Crop Energetics and Horticulture

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Since crop productivity depends directly on photosynthetic efficiency, it is desirable to understand the environmental and internal factors that regulate photosynthetic rate. The purpose of this article is 1) to outline some general features of horticultural plants which enable them to utilize the aerial environment and to compare their photosynthetic behaviour with that of some other rapidly growing crop species and 2) to see if information on the physiology of energy utilization by plants is relevant to horticulture.

THE COMPARATIVE PHYSIOLOGY OF PHOTOSYNTHESIS

Economic productivity is the outcome of the plant’s ability to both generate and distribute its photosynthetic products. The initial formation is most clearly related to how efficiently their leaves exploit the aerial environment with respect to light and CO₂ absorption. Light absorption is a function of leaf presentation and canopy architecture generally, while the CO₂ scavenging capacity of the leaves (at a saturating intensity of light) depends upon leaf porosity and the steepness of the CO₂ concentration gradient from the atmosphere to the chloroplasts. Internal factors determine this gradient.

The advent of infrared gas analyses as tools for horticultural research has enabled studies of CO₂ exchange by single leaves, by whole plants, and even by whole communities of plants such as a field of corn, a vineyard, or an apple orchard. Rates of CO₂ uptake per unit leaf surface vary, even under favorable conditions, over almost 2 orders of magnitude. Some broad scale comparisons of generalized groupings are made in Table I. The comparisons are in no way exhaustive and are not mutually exclusive categories, but are included to illustrate observed photosynthetic rates in various types of plants. The real situation is far more complicated than Table I suggests because of variation due to environmental factors and differing physiological states. Despite the gross approximations of such a survey, 2 distinct categories of plants emerge: group A represents those plants in which CO₂ fixation depends upon the enzyme ribulose diphosphate carboxylase (RUDP). They possess the reductive pentose phosphate or Calvin cycle of CO₂ fixation. This group includes the vast majority of plant species. Such plants are commonly called C₃ plants because the initial product of CO₂ fixation by their chloroplasts is a 3 carbon compound. The second group B includes plants which possess a different CO₂ fixing system in addition to the C₃ pathway.

They have almost universally higher rates of photosynthesis and represent a more recent evolutionary advance, thought to be the outcome of environmental pressures for short term rapid growth. Associated with their high rates of photosynthesis, compared to C₃ plants, is an enhanced translocation efficiency of their photosynthetic products (18), a lower resistance to inward diffusion of CO₂ (11), a virtual absence of photorespiratory CO₂ evolution and apparent CO₂ compensation points close to zero (12). These features all contribute to a steeper CO₂ concentration gradient i.e. a lower CO₂ concentration at the chloroplast, thus favouring CO₂ diffusion into the leaf. They also have bimorphic chloroplasts with specialized plastids in mesophyll versus vascular bundle sheath cells (2,23). Their CO₂ fixation is principally due to the enzyme phosphoenolpyruvate carboxylase (PEP) with entry of fixed carbon into a C₄ dicarboxylic acid. This enzyme functions in the mesophyll cells of the leaf. Subsequent biochemical transformations, analogous to those of the Calvin cycle of C₃ plants, then occur within the larger chloroplasts of parenchyma cells in the vascular bundle sheath.

To differentiate this category of plants from the former group (A) they are referred to as C₄ plants.

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FEATURES

Agricultural Books for Biology Majors?

Suppose you were asked to suggest 7 book titles, and only 7, to serve as a library holding in agriculture for undergraduate students in biology. Which of the following would you include?

- Plants, Man and Life, E. Anderson
- Agricultural Genetics, J. L. Brewbaker
- Silent Spring, R. L. Carlson
- Environmental Conservation, R. F. Dasmann
- Marine Aquaria, L. A. J. Jackman
- Poisonous Plants of the United States and Canada, J. M. Kingsbury
- From Fish to Philosopher, H. W. Smith

Chances are, if you are a typical professional in the field of agriculture you would include only the second title listed. But believe it or not, these 7 titles were the only one listed under agriculture in Guidelines and Suggested Titles for Library Holdings in Undergraduate Biology, recently published by the Commission on Undergraduate Education in the Biological Sciences supported by a grant from the National Science Foundation to AIBS.

At a time when undergraduate interests in the plants, animals and natural resources around them are stronger than ever, and when the emphasis is clearly on relevance, it is unbelievable that any group could be so far off-base with its recommendations. There are literally hundreds of modern texts in agriculture that more logically might have been included. One is tempted to ask why the sponsoring organization, AIBS, did not seek the advice of bona fide agriculture, or, alternatively, suggest that CUEBS not attempt to make recommendations outside its area of competence.
Table 1. Comparative rates of maximum photosynthesis (21).

<table>
<thead>
<tr>
<th>Type of plant</th>
<th>Maximum photosynthesis (mg CO₂ dm⁻²·hr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slow growing perennials (desert spp. orchids, some Crassulaceae)</td>
<td>1.0</td>
</tr>
<tr>
<td>Evergreen woody plants (tropical and subtropical trees and shrubs and temperate zone evergreen conifers)</td>
<td>5.0</td>
</tr>
<tr>
<td>Deciduous woody plants (horticultural plants and trees) and temperate zone deciduous broad leafed trees and shrubs</td>
<td>15.0</td>
</tr>
<tr>
<td>Rapidly growing agronomic plants (wheat, soybeans, sugar beet, sunflower) and temperate zone herbs.</td>
<td>20.0</td>
</tr>
<tr>
<td>Tropical grasses and other plants with the carboxylase acid fixation pathway (sugar cane, corn, Amaranthus, Atriplex)</td>
<td>50.0</td>
</tr>
</tbody>
</table>

2 Based on projected leaf area.

One further distinction between C₃ and C₄ plants is their energy requirement for CO₂ assimilation. Hatch and Slack (15) estimate that 5 moles of ATP and 2 moles of NADPH₂ would be required for incorporation of each mole of CO₂ into carbohydrate via the C₄ pathway. By contrast, CO₂ assimilation via the Calvin cycle requires only 3 moles of ATP and 2 moles of NADPH₂. The C₄ pathway is thus more energy efficient, but this slight inefficiency is more than offset by the absence of photorespiration, which in C₃ plants commonly lowers the overall efficiency of CO₂ assimilation by about 33%. The C₄ plants do however seem geared to cope with this slightly higher energy requirement; Black and Mayne (6) have pointed to the relatively higher level in C₄ plants of specific chlorophylls (e.g. P 700) directly involved in photochemical events, which generate proportionately more ATP in photosynthesis than in C₃ plants, and thus satisfy the greater ATP requirement of the C₄ fixation pathway.

The raw materials of photosynthesis including light, CO₂ concentration, and water supply. We should also include under "environmental" those factors that influence the rate or end products of photosynthetic reactions. These include: temperature, O₂ concentration, nutrient supply, exogenous chemicals, light quality as well as intensity, and even day length.

Inevitably these 2 groupings (internal and environmental) tend to be artificial because, in nature, many different factors interact continuously to dictate plant performance. Furthermore, an environmental factor such as light which is known to produce a well defined photosynthetic response really operates via internal control systems such as photochemical activity, and enzyme level which are under direct genetic control, and diffusive resistance of the leaf. A clear discrimination between environmental and internal controls, for every situation, is therefore impossible. Similarly, to examine a single environmental parameter, and exclude all others, in the hope of gaining complete understanding of the natural ecological situation is unrealistic. Since it's virtually impossible to comprehend all possible interactions, we will deal here with some major control systems and then consider the practical significance of some interactions.

Internal factors

Enzymes govern the rate, and sometimes the direction of metabolic events. This is especially true for photosynthesis since gas exchange studies on single leaves (Table 2) show that internal "resistances" to CO₂ fixation (Fig. 1) can be rate limiting, especially where low rates of photosynthesis are observed. In other words, the rate of CO₂ fixation by the chloroplast is often the chief "impedence" to photosynthesis.

While photosynthesis is enhanced by higher activity of its carboxylating system, the converse is true in C₃ plants at least with respect to activity of enzymes in the closely linked photorespiratory system. This system which is partly housed in the peroxisome (Fig. 1) generates CO₂ in close proximity to the chloroplasts within the cell. It is therefore linked to photosynthesis in C₃ plants. As light energises the photosynthetic machinery of the leaf, there is a concomitant enhancement of CO₂ evolution which depends upon the presence of O₂. The rate of photorespiration is zero or near zero in the absence of oxygen and increases with increased oxygen concentration. The substrate for photorespiration is probably an intermediate from the Calvin cycle, and the enzyme glycylate oxidase plays a central role in its dissimilation. By chemically inhibiting the activity of this enzyme, Zelitch (31) was able to show an increase in tobacco leaf photosynthesis. Understandably the tobacco leaf then showed other characteristics of C₄ plants which are correlated with the virtual absence of photorespiration, such as low CO₂ compensation point and higher optimum temperature for photosynthesis, as well as a generally elevated rate of CO₂ fixation.

The consequences of photorespiration are extensive; firstly

CONTROL SYSTEMS FOR PHOTOSYNTHESIS

For convenience we can divide the factors regulating photosynthesis into categories of internal and environmental factors. We shall then examine how they influence rates of photosynthesis. By "internal" we imply some response on the part of the plant whereas "environmental" covers all factors imposing from outside the leaf such as

Table 2. Comparative photosynthesis among species in relation to CO₂ diffusive resistances (11).

<table>
<thead>
<tr>
<th>Species</th>
<th>Photosynthesis (mg CO₂ dm⁻²·hr⁻¹)</th>
<th>Transpiration (g H₂O dm⁻²·hr⁻¹)</th>
<th>Leaf stomatal resistance (sec cm⁻¹)</th>
<th>Internal Resistance (sec cm⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corn</td>
<td>63 ± 2</td>
<td>3.3 ± 0.2</td>
<td>1.5</td>
<td>1.0</td>
</tr>
<tr>
<td>Sunflower</td>
<td>50 ± 1</td>
<td>3.5 ± 0.2</td>
<td>1.7</td>
<td>1.5</td>
</tr>
<tr>
<td>Cotton</td>
<td>38 ± 1</td>
<td>3.1 ± 1.0</td>
<td>2.0</td>
<td>2.9</td>
</tr>
<tr>
<td>Oats</td>
<td>31 ± 1</td>
<td>3.6 ± 1.6</td>
<td>1.7</td>
<td>4.1</td>
</tr>
<tr>
<td>Soybean</td>
<td>25 ± 1</td>
<td>2.3 ± 0.6</td>
<td>2.7</td>
<td>5.5</td>
</tr>
<tr>
<td>Hibiscus</td>
<td>23 ± 5</td>
<td>3.1 ± 0.7</td>
<td>1.9</td>
<td>7.3</td>
</tr>
<tr>
<td>Thespisn</td>
<td>18 ± 5</td>
<td>2.8 ± 0.5</td>
<td>1.1</td>
<td>9.7</td>
</tr>
</tbody>
</table>
Fig. 1. A highly schematic view of gas exchange by a leaf. Fluxes and resistances are shown in the form of an electrical analogue (with open circuit!). chl = chloroplast; m = mitochondrion, p = peroxisome, vac. = cell vacuole, r_a & r_5 = stomatal resistance (to H_2O and CO_2 exchange respectively), r_a & r_5 = stomatal resistance (to H_2O and CO_2 exchange respectively), r_c & r' = cuticular resistance (to H_2O and CO_2 exchange respectively), r_m = mesophyll resistance to CO_2 diffusion, r_x = carboxylation "resistance" (in effect r_x embodies all the biochemical limitations to CO_2 assimilation). The term leaf resistance (r_{L1}) is also commonly employed in the present context, and refers to the summation of stomatal and boundary layer resistances i.e. r_{L1} = r_a + r_5 or r_{L1} = r_a + r_5.

the CO_2 evolved close to the chloroplast reduces the CO_2 concentration gradient between the chloroplast and the atmosphere. This reduces the flux of CO_2 into the leaf; secondly, if the precursor for the CO_2 evolved comes from the Calvin cycle, this will lower the concentration of potential CO_2 acceptor molecules; and, thirdly, the photorespiratory CO_2 by recycling into the CO_2 fixing system competes with the CO_2 from the atmosphere. All of these events contribute to a reduction of net photosynthesis.

During photosynthesis in algae and in C_3 plants, up to 50% of the carbon fixed may have to pass through the glycolate "cycle" enroute to sucrose (for transport elsewhere in the plant) so that photorespiration in C_3 plants must be regarded as an integral part of carbon assimilation and not simply an addendum to photosynthesis.

Leaf resistance to gas exchange. Since CO_2 reaches the chloroplasts initially via the open stomata, the resistance offered by these pores to gaseous diffusion could help regulate photosynthesis. Fig. 1 shows the pathways for gaseous exchange between the outside air, and the reaction centres of the leaf (chloroplasts, mitochondria and peroxisomes) in a schematic form, and demonstrates how both H_2O and CO_2 exchange are under stomatal control. In C_4 plants, internal resistance is generally of the same order of magnitude as leaf resistance, and does not in itself represent the major limitation for photosynthesis (see Table 2). For these C_4 plants, leaf resistance (controlled primarily by stomatal aperture) does appear to regulate photosynthesis (11).

The means of regulation differs for C_3 plants (Table 2), especially in the

Fig. 2. Both photosynthesis and transpiration are under stomatal control. As stomatal aperture decreases (i.e. resistance rises) both H_2O and CO_2 exchange are affected, although disproportionately (22). (See also next Fig.)

Fig. 3. During the initial phases of stomatal closure orange leaf transpiration is affected to a greater degree than is photosynthesis. The ratio of H_2O vapor/CO_2 exchange therefore declines as leaf resistance rises (22).
tropical evergreens with low rates of photosynthesis (see Table 1). Although both H₂O and CO₂ exchange are partly controlled by leaf resistance (some data for orange leaves are shown in Fig. 2 and 3) there is a greater reduction in transpiration than in photosynthesis as stomata begin to close — i.e. the ratio of transpiration/photosynthesis is reduced (Fig. 3). These data suggest that internal resistances (including the leaf's carboxylating efficiency) offer a substantial resistance to CO₂ fixation. Gastra (14) arrived at a similar conclusion more than a decade ago following his work on a variety of other C₃ plants.

The demand for photosynthesize. The central issue here is whether a plant grows faster because it photosynthesizes more vigorously, or whether controlling factors call for a change in growth, and then photosynthesis responds accordingly. The evidence reviewed by Neales and Incoll (26) gives the impression that photosynthesis is the consequence rather than the cause of a given rate of growth.

By analogy with the law of mass action, the greater the demand imposed upon photosynthesis, then up to a certain point, the greater will be the photosynthetic yield. The converse should also apply. There are numerous instances of such compensatory resistances. They can be evoked by reducing the leaf surface supporting a given crop which increases CO₂ assimilation per unit of leaf area, or by reducing the demand for assimilates by fruit thinning, meristem removal which causes the photosynthetic rate to decline.

In view of the hormonal control of photosynthesis known to occur (see below), it is insufficient to attribute such responses in photosynthetic rate to alterations in the demand for assimilation. Although terminal meristems or fruits do represent such "sinks", they also act as sources of hormones which might be regulating events at the point of photosynthesize supply, i.e. at the chloroplast.

Hormonal control. Hormonal regulation of a wide range of physiological events can be regarded as axiomatic, and photosynthesis seems to be such an event. CO₂ fixation is influenced by both leaf resistance and internal resistances and since both of these parameters are under hormonal influence, the effects of hormones on leaf photosynthesis could be usefully analyzed in terms of diffusive resistances.

One research groups in Aberystwyth, Wales have reported clear instances where gibberellin and cytokinin have elicited an increase in photosynthesis. The treated plants also showed a higher carboxylating activity, due apparently to enzyme activation rather than de novo synthesis (25). Previous experiments reported by this group had shown an increase in photosynthesis, following partial defoliation, which was again matched by a greater activity of carboxylating enzymes. It is nevertheless difficult to attribute quantitatively all the enhanced assimilation in remaining leaves to higher enzymatic activity as measured on extracts, because the component resistances to CO₂ fixation by the intact leaf were not derived. The need for such data is heightened by other observations on stomatal responses to applied cytokinins. Meidner (25) for example, reports that 3 x 10⁻⁵M kinetin caused a 12% increase in photosynthesis within an hour, but this increase was associated with a lower leaf resistance (increased stomatal aperture) and reduced CO₂ compensation point. Such observations immediately raise the question as to whether leaf resistance or internal resistance was altered by the cytokinin.

Since available evidence suggests both resistances are under hormonal influence, the question must remain open.

Growth stimulations caused by endogenous or applied plant hormones are likely to elicit a response in photosynthetic activity. This could be either the result of an increased demand for assimilates, or a direct effect of the growth regulator on photosynthesis. A third possibility is that newly formed tissue, i.e. the outcome of the growth stimulation, manufactures its own complement of hormones, which then regulates photosynthesis in the existing leaves.

Genetic makeup. A plant's photosynthetic activity, as well as its overall response to environmental conditions, and hence its growth rate, are all species dependent. Furthermore a plant's ability to utilize the aerial environment (leaf arrangement and light interception) as well as its capacity to adapt to new situations, such as changing from high to low light intensity, may be genetically determined. Evolutionary pressures of this kind can then lead to genetically distinct races and cultivars as developed by plant breeders (17).

Genetic control can be exerted on both the CO₂ fixing system and the CO₂ transporting system of the leaf. These influences would express themselves in Table 2 for example, as variation in internal resistance, or in leaf resistance, respectively. To a limited degree, the CO₂ fixing capacity of the leaf can be related to internal resistance, thus a lower internal resistance tends to correspond to a more efficient CO₂ fixing system.

The leaf's biochemical capacity to fix CO₂ is partly a function of the enzyme complement of its chloroplasts, which in turn is under the control of both the genotype and the organelle's own genetic machinery. Since the chloroplast can transmit its own genetic information independently, there is an opportunity for genetically based variation in photosynthesis.

Extensive studies on different clonal lines of woody plants, such as the low bush blueberry (13) show that slight but consistent differences do occur, but they are of small order compared to environmental influences. Similarly, the photosynthetic activity of hybrid and imbrided lines of corn has been compared by Elmore and co-workers in Arizona and again consistent differences existed, but any relationship with productivity was difficult to prove(10). This discouraging picture of only minor differences between closely related cultivars or species is of little encouragement to plant breeders who might wish to produce material with an intrinsically higher photosynthetic capacity. A large part of the difficulty resides in the cost and complexity of measuring photosynthesis. Instead of basing his selection upon some clear anatomical criterion, or outstanding feature of plant growth, the plant breeder is confronted by complicated measurements that need to be put on a routine basis. Many features of the plant's physiological status, as well as environmental factors, can lower photosynthesis. Before making valid comparisons between progeny it is therefore necessary to optimise factors determining leaf performance; a time consuming procedure that requires days or at best many hours. This problem of making selections based on photosynthetic rates is exemplified in the red kidney bean where the genetic mechanism controlling cultivar differences indicates dominance for low photosynthetic efficiency (20).

Under natural conditions, genetic control of photosynthesis is expressed, and the emergence of ecological races within a given genus does reflect the plant's ability to make useful alterations between its two environments. Probably the most impressive instance has been the emergence of C₄ plants as a physiologically distinct group that cuts across a large number of taxonomically unrelated genera. While evolutionary pressures for rapid growth over relatively short periods, as encountered in monsoonal climates, have produced the genetically distinct C₄ plant, adaptation to situations when growth is severely restricted (e.g. by light) can also have a genetic background. Ecological races of Sonchus illustrate some remarkable adaptation of this type which have been intensively studied both in Sweden and California.
Bjorkman and Holmgren (3) report their findings in a series of papers dating from 1963. These workers first compared the sun and shade races of Solidago and then the hybrid clones of an F1 population from a cross between the 2 races. The progeny showed a wide variation in photosynthetic behaviour with parental characteristics being recombined in many different ways. Differences in photochemical efficiency, carboxylase activity, leaf resistance, and internal resistance had all contributed to the divergence between the original parents.

Environmental factors

Light intensity. The availability of sunlight is often the most significant determinant of plant productivity in agricultural situations, and since the photosynthetic activity of individual leaves eventually limits the plant's productivity, there is obvious merit in understanding how individual leaves respond to light intensity. For present purposes, we will deal with the "instantaneous" responses to light, not the adaptive changes that can occur within the leaf such as chloroplast rearrangement, altered photochemical efficiency or modified anatomy.

Since the photosynthetic activity of a leaf depends upon a continuous supply of raw materials, in particular light and CO2, Blackman's (5) principle of limiting factors should operate, i.e. "when a process is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the slowest factor." Accordingly, the interaction of light and CO2 in determining photosynthesis should produce a family of curves as in Fig. 4. The slope of the response curve will be governed by the leaf's photochemical activity, whereas the availability of CO2 will dictate the light saturated rate of photosynthesis; hence the stepwise increments in Fig. 4.

Regardless of the general validity of Blackman's principle, real plants do not behave precisely this way. The light response curve does not show a sharp inflexion point, but rather a gradual transition from a linear increase at lower light intensity, to a plateau at light saturation (Fig. 5). Apparently, the gradient in light intensity within the leaf has something to do with the discrepancy between Fig. 4 and 5, because the behaviour of optically thin leaves, and especially thin algal suspensions, approximates the theoretical picture (19).

Additional differences between C3 and C4 plants can now be viewed in terms of their light response curves. Fig. 5 taken from the data of Hesketh and Moss (16) shows some broad scale comparisons. The initial slopes are comparable (except for philodendron) but the light saturated rates of C4 and C3 plants are substantially different, in fact the sugarcane leaf is not convincingly light saturated even at the highest light intensity used (virtually full sun). We can conclude that C3 and C4 plants do not differ significantly in photochemical activity, but are enormously different in terms of CO2 fixing capacity; i.e. they have different internal resistances (Table 2).

Carbon dioxide. The prevailing level of CO2 in the earth's atmosphere is generally insufficient to allow full expression of a leaf's photosynthetic activity. It seems anomalous that a leaf should be operating at less than its potential for so much of the time, but this pragmatic view is supported by a number of lines of evidence.

The photosynthetic response curves of Fig. 6 adequately demonstrate the increase in photosynthesis elicited by CO2 concentrations well above the ambient levels in the atmosphere (around 300 ppm). Obviously the availability of light will influence a leaf's ability to respond to added CO2, but at intensities approaching full sunlight photosynthesis responds to concentrations approaching 1000 ppm.

HORTICULTURAL APPLICATIONS

Selection of highly productive material

Since we rarely know the key determinant of plant productivity it is difficult to establish the right parameters for measurement, but assuming photosynthetic capacity is of fundamental significance and that it is the major determinant of a plant's economic productivity, then the plant's photosynthetic capacity would be a useful datum. To make valid measurements it is necessary to eliminate, or at least insure equivalent influences of internal and external controls on the photosynthetic rate of the material being compared. One approach, based on our foregoing discussion, would be to insure that environmental conditions such as water supply, light intensity, CO2 concentration and temperature are the same, and then perform the measurements. Even assuming that every individual in the whole population responded similarly to environmental parameters, and that's dubious, there is no guarantee that the internal restraints that do exist within plants have been minimized or made ideally the same. These internal controls are especially difficult to manipulate because of variation in leaf age, crop-load, and a host of other influences that are
embodied in the vague phrase "the physiological status of the plant."

Despite these difficulties in equating the physiological states of different plants it is possible to make photosynthetic comparisons between progeny, and the most realistic approach would be to derive component resistances to CO₂ fixation in single leaves. The plant breeder, cum physiologist, is now able to at least explain differences in photosynthetic efficiency and decide whether environmental controls are operating, say via stomatal resistance; or whether performance differs on the grounds of internal resistances. This is a more elusive parameter, but one which is more likely to be an inherent characteristic of the plant.

A
dditional factor in photosynthetic activity that warrants attention is cropload. Earlier in this discussion we outlined briefly the responsiveness of leaf photosynthesis to the demands placed upon it, that is, part of the internal control referred to above. One feature of particular interest was a leaf's capacity to respond to greater cropload by increasing photosynthetic rate. The plant breeder in making progeny comparisons would therefore need to ensure all of his material had reached the plateau of this response "curve."

Changing photosynthetic characteristics

Since C₄ plants show superior photosynthetic capacity, could this feature be transmitted to the C₃ horticultural plant without losing other desirable features of the commercial species? The exuberant growth of _Amaranthus_ (a C₄ plant and one of the most vigorous weeds) would for example, be a desirable trait in something other than a pest! Hybridization between C₃ and C₄ plants would seem a possibility, but even assuming that matching C₄ families were available for horticultural plants it would not be sufficient to simply equip the progeny with the necessary biochemical machinery for C₄ fixation. C₄ plants function as such because of their unique anatomical distribution of C₃ and C₄ fixing systems. The C₄ type of fixation occurs in the mesophyll cells of the leaf but this must be coupled to the C₃ fixing system of the parenchyma cells forming a sheath around each vascular bundle. Intermediate metabolites of the two fixation systems are then interchanged between cells of the mesophyll and of the vascular bundle. Only when these 2 CO₂ fixing systems have the right spatial arrangement, does the plant show the full spectrum of C₄ characteristics. Consequently, the inheritance of C₄ properties becomes more complicated.

The genus _Atriplex_ offers suitable species for experimentation. _Atriplex rosea_ is a C₄ plant, whereas _A. patula_ is a C₃ plant, but it's apparently not possible to incorporate enough of the C₄ plant characteristics into the C₃ plant to make it perform as a C₄ and yet resemble the parent C₃ in other respects. This experience was gained by Björkman and colleagues (4) at Stanford during the hybridization and subsequent segregation of a relatively small number of F₂ progeny using _A. rosea_ and _A. patula_ as parents. At the present stage this outcome is hardly encouraging for horticulturists concerned with modifying photosynthesis.

**Light utilization**

The manipulation of whole stems or vines to improve the plant's utilization of the aerial environment appears a more tangible goal than altering basic photosynthetic efficiency. While the intrinsic photosynthetic capacity of individual leaves imposes an upper limit on the tree's total dry matter productivity, this is rarely even approached because the canopy as a whole tends not to expose all of its foliar surface to a saturating intensity of sunlight. Admittedly, other environmental factors would counteract even if this level of exposure was approached in nature, but in horticultural situations, environmental limitations can be relieved. Some significant improvements in productivity and fruit quality have been achieved from an altered canopy architecture which provided better "ventilation" as far as solar radiation and gaseous exchange are concerned. The 'Concord' grape is a case in point, its canopy develops a pendulant form so that only the outer leaf layers intercept enough sunlight to saturate their photosynthetic machinery. By opening the canopy into a 'double curtain' Shaulis and co-workers (27) virtually doubled productivity over that from conventional single wire trellis which had favored the dense pendulant and poorly 'ventilated' type of canopy.

Some fruit trees might lend themselves to this same type of treatment as shown in related experiments on apple trees whose canopy has been opened horizontally instead of vertically as with the grapes (7). The altered apple tree canopy has the additional advantage of facilitating mechanical removal of fruit.

Close familiarity with the crop in question can amplify the horticulturist's appreciation of these changes in vine or tree form, because additional, and indeed unexpected benefits are available. For example, in grape vines, the improved exposure of growing shoots, especially on isolated vertical ones, can increase the percentage of buds on the subsequently mature cane which are reproductive rather than simply vegetative (24). Since the potential cropload is one determinant of photosynthetic rate and eventual commercial productivity, the consequences of altered canopy form were two-fold; one derived on the basis of improved leaf exposure, the other obtained empirically and awaiting physiological explanation.

**Carbon dioxide availability**

Since photosynthesis shows such an impressive response to CO₂ concentration, there is the prospect of enhancement for practical gain. Clearly the nature of this "fertilizer" limits its use. Being a gas it needs to be contained, and greenhouse application seems most realistic. Since CO₂ uptake is the outcome of physical diffusion followed by biochemical fixation, there will be some temperature component in the overall photosynthetic response (greater than would be expected from a strictly physical system). This is to be anticipated from the data in Fig. 6 and is also borne out in practice (1). Simply replenishing the air in a greenhouse and then maintaining reasonable turbulence will have a favorable effect on growth (30) due principally to improved CO₂ supply; one major effect of turbulence being a reduction in boundary layer resistance (see Fig. 1).

This enhanced CO₂ supply, especially in CO₂ enrichment experiments, does not necessarily improve yield. Excessive concentrations, say above 1000 ppm, are phytotoxic (14, 8) but even below this injurious level, the long term productivity of a plant population does not match the short term response in the laboratory. Firstly the higher CO₂ tension can lead to stomatal closure, thereby offsetting the improved availability of CO₂; and secondly, plants can show morphogenic responses at high CO₂ tension, such as reduced leaf area so that productivity by the whole plant, or by the population of plants does not increase in direct proportion to the unit rate of photosynthesis (28).

Despite these unfavorable side reactions to supplementary CO₂, total productivity is undoubtedly enhanced (1) and it only remains for the economist to weigh the cost of supplying and monitoring CO₂ against the added return from the improved photosynthetic activity. Based upon these criteria, atmospheric enrichment to about 1000 ppm CO₂ maximises potential profit. With further increases in CO₂ content the photosynthetic activity shows diminished response whereas running costs continue to rise steadily. Moreover, if sustained concentrations above 1000 ppm CO₂
are phytotoxic (14, 8) there is little merit in continuing CO₂ fertilisation beyond this level.

CONCLUDING REMARKS

Plant physiologists make an unfortunate distinction between the philosophies of “applied” as opposed to “basic” work. The “basic physiologist” tends to deal in ideas and principles and chooses material for his convenience. It is often difficult to extrapolate from these principles directly to the field and furthermore, the basic worker tends not to follow up his work in this direction. The applied physiologist (e.g., horticulturist) on the other hand, tends to deal with practicalities and on the basis of long term experience generally limits himself to a specific crop, or at least a certain category of crops e.g., pome fruit, citrus, cucurbits etc. Consequently, fundamental work based on plant material other than his own specialty will tend to be overlooked despite its potential usefulness. If the basic researcher fails to follow up his new findings in the direction of field applications, while the person with an applied philosophy overlooks potentially useful material simply because the work was done on the “wrong” plant, then inevitably there will tend to be an explosion of information out of all proportion to its application. The question arises as to how these divergent patterns can be reconciled.

For the horticulturist, basic physiology can have either explanatory or predictive value. In the first case, laboratory data might point to a mechanism which now explains what horticulturists already know about the behaviour of their material. In these instances, the horticultural technique has often been arrived at empirically, and the physiologist subsequently offers an explanation. (This pattern has been exemplified in the chemical regulation of development). By contrast, the predictive type of exercise is based on a detailed understanding of the plant’s physiological make-up; or at least a significant portion of it, so that the plant can now be manipulated as desired on a sound basis (which is pleasing to the originator, at least intellectually!). Mathematical modelling is gainfully employed for this type of undertaking, and has achieved success in environmental control of plant growth — especially in the agronomic situation (see Donald (9) and literature cited).

Unfortunately, horticultural plants, or at least the woody perennials, are not readily adaptable to this type of modelling, and our lack of knowledge of internal control systems prevents us from anticipating performance, or predicting treatment effects. Basic data can nevertheless find application given the right horticultural bias!

Literature Cited