PHYSIOLOGICAL LIMITATIONS OF PRODUCTIVITY

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The crop breeder who attempts to increase economic yield potential traditionally proceeds in an empirical fashion. This approach has worked well in the past, but it has its obvious drawbacks. First, it is slow, particularly in the case of tree crops, and, second, the results are not necessarily general. That is to say, the yield of a crop is as much a reflection of its genetic make-up as it is of the environment in which it grew.

By attempting to isolate specific attributes that control productivity we may hasten the selection process and make the results more generally valid. But, in fairness to crop breeders, it must be recorded that neither crop physiologists nor crop ecologists have set out specific goals for breeders to attain.

We will indicate here two principal aspects of productivity in which both environment and crop interact to result in a physiological ceiling of performance. The first is light utilization in photosynthesis and the second is the water balance.

Light Utilization

A given site is characterized by a given photosynthetic light climate as measured by the spectrally distributed radiant energy per unit horizontal surface and per unit time (day, month, year) in the wave band from 0.4 to 0.7 microns. On the basis of present knowledge, there is no important difference in the effectiveness for photosynthesis of light within this broad band (Federer and Tanner, 1966). There is some difference in light absorption in that the green light is absorbed less than the other colors, giving foliage its color, both in reflected and transmitted light. Again, within the 0.4 to 0.7 micron waveband, the spectral composition of natural light does not vary greatly. We can, therefore, measure the "plantwatts" per square meter or PAR (photosynthetically active irradiance), in first approximation, with a standard pyranometer with a heat absorbing filter that cuts off at 0.4 and 0.7 microns, (McCree, 1966). Sometimes, a standard fraction of the total measured short wave radiation (0.3 - 2.3 microns) is used to arrive at PAR but this is a much worse approximation.

The question is what use the crop canopy can make of the incident radiant flux so defined and measured. First of all, this is a physical problem in light interception and it is laid out in terms of sun angle, leaf angle, leaf area index, and other geometrical and morphological characteristics of the canopy. The calculations become very complicated and solutions can be found only by computer simulation.

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So far, work of this sort has been done for broadleaved canopies only and it has given us some insight into the optimum morphology of plant stands (Duncan, et.al., 1967). No efforts have been made to deal in the same way with canopies of needle-shaped leaves.

The fate of intercepted light depends upon radiative properties of foliage. It remains yet to be seen whether there are significant differences between species and within progenies in a breeding program, that could be the basis of selection.

Finally, the utilization efficiency of absorbed light in photosynthesis may also vary as the result of differences in internal leaf structure or in biochemical factors. Experimentally, the two categories of effects are lumped together when we measure the CO2 fixation rates of individual leaves as affected by varying levels of incident light.

It appears that a consideration of the growth habits of trees in regard to leaf angle, leaf area index distribution, leaf size and shape is one parameter that deserves study and could be the basis of rational selections.

Another possible useful parameter is the "light-saturation" curve of individual leaves at standard levels of carbon dioxide concentration and at standard leaf temperatures.

Water Balance

The potential of a leaf array in a given light environment for photosynthesis and growth can only be realized when a favorable water balance in the leaf exists. The explanation of adverse effects of water deficits upon photosynthesis is not fully established (Slatyer, 1967), but at least a partial explanation resides in the closure of leaf stomata that results from a decrease in water potential and water content. Regardless of cause, the necessity for minimizing water deficits calls attention to at least three physiological factors with physical significance.

First, we must consider the nature of root systems. The leaf water potential is always lower that the root water potential and the latter is lower than that of the soil water potential by the following amount (Gardner, 1960):

$$\Delta \psi = \frac{E}{4 \pi d K L} \ln (1/ \pi L r^2)$$

E is the rate of water use by the canopy and L the root density in cm . Further, d is the depth of the rooting zone, K the hydraulic conductivity of the soil and r the root radius. The important thing about this equation is that **it** shows how the potential drop involved in water transfer from soil to root is directly related to both depth and density of rooting. The product dL could be called a root proliferation index and it could well be an important basis for early selection.

Second, an additional drop in water potential is represented by the translocation of water from root to leaf. The conductivity of stems or trunks for water is considerable and Scholander (1965) has demonstrated in certain cases that the potential drop can be accounted for on the basis of elevation alone. This may not be so always and further studies should be made of the role of the distance between leaf and root on leaf water potential. It may turn out that tall trees are not the most efficient ones, in part because of the adverse effect of height upon leaf water balance. Such a consideration would have an important inference for selection.

Thirdly, the depression of leaf water potential relative to the potential of soil water is directly proportional to the actual rate of water loss, or the transpiration. This parameter is, in part, controlled physiologically through the stomata in the following way (see Van Bavel, 1967).

$$E_a = E_o\ (\varepsilon + 1)/(\varepsilon + 1 + r_s\ C_d\ u)$$

E_0 is the potential or maximum possible water loss, determined by the weather. E_a is the actual water loss, ε a number dependent upon temperature, C_d a crop constant (drag coefficient) and u the windspeed. The role of the stomata is in the factor r_s, which, in first approximation, can be equated to:

$$r_1\ /\ LAI$$

the leaf resistance divided by the leaf area index. In turn, r_1 is determined by the number of stomata per unit leaf area, and the length and hydraulic radius of ;the individual stomata. On broad leaves r_1 can be readily measured (Van Bavel, et.al., 1965).

It can thus be seen that water use can be regulated by stomatal morphology and physiology. Decrease in water use results in maintenance of leaf water balance at a higher level.

At the same time, stomatal aperture influences CO_2 entry and photosynthesis. The optimum value for the parameter r_s and r_1 can only be determined by direct experimentation on the water use efficiency of individual leaves, and leaf arrays. When properly carried out such studies could be a valuable tool in selection of promising strains. In such tests it is essential that the environment be known, controlled and realistic. Currently available environment chambers leave much to be desired with regard to the light factor and the control over CO_2 concentrations.

Conclusion

Only two important aspects of plant foliage and of canopies that control plant productivity have been discussed. These characteristics of the plant cover can be specifically identified and measured in a physically justified way. These traits may be useful as criteria in the selection of high-yielding strains in a breeding program, but not enough work has been done to assure the breeder of success in this way.

There are certainly very special problems when trying to measure the physical properties of needle-like leaves. Light climate studies under canopies of needles (Logan and Peterson, 1964) are not sufficient; we must know why and how such climates come about. Also,the light must be measured in a physiologically meaningful way. But, apart from this, modeling of light interception and light utilization by needle canopies is going to be difficult.

There are indications (Szeicz, et.al., 1969) that in a pine forest the role of stomata in water loss is dominant over other foliage parameters. To what extent this applies to CO_2 exchange is an open question. Controlled studies of water use efficiency in needle canopies and the variation between species and strains appear an appropriate field of research that could give direction to the efforts of breeders.

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