respiration, and translocation can produce significant and rapid changes in tissue dry weight (Kramer and Kozlowski, 1960). Over long periods of time, progressive cell wall thickening usually causes significant dry weight increase. Hence changes in percentage water content of different tissues under various conditions may reflect changes in actual water content alone, in dry weight alone, or both. When changes occur in the actual amount of water in tissues as well as in dry weight, the changes in the latter often are considerably greater. A few examples of changes with time in actual moisture content and dry weight of various tissues will be given.

Kozlowski and Clausen (1965) showed that seasonal increases in percentage moisture of buds of trees were traceable to rapid movement of water into the buds. During the same period the buds also increased in dry weight, but at a lower rate than that at which water moved into them. Unlike the pattern in buds, percent moisture in angiosperm leaves decreased rapidly in the early part of the growing season and slowly after mid-summer. These decreases were the result of relatively greater increase in dry weight rather than a decrease in actual water content. In one experiment the moisture content of leaves (as % of their dry weight) decreased with time whereas dry weight increased. And no significant differences occurred in the actual amount of water per leaf. Thus the decrease in moisture content reflected primarily a dry weight increase.

Clausen and Kozlowski (1965) studied seasonal changes in moisture contents of *Picea glauca* and *Larix laricina* cones. An early increase in percentage moisture content of cones between late May and early June was the result of an increase in actual water content that exceeded the dry weight increase for the same period. Thereafter, percent moisture decreased markedly even though the actual moisture content remained about the same or even increased. Decrease in percentage moisture, although actual moisture content remained high, was traceable to a greater proportional increase in dry weight. After the beginning of August, by which time the seasonal increase in cone dry weight was completed, the cones began to dehydrate.

In another study Chaney and Kozlowski (1969) showed that percentage moisture content of reproductive tissues of angiosperm species (Acer rubrum, Quercus rubra, Prunus serotina) was variously influenced by water uptake or change in dry weight, or both of these. Such observations emphasize that moisture content alone is not necessarily an accurate indicator of internal water balance of plants and should be interpreted in relation to both water weight and dry weight change of tissues.

Use of Herbicides

Because of their effectiveness together with their low costs and speed and ease of application, herbicides can save time and manpower to such a degree that they may be considered necessary in forest practice. For example, their usefulness has been demonstrated in stand regeneration, release of conifers and crop trees, brush control, stand improvement following harvest cuts, plantation establishment, production of nursery stock, fire-lane and utility line maintenance, roadside maintenance, and control of tree diseases. We are only beginning to understand the vast potential of chemical control over forests. At the same time, however, we are becoming increasingly aware that use of herbicides poses dangers of toxicity to the very trees we wish to foster. The really skillful use of herbicides in forestry calls for an appreciation of herbicide characteristics and of specific physiological responses to various herbicides of both plants to be fostered and those to be eliminated.

A body of evidence has accumulated which shows the extreme toxicity of improperly used herbicides to forest trees. Such toxicity has taken many forms and includes arrested growth of trees as well as their morphological deformation and outright killing (Kozlowski, 1960; Kozlowski and Torrie, 1965; Kozlowski and Sasaki, 1968; Winget et al, 1963; Wu et al, 1971; Kozlowski, 1971a). Herbicides often show a delayed toxic effect. Sometimes an undesirable tree is treated with an herbicide and several adjacent trees are subsequently killed by "backflash" or translocation of herbicides from one tree to another through root grafts (Cook and Welch, 1957).

The observed toxicity of herbicides to trees is influenced by a host of herbicide, plant, and environmental factors. Toxicity or selectivity of an herbicide should not be considered as a generalized have or have-not attribute. We often are asked the general question of whether or not a particular herbicide is toxic to a given species. Such a question is not easily answered unless we also know the soil type, the environment, the herbicide dosage, the growth stage of the treated plants, the manner of herbicide application, etc. All of these will affect the observed toxicity. Furthermore, if we are dealing with herbicides which persist in the soil we need to know the probable amplitude of environmental factors for a long time after herbicide application.