

13

ENVIRONMENTAL AND EVOLUTIONARY CONSTRAINTS ON THE PHOTOSYNTHETIC CHARACTERISTICS OF HIGHER PLANTS

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PLANTS DIFFER in their photosynthetic capacity by over two orders of magnitude (Figure 13.1). Relative carbon-gaining capacity is a critical parameter in plant competitive relationships (Mooney, 1977). It is understood that factors other than carbon gain per se, such as reproductive output or success, may determine long-term fitness, but these in turn cannot be completely divorced from carbon-gaining capacity. In view of this dependence, we explore here a theoretical framework for the physiological and evolutionary basis of this variation in photosynthetic capacity among plant species. We then consider the implications of these constraints on photosynthesis for carbon allocation within the plant.

To structure this analysis, we employ the electrical analogy in which the photosynthetic rate (P) of a leaf is determined by the difference in the CO_2 concentration between the bulk air (C_a) and the leaf interior (C_i) divided by the various transport resistances to CO_2 , which include a boundary-layer resistance (r_a), a stomatal resistance (r_s), and a "biochemical" or mesophyll resistance (r_m) (Gaastra, 1959):

$$P = \frac{C_a - C_i}{r_a + r_s + r_m} \quad (1)$$

The limiting resistances are determined in a complex manner by environment, leaf morphology, and biochemistry. We consider the effect of the relationships between environment and physiology on each of these resistances in turn. As the boundary-layer and stomatal resistances have already been examined extensively in terms of water-use efficiency, we review these ideas briefly and focus on the mesophyll or “biochemical” resistance.

Throughout the remainder of the discussion, we use the term “conductance,” the reciprocal of resistance, in place of resistance. The boundary-layer conductance decreases with increased leaf size and increases with wind speed, as indicated in Figure 13.2. At wind speeds above $50 \text{ cm} \cdot \text{sec}^{-1}$, the boundary layer becomes quite small for most leaves. Generally, under natural conditions, the boundary-layer conductance is not a significant limitation to CO_2 diffusion into leaves.

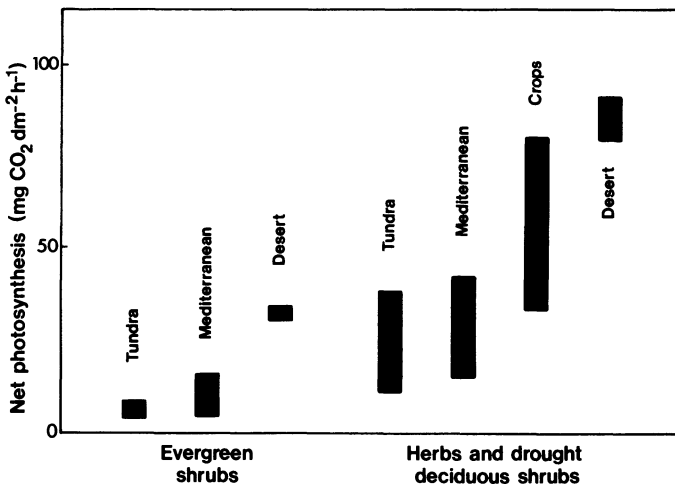


Figure 13.1. Rates of photosynthesis of diverse plant types measured under natural conditions. Tundra values from Tieszen, 1975 (herbs, 26 species; evergreens, 3 species); Mediterranean from Mooney, 1977 (evergreens, 5 species; drought deciduous, 7 species); crops from Elnore et al., 1967 (7 species). Desert values for Death Valley plants from Mooney et al. (1977), and unpublished data.

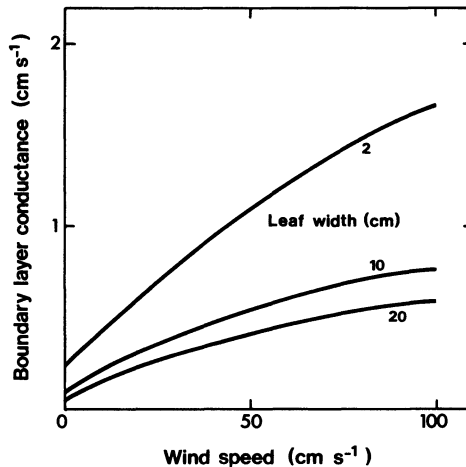


Figure 13.2. Influence of leaf size and wind speed on boundary-layer conductance of a flat leaf to CO_2 . The boundary-layer conductance in still air equals $(8 D d_L^{0.6})/\pi$, where d_L is the effective leaf diameter and D is the CO_2 diffusion coefficient ($0.147 \text{ cm}^2 \cdot \text{s}^{-1}$). In moving air, the boundary-layer conductance in flat leaves has been found empirically to equal $(U^{0.56}/0.89 d_L^{0.44}) D$, where U is wind speed (Bannister, 1976).

The stomatal conductance is dependent on stomatal depth, area, and number. The diameters of open stomata generally vary between 3 and 12 μm and may number between 20 and 1000 per square millimeter (Kramer, 1969). Leaves with a high stomatal frequency and with fully open stomata have a high diffusion conductance (Fig. 13.3).

Stomatal conductance is variable. Stomata close in response to a wide variety of environmental parameters, including light, CO_2 , humidity, and leaf water potential. When closed, conductance to CO_2 diffusion is very low. Thus, the differences we see in photosynthetic rates between plants are partly due to differences in the kinds and behavior of stomata.

From what we have said thus far, it is clear that the most efficient leaf, in terms of transport of CO_2 , would be a small leaf with numerous stomata. Since all leaves are not of this type, obviously there are other considerations in the evolution of leaf form, as pointed out by Parkhurst and Loucks (1972). We explore what these considerations might be before returning to a consideration of the other major component causing variability in photosynthetic capacity, the mesophyll conductance.

If leaves were nothing but chlorophyll-packed, moist cells exposed to the atmosphere, there would be little resistance to CO_2 diffusion from the atmosphere to the sites of carboxylation in the chloroplasts, and high photosynthetic rates would prevail, given a full complement of the photosynthetic machinery. Conversely, there would be little resistance to the diffusion of water from the mesophyll to the atmosphere. Water is lost from leaves via the same pathway as CO_2 enters, except that the pathway is shorter since there is no mesophyll component. Transpiration can be expressed as

$$T = \frac{C_a - C_i}{r_a + r_s} \quad \text{or} \quad \frac{(C_a - C_i)C_a C_s}{C_a + C_s} \quad (2)$$

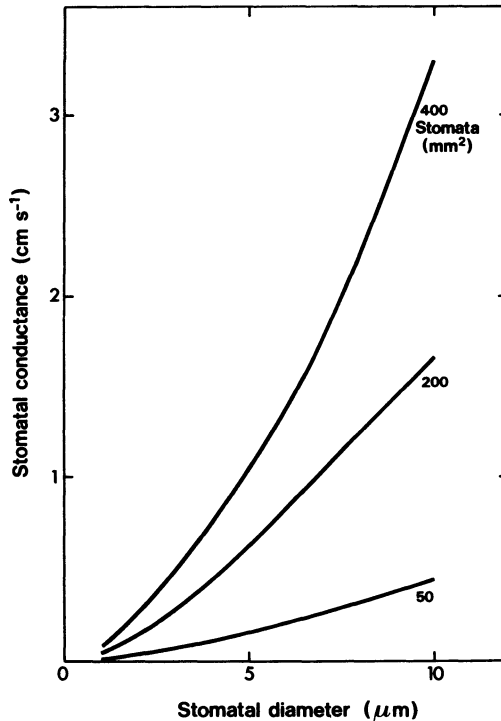


Figure 13.3. Influence of stomatal diameter and number on stomatal conductance to the diffusion of CO_2 . Stomatal conductance equals the reciprocal of $(1/nD) [a_s d_s / (L_s d_s + a_s)]$, where L_s is stomatal depth (taken as $5 \mu\text{m}$), a_s is stomatal pore area, d_s is stomatal diameter, D is diffusion coefficient of CO_2 , and n is stomata per square millimeter (from Bannister, 1976).

using conductance, where C in this case is the water-vapor concentration of the bulk air (C_a) and the leaf interior (C_i).

Water loss from plants is several orders of magnitude greater than the simultaneous carbon gain, even though the same general pathway is used. This is true for two reasons: The diffusivity of CO_2 is 1.5 times greater than H_2O ; and, of considerably more importance, the normal concentration gradient between bulk air and the site of CO_2 carboxylation can be no more than about 0.02 percent, whereas the concentration gradient of water vapor from the saturated mesophyll cell walls to the atmosphere on a sunny day is several percent. It is this commonality of the diffusion pathways of both CO_2 and H_2O that leads to constraints on leaf form and function which have implications to the diffusion-limited aspects of photosynthesis.

In most terrestrial habitats, atmospheric water loss precludes the viability of water-filled, permeable cells. Putting an impermeable layer containing variable conductor stomata over the leaf mesophyll has been the general evolutionary solution to this problem. This gives the plant control over water loss and the possibility of utilizing differing strategies to optimize the ratio of carbon gained to water lost. This particular optimization process has recently been discussed by Parkhurst and Loucks (1972), Mooney (1975), Givnish (1976), Miller (1978), and Orians and Solbrig (1977).

Here we review the variety of strategies that plants have used to achieve high water-use efficiencies, that is, how plants have maximized carbon gain per unit of water loss. Since water-use efficiency is of greatest evolutionary significance in arid environments, we consider, in particular, plants from such environments.

TEMPORAL MECHANISMS TO ENHANCE WATER-USE EFFICIENCY

Crassulacean Acid Metabolism

It has been shown that those succulents that have crassulacean acid metabolism (CAM) have a high water-use efficiency (WUE, ratio of carbon gained to water lost), since they open their stomata at

night, when vapor pressures are low and water loss is minimal. Exogenous carbon dioxide fixed into organic acids at night is refixed into carbohydrate during the day through utilization of light energy while the stomata are closed. This process is quite inefficient as a photosynthetic process, and rates of carbon gain are low. CAM plants are, of course, most prevalent in desert environment where there is limited light competition but where long-term survival to drought is important. Not all succulents use CAM, nor do all of those that use it do so exclusively. It has been found that those species having flexible photosynthesis—that is, employing Calvin cycle (C_3) photosynthesis part of the time and CAM during other periods—are generally leafy succulents (Mooney et al., 1974, 1977a). These plants generally do not have extensive water-storage capacity and can become desiccated during extended droughts. While water is available, they may have unusually high photosynthetic rates for a succulent (Bloom, unpublished data).

Stomatal Control

As shown above for succulents, closure of stomata during daylight periods of high vapor-pressure deficit (VPD) can result in high WUE, but with a significant concomitant loss in photosynthetic efficiency. Can plants manipulate stomata during the day to enhance WUE? We examine this possibility using a plant native to Death Valley, *Prosopis glandulosa*, which is known to have stomata sensitive to a number of environmental parameters, including vapor-pressure deficit.

We determined the effect of stomatal conductance on WUE using an energy balance model. Light and temperature response curves for *Prosopis* were used in conjunction with micrometeorological data for a mid-June day in Death Valley to determine net photosynthesis, transpiration, and water-use efficiency throughout the day at different stomatal conductances.

In Figure 13.4, the daily courses of transpiration and net photosynthesis are shown for the conductances giving maximum water-use efficiency. Stomatal conductance increased during midday but was relatively high throughout the day. Water-use efficiency was highest during the morning and declined steadily thereafter. Two

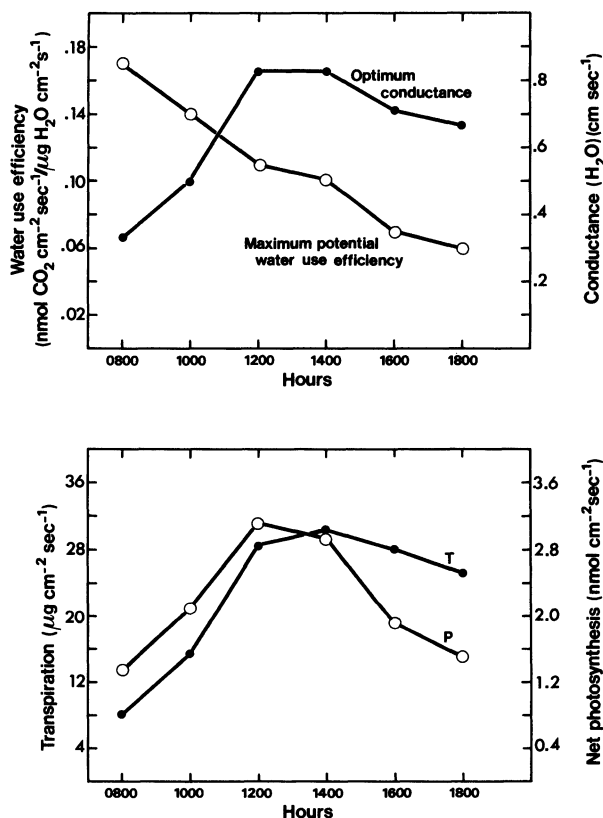


Figure 13.4. Daily courses of stomatal conductance to water vapor, transpiration, and photosynthesis for *Prosopis glandulosa*, where stomatal conductance has been optimized to obtain maximum water-use efficiency. Daily courses of temperature, solar irradiation, infrared irradiation, and water-vapor density of air were measured in Death Valley in mid-June. Leaf temperatures as a function of stomatal conductance were then obtained from the energy balance equation, assuming a boundary-layer resistance of $0.05 \text{ sec} \cdot \text{cm}^{-1}$. Using photosynthetic light and temperature response curves for *Prosopis*, the photosynthetic rates were determined for the incident Phar over the possible range of stomatal conductances.

factors account for maximum water-use efficiencies occurring at such high stomatal conductances. First, the light response curve of the species does not saturate, even with full noon sun, and the calculated mesophyll conductance is quite high (>1). Thus, during

midday, stomatal conductance has an approximately multiplicative effect on photosynthesis, and this offsets the increased transpiration. In the late afternoon, mesophyll conductances are lower owing to the decreased light level. However, temperature increases until after 1600 hours, and leaf temperatures are about 10° above the optimum for photosynthesis. Under these conditions, even small increases in leaf temperature owing to stomatal closure reduce photosynthesis to a relatively greater extent than transpiration. The responses just described appear to be typical for many desert plants and suggest that, in high light environments, increasing photosynthesis rather than decreasing water loss will result in the greatest water-use efficiency. We must emphasize, however, that this mode is effective only if water is available to the plant to sustain relatively high rates of transpiration.

C₄ Plants

As noted above, the way to achieve optimum water-use efficiency is to have a higher photosynthetic rate. In general, plants using the C₄ photosynthetic pathway have high photosynthetic rates owing, in part, to their lack of photorespiration. Furthermore, since photosynthesis is saturated at a relatively low internal CO₂ concentration, partial closure of stomata will not result in decreased photosynthesis, although transpiration is reduced. These features partially explain the prevalence of C₄ plants in hot regions of the world.

The question has often been posed, why C₄ plants are not more prevalent than they are, because of their generally superior carbon-gaining properties. Ehleringer and Björkman (1977) have found that, in contrast to C₃ plants, the quantum yield (moles of CO₂ fixed per mole of photosynthetically active radiation) of C₄ plants is temperature-insensitive; C₃ plants have a higher quantum yield than C₄ plants at lower temperatures, and a lower yield at higher temperatures. Utilizing these facts, Ehleringer (1977) has noted that C₃ plants would have a carbon-gaining advantage in cool and shady habitats. He successfully predicted distribution patterns and seasonal activity displacements between C₃ and C₄ grass species (Figure 13.5).

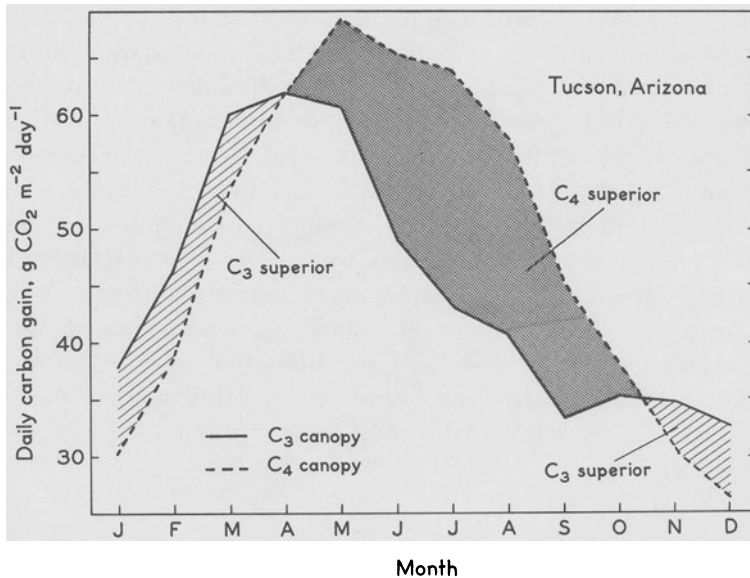


Figure 13.5. Simulations of daily carbon gain by C₃ versus C₄ grasses at Tucson, Arizona, during different months (from Ehleringer, 1977).

LEAF-TEMPERATURE CONTROL AND PHOTOSYNTHETIC CAPACITY

As noted above, in hot habitats, closure of stomata may not result in an increase in water-use efficiency, since leaf temperature may rise above the optimum for photosynthesis. A number of mechanisms have been found that reduce potential leaf temperature during periods when stomata close owing to drought stress in the desert. One example is the mechanism utilized by *Atriplex hymenelytra*, another native of Death Valley. This species conserves water through effective leaf-temperature reduction by decreasing its radiant energy absorption during the drought period and by having steeply angled leaves (Figure 13.6) (Mooney et al., 1977b). *Atriplex* modifies its leaf absorptance characteristics by utilizing salt glands. Another native of Death Valley, *Encelia farinosa*, accomplishes the same thing by changing leaf hair length and density (Ehleringer et al., 1976). In both cases, however, the amount of photosynthetically active radiation absorbed by the leaf is also reduced.

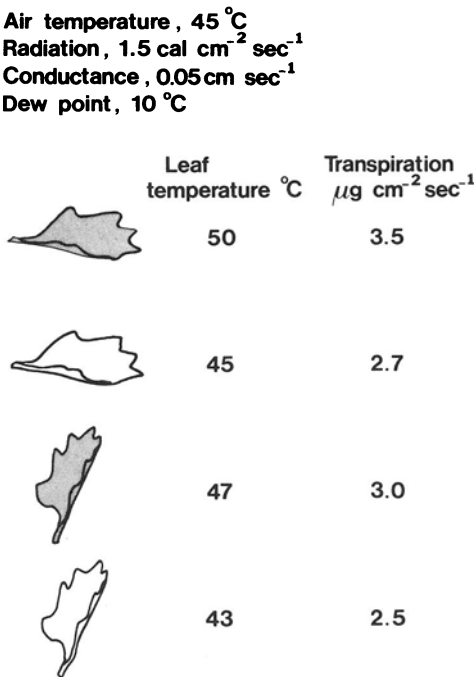


Figure 13.6. Leaf temperatures and transpiration rates of leaves of *Atriplex hymenelytra* having different angles and reflectivities. Values determined from the energy balance equation for physical and physiological parameters prevailing in Death Valley during the summer (from Mooney et al., 1978).

THE LIMITING ROLE OF THE CARBOXYLATING ENZYME IN PHOTOSYNTHESIS

It can be shown that plants that have comparable stomatal and boundary-layer conductances may still have quite different photosynthetic rates owing to dissimilarities in their mesophyll conductances. Tieszen and Wieland (1975) note that mesophyll conductances are generally only one-third to one-tenth as high as total leaf conductances $1/(r_a + r_s)$. The mesophyll conductance is principally biochemical rather than diffusional and most likely relates directly to the concentration of the photosynthetic carboxylating enzyme. Treharne (1972) and Tieszen and Wieland (1975) have shown a strong relationship between optimal photosynthetic rates and car-

boxylase activity. Since the principal carboxylating enzyme of plants, ribulose biphosphate carboxylase, makes up a substantial fraction of the total leaf protein (Björkman, 1968), it is not surprising to find a strong relationship between leaf photosynthetic rate and leaf nitrogen content under equal carbon dioxide conductivities (Fig. 13.7) (see also Natr, 1975).

In view of the relationship between carbon-gaining capacity and fitness noted initially, we now consider why all plants do not have high leaf protein contents, and hence high photosynthetic rates. We propose a theoretical framework based on the carbon-gain return on

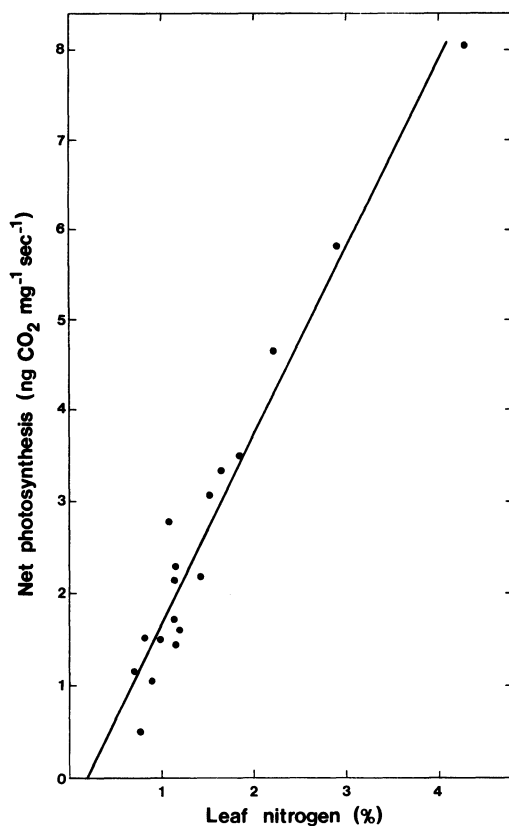


Figure 13.7. Relationship between photosynthetic rate and leaf nitrogen content in *Eucalyptus* (Mooney et al., unpublished data).

protein invested, the time course of resource availability,¹ and, possibly, the degree of predation pressure to answer this question.

Shade plants have lower light-saturated photosynthetic rates than sun plants (Björkman, 1968). This is most likely due directly to the lower contents of enzymes, especially the carboxylating enzyme, and electron carrier of the shade plants (Björkman, 1968, 1973; Gauth, 1968), although alternative hypotheses have been suggested (Nobel et al., 1975). The relationship between leaf enzyme content, light intensity, and photosynthetic rate is illustrated in Figure 13.8. Plants grown under conditions of either low light or low nitrogen have lower light-saturating photosynthetic rates than plants grown under high light and high nitrogen. This correlates with the content of carboxylating enzyme maintained in the leaf under these conditions (Medina, 1971).

We propose that a low investment in leaf protein is adaptive in shade plants because there is insufficient light energy to efficiently utilize higher levels for photosynthesis. This relationship is expressed graphically in Figure 13.9, showing the net photosynthetic rate P as a function of leaf enzyme content E in shade (low P) and sun (high P) habitats. These curves are derived from light response curves of plants grown in sun and shade conditions. The net gain dP/dE of carbon return for an incremental unit of protein invested approaches zero as the photosynthesis curves level off. When dP/dE equals zero, additional protein will not result in any additional carbon gain and would thus represent "wasted" energy. In the low-light habitat, dP/dE approaches zero more quickly,

¹To clarify our use of such terms as "resource," "gain," or "loss" in regard to plants, certain intrinsic differences in the meaning of these terms when applied to plants and animals must be explained. In the case of animals, the resource sought, such as food or nesting space, is directly identifiable with the resource gained. With plants, however, we can consider the primary resource to be carbon dioxide, which is reduced with light energy to form organic compounds. Light thus becomes a secondary or indirect resource, because it is not possible to measure a gain in light, only an increase in fixed carbon. Similarly, limitations of water, temperature, and, to a greater extent, mineral nutrients are most meaningfully measured in terms of carbon gained, or net productivity. Further, we also consider tertiary relationships. For example, water limitation may induce a plant to restrict the gas diffusion pathways to the extent that increases in the level of carboxylating enzyme do not result in additional carbon gain equal to the cost of construction. In this case, productivity is actually limited by carboxylating enzyme levels, but ultimately by lack of water.

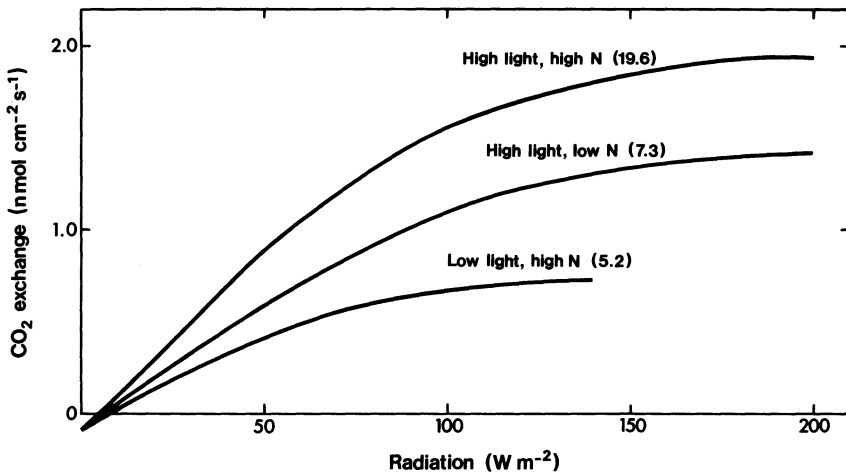


Figure 13.8. Light-related photosynthetic rates of *Atriplex patula* ssp. *hastata* grown under different light levels and nitrogen concentrations. The numbers in parentheses represent the activity of ribulose biphosphate carboxylase in micromoles of CO_2 per square centimeter of leaf area per second (from Medina, 1971). Radiation is photosynthetically active radiation (400–700 nm; $200 \text{ W m}^{-2} = 92 \text{ nE cm}^{-2} \cdot \text{s}^{-1}$).

and thus the optimum enzyme level is lower than in the sun habitat.

We now suggest a similar relationship between photosynthetic rate, protein content, and the water resource in the habitat (Mooney and Gigon, 1973). In Figure 13.10, the photosynthetic rates P as a function of enzyme content are compared for moist and dry conditions. In the dry condition, photosynthesis is primarily diffusion-limited because stomata are closed to conserve water. Here we introduce the net marginal gain G , which includes the added costs in connection with any incremental increase in enzyme content. We have explicitly added a cost term dC/dE , such that net marginal gain G equals $dP/dE - dC/dE$. The cost C is considered to be a rate of expenditure for the entire leaf, including enzyme synthesis. Fixed costs would be averaged over the life of the leaf. Consider that, when G equals zero, additional enzyme would represent a nonadaptive allocation of plant energy. In the moist region, the optimal enzyme level ($G = 0$) is higher than in the dry habitat.

The leaf-cost term includes the direct carbon cost of construction, dark respiration, and indirect costs of concentrating the necessary minerals, additional root growth, and possible increased preda-

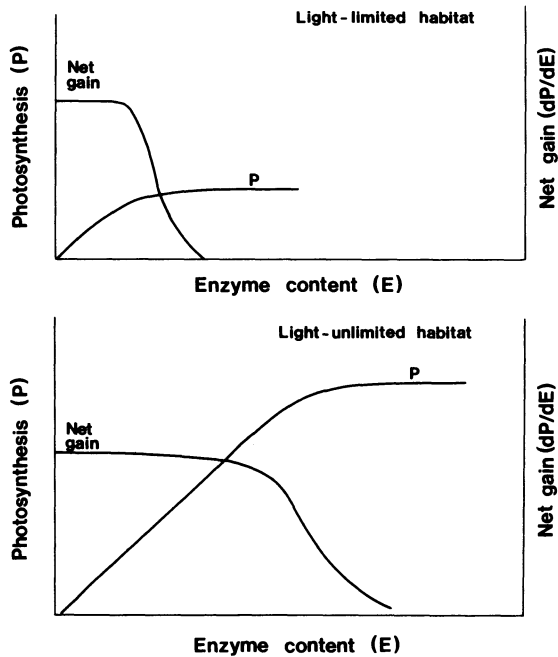


Figure 13.9. Hypothetical rates of photosynthesis of plants versus carboxylating enzyme content in light-limited and light-unlimited habitats. Curve shapes are derived from light response curves of plants grown in sun and shade habitats. The net gain in photosynthesis per unit enzyme investment (dP/dE) fall to zero at a lower enzyme concentration in the light-limited habitat. Further enzyme investment under these conditions would be nonadaptive; in fact, shade-adapted plants are found to have lower enzyme concentrations than sun-adapted plants.

tion losses. The shape of the relationship between total cost and enzyme content is unknown but would be at least a linear, and most likely an upward-bending, function. Figure 13.11 illustrates the effect of two hypothetical cost functions on net marginal gain, and thus optimal enzyme content of the leaf. (Figure 13.8 contained an example of increased leaf cost.) In the low-nitrogen condition, the cost of taking up nitrogen for protein was increased, and the resulting enzyme content was lower than in the high-nitrogen condition.

Leaf cost will be affected by environmental parameters such as temperature, soil moisture, and available nutrients, and by predation intensity. By decreasing the effective leaf size, predation loss scales up all the other leaf costs in proportion to its severity. There is some

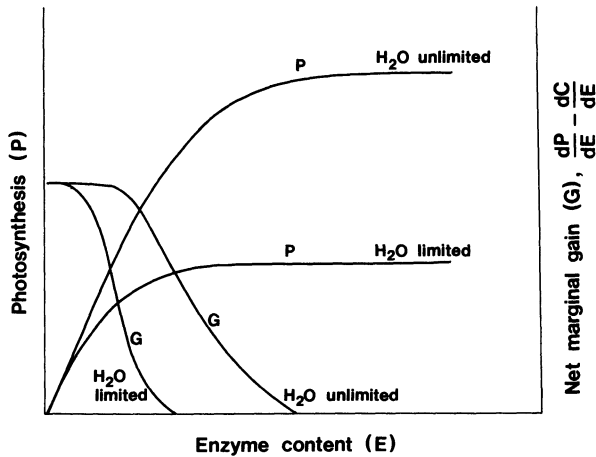


Figure 13.10. Hypothetical light-saturated rates of photosynthesis of plants versus carboxylating enzyme content in water-limited and water-unlimited habitats. The net marginal gain (G), or the difference between increased photosynthesis and increased cost per incremental increase in enzyme concentration ($dP/dE - dC/dE$), varies in these two habitats. Where water is limited, the net marginal gain reaches zero at a lower leaf enzyme content than in plants living in habitats where water is unlimited. In computing the cost of the leaf, C is taken as the total energetic rate of expenditure of leaf synthesis and maintenance, including mineral uptake, etc. Fixed costs are averaged over leaf life span.

evidence to indicate that predation intensity increases with increased leaf protein contents. Soo Hoo and Fraenkel (1966a,b) have shown that, for a typical polyphagous insect (*Prodenia eridania*), plants most readily accepted by larvae had higher protein contents than plants least accepted. Such a pattern, if general, would result in an upward-bending cost function for leaf protein, such as shown in Figure 13.11a. Furthermore, it has been suggested (Mattson and Addy, 1975) that plant foliage provides only marginally adequate nutrition to its usual insect consumers. To the extent that this is true, small variations in leaf protein content would produce relatively greater feeding and growth responses by the insect grazers. An evolutionary alternative to predation loss is production of predator protection mechanisms such as secondary compounds lethal or distasteful to predators or physical structures which protect the leaves mechanically or make the resources unavailable to predators. These mechanisms would have an associated cost of construc-

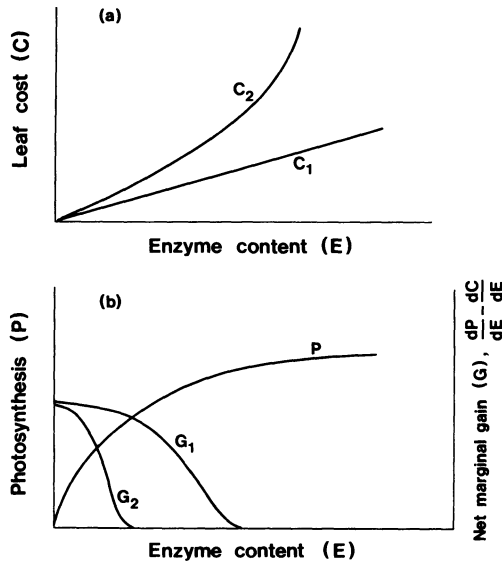


Figure 13.11. (a) Hypothetical relationships between leaf cost and enzyme content in two contrasting environments. (b) For C_2 , incremental leaf costs increase at higher leaf enzyme contents as a result of, for example, increased predation on protein-rich leaves or decreased nitrogen availability. The differences in the cost function result in different zero intercepts of the net marginal gain in the two environments.

tion, and maintenance and possibly indirect costs of increased nutrient uptake and root growth. Whether or not they result in an optimum productive system depends in part on the actual photosynthetic rate and predation intensity as functions of enzyme content.

This is illustrated for an hypothetical example in Figure 13.12. We consider, as in previous sections, two photosynthetic functions of enzyme content, high photosynthesis (P_1) and low photosynthesis (P_2), and two cost functions, in the absence of predation (C_1) and with predation (C_2). In this case, the difference between C_1 and C_2 is the proportion of leaf lost to predation. As shown in Figure 13.12, the optimum leaf enzyme content for photosynthetic function P_1 and predation-cost function C_2 is substantially lower than that for P_1 and C_1 (no predation). Further, the slope of the cost function C_2 at the optimum enzyme content (shown as a dashed line) defines an upward bound for expenditure on predator protection. If the cost of protection plus the residual predation lies between this bound and

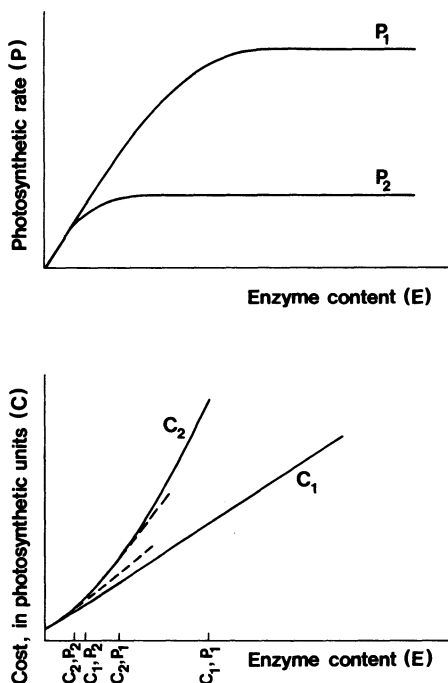


Figure 13.12. (a) Two photosynthetic functions of enzyme content, high (P_1) and low (P_2). The low function represents a plant that is light- or water-limited. (b) Solid lines represent two hypothetical cost functions, C_1 (no predation) and C_2 (predation). The dashed lines are the slopes of the cost function C_2 at the optimum enzyme contents for P_1 and P_2 ($dP/dE = dC_2/dE$). The difference between C_1 and the dashed line for each photosynthetic function P defines a potential expenditure for predator protection which would result in higher net productivity than no protection in the presence of predation (C_2).

C_1 , in the vicinity of C_2P_1 , then protection will result in greater net productivity than no protection. If the lower photosynthetic curve P_2 is analyzed in a similar manner, we also get an upward bound for predator-protection cost (in the vicinity of C_2P_2), but it is much closer to the minimum leaf cost C_1 . That is, the additional amount that the P_2 (low P) plant could spend on predator protection with a net increase in carbon gain is lower than the expenditure available to the P_1 (high P) plant. Thus, the net marginal gain for investment in predator protection mechanisms depends upon the photosynthetic rate, the predation intensity, and the relation between cost and

effectiveness of the actual mechanism used. Note that the net gain would also be affected by the basic cost C_1 . Thus, longer-lived leaves, with a lower mean cost, could "afford" more predator protection. Similarly, leaves that are short-lived but have very low fixed costs would also have greater margins for predator protection costs.

Resources and predation intensity vary temporally (e.g., available soil moisture) in most habitats, and thus enzyme contents and intrinsic photosynthetic rates should also vary, since investment in enzyme can be reclaimed and reinvested in functions with greater return for a specified season (Mooney, 1972). For example, *Larrea divaricata*, a desert shrub common in Death Valley, changes its temperature-related photosynthetic capacity with the changing seasonal thermal conditions (Fig. 13.13). The mechanism for this thermal shift in photosynthetic capacity is complex and involves an increase in thermal stability of the photosynthetic apparatus in high-temperature-grown plants and apparently an increase in a rate-limiting enzymatic step in cold-temperature-grown plants (Mooney et al., 1977c). Since cost functions may also vary in time, the model predicts that enzyme levels should fluctuate in response to enzyme costs as well as to environmental limitations on photosynthesis.

Alternatively, plants may construct leaves specifically adapted to a band of the total environmental regime and shed them at other

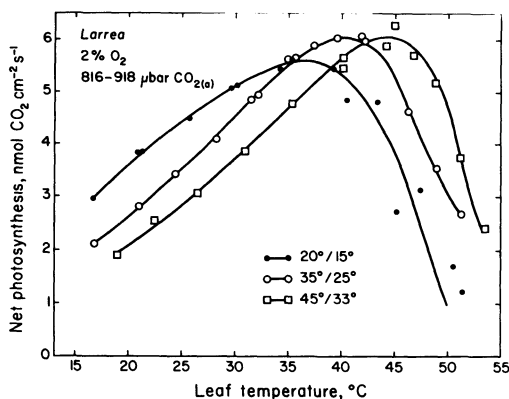


Figure 13.13. Temperature-related photosynthetic response of the desert shrub *Larrea divaricata* from three different thermal regions. Analyses were performed under low oxygen and high CO₂ to eliminate diffusion limitations and photorespiration effects (from Mooney et al., 1977).

periods. In habitats where resource availability varies greatly during the season, plants may construct leaves that have a very high photosynthetic rate or low cost (high G) for the brief time of nonlimiting resources and then shed them during resource-limited periods, rather than investing more carbon in protecting the leaves (from limited water, for example) during periods of resource limitation (Orians and Solbrig, 1977). Alternatively, plants may invest the additional carbon in protection that will be repaid by the greater time period of carbon gain by the leaf (Mooney and Dunn, 1970a,b). In many habitats, particularly those that are light-unlimited, these plant types coexist. Thus, physical conditions of the habitat can greatly influence the intrinsic rate of photosynthesis of a leaf through influences on enzyme production both directly and indirectly through an adaptive response by the plant.

PHOTOSYNTHESIS AT THE PLANT LEVEL

In addition to being dependent on the photosynthetic capacity of each leaf, the productivity of a plant is also controlled by the proportion of the photosynthate that is reinvested into expansion of the carbon-gaining system, the leaves. The effect of carbon allocation on subsequent carbon gain has been discussed by Monsi (1968), Ledig (1969), Mooney (1972), and others.

Monsi starts with a simplest case model of continuous exponential growth,

$$W_t = W_0 e^{k(mP - nr)t} \quad (3)$$

The weight at time t (w_t) is given as the initial weight W_0 times an exponential function of construction efficiency k , proportion of production allocated to the photosynthetic system m , proportion allocated to support and root systems n ($m + n = 1$), the net photosynthetic rate P , the respiration rate of nonphotosynthetic tissue r , and time t . The factors n and m are constant and equal the distribution of biomass at $W = W_0$. Thus, productivity increases as m approaches 1. If $m = 1$, the plant has no roots or stems. Epiphytes

and vines are examples of adaptations maximizing m , but both these groups require other plants or physical structures for support. Root and stem parasites have also maximized m , and these groups depend on other plants for nutrients.

Even among free-standing plants, however, the ratio of photosynthetic tissue to nonphotosynthetic tissue varies greatly and in a systematic fashion among plants of different environments. For example, plants from environments characterized by low soil-nutrient or water availability will invest less into leaves than plants growing where light or nutrients are abundant (Mooney, 1972). This variation hinges upon the relationship between net photosynthetic rate P and leaf allocation fraction m . The growth rate is proportional to the product mP , so that, if an increase in m causes an equal or greater decrease in photosynthetic rate, no net gain in productivity will result. Photosynthesis may be limited by the availability of water or minerals, and these resources are supplied through roots and stems. Thus, where one or more resources are strongly limiting, decreasing the proportion of nonphotosynthetic tissue may result in a reduction of net photosynthetic rate which overbalances the potential gain of an increase in leaf area.

A hypothetical relationship between leaf net photosynthesis and the structural allocation to roots (n) in a normally wet and normally dry environment is shown in Figure 13.14. The photosynthetic rates $P(n)$ are considered functions of the form

$$P(n) = b(1 - e^{-an}) \quad (4)$$

There is no experimental evidence for the precise shape of such functions. Our argument derives solely from the assumption that, in a water-limited (or nutrient-limited) condition, the leaf photosynthetic rate increases more slowly as a function of root allocation n than in a less limited condition. This is equivalent to saying that the specific root activity (rate of uptake of an essential nutrient per unit root weight) is lower under nutrient- or water-limited conditions, and this has been experimentally demonstrated (Troughton, 1968; Davidson, 1969; Hunt, 1975). We can substitute the $P(n)$ from Figure 13.14a into the growth rate term $R = k(mP - nr)$ from Equation (4),

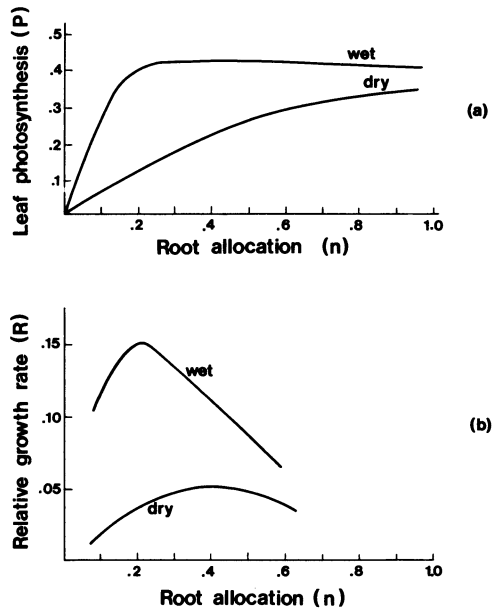


Figure 13.14. (a) Hypothetical relationship between leaf net photosynthetic rate P and structural allocation to roots n in normally dry and wet habitats. Functions are of the form $P(n) = b(1 - e^{-an})$. (b) Calculated relative growth rates [$R = k(mP - nr)$, assuming k of 0.5 and r of 0.05, and P as above] in the same habitats as a function of the root allocation factor. In the dry habitat, fractional allocation to roots of 0.4 is optimal for growth, and in the wet habitat 0.2 is optimal.

so that

$$R(n) = k[(1 - n)b(1 - e^{-an}) - nr] \quad (5)$$

Maximum growth occurs when $dR(n)/dn = 0$. The growth rates $R(n)$, derived from Figure 13.14a, are plotted in Figure 13.14b. Where water or nutrients are limited, there will be a greater return in carbon by investment in the means (i.e., roots) for gathering more of the limiting resource than in making more resource-limited leaves.

Since Equation (4) is based on continuous growth, it does not take into account the frequency of leaf replacement or leaf life-length. The longer the life of the photosynthetic tissue, the greater the return in the invested carbon of construction or the lower the mean cost. This relationship has been discussed in general by Monsi (1968) and for specific systems by Mooney and Dunn (1970a,b) and

Miller and Mooney (1974). Leaves vary in their lifespan from days or weeks, in the case of such plants as desert annuals, to decades, in the case of certain conifers. For a given habitat type, there is a strong inverse relationship between the length of life of a leaf and its inherent photosynthetic capacity (Johnson and Tieszen, 1976; Harrison et al., 1971; Mooney et al., 1976a).

SUMMARY

The wide variation in photosynthetic rates among plant species can be partitioned primarily into variation in stomatal conductance and mesophyll conductance. Stomatal conductance has been considered mainly in terms of water-use efficiency. We have focused on mesophyll conductance, which appears to be closely correlated with carboxylating enzyme activity and hence total protein in the leaf. Through a theoretical framework based on maximization of net carbon gain (gain-cost) and existing knowledge of the photosynthetic process, we have demonstrated unique optima for leaf enzyme contents in different environments or in the same environment at different times. Insofar as net carbon gain can be considered a primary component of fitness, deviation from these optima would be maladaptive. The theory provides testable relationships between environmental parameters and plant responses.

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