Carbon Gain by Plants in Natural Environments

Carbon assimilation analysis provides an understanding of how plants function in diverse environments

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P hysiological ecologists have long been concerned with photosynthesis, which incorporates carbon to provide plants with all their energy and structural building blocks. This carbon gain is an important aspect of plant performance in natural environments. The acquisition and use of other resources, such as nitrogen and water, are tightly linked to photosynthetic performance. For example, energy from photosynthesis is employed for nitrogen acquisition and reduction, and photosynthetic capacity is strongly coupled to leaf nitrogen content (Chapin et al., p. 49, this issue). Photosynthesis is also closely related to water movement in a plant. To facilitate absorption of carbon dioxide for use in photosynthesis, a leaf must have wet cell surfaces. As a consequence, transpiration uses nearly all of the water taken up

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by the roots. Thus, water is, in effect, traded through the stomata for carbon dioxide.

There are strong links between resource availability, the ability of plants to use resources for carbon gain and productivity, and, at the population level, parameters such as size, survival, and reproductive output (Bazzaz et al., p. 58, this issue). Ecological functions, such as plant and population reproductive output, correlate with net primary productivity (Pitelka et al. 1985). Moreover, within populations, plant size and survival are correlated (Solbrig 1981). Local environmental variations in resource availability, due either to competition or microsite quality, probably influence these correlations more strongly than do genetic differences between individuals.

Although leaf photosynthetic rates have been studied extensively, more information is needed to understand what factors control plant carbon gain (which is computed by multiplying the carbon dioxide uptake rate per unit of photosynthetic surface area by a plant's overall photosynthetic surface area, and then subtracting any losses due to such factors as respiration and consumption by herbivores). Plant architecture plays an important role in determining how much light is intercepted by any leaf and, hence, its photosynthetic rate. Moreover, carbon gain is a dynamic process. Leaf photosynthetic capacity is age dependent and, as the plant grows, canopy structure and other such changes modify the environment of a particular leaf. Allocation of car-

bon and nutrients to new leaves is an especially important "reinvestment," because it drives growth in an exponential fashion.

Leaf photosynthetic capacity

Leaf photosynthetic capacity—defined as the photosynthetic rate per unit leaf area when incident light is saturating, CO_2 and O_2 concentrations are normal, temperature is optimum, and relative humidity is high—varies nearly 100-fold (Mooney and Gulmon 1979). Generally, the plant species found in resource-rich environments have much higher photosynthetic capacities than those found where water, nutrients, or light is in short supply. Thus, species native to high light environments have higher photosynthetic capacities than shade-adapted species, and agricultural weeds have higher rates than species native to less fertile habitats. In addition, species native to resource-poor environments (e.g., with low light or low nutrients) tend to respond less to an increase in resource availability than do those species from resource-rich environments.

Highest photosynthetic capacities are found among annuals and grasses indigenous to deserts, where light is not limiting and other resources are intermittently abundant (Ehleringer and Mooney 1984). Evergreen desert shrubs, however, which must endure periods of low water availability, have very low photosynthetic capacities. The photosynthetic capacity of the leaves of most species is very plastic, depending strongly on the

availability of resources. For example, sun- and shade-grown leaves of the same species often exhibit up to a fivefold difference in photosynthetic capacity (Björkman 1981). Photosynthetic capacity is also strongly dependent on nitrogen availability (Chapin et al., p. 49, this issue).

In addition to control by the environment, there may be internal controls on photosynthetic capacity. For example, experimentally removing carbon sinks, such as developing fruits, frequently results in lowered leaf photosynthetic capacity (Gifford and Evans 1981). Removing some leaves, however, often leads to an increased photosynthetic rate in those remaining. Because such experiments usually have been done with crop species growing under resource-rich conditions, the results may not predict how wild plants growing in resource-limited environments will behave. Some observations based on partial defoliation of range grasses and trees indicate that photosynthesis increases in the remaining leaves after some are removed. This effect may be due to such resources as nitrogen and water becoming more readily available to the remaining leaves (Detling et al. 1979, Heichel and Turner 1983). Accumulation of starch or soluble carbohydrates is not likely to control photosynthesis by direct feedback, except under extreme situations, such as when the photosynthetic rate has been increased by continuously elevated levels of both CO_2 and light (Azcon Bieto 1983).

The leaf photosynthetic capacity is determined primarily by the amounts and catalytic activities of photosynthetic enzymes. Although stomatal CO_2 conductance was believed to be a major factor limiting photosynthetic capacity, current evidence suggests otherwise (Farquhar and Sharkey 1982). There is a strong correlation between stomatal conductance and photosynthetic rate (Wong et al. 1979), but it seems more likely to represent an adjustment of stomatal conductance to match the intrinsic photosynthetic capacity rather than a causal relationship. According to a theoretical model for stomatal control, the stomata may minimize daily transpiration for a given daily carbon gain. In other words, if a certain amount of water can be acquired for

transpiration, stomata should act to maximize photosynthesis within this constraint (Cowan and Farquhar 1977).

According to another model describing the relationship between the biochemistry and photosynthetic capacity of leaves, activity of the primary carboxylating enzyme, ribulose-1,5-bisphosphate carboxylase-oxygenase (RUBISCO), determines the intrinsic photosynthetic capacity of a leaf having the C_3 photosynthetic pathway (von Caemmerer and Farquhar 1981). The carboxylation rate depends on the amount of active enzyme present and any limitations imposed by substrate concentrations, such as low levels of CO_2 that may be due to stomatal closure (Figure 1). In addition, atmospheric O_2 competitively inhibits CO_2 fixation by RUBISCO, leading to photorespiration. As CO_2 levels in the leaf are depleted, the ratio of O_2 to CO_2 increases, and the enzyme's activity is reduced. Because regeneration of the substrate ribulose-1,5-biphosphate (RuBP) depends on electron transport and photophosphorylation, these processes ultimately limit the photosynthetic rate at high CO_2 concentrations or in low light. At the transition from CO_2 to RuBP limitation, electron transport capacity and carboxylation capacity can both limit photosynthesis.

Stomata appear to operate so as to keep CO_2 concentrations in the chloroplast close to this transition level. Hence, there is neither a great excess of electron transport capacity nor of carboxylation capacity, and the system may be operating at maximum efficiency with respect to investments in these two capacities (Farquhar and Sharkey 1982). However, this interpretation of leaf gas exchange may be oversimplified since other factors, such as chloroplast inorganic phosphate supply (Sharkey 1985) or the light-activation requirement of RUBISCO (Perchorowicz et al. 1981), may be limiting under certain circumstances. Despite its simplicity, the model developed by Farquhar and his colleagues can account for the photosynthetic response of leaves to a wide variety of conditions, and thus is highly useful.

How can we expect the photosynthetic apparatus to vary among plants in environments with different re-

source levels? Mooney and Gulmon (1982) used econometric models to predict how carboxylation capacity may be modulated to match the most limiting environmental resource. Assuming plant leaves obtain the highest photosynthetic capacity commensurate with prevalent resource limitations, carboxylation capacity should be less for shaded rather than well-illuminated leaves and where nutrients are scarce compared to where they are abundant. Moreover, where water is limited and stomatal conductance presumably reduced, carboxylation capacity also should be reduced (Figure 2).

These predictions agree qualitatively with observed differences in photosynthetic capacity. However, such models have not yet been tested quantitatively. Moreover, under some circumstances, production of two leaves with lower photosynthetic capacities may be favored over maximizing the photosynthetic capacity of an individual leaf. An exciting prospect is the combination of the more detailed mechanistic models, such as the one developed by Farquhar et al. (1980), with the econometric models to determine whether the allocation of resources within the photosynthetic apparatus is optimal. Physiological ecologists then would be able to address such questions as whether in shady environments an elevated ratio of electron transport to carboxylation capacity provides optimal use of resources.

Alternate metabolic pathways for photosynthesis

Besides the important quantitative differences in leaf enzyme levels within a single plant or between one plant and another, qualitative differences in the photosynthetic metabolic pathways employed by different species of higher plant can have a great impact on carbon gain and other responses of an individual plant to its environment. Identification of the pathway called C_4 ranks as one of the most exciting discoveries in plant biology of this quarter century. The pathway's potential ecological consequences were recognized almost immediately, thus bringing together physiological ecologists, plant physiologists, and biochemists to meet a

new challenge. Because of the biochemical similarities, the discovery of the C_4 metabolic pathway helped elucidate another photosynthetic pathway, called the crassulaceaean acid metabolism (CAM) pathway, which is found in many succulent species. The discovery promoted work on the physiological ecology of plants within both categories. The ties created between physiological ecologists and metabolic plant biologists by the C_4 discovery continue to be strong.

Several thousand species in at least 17 families of angiosperms follow the C_4 pathway, although the C_3 metabolic pathway predominates throughout the plant kingdom. The C_4 photosynthetic pathway is believed to have evolved multiple times and also relatively recently, because C_4 metabolism is found only in phylogenetically advanced families, and even within a family only in the more advanced genera (Osmond et al. 1980). CAM is as widespread as C_4 photosynthesis, but it is also found in primitive groups, such as ferns and fern allies (Isoetes), and the primitive gymnosperm, *Welwitchia*. Many genera with CAM species also contain C_3 species. A few genera contain both C_3 and C_4 species, and several species with intermediate C_3-C_4 metabolism have been identified (Monson et al. 1984). These species seem to have more C_3 than C_4 characteristics and may represent a step in the evolution of C_4 photosynthesis. They may prove valuable in understanding how the complex process of C_4 photosynthesis has evolved.

Whereas C_3 photosynthesis requires only one carboxylation, photosynthesis by C_4 and CAM plants requires two carboxylations. First, CO_2 is fixed into a 4-carbon, rather than a 3-carbon, compound by the enzyme phosphoenol pyruvate (PEP) carboxylase. Then it is released and fixed again by RUBISCO, the same enzyme found in C_3 species. In CAM plants, the two carboxylases are found within the same cells, but the reactions occur at different times. In C_4 plants, the two carboxylations occur in separate cells, with the C_4 pathway pumping CO_2 from the mesophyll to the bundle sheath cells to maintain high CO_2 concentrations near RUBISCO. As a consequence, the competitive inhibition of RUBISCO by oxygen
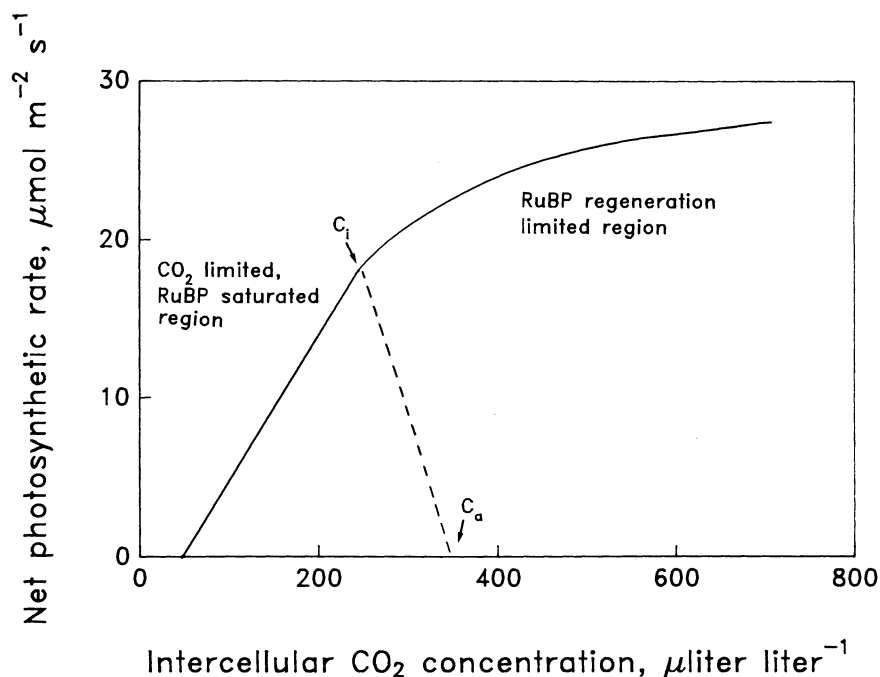
Figure 1.The relationship between intercellular CO_2 concentration and photosynthetic CO_2 fixation in a C_3 leaf. The arrows indicate the intercellular (C_i) and ambient (C_a) CO_2 concentrations, while the slope of the dotted line is proportional to stomatal conductance. Adapted from Farquhar and Sharkey (1982).
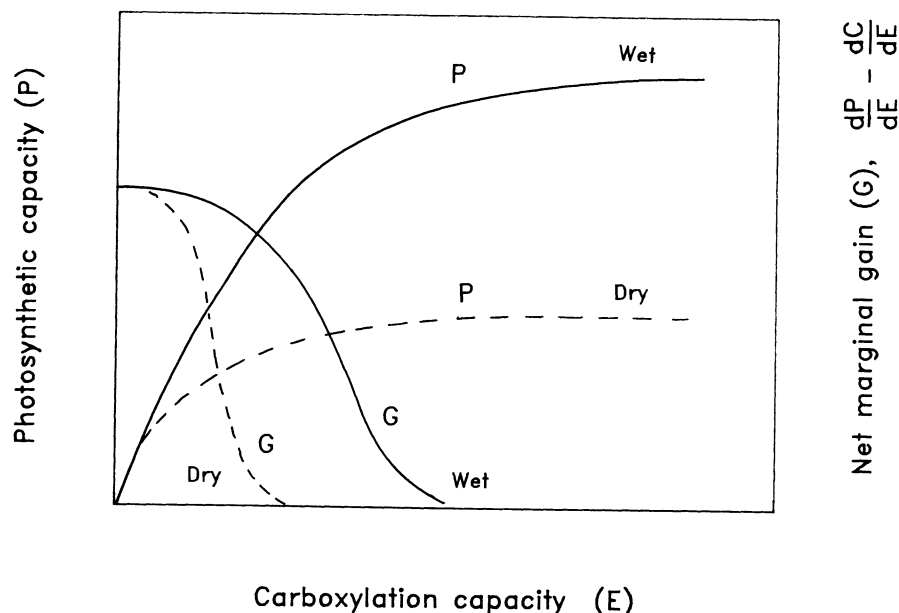
Figure 2. The hypothetical relationship between photosynthetic (P) and carboxylation (E) capacities for leaves of plants in wet and dry environments. The net marginal gain (G) for an increase in carboxylation capacity is a function of the difference in the rate of increase in P and the rate of increase in the associated costs. E is a function of the investment in photosynthetic enzymes, electron carriers, and related components in the leaf. P increases asymptotically with increasing E, but reaches different maximal levels under wet and dry conditions, because of differences in stomatal conductance. E is optimal when G equals O. Adapted from Mooney and Gulmon (1979).

and photorespiration is eliminated. The greatest benefits of the C_4 pathway may accrue at warm temperatures, because C_3 plants experience greater O_2 inhibition and photorespiration as temperatures increase (Björkman 1973).

The CO_2 pump of the C_4 pathway also allows for higher photosynthetic rates when CO_2 concentrations are low in the intercellular air spaces. Consequently, for any given photosynthetic rate, C_4 plants can have lower stomatal conductances and, therefore, higher water use efficiencies (the ratio of photosynthesis to transpiration) than do C_3 plants. Nitrogen use efficiencies (photosynthetic rate per unit of leaf nitrogen) also are higher in C_4 than C_3 plants because the enzyme RUBISCO is saturated with the substrate CO_2 and therefore is more efficient. Moreover, the RUBISCO variant present in C_4 plants is catalytically superior at high CO_2 concentrations (Seemann et al. 1984). Its greater efficiency means that C_4 plants need to make less enzyme compared to C_3 plants, a metabolic savings that more than offsets the additional investment required for the other C_4 enzymes. However, the CO_2 pump has an extra cost to C_4 plants of at least two molecules of ATP for each molecule of CO_2 that is fixed.

Thus, the relationships between photosynthetic capacity and supplies of water, nitrogen, and light differ substantially for C_4 and C_3 plants. Even so, the same general constraints seem to hold. For example, among C_4 Hawaiian shrubs and trees of the *Euphorbia* genus there is a marked decrease in photosynthetic capacity from the species occupying arid, highly illuminated habitats, where resources are at least temporarily abundant, compared with those species found in mesic and wet forests, where light is low and nutrients may be limiting (Pearcy et al. 1983). A similar, though less dramatic, shift in photosynthetic capacity along the same environmental gradient occurs in the C_3 *Scaevola* species (Robichaux and Pearcy 1984).

The C_4 pathway thus appears to be a specialized adaptation for yielding high photosynthetic activity and, hence, rapid growth when temperatures are warm and solar radiation is high. Tropical grasslands and savan-

nas, where water is available temporarily during the warm summer months, are dominated by C_4 grasses. In the central great plains of North America, C_3 species of grass flora are active during the spring, whereas C_4 species are active in the summer. Similarly, summer desert annuals are almost exclusively C_4 and winter desert annuals C_3 (Mulroy and Rundel 1977). The water use efficiency of C_4 plants is about twice that of C_3 plants. This enhanced efficiency also may increase productivity. Among woody plants, C_4 photosynthesis is common only in the Chenopodiaceae, which are found primarily in saline desert regions. However, C_3 plants can also be successful under arid conditions; desert perennials, for example, are predominantly C_3 plants.

The relative scarcity of C_4 plants in cool, shaded, and mesic environments may be due more to such factors as sensitivity to chilling. These traits may reflect C_4 plants' evolutionary origins in warm regions rather than any disadvantage directly linked to C_4 photosynthesis. The lower quantum yield in C_4 plants is about equal to the energy losses due to O_2 inhibition and photorespiration in C_3 species (Björkman 1981). This apparent balance depends on temperature and the particular species (Pearcy and Ehleringer, 1984), but C_3 photosynthesis is favored only in the cooler northern forests, whereas tropical forest understories are not sufficiently warm to favor C_4 photosynthesis.

Indeed in Hawaiian forests, where several C_4 *Euphorbia* species occur in the shaded understory, C_4 photosynthesis confers no apparent advantage or disadvantage in terms of carbon gain or growth relative to when the C_4 plants are compared with neighboring C_3 species (Pearcy and Calkin 1983). Presumably, the occasional occurrence of C_4 species in cool or shaded habitats is a result of secondary adaptations to these conditions. This seems clearest in the Hawaiian *Euphorbia* species, since those native to wet and shaded habitats seem to have evolved from arid-habitat species.

Although biochemically similar to C_4 photosynthesis, CAM provides a different mode of carbon gain. In CAM plants, stomata are open at night and CO_2 fixation depends on

the enzyme PEP carboxylase, which yields C_4 acids. During the day when the stomata are closed, the C_4 acids are decarboxylated, and the CO_2 is recaptured by RUBISCO. Because transpiration is restricted by cool temperatures and high humidities at night and by closed stomata during the day, CAM plants typically use water very efficiently.

Many variations of CAM photosynthesis exist. For example, under drought stress some species—mostly leaf succulents—switch from purely C_3 photosynthesis to CAM or a combination of C_3 and CAM photosynthesis. Many stem succulents, on the other hand, undergo "CAM idling," where stomata remain closed both day and night, but CAM metabolism continues and CO_2 is internally recycled. The advantage of CAM idling is that, during the drought period, a fully active photosynthetic apparatus is maintained that can rapidly resume CO_2 uptake whenever it rains. For example, after a drought the night CO_2 fixation rates of *Opuntia basilaris* fully recover within 24 hours following rain (Szarek et al. 1973), whereas regrowth of leaves in a drought-deciduous species may require a week or two. CAM idling, coupled with the rapid regrowth of root systems and water storage that typifies desert succulents, allows plants to use efficiently brief and unpredictable rainfall.

Although desert succulents provide perhaps the best examples, CAM also is found in plants from a much wider range of microenvironments where water supplies can be limited. These include rock outcroppings in temperate humid environments, grasslands, and tropical forest tree canopies where many epiphytes rely at least partly on CAM. In the latter environment, CAM species show a clear preference for the upper, dryer parts of the canopy, whereas the C_3 species are found in the lower canopy (Winter et al. 1983).

CAM metabolism is used by plants in several unusual ways. For instance, *Isoetes howellii*, an aquatic plant, uses CAM as a CO_2 trapping mechanism. This native California species is found in vernal pools where CO_2 can be depleted during the day by photosynthesis but builds up at night because of respiration by plants and

other organisms. CAM enables plants to take up CO_2 at night when it is most available. Early in the morning, the plants shift to C_3 photosynthesis but, as CO_2 is depleted, the C_3 photosynthesis becomes dependent on the internal release of CO_2 from organic acids (Keeley and Busch 1984). Several other *Isoetes* species as well as species from other genera found in carbon-poor aquatic environments possess CAM, but most terrestrial *Isoetes* lack it. An exception is *I. andicola* (formerly *Stylites andicola*), a low rosette-forming plant native to Andean bogs above 4000 m in Peru. This species lacks stomata and takes up CO_2 through the roots (Keeley et al. 1984). After diffusion to the stems, CO_2 fixation may occur at least in part via CAM. CAM is also observed in the green roots of shootless epiphytic orchids (Cockburn et al. 1985). These roots lack stomata, and thus may take up CO_2 across the cortex by means of special aeration pathways.

Coping with respiratory losses

A considerable fraction of the carbon fixed by a plant is lost as CO_2 during respiration. However, quantitative information on respiratory losses and the relationship between carbon gain and respiration is suprisingly scarce. For example, it is not known conclusively whether the rate of leaf mitochondrial respiration is the same in the light and dark. Experimentally, respiration rates are difficult to separate from photosynthetic rates. Thus, gauging true respiratory losses from leaves is also difficult. Moreover, photosynthesis may directly replace some of the energy usually derived from respiration in nongreen tissues.

Respiration serves many important functions, including the supply of energy and the structural building blocks required for synthesis of new biomass. Additional respiration also is required for maintenance of membranes, proteins, and ion gradients. Moreover, an alternative pathway of respiration, whose role and extent is controversial (Laties 1982), is found in many leaves and roots. No ATP is produced by it. Its role may be to consume carbohydrates that have accumulated in quantities exceeding growth needs (Lambers 1985).

The respiration losses required for building new biomass can be estimated from the chemical composition of the biomass and the biochemistry used for its synthesis (Penning de Vries et al. 1974). Alternatively, such estimates are made by analyzing the oxidation-reduction state of the tissue (McDermitt and Loomis 1981). Estimating maintenance respiration is much more difficult, but in theory it is the remaining respiration rate when the growth rate is extrapolated to zero (Amthor 1984). The proportion of respiration due to the alternative pathway can be estimated by applying inhibitors that block either it or the mitochondrial electron transport (Lambers 1985).

The respiration costs of biomass production are tied closely to the content of proteins, lignins, resins, phenolics, and other constituents of plant tissues. Because most leaf protein consists of photosynthetic enzymes, leaves with high photosynthetic capacities are more costly to construct and maintain than those with low photosynthetic capacities. Secondary plant compounds, many of which play a defensive role in plant leaves, also may account for a considerable proportion of the total leaf cost (Bazzaz et al., p. 58, this issue). While growth and maintenance components are difficult to disentangle, apparently only a small percentage of the CO_2 that is fixed daily goes for maintenance (Merino et al. 1982). In overall carbon balance, therefore, growth respiration represents the majority of the losses. Nevertheless, maintenance respiration is environmentally sensitive and therefore may play an important role in net carbon gain (Mooney and Gulmon 1982). One would expect maintenance respiration rates to be greater in tissues with high metabolic activity because of the greater protein turnover and greater costs for ion transport.

In agricultural crops, the correlation between high respiration rate and reduced productivity is often closer than that between photosynthetic rate and yield. Crop varieties with reduced respiration rates show better yields than those with high respiration rates (Lambers 1985). In contrast, there was no correlation measured between photosynthetic rate per unit leaf area (with saturating

light) and yield. The high-yielding varieties may have a greater capacity for adaptation to shaded conditions within dense crop canopies, enabling them to have a greater net photosynthetic efficiency at the canopy level. However, the physiological basis for the reduced respiration rates is not understood.

Acclimation of respiration to prevailing temperature conditions has been commonly observed in wildland plants. Thus, over the long term, respiration may be fairly independent of temperature changes within about a 10° C range. Because photosynthesis also acclimates within many of the same plants, respiration adjustments may maintain a balance between fixation and carbon use. Over the life of the plant, however, increased respiration as compared to photosynthesis, must inevitably lead to declining growth.

Leaf carbon balance

For a leaf to benefit a plant, the leaf's cumulative carbon gain must be at least marginally greater than the carbon costs of its construction, maintenance, and protection. Leaf development and aging follows a predictable sequence of events involving changing patterns of costs and carbon gain (Chabot and Hicks 1982, Mooney and Gulmon 1982). During the initial phases of expansion when photosynthetic capacity is low, the leaf imports much of its carbon for construction and the respiration rate is high. The maximum photosynthetic capacity is usually reached at about the time of full expansion. Finally during senescence, photosynthetic capacity declines as nitrogen is mobilized and exported before the leaf falls from the plant.

The time required before a leaf yields a net profit depends on the environment, the construction and maintenance costs, and the leaf's photosynthetic capacity. Evergreen leaves take longer to produce a net profit because they develop more slowly, can be more costly to produce, and have lower photosynthetic capacities than deciduous leaves (Chabot and Hicks 1982). In environments with pronounced seasonal variation, evergreen leaves should be favored where the cost of maintaining the leaf over

the unfavorable season plus the cost of the lower photosynthetic capacity is less than the cost of producing a new leaf. Based on such reasoning, Miller and Stoner (1979) correctly accounted for the elevational distributions of evergreen and drought-deciduous leaf types in the California chaparral.

Environmental constraints also play a major role in determining the long-term carbon gain of a leaf. Under unfavorable conditions, more time is required for a leaf to return a profit. In nature, conditions are usually not optimal, and photosynthesis is below full capacity because of water stress, temperatures being either too high or too low, light being either excessive and causing photoinhibition or too low, or humidity being so low that it causes partial stomatal closure (Figure 3).

These factors can reduce the daily average photosynthetic rate by as much as 40–70% (Schulze and Hall 1982). For example, wild strawberry leaves need only 12 days to meet construction costs in an open field, whereas in a deciduous forest understory they require more than 30 days (Chabot and Hicks 1982). The annual leaf carbon gain was limited to 35–45% of its potential maximum in several plant species growing in a European hedgerow community (Küppers 1984b). The principal limitation was low light, including effects of dawn and dusk, short photoperiods in the spring and fall, and cloudy days (Figure 4). Low temperatures and the short photoperiod in winter, as well as water stress in summer, reduce the annual carbon gain of the evergreen chaparral shrub *Heteromeles arbutifolia*, to about 52% of its potential (Mooney et al. 1975). Because such estimates do not include probable nutrient limitations, the actual reductions by both soil and climatic factors may be even greater. Moreover, repair mechanisms required to overcome the effects of stresses also must increase maintenance costs, further delaying net leaf profit.

Analyzing allocation effects

Monsi's (1960) analysis more than two decades ago illustrated how important reinvestment of fixed carbon and other resources into new leaves is to production. Because total plant photosynthesis is increasing, relatively small changes in allocation to new leaves compounds the investment, leading to large changes in plant size. Indeed, plant behavior is predicted very well by Monsi's model, and large differences in growth rates can be attributed to differences in allocation patterns.

For example, after five weeks' growth, the wild radish *Raphanus raphanistrum* × sativus accumulates twice as much dry weight as the cultivated radish, which invests much of its carbon into its swollen hypocotyl, even though both varieties have the same photosynthetic rate per unit leaf area (Mooney and Chiariello 1984). Allocation to roots, stems, and storage organs reduces the plant's maximal potential growth rate but is vital
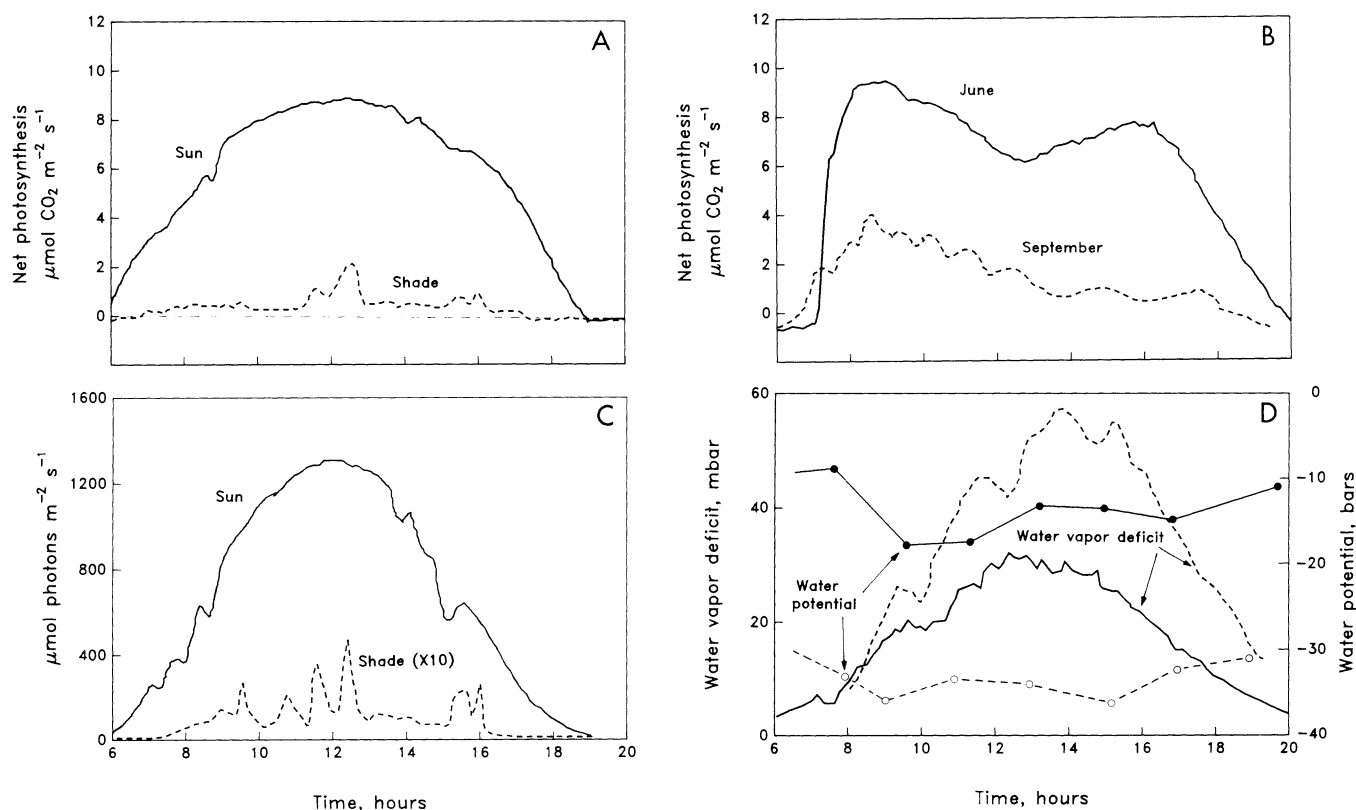
Figure 3. Diurnal course of CO_2 exchange for (A) sun and shade leaves of *Acer campestre* in a central European hedgerow and (B) leaves of *Quercus coccifera* in an evergreen scrub community in Portugal at the beginning (June) and end (September) of the dry season. Shown in the lower graphs are the diurnal course of (C) light received by the sun and shade leaves and (D) water vapor deficits from the leaf to the air and water potentials for *Q. coccifera*. Data for *A. campestre* from Küppers (1984a) and for *Q. coccifera* from Tenhunen et al. (1985).

for acquiring and distributing resources and displaying leaves. Storage is more complicated because it involves a savings that reduces current growth but may ensure long-term survival during stress periods as well as increased reproductive output.

Carbon gain should be optimized when resources are allocated to non-photosynthetic structures so that no single resource is more limiting than others. Despite this being an intellectually satisfying statement, its validity remains in doubt because there are still no conclusive tests of whether allocation patterns actually maximize carbon gain. However, some observations point in this direction. For example, changes in allocation to root systems during cowpea (*Vigna unguiculata*) growth are consistent with the proposed pattern. Thus, cowpeas invest only enough of their resources in building roots to prevent water stress; doing otherwise would reduce the plants' photosynthetic capacity (Schulze et al. 1983).

In a similar vein, Givnish (1982) predicted how forest herbs might optimize their investment in stem structures, based on certain mechanical considerations. To maximize carbon gain, an investment would need to be just sufficient to build the xylem and phloem required for transport and to provide the mechanical strength and height to raise the leaves above competitors. While herbs in denser communities tend to be taller than those in sparsely vegetated understory areas, the question of whether stem investments are optimal has not been tested.

Moreover, the structural needs may be greater and more costly than initially assumed because the support system must be able to bear loads resulting from falling twigs or other objects. The extra cost would depend on the frequency and nature of falling debris or other sources of damage, such as wind, and the probable benefit to be accrued from a surviving leaf. For instance, key support structures in several palms found in the understory of Costa Rican tropical forests can be from 3–100 times stronger than the minimum required to support the leaves (Chazdon 1986). Consideration must, therefore, be given not only to the immediate costs and benefits of a plant's carbon allocation
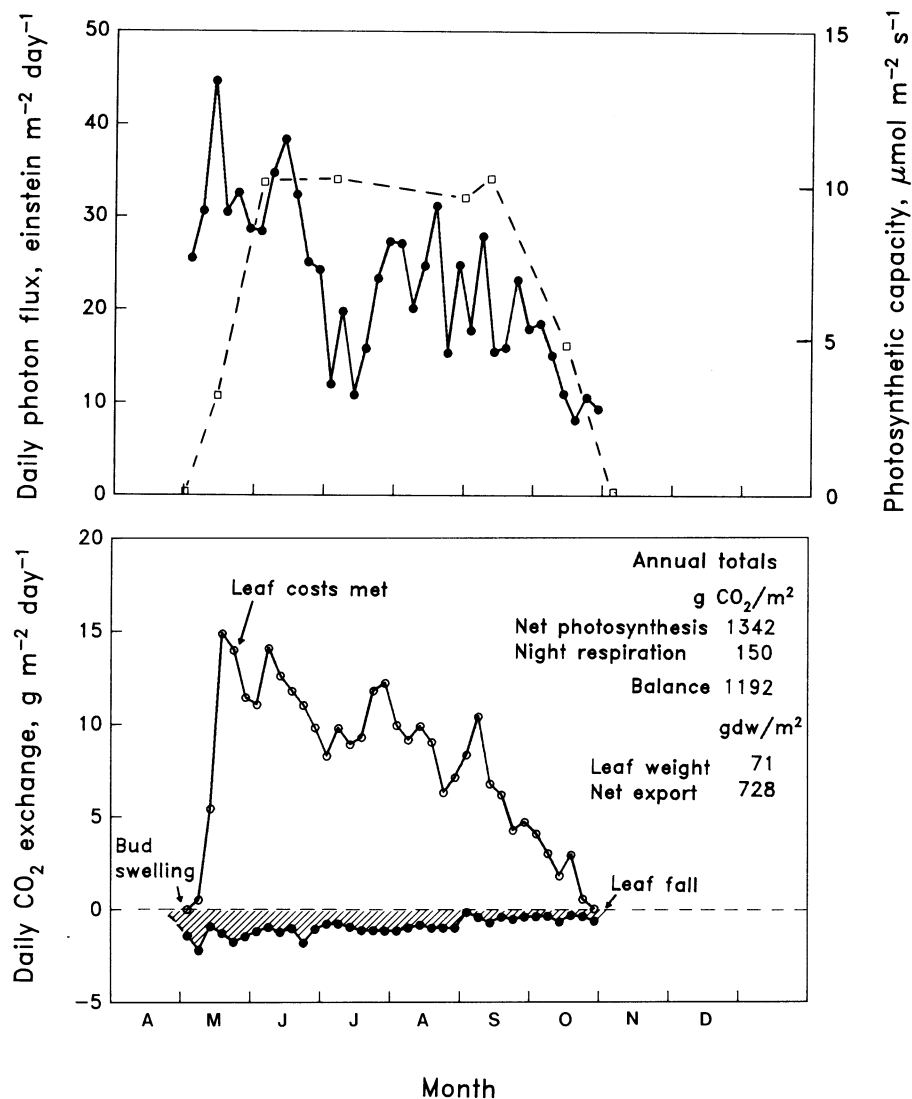

Figure 4. Annual course of photosynthetically active radiation (●, top graph), photosynthetic capacity(□), daily CO_2 uptake(○), and night respiration (shaded area) of *Acer campestre* during 1980. The data for respiration, CO_2 uptake, and daily radiation are 5-day means. The annual totals for dry weight exported (gdw) are based on a conversion between CO_2 fixed and biomass of 0.66. Adapted from data of Küppers (1984a and b.)

pattern but also to its influence on the lifespan of the leaves in the face of likely damage. Determining whether an allocation pattern is optimal or not is an exceedingly complex problem.

The influence of canopy structure

Canopy architecture determines how leaves are positioned in different microenvironments and how light energy is absorbed by the whole plant. Moreover, it also influences how limited resources must be distributed among leaves of different age and position to maximize whole-plant

carbon gain (Field 1983). Although the important role of canopy structure in agricultural systems has long been recognized, the issue has received relatively little attention in physiological ecology.

Chief among the crop traits correlated with high productivity is the capacity for rapid canopy closure to intercept maximal light (Gifford and Evans 1981). After canopy closure, steep leaf angles can increase productivity by allowing more light to be transmitted to lower layers (Duncan 1967). Although the same principles should apply to wild plants, other constraints may also play an impor-

tant role in canopy structure. For instance, horizontal leaves can shade competitors more effectively. Moreover, leaf angles play an important role in stress avoidance by reducing injury from photoinhibition or by altering energy balance relationships. Thus, the leaf angles and canopy structure of a particular plant reflect a compromise between the need to maximize its short-term photosynthetic rate and the need to avoid stresses that reduce long-term carbon gain.

Canopy structure studies have focused on theoretical treatments of the mechanical constraints that influence leaf display and, hence, light interception (Borchert and Tomlinson 1984). Branching patterns may serve to maximize the efficiency of leaf display to sunlight but also may be linked to reproductive functions or to the maintenance of many meristems so leaf area can be rapidly deployed (Miller and Stoner 1979). In two understory palm species, for which light apparently is the primary limiting factor, leaf display appears to maximize light absorption and minimize self-shading (Chazdon 1985). One species is more efficient at light interception because it uses less biomass to support its leaves, and so it can reproduce at a smaller size and occupy more shaded microsites than the other species.

Based on simulations taking into account energy balance, photosynthesis, leaf costs, and longevity, several (but not all) species of California chaparral shrubs appear to maintain leaf area indices (the ratio of leaf surface area to ground surface area) close to the optimum for maximal photosynthesis (Miller and Stoner 1979). And the high productivity of spruce (*Picea excelsa*), despite the low photosynthetic capacity of its needles, can be ascribed to its maintaining high leaf area indices (Schulze et al. 1977). Needles live as long as 12 years, and only 15% of the total needle biomass is renewed annually. In contrast, although leaf photosynthetic rates of the deciduous beech (*Fagus sylvatica*) are double those of spruce, the beech's annual productivity is 40% less. The difference is due largely to the much greater leaf area maintained by spruce and only in small part to the two species' different annual periods of photosynthesis.

Conclusions

Carbon balance, because it integrates many plant functions, has provided a very useful conceptual tool as well as a practical approach for studying how plants function in particular environments. It also has proved useful to treat carbon as the currency of the costs and benefits to a plant for having particular physiological or morphological mechanisms that allow it to cope with environmentally imposed limitations. While this use of carbon has been questioned, it still appears to be the most widely useful among the alternatives (Bazzaz et al., p. 58, this issue). The close link between carbon and other major resources, such as nitrogen and water, also allows the costs and benefits of their acquisition and use to be relatively easily expressed (see Chapin et al., p. 49, and Schulze et al., p. 30, this issue). However, in some instances, nitrogen or some other nutrient may be a more appropriate choice. Ideally, the chosen currency should allow for estimates of energy costs. Although the use of glucose equivalents provides an example (Penning de Vries et al. 1974), such an approach requires either detailed biochemical analysis or knowledge of the elemental composition of the plant tissue (McDermitt and Loomis 1981). Either one is difficult to obtain.

The concerns of physiological ecology, which are shared with fields ranging from biochemistry to evolutionary ecology, cover a size scale from molecules to ecosystems and a time scale from milliseconds to thousands (if not millions) of years (Osmond et al. 1980). The physiology of leaf photosynthesis and its response to the environment are relatively well understood, an achievement due in part to the sophisticated measurements made possible by the development of the infrared gas analyzer as well as the relative rapidity of conducting most experiments. Remarkable progress has also been made linking leaf biochemistry to gas exchange responses. In contrast, there has been less progress toward understanding many aspects of respiration. Similarly, knowledge of allocation patterns is largely empirical, and little is known about their control.

Within the broad space-time scale,

our knowledge is concentrated. We have the most detailed understanding of the mechanisms underlying leaf functions. Scaling up to understand the significance of these mechanisms for whole-plant performance in communities is still a difficult challenge. Merely extending results from single leaves to whole canopies requires a formidable sampling program (Leverenz et al. 1982), and results from single leaves may not provide the same perspective as those gleaned from whole plants (Caldwell et al. 1983). Moreover, we need a better understanding of how plants respond on a seasonal or annual time scale and, in particular, how they cope with the stochastic nature of the environment. Models that relate optimal plant performance to seasonal rainfall patterns may provide a useful framework in which to begin this task (Cowan 1982).

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