Physiology of Trees as Related to Forest Genetics

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After defining some terms, I shall present some specific examples which I hope will illustrate the relationship between genetics and physiology and show that an understanding of the physiological processes of forest trees is important to forest geneticists. It is also important to progress in the everyday task of forest management, but that is not my subject. In this discussion I have borrowed heavily from ideas introduced to me by Dr. Paul J. Kramer at Duke University, and from the book "Physiology of Trees" (Kramer and Kozlowski 1960).

What is forest tree physiology, and are there any unusual attributes of trees that make tree physiology a special area in the general field of plant physiology? Webster's Third New International Dictionary defines physiology as "a branch of biology dealing with the processes, activities, and phenomena incidental to and characteristic of life or of living organisms." B. M. Duggar (1911, p. 3) made this somewhat more specific: "Plant physiology . . . concerns itself with plant responses and plant behavior under all conditions; that is, with relations and processes readily evident or obscure, simple or complex, which have to do with maintenance, growth and reproduction of plants."

This seems to cover all angles, but are trees any different from other plants in their physiology? Kramer and Kozlowski (1960) describe clearly the differences that make trees distinctive:

> "The peculiar characteristics of trees are a matter of degree rather than of kind, however. They go through the same stages of growth and carry on the same processes as other plants, but their larger size, slower maturity, and longer life accentuate certain problems as compared with smaller plants with a shorter life span. The most obvious difference between trees and herbaceous plants is the great distance over which water, minerals, and food must be translocated in the former. Also, because of their longer life span, they usually are exposed to greater variations and extremes of temperature and other climatic and soil conditions than annuals or biennials. Thus, just as trees are notable for their large size, they are also notable for their special physiological development."

The only thing I would add to this is that in forestry we are primarily interested in the stem of the plant, rather than in the fruit, which is the object of main interest to scientists interested in field crops. This different emphasis may change somewhat the direction of physiological research on the part of those interested in forest tree physiology.

Keeping in mind these definitions of forest tree physiology, how then is it related to forest genetics or species improvement? To illustrate the association I would like to refer to the concept which, according to Kramer and Kozlowski (1960), was developed by the German physiologist Klebs and refined by others in this country. This concept emphasizes the principle that hereditary or environmental factors can affect the growth of a living organism—be it an alga, cotton plant, or tree—only by affecting the plant's internal processes and conditions; in other words, its physiology. These relationships are illustrated by the accompanying diagram.

HEREDITARY POTENTIALITIES OF TREES forest genetics and tree breeding	ENVIRONMENTAL FACTORS forest ecology and forest soils

PHYSIOLOGICAL PROCESSES AND CONDITIONS
tree physiology

TREE GROWTH
forestry and horticulture

(After Kramer 1956)

Thus, in order to understand how genetic factors may affect tree growth, wood quality, or other important features, we must learn how the factors affect the physiological processes involved.

Now I hope that this concept does not offend the geneticists present, since I seem to be saying that they cannot get anywhere without knocking on the physiologist's door. I do not intend to imply that physiology is more important than genetics.

In reality you can bypass physiology temporarily and, for example, develop a hybrid which grows faster than either parent species, without knowing why or how this growth increase occurs. For the greatest progress and for the widest application of our results, however, we eventually would have to try and determine what processes or conditions in the tree were changed to bring about an increase in growth. Rather than to attempt a comprehensive literature review of physiology-genetics work under way, let us just illustrate the relationship with some specific examples in several areas of forest genetics.

Selection

The phase of forest species improvement with which most of us are somewhat familiar here in the Southeast is selection. To illustrate how selection for a desired trait is related to tree physiology, let us use the example of selection for high oleoresin yield which has been conducted by the U. S. Forest Service at Olustee, Fla., since 1941 (Squillace and Dorman 1961; Squillace and Bengtson 1961).

The first step in this work was the selection of 12 slash pine trees for high gum-yielding potential from natural stands in north Florida and south Georgia. The yield of these trees was about double that of comparable non-selected trees. Subsequently, crosses were made among nine of these selected trees, and between the selected trees and average and low-yielding trees. By using a micro-chipping technique on young trees stemming from these crosses, it was shown that oleoresin yield is inherited, with a heritability of about 55 percent. These studies also showed that of the original nine rigid selections used, only three were outstanding in passing on their high gum-yield qualities to their progeny.

Now, how does physiology enter this picture? Schopmeyer et al. (1954) suggested that gum yield should be related to certain anatomical and physiological characteristics, namely, number and size of resin ducts, gum exudation pressure, and gum viscosity. Mergen et al. (1955) demonstrated that gum yield was inversely related to gum viscosity, and Bourdeau and Schopmeyer (1958) were able to prove that oleoresin exudation pressure was directly correlated with oleoresin yield. They concluded that the ratio of pressure to viscosity could be used for predicting yield potential of young trees.

So, what has happened here? The geneticist has selected high-yielding trees and proven that some of them pass to their progeny this high-yielding trait. The physiologist, working hand-in-hand with the geneticist (indeed, often they have been the same individual), has discovered why some trees yield more oleoresin than others. Now they have a tool which is available to improve selection techniques and to improve progeny testing. If techniques can be developed so that exudation pressure and gum viscosity can be measured on a seedling, the testing program can be speeded up considerably.

This research has revealed some physiological differences, but has raised many new problems for the physiologist to consider. Why do some trees have a higher exudation pressure? Why do some produce low-viscosity oleoresin? These questions will carry the researcher back toward more fundamental processes, e.g., photosynthesis, cell metabolism, gum synthesis. When you answer one "Why?" you generate a dozen new "Whys?".

Before we leave the subject of selection, let me just mention the physiologically complex problem of selection for fast growth rate. What are we really selecting for? Efficient photosynthesis, efficient utilization of water or minerals, some difference in cell metabolism that allows one plant to convert to cellulose more of the products of photosynthesis.

Breeding

Now let us move on from selection and consider for a few minutes the subject of breeding for desired traits and multiplication of genetically identical individuals once a desired strain is available.

One major deterrent to rapid progress in forest genetics is the flowering habit of most commercial tree species. They do not normally begin producing the organs for sexual reproduction in appreciable numbers until they are 10 or more years old, so breeding and progeny testing are delayed. Compare this with, say, corn breeding, where four crops of a 90-day maturing variety can be raised in one year by using a greenhouse during cold weather. The forest geneticist knows or can work out the techniques of breeding in the various species, but he cannot do breeding without flowers or strobili.

Some treatments, such as fertilizing, strangling, and root pruning, have been successful in stimulating precocious flowering, but there remains abundant opportunity for further advancement. Here again the physiologist can perhaps help. The U. S. Forest Service's Dr. R. L. Barnes and associates at the Research Triangle near Durham, N. C., are trying to determine internal physiological factors governing flowering. They are studying the biochemical changes which bring about "readiness to flower," and are attempting to identify the basic processes which initiate the changes. This work is far from finished, but when the controlling physiological processes have been identified and the biochemical steps determined, one can then make some logical "guesses" about methods of manipulating flowering with more hope of success in producing flowers or strobili on young saplings or even seedlings.

In this same area of genetics, it is desirable to have some reliable means of clonal reproduction of individuals with desirable traits. This requires grafting or some form of rooting, and raises many problems of a physiological nature. For example, with loblolly pine and many other species, rootability declines with age (McAlpine and Jackson 1959). What is the basic cause of this decline? Can rooting potential be restored? Also, cuttings from one part of a tree may root better than those from another (Grace 1939), and the resulting ramets may even have different growth characteristics (Libby and Jund 1962). What physiological processes of a cutting are affected by age of parent tree, or by its original position in the crown?

As for grafting, several techniques have been used successfully to establish the initial graft union, but in many instances a large number of the grafts later die. Some physiological difference between stock and scion causes an incompatibility which prevents normal functioning of some essential process. What causes the incompatibility, and can it be overcome? When the physiologist can answer some of these questions, the geneticist can make more rapid progress in species improvement and will be able to assess more precisely true genetic differences.

Application

As a final example, let us turn to the essential step of utilizing superior strains once they have been tested and proven. Let us suppose that selection, breeding, and testing at the University of Georgia have produced a strain of shortleaf pine highly resistant to littleleaf disease (Zak 1955). Now disease resistance is not of much benefit unless the tree also makes satisfactory growth. Can we expect good growth from this new strain throughout the natural range of shortleaf pine from New Jersey to Texas and in areas where it has been planted outside its natural range? We know that geographic races exist within species, and so we would assume that this new strain would be limited in the geographic range over which it could be expected to make good growth. We could make trial plantings of the new strain throughout the range of shortleaf pine and wait 20 to 40 years to assess the pertinent growth results. But as our knowledge of physiology of trees increases, perhaps we can arrive at some valid estimates of potential range by making certain physiological tests. For example, drought resistance of some species has been found to be related to stomatal control and rate of transpiration (Polster and Reichenbach 1957). Could we make estimates of soil moisture or rainfall limits of the new strain by measuring these characteristics on seedlings in the laboratory? Cold hardiness has been associated with the concentrations of certain cell constituents (Parker 1962). Could temperature limits for the new strain be determined by measuring cell sugars? The optimum temperature for maximum net photosynthesis has been established for some species (Decker 1944) and could be established for the new strain. Some species and races within species can tolerate shorter daylengths than others and still make satisfactory growth (Pauley and Perry 1954; McGregor et al. 1961; Allen and McGregor 1962; Watt and McGregor 1963). These limits also could be established for the resistant shortleaf pine strain.

By measuring the rates of the various physiological processes and determining the limits of optimum operation of these processes under various conditions, perhaps we could predict how well our new strain would perform in a certain locality in competition with other tree species. With continued research, this will be possible.

I seem to have raised many questions and given very few answers. However, I hope that I have contributed to your better understanding of physiology and of its relation to forest genetics. Let me summarize by saying that physiologists are interested primarily in how trees grow, while forest geneticists are interested in changing the way in which trees grow. The greatest progress will be made when the two work together to solve the many remaining problems.

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