Adaptation of Photosynthetic Processes to Stress

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Under optimum conditions plant productivity may exceed by at least an order of magnitude the average productivity of the earth (*1, 2*). The great variation in productivity that characterizes the land surface is due to the existence of large differences among habitats in environmental factors such as light, heat load, evaporative demand, and the supply of water and essential plant nutrients. Where one or more of these factors exceed certain limits (such as excessively high temperatures or inadequate water), a stress that inhibits plant growth may develop. Much of the energy and resources used in agriculture is used to eliminate such stresses. For example, it was estimated (*3*) that 100 pounds (45 kilograms) of nitrogen fertilizer requires an energy input of 840,000 kilocalories, and to provide 1 acre-foot (1,230 cubic meters) of irrigation water requires 905,000 kcal. Productivity in some intensively managed crops approaches within practical limits the efficiency of solar energy conversion by photosynthesis (*4*). However, the requirement for energy and other limited resources in modern technologically advanced agriculture is very high, and we are faced with a global energy and resource shortage. It would appear that we are faced with a dilemma in that, while we now have the technical capacity to increase the world's food supply greatly, in the long term we may lack the resources to do it.

I believe that we must endeavor to improve the efficiency of food production. Efficiency is often used synonymously with yield per area of cultivated land or percentage of solar radiation converted to plant growth. This usage may not reflect the real limitations to productivity in an environment. If we are to maintain or increase production in that environment while reducing the input of energy and resources, then we should use efficiency in a more general way to refer to output in terms of the resources limiting plant growth in a particular environment.

It seems to me that efficiency in these terms can be increased by making more effective use of the intrinsic capacities of plants. Natural communities of plants are capable of quite respectable productivity in a wide range of environments, many of which would be unsuitable for the growth of crop species. Apparently the plants native to these habitats have become functionally adapted to grow and survive under conditions that would impose severe stress on other plants, and hence they are more efficient in utilizing limiting resources.

Our knowledge of the limits of tolerance and efficiency that exist among higher plants is far from complete, and very little is known about the underlying mechanisms. We are only beginning to understand the tremendous complexity of the interactions between the environment and the productive processes of the plant. Further, most of the knowledge of environmental responses and adaptive differentiation that we do have has been derived largely from studies of economically important plants, and until recently these studies were restricted mostly to temperate regions of Europe and North America. However, if the objective is to gain an understanding of the environmental and evolutionary limits of adaptation and of the structural, physiological, and molecular mechanisms involved, then we should choose plants that are native to environments that are extreme in one respect or another. The use of wild plants native to extreme habitats rather than crop plants for these studies has the advantage of providing a much greater environmental range and therefore a greater probability of discovering adaptive mechanisms. It also avoids a problem that may exist with cultivated plants, namely that adaptive mechanisms may have been altered or obscured by cultural or breeding operations attendant to domestication.

In the remainder of this article, I will review several studies, drawn principally from the work of our group at the Carnegie Institution, of the photosynthetic processes of plants native to diverse natural habitats, and explain where possible in mechanistic terms some of the functional adaptations that have been discovered. Since photosynthesis is the source of organic carbon and energy for plant growth, understanding the environmental and biological control of photosynthesis is essential to understanding the complex relationship between the productivity of vegetation and the environment.

Some comments should be made about the photosynthetic process in general as it occurs in all plants before beginning to discuss functional differences among plants [for general reviews see (*1, 2, 4, 5*)]. The driving force of the process is the absorption of light, and the energy is stored in the form of reduced organic compounds which are formed from CO_2 obtained from the atmosphere. There are at least 100 steps linking the absorption of light to the formation of stable end products. Within microseconds of its absorption, light energy is utilized to effect a charge separation in photochemical reaction centers. These reactions are linked to membrane-bound electron transport reactions, which in turn are linked to enzyme-catalyzed oxidation-reduction reactions, which ultimately lead to the oxidation of water to O_2 and the reduction of CO_2 to the level of carbohydrate. These reactions require a very high degree of organization and are very fragile.

Three environmental factors determine the rate of photosynthesis in functionally intact tissue (which is usually assayed by measuring CO_2 uptake): (i) the input light intensity or energy; (ii) the temperature, which affects the capacity of the enzymatic steps linking the photochemical steps to CO_2 fixation; and (iii) the concentration of CO_2 at the site of its fixation, which may fall below that of the atmosphere because of restrictions to diffusion of CO_2 from the atmosphere to this site.

These factors affect the rates of different steps of the sequence. Since the rate of the overall sequence cannot exceed that of the slowest step, both the

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limiting factors and the site of limitation may change when the conditions are altered and considerable interaction between factors occurs. In this article the responses of single leaves to light, temperature, or CO_2 concentration will be described. Careful attention has been paid in these studies to selecting conditions to minimize interaction between factors. When comparing different species or genotypes it is important to keep in mind the characteristics of the particular environment in question. Characteristics which may be considered efficient in one habitat often are not efficient in another.

Sun and Shade Plants

Plants are capable of growth over a wide range of light intensities. During summer, for example, plants such as *Tidestromia oblongifolia* (S. Wats.) Standl. growing on the floor of Death Valley, California, receive about 6600 microeinstein per square centimeter per day (μeinstein cm^{-2} day^{-1}) of light in the spectral band 400 to 700 nanometers (*6*). *Atriplex patula* ssp. *hastata* (L.) Hall and Clem. growing on a coastal strand receives 4500 μeinstein cm^{-2} day^{-1} (*7*), and *Alocasia macrorrhiza* (L.) G. Don growing on the floor of a rain forest in Queensland, Australia, receives only 22 μeinstein cm^{-2} day^{-1}, which must be very near the lower limit for plant growth (*8*). The quantum flux received by these plants in their native habitats differs by a factor greater than 300.

The response of leaves of these plants to light intensity is shown in Fig. 1. The arrow on each curve indicates the average light intensity to which the plant was exposed during growth. Leaves of plants that are native to and have developed under high light intensity have much higher maximum photosynthetic rates, but require high light intensity to achieve these rates. In bright environments they are clearly more productive than the shade plant, which would in fact be injured by exposure to full sunlight. The maximum rate of *Alocasia* at high light intensity is only a fraction of that of *Tidestromia*. This is, however, not necessarily a disadvantage in its native habitat. The low light intensity of the forest floor is not sufficient to support high rates of photosynthesis, and in such an environment the capacity to achieve high rates at high light intensity could be of little value. In fact, at the low light intensity of *Alocasia*'s native habitat, neither species native to sunny habitats would be able to sustain net CO_2 fixation. They would be below their light compensation points (see Table 1). These species have much higher rates of dark respiration than *Alocasia*, and at these light intensities the rate of gross photosynthesis would not exceed the respiratory rate; hence the leaves would evolve CO_2 by drawing on the reserves of the plant. At the light intensities of its native habitat, the rain forest species is capable of net photosynthesis partly because its respiratory rate is lower than that of the plants native to sunny habitats.

Plants such as *Alocasia macrorrhiza* are highly specialized and grow only in habitats with low light intensities. It is interesting, however, that even plants that occur in sunny habitats have differing light response characteristics depending on the light intensity used for growth. Figure 2 and Table 1 show that leaves of *Atriplex patula* ssp. *hastata* which developed under low light intensity have response characteristics similar to those of *Alocasia*, but not nearly as extreme.

Are the photosynthetic properties of the leaves which developed under low light intensity an inevitable result of development at that intensity? Or do they reflect modifications which adapt the leaf to low light? The best answer to this comes from a mechanistic analysis of how these differences are caused and what their impact is on the efficiency of the leaf at low light intensity. In general, the leaves of plants which developed under low light intensity have about the same chlorophyll content as those of plants from open habitats, but have a lower soluble protein content (Table 2). No indication of a change in the nature or basic efficiency of the photosynthetic apparatus has been ob-

Table 1. Physiological properties of *Alocasia macrorrhiza* which developed in its native habitat and *Atriplex patula* ssp. *hastata* leaves which developed under different light intensities (*17, 23*).

Plant	Light intensity (nanoeinstein cm^{-2} sec^{-1})		Rate (nmole CO_2 cm^{-2} sec^{-1})	
	Average for growth	Compensation point	Light-saturated photosynthesis	Dark respiration
Alocasia macrorrhiza	0.34	< 0.2	0.32	0.008
Atriplex patula ssp. *hastata*				
High light	92	6.3	3.4	0.35
Intermediate light	29	3.7	2.35	0.21
Low light	9.2	1.7	0.67	0.08

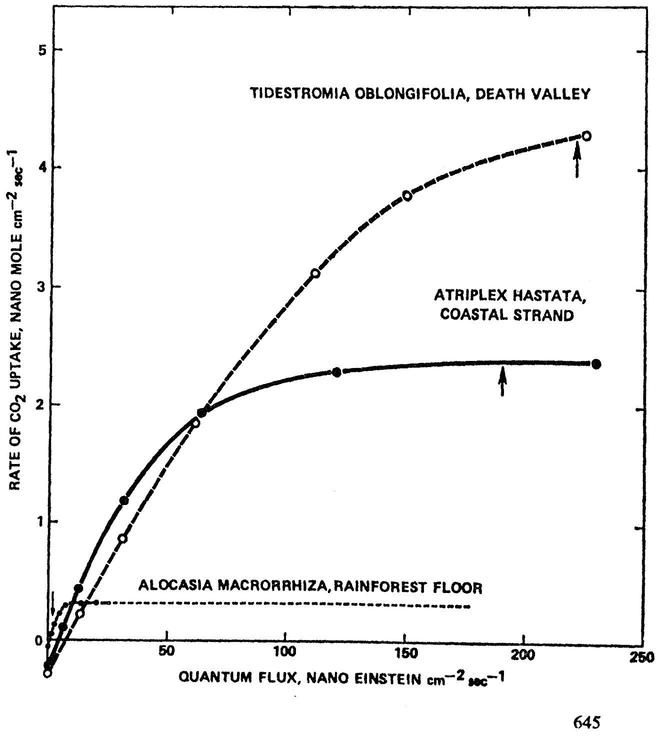

Fig. 1. Light dependence of net CO_2 uptake by single attached leaves, grown under the contrasting light intensity regimes of their natural habitats. Rates were determined at near-optimum temperature for each species, a CO_2 partial pressure of 320 μbar, and an O_2 concentration of 21 percent by volume. The arrows indicate the average maximum light intensities to which the plants were exposed during growth. [Source: (*7*)]

Table 2. Composition and in vitro catalytic activity of preparations from leaves of *Alocasia macrorrhiza* which developed in its native habitat and *Atriplex patula* ssp. *hastata* which developed under different light intensities (*17, 23*). The catalytic activity is given as a percentage of the light-saturated photosynthetic rate of the corresponding intact leaf, measured in vivo and expressed in equivalent units.

Plant	Composition				In vitro rate (%)		
	Chlorophyll (a + b) (mg cm^{-2})	Soluble protein (mg cm^{-2})	Chlorophyll/ P700 (molar ratio)	Chlorophyll/ cytochrome f (molar ratio)	RuDP carboxylase	Photo-system 1 electron transport	Photo-system 2 electron transport
Alocasia macrorrhiza	0.58	0.16	570	1120	242	323	128
Atriplex patula ssp. *hastata*							
High light	0.51	0.70	430	330	162	129	120
Intermediate light	0.51	0.61	434	509	177	134	107
Low light	0.42	0.29	468	689	199	238	168

tained. However, the relative capacities of several of the component steps of the photosynthetic process, such as the CO_2 fixing activity of extracts of the leaf or electron transport by photosystem 1 or 2 (also shown in Table 2), vary in direct proportion to the total photosynthetic capacity of the intact leaf. Since the capacity of each step is related to the amount of specific protein [such as ribulose-1,5-diphosphate (RuDP) carboxylase or cytochrome f], we may conclude that the investment of energy and nutrients into synthesis of leaf proteins has been closely metered. No single step or protein can be specified as causing the limitation of the light-saturated rate; rather the data suggest that the steps are balanced so as to give high catalytic use of each of the component enzymes synthesized and thus efficient use of the resources invested. Protein synthesis requires energy and nutrients, which must be derived from the limited amount of photosynthesis which the leaf (or the leaves of the plant) can perform in its environment. It is also likely that after the protein is synthesized, energy is still required to maintain it. This may be one reason why leaves which developed in high light and have abundant protein also have high rates of respiration.

These energy costs are especially important because the growth rate is very sensitive (exponentially) to the amount of new photosynthetic capacity that can be made for each unit of carbon gained in photosynthesis. In the low light intensity of the forest floor the *Alocasia* plant must absorb more light to increase its photosynthetic capacity. To do this it must increase its leaf area. The leaf this plant has synthesized is very "cost effective." This low-protein leaf is not only less costly to synthesize but also less costly to maintain because of a lower requirement for respiration.

It is probable that the *Alocasia* plant could not survive in its native habitat without these economies. By contrast, plants which develop at much higher light intensities are not limited by light intensity. They can utilize larger quantities of protein per unit of leaf area and can afford the additional cost of respiration. Under these conditions the appropriate strategy for synthesis of new photosynthetic capacity is different, and it changes as the light intensity for growth is changed.

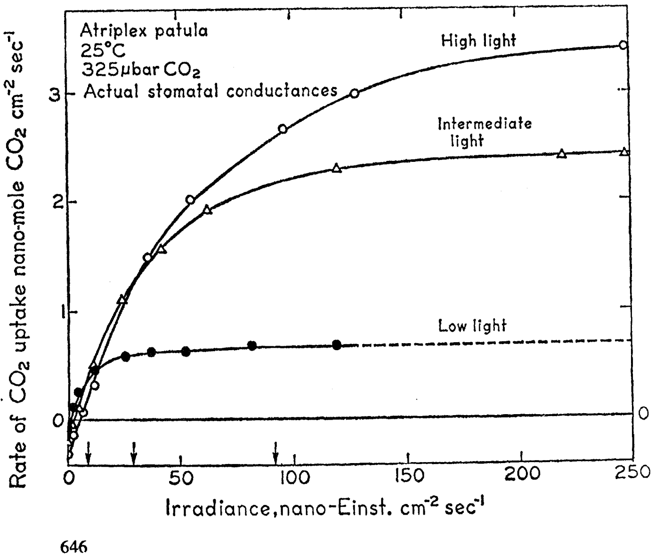

Fig. 2. Light dependence of net CO_2 uptake for single attached leaves of *Atriplex patula* ssp. *hastata* grown at high, intermediate, and low light intensity. These intensities are given in Table 1 and are indicated by arrows on the abscissa. Conditions were as given for Fig. 1. [Source: (*23*)]

The environmentally induced modifications of the photosynthetic characteristics of leaves of a single genotype (Fig. 2) have relevance in nature. Leaves that are shaded by other leaves of the same plant experience limitations similar to those experienced by a plant shaded by other plants. By these mechanisms not only the plant but individual leaves of the plant are capable of adaptation to their environmental conditions. It is easy to suppose that natural selection among competing plants has resulted in the evolution of genotypes possessing these adjustments in the constitution of the photosynthetic apparatus and the ability to adjust to differing light climates. These adjustments adapt the leaf to perform efficiently at the light intensity under which it develops, while apparently keeping the energy and nutrient investment in new leaf area low. The nature of the adjustments also indicates that adaptation to function with unusual efficiency at one extreme (low light intensity) precludes high efficiency at the other extreme.

In more general terms, these studies indicate a considerable degree of evolutionary control over energy and nutrient allocation for synthesis of new photosynthetic capacity. Such control probably also extends to many other aspects of plant metabolism. Selective pressures in diverse environmental regimes could by themselves lead to some degree of optimization of the resource allocation strategy. Breeding or chemical treatment to modify a plant's internal control of resource allocation might be beneficial, but it might also cause unexpected or undesirable results when applied without some knowledge of the costs and benefits involved in such modification.

Adaptation to Different Thermal Regimes

The extremes of high or low temperature also place quite different demands on the photosynthetic apparatus of a leaf. The extent of differentiation between plants that grow under hot or cool conditions is illustrated in Fig. 3, which shows the photosynthetic responses of *Atriplex glabriuscula,* a native of cool (10° to 20°C) marine climates adjacent to the North Atlantic, and *Tidestromia oblongifolia,* which grows during the hot summer in Death Valley, California (40° to 50°C). These plants were grown in the thermal regimes of their native habitats and assayed under common conditions of saturating light intensity. The temperature range of optimum photosynthetic capacity is clearly different in the two plants. However, the maximum rate of each is high, especially at the temperature extreme that characterizes its native environment (near 10°C for *Atriplex* and 45°C for *Tidestromia*). Somewhat higher photosynthetic rates (in the range of 3 to 6 nmole cm^{-2} sec^{-1}) have been measured at 25° to 35°C in plants (including crop species) native to and grown under conditions normally considered optimal for plant growth (*9*). However, at higher or lower temperatures the photosynthetic capacity of these plants falls, and it is far below that of *Tidestromia* or *A. glabriuscula,* respectively. This phenomenon is also evident in the poor performance of *Tidestromia* at low temperatures or *A. glabriuscula* at high temperatures. The results again indicate that trade-offs must exist at a mechanistic level such that optimization for one environmental condition leads to less efficient performance under other environmental conditions. Such trade-offs also make it likely that the capacity to tolerate or to function efficiently over a broad range of conditions may necessitate suboptimal efficiency at any one temperature.

The mechanisms responsible for the considerable difference in optimum photosynthetic activity of these species are not yet fully understood, nor is it understood why the trade-offs seem to exist. It is clear, for example, that the photosynthetic apparatus of *Tidestromia* is quite stable at high temperature. Perhaps this is because of changes in the composition of the chloroplast membranes (*7*). Likewise the high photosynthetic capacity of *A. glabriuscula* at low temperatures is in part due to massive quantities of enzymes that catalyze steps which become limiting under cool temperatures (*10*). It is not at all clear that these changes should be of any liability at higher or lower temperature. But *Tidestromia* is not capable of growth at temperatures below 20°C, and *A. glabriuscula* cannot tolerate temperatures above 42°C (*11*). An understanding of the reason for these limitations is of fundamental importance to understanding the biology of adaptation.

Water Use Efficiency and C_4 Photosynthesis

Plants use a great deal of water, most of which evaporates from the leaf and escapes to the atmosphere. This large flux of water through the plant does not appear to be essential to the plant, rather it seems to be the inevitable result of growing in a terrestrial habitat. Water vapor is lost from the leaf by diffusion from the air spaces within the leaf to the dry atmosphere. The leaf can regulate the rate of this

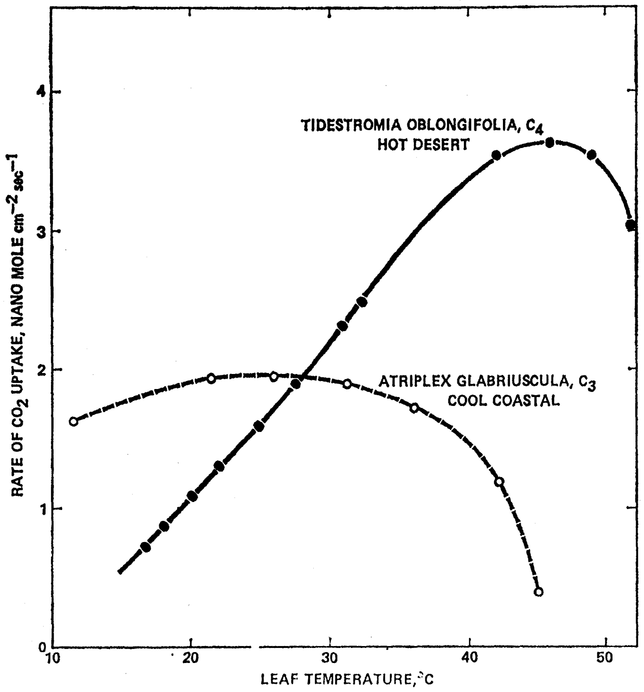

Fig. 3 (left). Temperature dependence of photosynthesis in *Tidestromia oblongifolia* and *Atriplex glabriuscula* at high light intensity of 160 nanoeinstein cm^{-2} sec^{-1}, a CO_2 partial pressure of 320 μbar, and an O_2 concentration of 20 percent by volume. Stomatal conductances were almost identical in the two species. The plants were grown under the light and temperature regimes of their respective habitats. [Source: (*7*)]

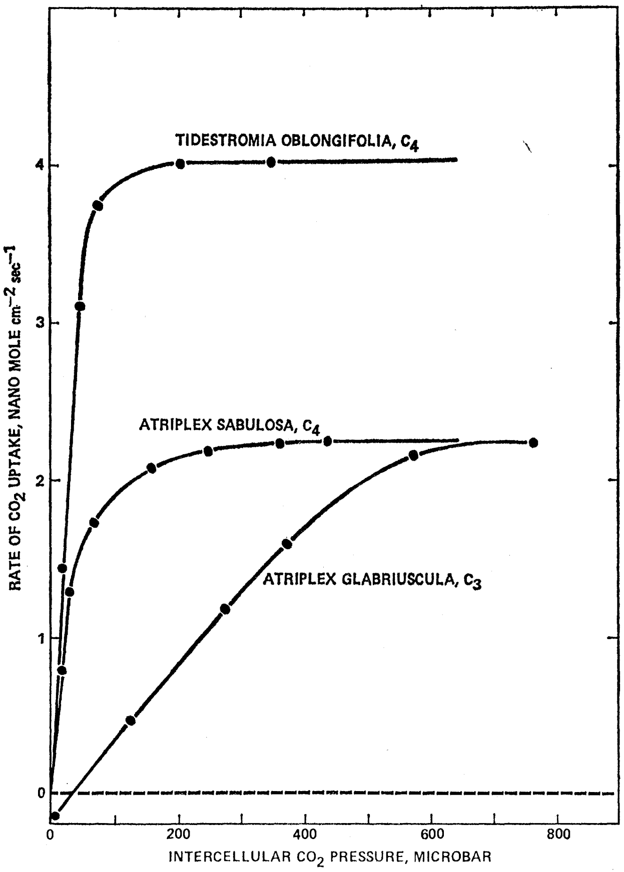

Fig. 4 (right). Photosynthesis as a function of the CO_2 concentration in the intercellular spaces in C_3 and C_4 species, grown under a temperature regime of 40°C by day and 30°C by night. Measurements were made at a leaf temperature of 40°C, a light intensity of 160 nanoeinstein cm^{-2} sec^{-1}, and an O_2 concentration of 21 percent by volume. [Source: (*7*)] process by physiological mechanisms that govern the opening and closing of stomatal pores which penetrate the leaf epidermis. However, the leaf is faced with a dilemma. Carbon dioxide is required for photosynthesis. This CO_2 must diffuse to the site of reaction inside the leaf from the atmosphere by the same path that water vapor would take to escape from the leaf. As a result, closing the stomata to prevent water loss also prevents CO_2 uptake, which is needed to store the energy gained by photosynthesis. Thus, plants must tolerate water loss if they are to photosynthesize and grow. In cool mesic conditions water loss may not stress the plant since the evaporative demand is low and the lost water can readily be replaced from the soil. Plants that grow when evaporative potential for water is very high or when temperature is high are more likely to develop water stress and to be CO_2 limited. A mechanism is now known which adapts plants to this stress. This may be best illustrated by a practical example.

Just after the turn of the century, a group led by Shantz (*12*) investigated the amount of water required for each gram of dry weight increase (water use efficiency for growth). Under summer conditions at Acron, Colorado, they found that the amount of water used for each gram of growth ranged from about 300 g for sorghum to 900 g for alfalfa. They could detect no advantage to the alfalfa plant of the threefold higher rate of water loss than sorghum under identical conditions. In fact, in those arid conditions it could be considered a liability if the total water supply was limiting. Shantz recognized that the lower rate of transpiration of sorghum was partly due to its leaves having a higher resistance to transport of water vapor. However, he also recognized that this would impair CO_2 transport. He stated that (*13*) "it is difficult to conceive of sorghum absorbing CO_2 as rapidly as alfalfa, under the conditions just mentioned." Shantz resisted making the statement that sorghum was more efficient at absorbing CO_2 than alfalfa, but it is now established that this is indeed the basis of their difference in water use efficiency (*14*). Plants, such as sorghum, that are more efficient at absorbing CO_2 when the concentration of CO_2 is low can maintain a reasonable rate of CO_2 uptake even if there is a considerable barrier to diffusion between the atmosphere and the site of CO_2 fixation. Since this diffusion barrier also limits the rate of water vapor loss from the leaf, a plant with higher efficiency of CO_2 uptake could absorb more CO_2 at any diffusion limitation (or transpiration rate) than a less efficient plant.

About 10 years ago workers at the Hawaiian Sugar Planters Association (*15*) discovered that some plants fix CO_2 by a mechanism that had not been previously described; it was later discovered that sorghum is one of these plants (*16*). The biochemical foundation of this mechanism is that the enzymatic reaction by which CO_2 is initially fixed into a stable organic compound is fundamentally different. This reaction in plants such as sorghum—referred to as C_4 plants—is between CO_2 and phosphoenol pyruvate (PEP), and the product is the C_4 dicarboxylic acid, oxaloacetic acid. In the analogous reaction of other plants—referred to as C_3 plants —CO_2 reacts with RuDP and the product is 3-phospoglyceric acid.

The C_4 mechanism leads to greater efficiency of CO_2 uptake at low CO_2 concentrations. Response curves indicating the rate of photosynthesis as a function of the concentration of CO_2 in the intercellular air spaces are shown in Fig. 4. These curves are from experiments in which the responses of leaves to the concentration of CO_2 in the atmosphere was measured at saturating light intensity. The CO_2 concentrations plotted have been adjusted to compensate for diffusion gradients that develop between the atmosphere and the inside of the leaf, so the responses plotted represent what would have been obtained if there were no diffusion barrier [for details see (*5*)]. Most plants show a concentration dependence similar to that of *Atriplex glabriuscula*, a C_3 plant. This plant requires a CO_2 concentration higher than that of the normal atmosphere (320 ± 20 microbar) to saturate its rate, and in air containing oxygen there is a CO_2 compensation point below which CO_2 evolution rather than uptake occurs. In contrast, *Tidestromia oblongifolia* and *Atriplex sabulosa* Rouy, which have C_4 photosynthesis, are saturated at much lower CO_2 concentrations and have much lower CO_2 compensation points. This is a very significant difference since the concentration of CO_2 in the atmosphere is saturating for C_4 plants and not saturating for C_3 plants. In essence, plants with C_4 photosynthesis may be considered more efficient at absorbing CO_2 from air of low CO_2 concentration.

Our studies of wild C_4 plants indicate that they typically form a sparse vegetation cover in regions of the southwestern deserts and the Great Plains which receive summer rainfall. Metabolic activity is usually greatest in the hot summer months, and plant growth is often limited by the amounts of summer rainfall. Both the limiting amounts of water and the high summer temperatures could be stresses to the plants. In addition to conferring a potential for more efficient use of water, C_4 metabolism leads to greater efficiency of photosynthesis at high temperature. Thus C_4 metabolism may adapt the plant to cope better with both stresses. *Tidestromia* is a C_4 plant, and its high rate of photosynthesis at high temperatures (see Fig. 3) is partly due to its high efficiency of CO_2 uptake. Even at 47°C and full sunlight, photosynthesis by leaves of this plant is not limited by the CO_2 concentration of the atmosphere. In contrast, the concentration of CO_2 is an important factor in limiting the rate of photosynthesis of C_3 plants at high temperature and high light intensity. The photosynthetic rate of *A. glabriuscula*, a C_3 plant, can be increased at high temperature by providing CO_2 to the leaf at two to three times the normal atmospheric concentration. Even then photosynthesis declines at temperatures above 30°C, and the leaf is not capable of tolerating temperatures higher than it can under normal CO_2 concentrations. Thus other factors in addition to an improved efficiency of CO_2 absorption would be required to adapt the plant to high temperature.

It might be argued that the poor performance of *Tidestromia* at low temperature is a result of its having C_4 photosynthesis. This is not true. There are plants native to cool habitats which have C_4 photosynthesis. *Atriplex sabulosa*, for example, is a C_4 plant that grows in the same habitats as *A. glabriuscula* (10° to 20°C), and it has high rates of photosynthesis at cool temperature (*7, 11*).

One fact which has puzzled many of us who study the distribution of vegetation in arid areas is that a great many of the plants of these regions do not have C_4 photosynthesis (*18*). It is apparently possible for plants to adapt to the same environment in different ways. For example, many C_3 plants in such areas confine their metabolic activity to the cooler, more humid winter and spring months.

Because C_4 plants appear to be relatively more efficient in hot and arid environments, it seems likely that they evolved from C_3 plants in response to stresses imposed by these conditions. This mechanism is a discrete functional dichotomy. It is not the result of quantitative adjustments of the capacity of the component steps of photosynthesis, as has been suggested to explain adjustments of the photosynthetic apparatus to function more efficiently in different light or temperature regimes. In this case a plant may be characterized as either possessing or lacking the mechanism of C_4 photosynthesis.

The enzymes that catalyze the CO_2 fixation reactions in C_3 and C_4 plants are quite different. Perhaps the most important difference is that the enzyme which catalyzes the reaction of CO_2 with RuDP also reacts with and is inhibited by oxygen, whereas the reaction of CO_2 with PEP is not affected by oxygen (*19*). As a result of the interaction of the enzyme with oxygen, photosynthesis in plants with C_3 photosynthesis is inhibited by the oxygen of the atmosphere. This inhibition is greatest at low CO_2 concentration and at high temperature. It is under these conditions that C_4 photosynthesis appears to be superior to the C_3 mechanism.

As might be imagined, it is not a simple matter to alter the initial step of such a biochemical sequence and leave the remainder unchanged. Subsequent steps in the C_3 mechanism are keyed to receive 3-phosphoglyceric acid, not oxaloacetic acid. It is now known that the C_3 mechanisms are not eliminated in C_4 plants. Instead, the C_4 mechanism serves as a CO_2-gathering mechanism for the leaf and provides the CO_2 to the site of its reaction with RuDP. This is possible because of the coevolution of a unique tissue (the bundle sheath), which is not found in leaves of C_3 plants, and the physiological specialization of this tissue to link C_3 and C_4 mechanisms (*16, 20*).

Clearly the evolution of the C_4 pathway is not a trivial genetic step. Yet it appears quite likely that it has occurred several times independently in different groups of higher plants. Species with C_4 metabolism occur in at least eight separate families, often in a single genus or species group.

Nobs has successfully hybridized several *Atriplex* species which have C_4 photosynthesis with *Atriplex* species lacking it (*21*). Neither these crosses nor the selection of progeny of the crosses has resulted in breeding of a new C_4 plant. The several characteristics a plant must have to have a functional C_4 mechanism are specified by separate genes, and these must all be present in the same individual, a very unlikely event and difficult to achieve in laboratory breeding experiments (*21*). That it has evolved several times in nature illustrates the massive difference in scale between the processes of nature and laboratory efforts at genetic manipulation. Sexual reproduction from generation to generation over geologic time scales constantly brings into existence new combinations of genetic material in individual plants. Selective pressure favoring C_4 photosynthesis exists for vast numbers of plants growing in warm, arid areas.

Such large numbers of plants are impractical in breeding experiments. The probability of success in transferring such a multigene adaptation by plant breeding could, however, be improved greatly by selecting for individual components of the mechanism rather than selecting at a functional phenotypic level, which would require the presence of the complete mechanism. Thus, the plant breeder could transfer individual genes and accumulate these stepwise instead of awaiting their coincidence. Such an analytic approach, however, requires considerable knowledge of the physiological and genetic basis for the adaptation.

Conclusion

I have focused on examples of plant adaptations to environmental conditions that range from adjustments in the allocation of metabolic resources and modification of structural components to entirely separate mechanisms. The result of these modifications is more efficient performance under the stresses typically encountered in the plants' native habitats. Such adaptations, for reasons which are not entirely clear, often lead to poorer performance in other environmental conditions. This situation may be a fundamental basis for the tendency toward specialization among plants native to specific niches or habitats. The evolutionary mechanisms that have resulted in these specializations are very large-scale processes. It seems reasonable to suppose that the plants native to particular habitats are relatively efficient in terms of the limitations imposed by those habitats, and that the adaptive mechanisms these plants possess are, compared to those which have evolved in competing organisms, the most succesful biological means of coping with the environmental stresses encountered.

I believe that we can learn from nature and utilize the adaptive mechanisms of these plants in agriculture to replace in part our present reliance on resources and energy to modify the environment for plant growth. By analogy with natural systems, improved resource utilization will require specialization and greater knowledge of the limitations of a particular environment and plant genotype. For example, the cultural conditions, plant architecture, and physiological responses necessary to achieve high water use efficiency from our crop species with C_4 photosynthesis probably differ from those required to achieve maximum total growth. Also, efforts to control water application to eliminate waste carry with them the risk that the crop could be injured by inadequate water. Thus, greater demands would be placed on the crop physiologist, the plant breeder, and the farmer. Planting and appropriate management of adapted crop genotypes could enable cultivation of many areas presently considered unusable because of environmental extremes or shortage of resources, and may lead to more efficient resource utilization on land already under cultivation. The costs or benefits of this cannot yet be estimated. However, I suspect that the greatest potential for application of such techniques will be in the developing rather than the developed regions of the world.

The genetic and functional diversity of plants is a tremendous biological resource. The capacity of plants to adjust in the future to changing environmental conditions depends on this diversity and on evolutionary processes of nature. Wild plants may provide a source of genetic material to improve crop plants. Also, as advocated by McKell (*22*), wild plants can be utilized to a greater extent directly by man. Long-term research efforts and commitment to preserve natural habitats and their populations of wild plants will be required to maintain and more effectively utilize this resource.

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