

RELATION BETWEEN GROWTH AND UNIT RATE OF PHOTOSYNTHESIS

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Increases in stem height and diameter, the usual yardsticks of growth in forest trees and seedlings, are the result of the increase in dry matter of the tree as a whole and the distribution of that dry matter into stem, roots, foliage. The net increase in dry matter is the sum of the products of photosynthesis and mineral uptake minus the amount lost in respiration, leaching, guttation, leaf and twig abscission, and death of roots. Actually, photosynthesis accounts for 80 to 90 percent of the gross dry weight increase, and respiration can use from 20 to 40 percent of the manufactured food.

A faster growing plant is thus one which accumulates more dry matter per unit of time. This rate is dependent upon the amount of cell material actively engaged in assimilation and its efficiency. Dry matter increment per unit of "growing material" should remain constant for a given plant under constant environmental conditions and could be considered as a measure of its growth efficiency. Such constant rates were found in populations of yeast cells (Slator, 1913) where all the matter is engaged in growth. In higher plants, however, the situation is more complicated because only a fraction of the total dry matter is participating in assimilation and this fraction changes continuously as the plant develops.

Several attempts have been made in the past to define growth constants in higher plants which might be used as growth efficiency criteria. Two of them will be mentioned.

The first is Blackman's efficiency index (1919). By applying compound interest law to plant growth, he reasoned that leaf area increased as growth proceeded and that this brought about a corresponding increase in photosynthates which produced more growth, more leaf area, and so on. He proposed the formula $W_1 = W_0 e^{rt}$ to express the relationship between final and original weight with r as the rate of interest or efficiency index. It was found that r varied considerably from species to species under similar environmental conditions. It also varied with the stage of development of the individual plant.

The second concept is that of unit leaf rate (Briggs, Kidds and West, 1920) also known as net assimilation rate (Gregory, 1926). Briggs et al. had found by plotting relative growth rates (R) of corn plants, i.e. amount of dry matter change (dW) per unit of dry matter (W) per unit of time (dt), or $R = 100 \frac{dW}{W dt}$, that the curve obtained was almost parallel to the curve expressing $\frac{WT}{w}$ the leaf-area ratio (A), i.e. the ratio of leaf area (L) to dry weight (w). This suggested that the increase in dry weight per unit leaf area ($E = 1/L \frac{dW}{dt}$) should remain fairly constant. Actually it varies in annual plants, first going up very rapidly, then being uniform for a fairly long period, then falling off gradually. Relative growth rates are thus the product of leaf-area ratio and net assimilation rate: $R = 100 AE$.

Williams (1939) and others improved upon Gregory's E by expressing it on the basis of unit leaf protein nitrogen (E_p) instead of unit leaf area. Watson (1947) made a thorough analysis of growth data for several field crops over several years. He found that net assimilation rates varied under similar environmental conditions from species to species and even among varieties of the same species. Leaf-area ratios varied similarly and actually accounted for more variation in yield than did the differences in net assimilation rates.

The preceding ways of evaluating the growth efficiency of plants have one serious drawback; it is necessary to grow the plants for long periods of time and sample them at regular intervals to determine leaf-area ratios and net assimilation rates. Since the latter (increase in dry weight per unit leaf area per unit time) are largely determined by the difference between total photosynthesis and total respiration over a given length of time, they might be estimated by making direct measurements of the two processes under standard conditions. A comparison between growth rate and unit rates of photosynthesis and respiration will show whether or not there is a good correlation between the three processes; in other words whether growth differences are due more to differences in the efficiency of the photosynthetic apparatus or to its size (leaf-area ratio) or to some duration factor (length of time during which photosynthesis is carried on).

If a good correlation between growth and unit rates of photosynthesis and respiration can be established it will be possible to determine rapidly the effect of environment or heredity on present and even future growth. Early detection of potentially fast-growing or more efficient seedlings could be made in nursery beds. Selection of parent trees for controlled breeding could be made, as John Decker suggested in 1953, by measurements of photosynthetic and respiratory rates on branches of the prospective parents. For instance trees with high total photosynthetic rates but high respiratory rates could be selected to be crossed with trees of low respiratory rates to obtain progeny of high net photosynthetic rates, thus efficient dry matter accumulators.

Such a prospect is very appealing. The basic idea is simple and measurements of photosynthetic and respiratory rates can be made fairly rapidly with an infrared CO₂ gas analyzer. There are many pitfalls, though. First, to have comparable data it is necessary to make the measurements under uniform and standard conditions of temperature, light intensity and quality and CO₂ concentration. Other difficulties reside in the plant material itself. It is often impractical to make the measurements outdoors because of the extreme variability of environmental conditions and the bulk of the equipment, although it might be possible to design a portable set-up with provisions for light and temperature control. Branches can be severed and brought indoors for measurement, since Clark (1953) showed that severing does not affect photosynthetic rate. In studies involving seedlings which are not to be destroyed, the best solution is to use detached leaves or needle fascicles. The results obtained at Valhalla indicate, in agreement with Willst9tter and Stoll (1918) that rates of detached leaves are comparable to those of intact foliage for several hours, provided that the petioles or needle bases are in water and that a high relative humidity is maintained in the system. Another source of trouble is that rates of photosynthesis vary with the age of the leaf and the light intensity under which it developed. This makes it necessary, when comparing different plants, to use leaves of the same degree of development and grown under comparable light conditions. It has also been shown that an induction period is required to reach steady rates of photosynthesis. The length of this period varies greatly with

the species, the individual and even the individual leaf sample and also with the pre-treatment. Quite often as much as 1 hour is required. In addition, due to some internal factors, rates of photosynthesis may fluctuate under uniform environmental conditions by as much as 10 to 20 percent without any apparent reason. These fluctuations sometimes show a regular pattern but often are quite erratic (Rabinowitch, 1951, p. 879). Finally the variability in rate of photosynthesis between individuals of the same species or even the same clone can be very great. As a result, although definite trends may appear in average rates, statistically significant differences often fail to materialize unless numerous replications are taken. Respiration rates, on the contrary, are less variable.

In view of the potentialities and limitations of this approach to the study of growth efficiency, it might be desirable to review briefly some of the work done along these lines with forest trees.

Polster (1955) compared Douglas fir, eastern white pine and Norway spruce planted in Germany, where Douglas fir can produce about twice as much dry matter per Ha as spruce or 50 percent more stem volume. His determinations of photosynthesis and respiration were made outdoors on attached twigs of large trees using an open system. Rates were recorded at short intervals together with light intensity, temperature and humidity. It was found that Douglas fir carried on photosynthesis at consistently higher unit rates than white pine and spruce, the differences being greater the more favorable the environmental conditions. For instance on a given day the average rate was 1.41 mg CO₂ per gm. needle fresh weight per hour for Douglas fir, 0.84 for white pine, and 0.74 for spruce. By combining data on photosynthetic rates and foliage mass a good correlation was found with total dry matter production.

Huber and Polster (1955) made a similar study but this time restricted to clones of poplars, mostly hybrids of the sections Aigeiros and Tacamahaca. Large differences were found in unit rates of photosynthesis and respiration (from 2.19 to 4.56 and .35 to 1.99 mg CO₂/ dm²/ hour respectively).

Poplars in general proved to have relatively high photosynthetic rates and low respiration rates when compared to other species, which may account for their high growth rates. Among the 16 clones investigated, very good agreement was obtained between unit rates of photosynthesis and production of wood per ton of foliage. Combination of unit rate and leaf mass ratio were again well correlated with production per Ha.

McGregor and Kramer (1957) on the other hand, studied the relationship between photoperiod (9.5 and 15 hr.), growth and photosynthetic rate in loblolly pine and found that greater growth under long photoperiod was not due to greater unit rate of photosynthesis but to greater rates per seedling.

Some exploratory measurements on seedlings growing in nursery beds and in the greenhouse were made at Valhalla. The apparatus consists of a Liston-Becker infrared gas analyzer which can detect changes in CO₂ concentration of less than 5 ppm, and an Esterline-Angus recorder. The shoot or leaves are enclosed in a Lucite chamber forming a closed system with the sample tube of the analyzer, a diaphragm air pump and a flowmeter. The light source is a Fluomeric bulb, a new type of lamp which combines incandescent filaments and mercury arc and has a spectral energy distribution well distributed in the visible range (L00 to 700 mu). Light intensity is varied by varying the distance of the light to the chamber or by using gauze screens. Cooling is effected by the inter-position of a cold water layer the circulation of which is controlled by a Thermocap relay. Temperature can be kept within ± .5°C in this manner.

Measurements of photosynthesis were made at 25⁰C under 1 or more light intensities, the highest one being 2,500 foot candles. Detached leaves or fascicles were mostly used, placed horizontally and with their base in water. An induction period at the highest light intensity, as long as necessary to obtain steady photosynthetic rates, preceded the actual measurement. When fluctuations in rate occurred, the maximum rate attained was considered as the most valid one. Respiration rates were determined from measurements of CO₂ output in complete darkness at the same temperature.

A number of species were compared. For instance Douglas fir (variety viridis) and Norway spruce seedlings of the same age growing side by side in a nursery bed gave average (P+R)/R ratios (P = apparent photosynthesis at 2,500 foot candles and 25⁰C, R = respiration rate at 25⁰C) of 2.47 for the Douglas fir and 1.80 for the spruce, a difference which was reflected by the better height growth of the Douglas fir in this particular case. Jack pine seedlings in the same nursery gave a ratio of 2.0 although they were bigger than the Douglas fir. However, the leaf-area ratio was much greater which compensated for the relatively low unit rate of net photosynthesis.

Among seedlings grown in the greenhouse, Monterey pine and Pinus pinea had (P + R)/R ratios of respectively 5.36 and 6.36, with a much lower leaf-ratio for the latter probably causing the appreciable difference in total growth. Sand pine, another fast-growing species gave a ratio of 6.37 while the slower-growing Austrian pine had a ratio of only 2.15.

In the preceding measurements, respiratory rates at 25⁰C varied from .48 to 1.63 mg CO₂/g fresh weight/hour and apparent photosynthetic rates at 2,500 f.c. varied all the way from .19 to 5.28 mg CO₂/g fresh weight/hour.

These data suggest that unit rates of photosynthesis or (P+R)/R ratios have some usefulness in estimating growth efficiency but that as much attention has to be paid to the foliage ratio.

Individuals of the same species showing obvious differences in growth rates were studied. In one test rates were determined on small, medium and large slash pine seedlings grown in close association in large pots. Although the smallest seedlings were in most cases less than a third the height of the largest ones, no differences at all were found in the unit rates. It is possible of course that the growth differences were due in part or mostly to differences in seed weight, microenvironment or time of germination.

Similar tests are under way with black and northern red oak seedlings and so far a definite trend appears, showing larger unit rates and (P+R)/R ratios in the larger plants.

In the last few months, F. Mergen has been conducting a study on colchicine--induced polyploidy in slash pine. Polyploid shoots were grafted on normal stocks and this provided an opportunity to measure photosynthesis and respiration in diploid and polyploid needles growing on similar root systems. In primary needles the (P+R)/R ratios were 1.99 for the diploids and only 1.65 for the polyploids, and in secondary needles 2.04 and 1.47 respectively. Average respiration rates on the other hand were almost identical. These differences in photosynthetic efficiency are well correlated with differences in growth rates, the polyploids being markedly more sluggish than the diploid shoots.

In conclusion it seems that the use of rapid measurements of photosynthetic efficiency offers some promises in the selection of potentially fast-growing individuals but the method has certain serious limitations and much more work needs to be done to ascertain its value.

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