

## POSSIBILITIES IN THE PHYSIOLOGICAL ANALYSIS OF GROWTH

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Crop breeders seeking to improve yields have usually been interested in a single aspect of plant growth, i.e., storage of food in the reproductive structures. Because grain yield and plant size are not correlated (e.g., Asana, 1965), the International Rice Research Institute has been able to increase yields tremendously through production of a dwarf rice plant. However, wood yield and tree size are always correlated. Consequently, tree breeders interested in yield are concerned with total accumulation of dry matter by the tree or at least in production of the structural bulk of the plant.

The possibilities of increasing the efficiency of total energy capture and CO<sub>2</sub> fixation have received relatively little attention from the crop breeders. In contrast, tree breeders very early considered the possibility of using photosynthetic rate (i.e., CO<sub>2</sub> assimilation) as a selection criterion. Thus for example, Bourdeau (1958) spoke of these possibilities at the Fifth NEFTIC meeting. Ecologists and silviculturists interested in forest productivity and species competition have often used measurements of photosynthesis upon which to base their conclusions on relative tolerances and the causes of succession.

However, other factors besides photosynthetic rate per se are important in dry matter accumulation. There are at least three major physiological functions which are important in this aspect of tree growth: (1) photosynthetic and respiration rates, (2) distribution of the photosynthate (i.e., growth) within the tree, and (3) duration of active growth (i.e., assimilation). In contrast to photosynthetic rate, the relative distribution of photosynthate and the duration-intensity aspects of assimilation have been much neglected in studies of dry matter production. Each of these shall be discussed in detail.

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## PHOTOSYNTHESIS

The research of many investigators has indicated that a number of variables must be considered in measurements of photosynthetic rate. These variables are classified in table 1. The first group of factors listed can lead to differences in photosynthesis among leaves or branches on the same tree or among trees even if their genotypes are identical. The rate of CO<sub>2</sub> assimilation as a biological reaction is a function of, or dependent on the levels of the second group of factors at the time of measurement (table 1). Environmental influences operating prior to the period in which photosynthesis is measured precondition a plant's response to light, temperature, soil moisture, and CO<sub>2</sub> concentration by their effect on the items listed in the first group. Because of these considerations, it is obvious that it would be difficult to make selections for superior individuals by measuring photosynthesis in tree crowns or on cuttings of mature trees, at least during a relatively short time period.

Most investigators have found either a weak correlation or none at all between measurements of photosynthesis and growth. In the best correlation reported, Huber and Polster (1955) accounted for some of the variation in growth among clones of poplar (Populus L.). In the work by Campbell and Rediske (1966) genotypic correlations of photosynthetic rate and seedling dry weight in Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] were high but apparently phenotypic correlations were low or negative. Reines and his co-workers have found no general relationship between vigor and photosynthetic rate in Southern pines (Reines, 1962; Robertson and Reines, 1965; Burkhalter, Robertson, and Reines, 1967).

Frequently there is a negative correlation between seedling size and unit photosynthesis. This is true for sweetgum (Liquidambar styraciflua L.) as shown by Zobel (1965) and in loblolly pine (Pinus taeda L.) according to Ledig and Perry (1967). Greater size means more leaves, greater depth of the seedling crown, and therefore, self-shading or a reduction in the average light intensity reaching the leaves (Kramer and Clark, 1947). This implies that seedlings with high photosynthetic rates, potentially fast growing, begin to experience self-shading sooner than seedlings with low photosynthetic rates; as a result, their relative growth rate declines. (Relative growth rate is the increase in weight per unit plant.) In other words, differences in growth rate (and growth) become partially erased if variation in growth depends only on unit photosynthetic rate.

## DISTRIBUTION OF GROWTH

More interesting than a weak negative correlation of photosynthetic rate and size are results such as those of Sorensen (1964). Even though Douglas-fir seedlings grown at a high temperature had photosynthetic rates 65% greater and respiration rates 50% lower than those grown at cool temperatures, their dry matter production was less. This seems anomalous since virtually all dry matter growth of the seedling is some multiple of the amount of carbon assimilated as CO<sub>2</sub> in photosynthesis minus that lost in respiration.

The explanation may be that seedlings with different genotypes or with similar genotypes but grown in different environments differ in the proportion of photosynthate that they allocate to the production of leaves. Under conditions of adequate moisture and nutrition, the genotype which distributes its photosynthate in such a manner as to favor leaf growth will increase its photosynthesizing surface rapidly and will be at an advantage in total dry matter growth (providing that the phenotype produced is reasonably balanced and capable of surviving in its habitat).

Table 1. Nongenetic causes of variation in measurement of photosynthetic rate.

<u>Source of variation</u>	<u>Example</u>
<u>Physiological-Morphological Factors</u> <sup>1/</sup>	
Age of leaf.	Sestak (1963), Clark (1961), McGregor (1958).
Age of meristem when leaf primordia was produced.	Bormann (1956).
Structural adaptation of the leaf.	In sun vs. shade leaves as shown by Björkman and Holmgren (1963, 1966), Clark (1961), and as governed by origin of sample according to height and aspect in the crown as shown by Reines (1962).
Mineral content of the leaf.	Peaslee and Moss (1966), Post (1962).
General vigor of disease status.	Sestak (1963), Decker and Tio (1958).
Endogenous diurnal cycle.	McNaughton (1967), Ledig (1967), Hoffman and Miller (1966), Palmer, Livingston, and Zusy (1964), Reines (1962), Hastings, Astrachan, and Sweeney (1961).
Seasonal cycle.	Bamberg, Schwarz, and Tranquillini (1967), Negisi (1966), McGregor and Kramer (1963), Bourdeau (1959).
Developmental stage.	Kreuger and Ferrell (1965), Bormann (1956, 1958), perhaps as controlled by degree of mutual shading as shown by Kramer and Clark (1947).
<u>Transient Environmental Factors</u> <sup>2/</sup>	
Light - Quality, intensity, and duration.	Negisi (1966), Milner and Hiesey (1964), Kramer and Decker (1944).
Temperature.	Negisi (1966), Tranquillini (1955).
Soil moisture.	Negisi (1966), Post (1962), Clark (1961), Bourdeau (1954).
CO <sub>2</sub> concentration.	Milner and Hiesey (1964), Billings, Clebach, and Mooney (1961), Thomas and Hill (1949), Decker (1947).

<sup>1/</sup> Modifications of plant physiology or morphology because of inherent developmental patterns or due to environmental factors exerting their effect through preconditioning sometime prior to the period of measurement.

<sup>2/</sup> Factors operating at or very shortly before the time of measurement and not by inducing a permanent modification in plant behavior or structure.

Relative leaf growth is measured by the allometric constant, the slope of the logarithmic regression of the dry weight of the leaves on total dry weight [see Ledig and Perry (1965) for an explanation of allometry]. Based on current research on loblolly pine seedlings, the allometric constant can vary among families at least within a range from 0.87 to 0.93 (unpublished data). These values mean roughly that during the first growing season, the needles grow at a rate of 0.3 to **0.5g** for every gram of increase in total seedling dry weight (needles plus remainder). Figure 1A is plotted using values within this range and identical photosynthetic rates. A seedling with a relatively high distribution of photosynthate to the production of leaves rapidly outgrows a seedling with a lower rate of leaf to total seedling growth. Obviously, if the allometric growth rates are identical and photosynthetic rate varies, growth of the genotype with the higher photosynthetic rate must exceed that of the genotype with the lower rate in the idealized situation (fig. 1B). A case in which both photosynthetic rate and allometric growth of the needles varies is illustrated in figure 1C. Though the photosynthetic rate of *b* is nearly 4  $\frac{1}{2}$  greater than that of *a*, their cumulative growth at 150 days is reversed. The effect of the allometric constant may not always be apparent but it is important.

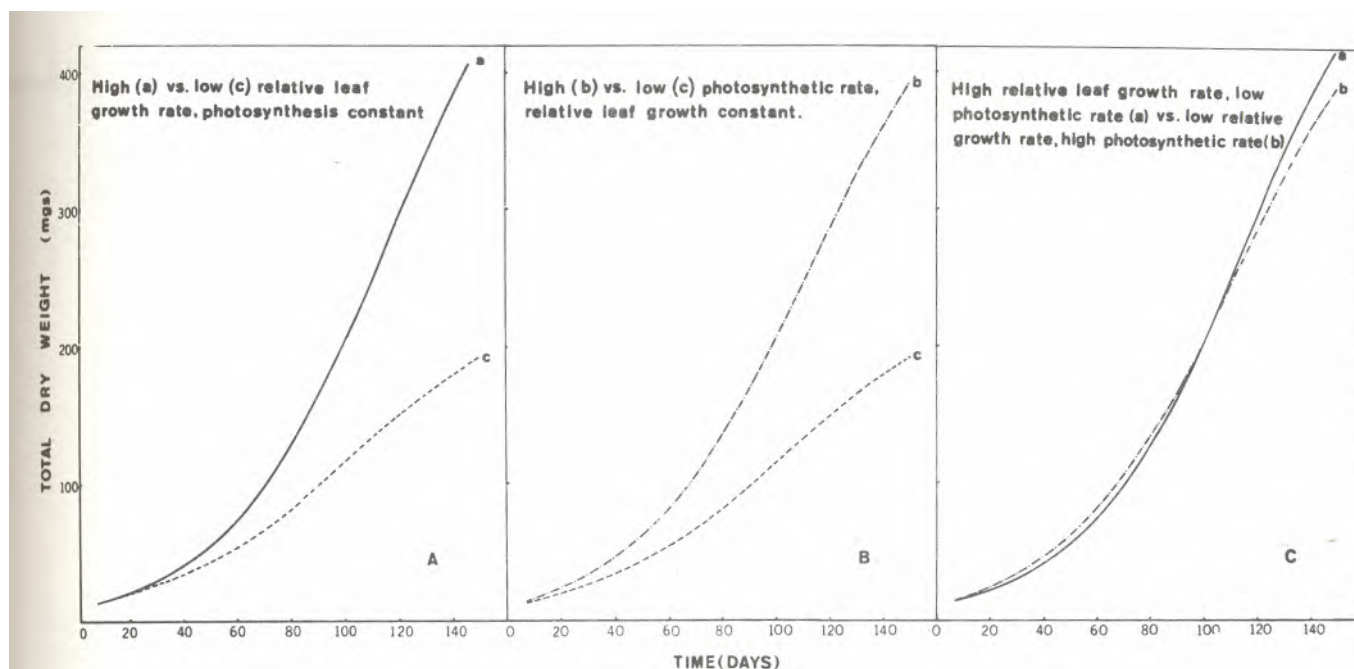


Figure 1. -- Cumulative growth in total seedling dry weight ( $Y_t$  in mg) computed from the model:

$$Y_t = Y_0 + \sum_{i=1}^t K \cdot L_{t-1} \cdot \frac{ACe^{-(B+Ct)}}{[1 + e^{-(B+Ct)}]^2} \cdot \frac{1 + e^{-(E+Pt)}}{D}, \text{ where } L_{t-1} = L_0 + R \cdot Y_{t-1}$$

R is the proportion of total photosynthate utilized for leaf growth, K is a constant to fix the relative level of photosynthetic rate, t stands for time in days, and  $Y_0$  and  $L_0$  are, respectively, initial first-week values for total seedling and leaf dry weights. Values for the constants A, B, C, D, E, and F are based on measurements of net assimilation on first-year loblolly pine seedlings.  
 A. Growth curves generated by the model when photosynthetic rate is identical for *a* and *c* ( $K=1$ ) and *a* distributes 40% of its current assimilate to leaf growth ( $R_a = 0.4$ ) and *c* distributes 30% of its current assimilate to leaf growth ( $R_c = 0.3$ ).  
 B. Growth when R is identical for *b* and *c* but the photosynthetic rate for *b* is 40% greater than that of *c* ( $K_b = 1.4$ ).  
 C. Growth when both K and R vary; for *a*,  $K_a = 1$  and  $R_a = 0.4$ ; for *b*,  $K_b = 1.4$  and  $R_b = 0.3$ .  
 A higher photosynthetic rate does not ensure more rapid growth throughout all stages of development.

seasonal changes in photosynthetic rate are a third factor which may lead to differences in growth. They are a greatly overlooked aspect of almost all growth studies.

Duration of seasonal growth, as measured by leader elongation, accounted for 40% of the variation in total height growth among provenances of loblolly pine studied by Perry, Wang, and Schmitt (1966). However, this correlation approaches circularity. Yet, if some individuals retain high rates of photosynthesis later in the fall than others, or reach peak rates sooner in the spring, or maintain the ability to carry on photosynthesis at significant levels in the winter, then they would have **areal** advantage in dry matter accumulation. This situation has been described by Negisi (1966) in comparisons of Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) versus Hinokicypress (*Chamaecyparis obtusa* Sieb. et Zucc.) and cryptomeria (*Cryptomeria japonica* D. Don) (fig.2). There are also differences between loblolly pine and white pine (*P. strobus* L.) in the seasonal course of photosynthesis (McGregor and Kramer, 1963).

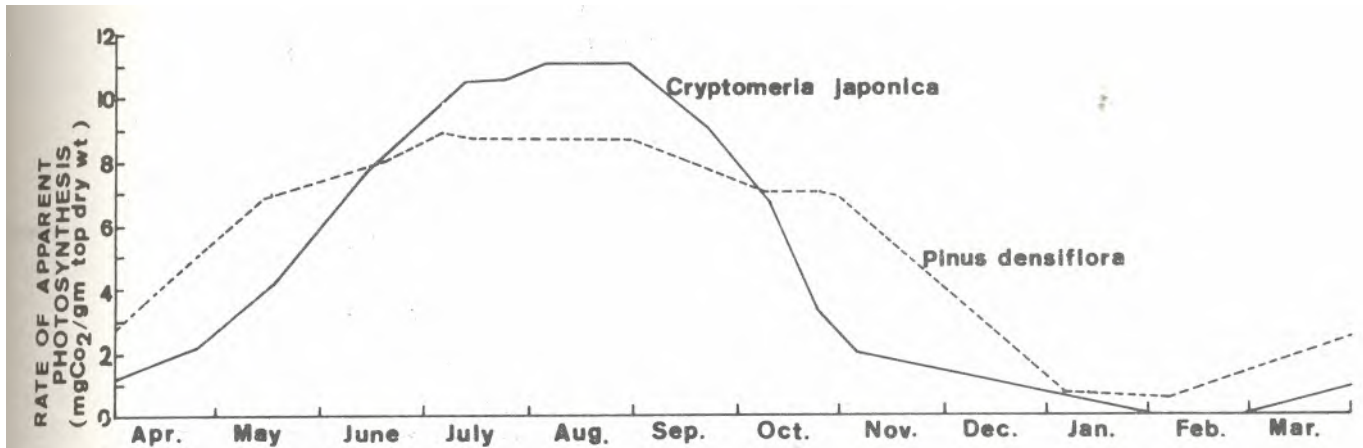


Figure 2. -- Seasonal trend of photosynthesis in *Pinus densiflora* and *Cryptomeria japonica*. Though peak rates of photosynthesis are higher in *C. japonica* than in *P. densiflora*, the latter achieves higher rates earlier in the spring and maintains its photosynthetic rate later in the fall and through the winter. Yearly growth in the two species is approximately equivalent (after data of Negisi, 1966).

We are not aware of any genetic study designed to reveal intraspecific variation among trees in the seasonal course of photosynthesis. There is reason to suspect that such variation might occur within species. For example, there are seasonal differences among races of Scotch pine (*Pinus sylvestris* L.) in chloroplast pigmentation (Gerhold, 1959) and among loblolly pine trees in chloroplast organization during the fall and winter (Perry and Baldwin, 1966).

If everything else were equal, the differences in area under two curves of the seasonal trend of photosynthesis should be a reflection of differences in growth potential. There are differences in the seasonal course of assimilation among progenies of loblolly pine as shown by figure 3. Potted seedlings were grown under natural conditions at Raleigh, North Carolina. Sample plants were removed, dried, and weighed on a weekly basis. Growth curves were fitted and net assimilation rates calculated by the methods of Hughes and Freeman (1967). The curves show that some genotypes maintain photosynthesis at nearly constant levels for a long period in their development while assimilation in others begins to decline rapidly after the first week. In individual cases, this variation in the seasonal or developmental trend of assimilation rate can be used to explain differences in growth. If these seasonal patterns are as constant from tree to tree in subsequent years as is time of bud break or bud set, phenological events with which they are undoubtedly linked, then they may have great value in studies of productivity.

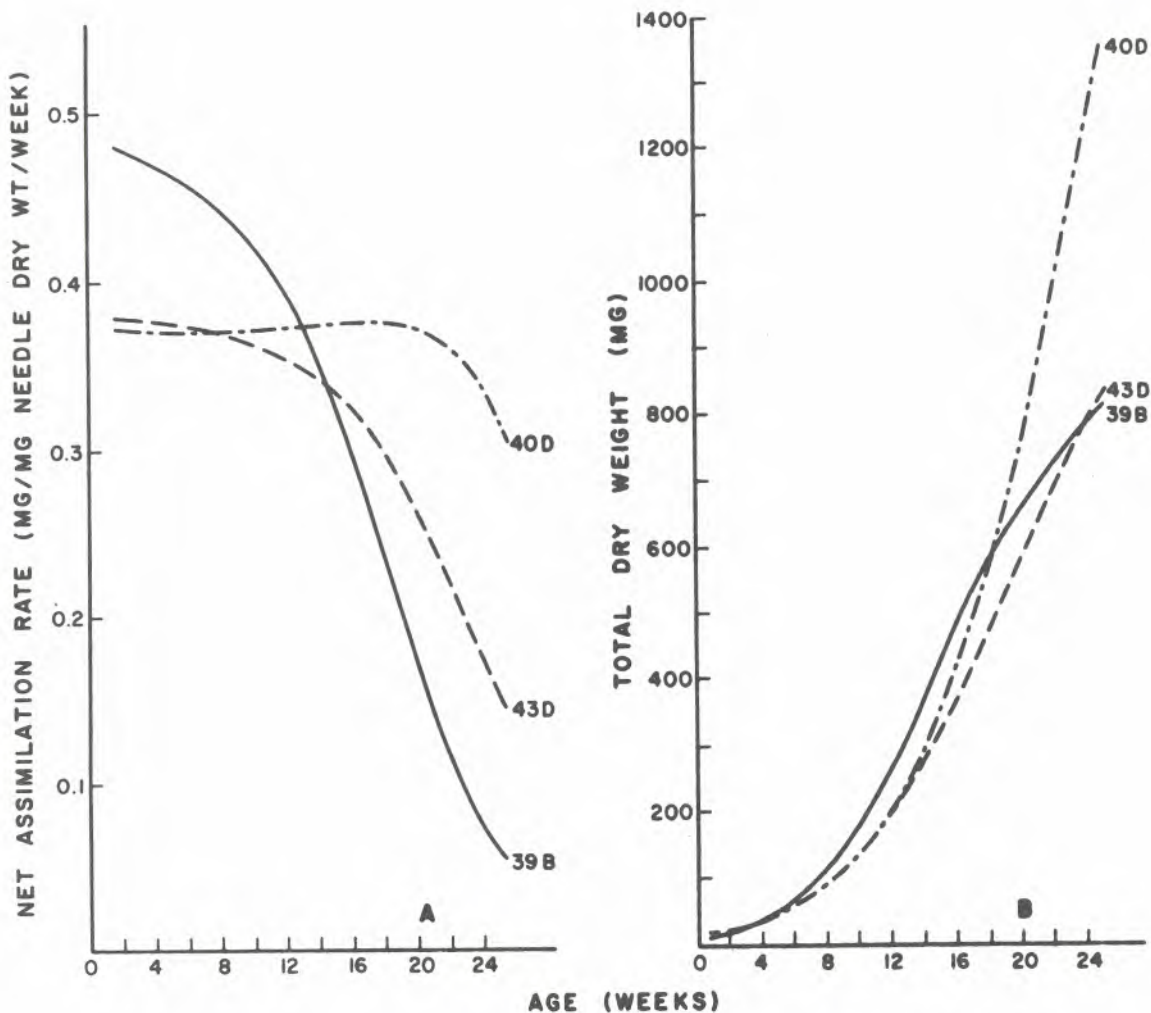


Figure 3. -- Duration-intensity aspects of photosynthesis and their effect on dry matter growth in loblolly pine.

- A. -- Net assimilation rate in family 40D remained constant for about 20 weeks after germination. Assimilation in 39B began to fall rapidly immediately after germination. The values for 43D are intermediate in this respect.
- B. -- Growth curves for the families cross; this can be rationalized on the basis of seasonal trends in assimilation rate. The areas under the curves in A are correlated with the growth of each family in B.

#### SUMMARY AND CONCLUSIONS

An attempt was made to portray dry matter growth in terms of three physiological concepts: (1) photosynthetic and respiration rates, (2) distribution of the photosynthate for growth between leaves and the remainder of the plant, and (3) duration-intensity aspects of the seasonal pattern of assimilation. It is emphasized that **measurements** of photosynthesis at a single period of time cannot account for growth. Variation among individuals in the amount of photosynthate allocated for leaf growth can affect productivity. Further, a seedling whose genotype enables it to carry on photosynthesis at a high rate at one stage of development may **not be superior** in this aspect at another stage. Intraspecific variation in seasonal patterns of net

assimilation rate was reported in loblolly pine and areas under the curves of net assimilation rate during one growing season were used to explain differences in growth.

Certain models are mathematically expressed which take these concepts into account. The effect of photosynthetic rate and relative leaf growth on accumulation of dry matter was demonstrated through computer simulation using simple models. A final step in the development of the model of growth is to express photosynthesis as a function not only of time but of light, temperature, and moisture, thereby extending its applicability to natural environments.

It seems possible that tree breeders may eventually be able to predict growth from measurements of physiological processes. However, the major contribution of this aspect of physiology-genetics will not be to allow precise discrimination among genotypes, rather, it will permit breeders to cull certain individuals and reduce costs of field tests by restricting attention to those progenies with the highest potential. It may also aid in increasing selection intensity by facilitating the testing of many more trees than has previously been possible.

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