FEATURES

Photosynthesis and Photorespiration: Biochemistry, Physiology, and Ecological Implications

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Over the past 15 years tremendous progress has been made in the study of photosynthetic pathways. It is now accepted that there are 3 distinct photosynthetic pathways in higher plants: the Calvin-Benson pathway (C_3 photosynthesis), the Hatch-Slack pathway (C_4 photosynthesis), and Crassulacean Acid Metabolism (CAM photosynthesis). Much progress has been made in describing the biochemistry and physiology of these pathways, but less is understood of the genetics, ecology, evolution, and regulation of these pathways. The purpose of this review will be to bring the reader up to date on the significant details of the biochemistry and physiology of the 3 photosynthetic pathways and to present an ecological/evolutionary view of the significance of differences in the pathways.

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Biochemistry, morphology and physiology

The biochemistry of all the photosynthetic pathways revolves around a central theme, the Calvin-Benson pathway. This is the so called C_3 photosynthesis, because the initial product formed in the pathway is phosphoglyceric acid (PGA), a 3 carbon molecule. Two molecules of PGA are formed as a consequence of carbon dioxide (CO_2) combining with ribulose bisphosphate (RuBP, a 5 carbon molecule) in a reaction catalyzed by the enzyme RuBP carboxylase. In this pathway, also known as the pentose phosphate reductive cycle, PGA is converted in a series of steps to reform RuBP to keep the cycle functioning. For each cycle one-sixth molecule of glucose is produced. The energy sources ATP and NADPH to drive this cycle come from the light reactions of photosynthesis. Both light and dark reactions take place in the chloroplasts.

Up until the mid 1960's it was thought that all plants possessed C_3 photosynthesis. At that time Kortshack el al. (33) and Hatch and Slack (28) found that in sugar cane the initial product of photosynthesis was not a three carbon molecule, but rather a four-carbon molecule, oxaloacetic acid (OAA). Thus, a new photosynthetic pathway, C_4 photosynthesis, was discovered. Extensive reviews of the biochemistry of C_3 and C_4 photosynthesis can be found in Hatch and Osmond (27), Björkman (5), Black (8), and Chollet and Ogren (17).

Basically, C_4 photosynthesis is simply a biochemical and morphological elaboration of the C_3 photosynthetic pathway in which CO_2 is initially combined with phosphoenolpyruvate (PEP) by the enzyme PEP carboxylase to form OAA. This reaction occurs in the mesophyll or outer cell layers. The OAA is converted to aspartate or malate (26,27), which then diffuses from the mesophyll cells through plasmodesmata to the bundle sheath or inner cell layers where decarboxylation of the C_4 acid occurs. The freed CO_2 is then able to combine with RuBP in the typical Calvin-Benson cycle previously described. The other product of decarboxylation, pyruvate, is used to generate PEP by the enzyme pyruvate Pi dikinase allowing the C_4 system to cycle again (27). The adaptations in function of the C_4 system allows concentration of CO_2 at the site where the RuBP carboxylase reaction occurs.

The key to the operation of the C_4 pathway is a spatial separation of the two carboxylation reactions (PEP carboxylase has a much higher affinity for CO_2 than does RuBP carboxylase) which occur simultaneously. Unlike the photosynthetic cells (palisade and spongy mesophyll) of a C_3 plant, there is a subdivision of function among the photosynthetic cells of the C_4 plants (Fig. 1). In C_4 photosynthesis, there is an outer circle of cells (usually mesophyll) which contain the PEP carboxylase activity while the inner circle of cells (usually bundle sheath) contain the RuBP carboxylase activity. This wreath-like arrangement, termed Kranz anatomy, is a prerequisite for C_4 photosynthesis. Typically, the inner Kranz cells are bundle sheath cells. There are several notable exceptions (such as *Glossocordia* (52), *Suaeda* (56), and *Triodia* (18)) to the general morphological arrangement in that the inner RuBP carboxylase cells are not bundle sheath cells but rather mesophyll cells. However, these species, which do not follow the conventional anatomy still have the same spatial separation of enzyme activities, with PEP carboxylase activity confined to the outer mesophyll cells and the RuBP carboxylase activity restricted to the inner mesophyll cells.

Crassulacean Acid Metabolism or CAM photosynthesis is a modified form of C_4 photosynthesis. In CAM photosynthesis, there is no spatial separation of PEP carboxylase and RuBP carboxylase activities as in C_4 plants, but there is a temporal separation of activities and both enzymes are located in the same cells. PEP carboxylase is active in the dark, while RuBP carboxylase is active during the day. In CAM plants, the stomates open at night allowing PEP carboxylase to fix atmospheric CO_2 into C_4 acids which are stored within the vacuoles, hence the large succulent cells in CAM plants (Fig. 1). During the day, the stomates close and the CO_2 taken up during the dark period is fixed by RuBP carboxylase after decarboxylation from the C_4 acids.

Advantages of different pathways

After having described the 3 photosynthetic pathways, one might wonder

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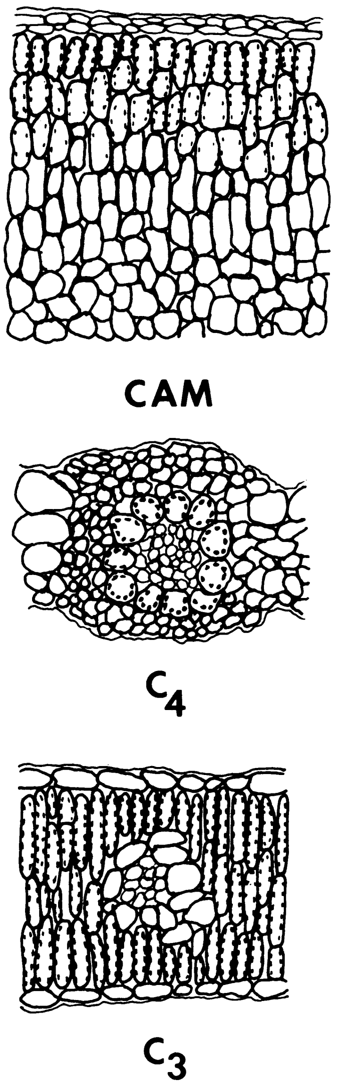

Fig. 1. Leaf cross-sections of CAM, C_4, and C_3 plants. In CAM plants the chloroplasts are located primarily near the epidermal cells and mesophyll cells are large and succulent. In C_4 plants, the photosynthesizing chloroplasts are restricted to the bundle sheath cells, and in C_3 plants the chloroplasts are distributed throughout the mesophyll cells.

why 3 (or possibly more) photosynthetic pathways should exist in nature. After all, might not one type of photosynthetic pathway work equally well in all environments? The answer is apparently no and we are just now beginning to understand the advantages and disadvantages of the various photosynthetic pathways. In evolutionary terms, the C_3 photosynthetic pathway is the oldest and most primitive. An apparent disadvantage of the C_3 pathway is a process known as photorespiration (5, 16, 17, 47). Photorespiration is a process occuring in the light in which CO_2 is evolved from photosynthetic tissues. It is now widely accepted that photorespiration arises because RuBP carboxylase has an oxygenase activity as well as carboxylase activity (47). Normally, RuBP carboxylase catalyzes a reaction whereby RuBP combines with CO_2 to produce 2 molecules of PGA. The oxygenase activity of this enzyme catalyzes the reaction whereby RuBP combines with O_2 to produce PGA and phosphoglycolate (11). CO_2 and O_2 compete for RuBP at the same active site on the carboxylase enzyme, hence CO_2 competitively inhibits the oxygenase reaction and O_2 competitively inhibits the carboxylase reaction (1, 10, 34). The competition between CO_2 and O_2 for RuBP at the active site of the carboxylase enzyme determines the relative rates of photosynthesis and photorespiration. Increasing the CO_2/O_2 concentration favors photosynthesis, while decreasing the CO_2/O_2 concentration favors photorespiration.

Fig. 2 summarizes the influences of CO_2 and O_2 on photosynthesis and photorespiration. Under normal atmospheric conditions (330 μbar CO_2, 21% O_2) the carboxylase enzyme appears to fix 4 CO_2 for every O_2 molecule (36). This ratio of activities has been observed with RuBP carboxylase extracted from leaves of spinach (1) and soybean (34). Under normal atmospheric conditions, we would expect that for every 10 RuBP that cycle through, there will be a net gain of 7 carbons. One CO_2 will be evolved for every 7 carbons gained, resulting in a loss of 14%. This percentage agrees well with direct measurements of CO_2 evolution by Ludwig and Canvin (37).

Decreasing the oxygen concentration to near zero should increase carbon fixation by about 43% (7C net gain to 10C net gain in Figure 2). This same percentage increase is photosynthesis is quite similar to values measured on intact whole leaves (4, 21, 24, 37). Laing et al. (34) and Ehleringer and Björkman (21) have shown that the ratio of oxygenase to carboxylase activity increased as temperature increased from 15° to 35°C, that is the ratio of CO_2/O_2 fixed by RuBP carboxylase decreases below 4. Thus productivity would be expected to decrease in C_3 plants as temperature increased, because of temperature dependent increases in photorespiration.

The advantage of the C_4 pathway is that the PEP carboxylase system acts to concentrate CO_2 causing a high CO_2/O_2 ratio at the site of carboxylation by RuBP carboxylase. The high CO_2/O_2 ratio means no detectable photorespiration in C_4 plants (27). That does not mean that the RuBP carboxylase of C_4 plants is not sensitive to O_2 *in vitro,* because it is (2). It does mean that in intact leaves of C_4 plants, photorespiration is not detectable. This indicates that, all other factors being equal, C_4 plants should be more productive than C_3 plants under high leaf temperature conditions.

The disadvantage of the C_4 pathway lies in its higher intrinsic energy cost. In the C_3 pathway, the light reactions must supply 3 ATP and 2 NADPH for every CO_2 fixed. The C_4 pathway requires a minimum additional 2 ATP per CO_2 fixed to operate the CO_2 pumping mechanism, resulting in a minimum of 5 ATP and 2 NADPH per CO_2 fixed (19, 29). In terms of whole leaf performance, Ehleringer and Björkman (21) have shown that the higher intrinsic cost of the C_4 pathway is reflected in a reduced quantum yield (CO_2 fixed per quantum of light absorbed) under low-oxygen conditions. Under normal atmospheric conditions, the quantum yields of C_3 and C_4 plants are similar at a temperature of 30°C. This is so, because the decrease in the quantum yield of the C_3 plant by photorespiration exactly offsets the decrease in the quantum yield of the C_4 plant because of its higher energetic cost. However, at temperatures below

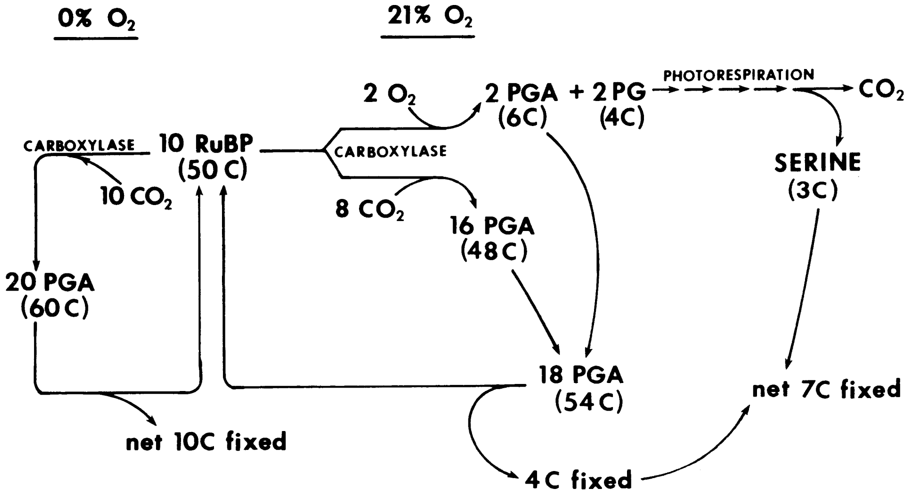

Fig. 2. Photosynthetic carbon reduction cycles in C_3 plants under 0% and 21% O_2. Based on Laing et al. (34).

30°C, the quantum yield of the C_3 plant exceeds that of the C_4 plant (reduced photorespiration in the C_3 plant), while above 30°C the quantum yield of the C_4 plant exceeds that of the C_3 plant. The implication here is that the C_4 plant may have a superior photosynthetic capacity at higher temperatures, but C_3 plants may be superior at cool and moderate temperatures or under low irradiance conditions.

In spite of the advantages of the C_4 pathway, a reduced quantum yield is a serious disadvantage. In C_3 plants, we find photorespiration under all conditions, and this, too, is a serious disadvantage in terms of production of dry matter. It seems puzzling that after millions of years of evolution, natural selection has not resulted in a RuBP carboxylase enzyme which does not have oxygenase activity, unless there is a natural selection advantage to photorespiration. Most studies on photorespiration in agriculture have attempted to find ways of reducing photorespiration under the assumption that this process is wasteful and serves no purpose to the plant other than to reduce productivity. It is possible that photorespiration may play an important role in plant survival under conditions of low water availability. Under drought stress situations in which the stomates close, the CO_2 available as substrate for RuBP carboxylase is reduced. Yet the photosynthetic machinery must continue to operate as the products of the light reactions are still being produced. Photorespiration may serve as a means of operating the photosynthetic machinery in an idling mode (cycling CO_2 through the system with no net carbon gain) (49). This would allow dissipation of the ATP and NADPH generated by the light reactions of photosynthesis, thus avoiding photodestruction of the photosynthetic apparatus.

The advantages of C_3 photosynthesis lie in the ability of this pathway to operate more effectively at cool to moderate leaf temperatures and under less than full sunlight conditions. At low to moderate leaf temperatures, photorespiration is reduced and the quantum yield for photosynthesis is higher. Under the low to moderate light levels typical of plant canopies, the C_3 pathway will be superior because of its lower intrinsic cost (higher quantum yield). Under shade conditions, such as the floor of a temperate or tropical forest, or inside large canopies the C_3 pathway should be superior to the C_4 pathway.

Two interesting additional features arise as a consequence of photosynthetic pathway differences. First, the root/shoot ratios of C_4 plants appear to be lower than for C_3 plants (66). Second, the nitrogen use efficiency in C_4 plants is greater than that of C_3 plants (12). That is to say a C_4 plant produces more photosynthate per gram of nitrogen (or for that matter any nutrient) than does a C_3 plant. This may place C_4 plants at a competitive advantage in low nutrient sites and especially in arid zones where nutrient levels are reported to be low.

An additional advantage of the C_4 pathway may lie in an increased water use efficiency over the C_3 pathway (5). The transpiration ratio (defined as the ratio of transpiration/photosynthesis) will be higher in C_3 plants. This is because the CO_2 pumping system allows the C_4 plant to attain the same photosynthetic rate as in a C_3 plant, but with a smaller stomatal opening (i.e., lower water loss). Under hot and/or arid conditions this could mean a much lower rate of water loss in a C_4 plant.

The CAM pathway represents an even further increase in water use efficiency over the C_4 pathway (Table 1). Because the stomates open only at night (cooler temperatures meaning lower transpiration rates), the transpiration ratio of CAM plants will be very low. The lower transpiration ratio may be misleading in terms of adaptation, because by opening stomates only at night, CAM plants may be simply better able to survive extreme drought than C_3 or C_4 plants. Szarek and Ting (61) have summarized the ranges of water use efficiency usually found in plants possessing the C_3, C_4, and CAM pathways. Their data (Table 1) show that CAM plants have transpiration ratios far below those of either C_3 or C_4. However, as a consequence of only nocturnal stomatal opening, the maximum rates of photosynthesis in CAM plants are also much lower than those of either C_3 or C_4 plants (Table 1).

Distributions of photosynthetic pathways

The C_3 photosynthetic pathway is found in all higher land plant families and is assumed to be the oldest of the 3 pathways. The C_4 and CAM pathways, however, seem to be taxonomically restricted to land plant families. It is interesting to note that both C_4 and CAM pathways have polyphyletic origins. That is both pathways seemed to have evolved in different families independently.

Table 1. Rates of maximum photosynthesis and ratios of transpiration to photosynthesis (transpiration ratio) for plants possessing different photosynthetic pathways. Data are from Szarek and Ting (61), Sestak et al. (55), and Mooney et al. (40).

Pathway	Maximum photosynthetic rate ($\mu mol\ m^{-2}\ s^{-1}$)	Transpiration ratio
C_3	10-60	450-600
C_4	30-60	250-350
CAM	3-10	25-150

The C_4 pathway is known to occur in at least 18 families (Table 2), many of which are distantly related. Since the discovery of this photosynthetic pathway is recent, the number of families in this list may be expected to increase as additional families of plants are examined. The C_4 pathway has been found in both monocots and dicots, but as of yet no C_4 gynmosperms or C_4 ferns have been found.

The CAM pathway occurs in ferns, gynmosperms, and angiosperms (Table 3). The CAM pathway is by far most common among the angiosperms, but is known to occur in at least one gymnosperm (*Welwitschia*) and two ferns (*Drymoglossum* and *Pyrrosia*). Several families contain all three photosynthetic pathways (Aizoaceae, Compositae, Euphorbaiceae, and Portulacaceae).

As mentioned previously, the phylogenetic distributions of C_4 and CAM pathways suggest that each pathway has arisen independently many times. One measure of how frequently the C_4 pathway has risen is to look at the number of genera possessing both C_3 and C_4 species. To date a total of 19 genera have been found containing both C_3 and C_4 species (Table 4). This high number of genera possessing C_3 and C_4 members implies that the evolution of the C_4 pathway under recent environmental conditions has been frequent. Within the genus *Atriplex*, C_4 photosynthesis is thought to have arisen independently twice (6). Of the genera in Table 4, at least two genera, *Mullugo* and *Panicum*, are known to have species which possess a C_4 type leaf anatomy, but functionally still have the C_3 photosynthetic pathway (25, 31, 32). Perhaps these species are "on the evolutionary road" to becoming C_4 plants. It is even more astonishing that within *Alloteropsis semialata*, Ellis (23) has found individuals that are C_3 and other individuals that are C_4.

It is likely that C_4 photosynthesis first evolved after the increase in oxygen concentration that followed the evolution of photosystem II (photosystem II splits water resulting in O_2 production and electrons for the light reactions of photosynthesis). Since CO_2 and O_2 compete for the same active site on the RuBP carboxylase enzyme, it is likely that natural selection would not favor the evolution of the C_4 pathway until O_2 concentrations were sufficiently high (58). Data regarding continental drift and the grass family (13) and more recent observations of grass fossils by Nambudiri et al. (44) suggest that C_4 photosynthesis had evolved by the Pliocene.

In ecological terms, the three photo-

Table 2. Families known to possess the C_4 photosynthetic pathway. Data are from Burris and Black (14), Sankhala et al. (53), and Winter et al. (67).

Acanthaceae
Aizoaceae
Amaranthaceae
Boraginaceae
Capparaceae
Cappardiaceae
Caryophyllaceae
Chenopodiaceae
Clemaceae
Compositae
Cyperaceae
Eyphorbiaceae
Gramineae
Nyctaginaceae
Polygonaceae
Portulacaceae
Scrophulariaceae
Zygophyllaceae

Table 3. Genera known to possess the Crassulacean Acid Metabolism (CAM) pathway. Data are from Burris and Black (14), Schulze and Schulze (54), and Mooney et al. (41,42).

Polypodiales	Polypodaceae
Gymnospermae	Welwitschiaceae
Monocotyledonae	Agavaceae Bromeliaceae Liliaceae Orchidaceae
Dicotyledonae	Aizoaceae Asclepiadaceae Bataceae Cactaceae Capparaceae Caryophyllaceae Chenopodiaceae Compositae Crassulaceae Cucurbitaceae Didiereaceae Euphorbiaceae Geraniaceae Labiatae Oxalidaceae Passifloraceae Piperaceae Plantaginaceae Portulacaceae Tetragoniaceae Vitaceae

Table 4. Genera which have been shown to possess both C_3 and C_4 species. Data are from Burns and Black (14) and Raghendra and Das (50).

Family	Genus
Aizoaceae	Mollugo
Amaranthaceae	Aerva Alternathera
Boraginaceae	Heliotropium
Chenopodiaceae	Atriplex Bassia Kockia Suaeda
Compositae	Flaveria Pectis
Cyperaceae	Cyperus Scirpus
Euphorbiaceae	Chamaesyce Euphorbia
Gramineae	Alloteropsis Panicum
Nyctaginaceae	Boerhaavia
Zygophyllaceae	Kallstroemia Zygophyllum

synthetic pathways segregate into different environmental regimes (Figure 3). Within North America, C_3 plants predominate in the cool and moist environments (41, 42, 43, 59, 62, 65), C_4 plants are found in warm to hot and wet environments (43, 60, 62, 65), while CAM plants are restricted to unpredictable and dry habitats (22, 41, 42, 63, 64). Similar distributions of C_3, C_4, and CAM plants are found in north African plants (68,69).

The distributions of the C_4 grasses can be accounted for on a physiological-biochemical basis. Ehleringer (20) has shown that the changes in abundance of C_3 and C_4 grasses in the Great Plains of North America are likely due to the changes in environmental temperatures and the dependence of quantum yield of photosynthesis in C_3 plants on temperature. In arid regions such as the Sonoran Desert where plants can be active throughout the year, C_3 grasses tend to be winter active and C_4 grasses to be summer active (43, 57). Again differences in the temperature dependence of the quantum yield account for the observed temporal distribution of pathways (Figure 4). A similar explanation may in part account for the observed distributions of C_4 dicots.

C_4 plants tend to predominate in salty soils of inland and maritime locations (7, 15, 36). This is presumably because of the greater water use efficiency, which allows for them a competation advantage over C_3 plants. The distribution of CAM plants seems related to aridity and precipitation unpredictability. In these habitats, natural selection may favor those perennial plants with a high water storage capacity and the capability of withstanding long periods without rain.

Within tropical epiphytic species it is interesting that both C_3 and CAM pathways appear (38, 39, 45). Thick leaved orchids possessed CAM photosynthesis, while thin leaved terrestrial and epiphytic orchids showed C_3 type photosynthesis (45). In contrast, within the bromeliads dry epiphytic or terrestrial habitats are occupied by plants possessing CAM photosynthesis (38, 39). Most tropical trees are C_3, but there are several C_4 tree *Euphorbia* species found in Hawaii (48).

Optimization and photosynthesis

The patterns related to the distribution of photosynthetic pathways and environment are becoming increasingly clear. There appear to be a strong correlation between specific environments and the abundance of plants possessing a specific photosynthetic pathway. Most habitats, however, do not have constant environments and the question becomes, can plants change photosynthetic pathways during the growing season so that at all times the plant is utilizing the photosynthetic pathway most suited for the current environmental situations? For grass species in Tucson, Arizona (Fig. 4) the answer must be "no". Rather than switching photosynthetic pathways, we find that grass species at this desert site tend to be inactive at times of the year when their photosynthetic pathway does not operate efficiently.

There are however, a large group of plants which are able to shift photosynthetic pathways (3, 9, 30, 64). It appears that many succulent perennials are able to shift from the C_3 pathway to the CAM pathway depending on environmental conditions. Under mesic conditions these plants turn off the CAM pathway and utilize C_3 photosynthesis for a higher rate of carbon gain. Under arid conditions, these plants use CAM photosynthesis and are better able to survive drought conditions than they could with C_3 photosynthesis. A variation on this theme is *Frerea indica,* a plant with succulent CAM stems and drought deciduous C_3 leaves (35). Not all CAM plants are able to shift from CAM to C_3 photosynthesis. The taxomonic and/or ecological relationships between those that can shift and

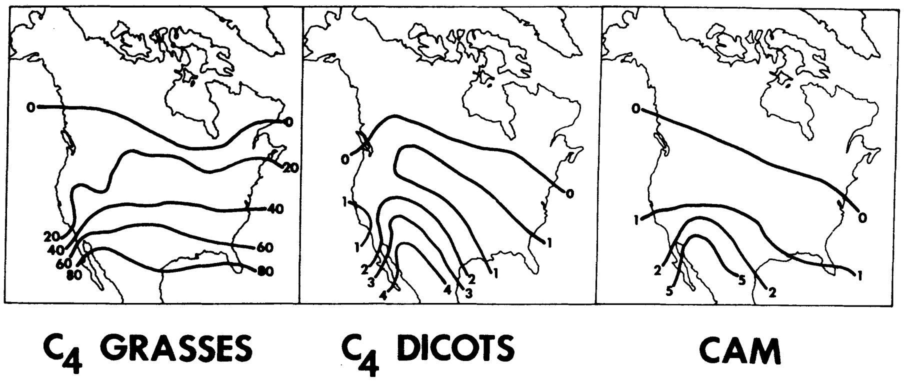

Fig. 3. Distributions of C_4 grasses, C_4 dicots, and CAM plants in North America. Isolines represent percentage abundance of the pathway type in the flora. Based on data from Terri and Stowe (62), Stowe and Terri (59), and Terri et al. (63).

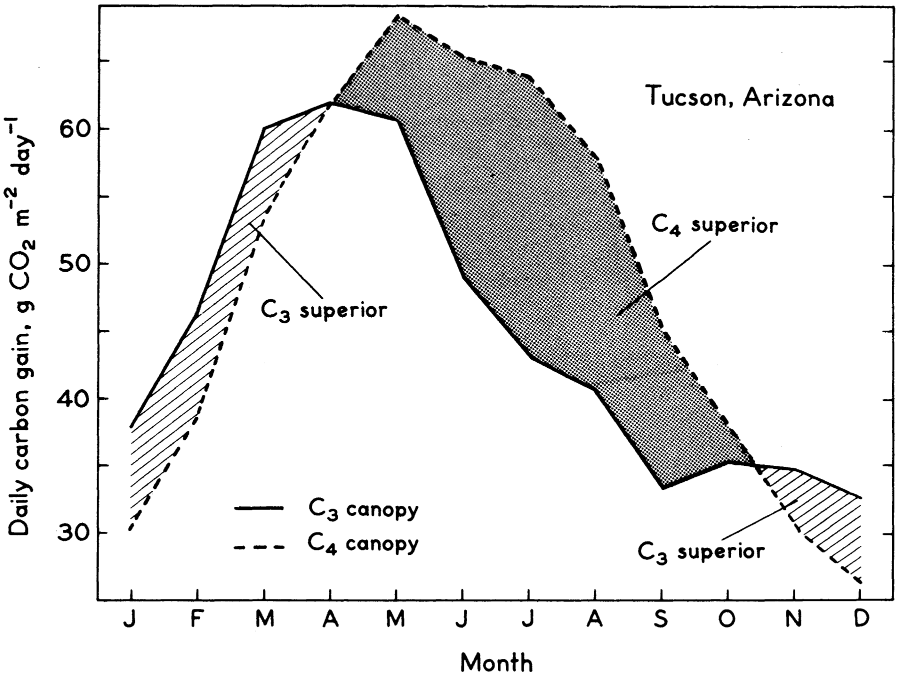

Fig. 4. Predicted carbon gain by C_3 and C_4 grass canopies throughout the year in Tucson, Arizona, a site within the Sonoran Desert. When plants with one pathway have a higher daily carbon gain they are predicted to be present and plants with the other pathway absent. From Ehleringer (20).

those that cannot are unknown.

One interesting example of a plant which shifts from C_3 to CAM photosynthesis is the facultative CAM plant *Mesembryanthemum crystallinum*, the ice plant (9). What makes this plant most interesting is that it is an annual and it shifts back and forth between C_3 and CAM pathways during the growing season. This plant varies the amount of CAM or C_3 photosynthesis depending on the soil moisture content (Fig. 5). Under mesic conditions of high soil moisture all of the photosynthesis is of the C_3 type, but as the soil dries out the percentage of CAM photosynthesis increases while the percentage C_3 photosynthesis decreases.

A single report exists in the literature suggesting that plants may shift between C_3 and C_4 photosynthesis. Raghavendra et al. (51) report that *Mollugo nudicalis* possess both C_3 and C_4 photosynthesis. They report that younger leaves possess the C_3 pathway, whereas older leaves are of the C_4 type. Changes in the morphology, biochemistry, and photosynthetic rates support their contention.

Breeding C_4 into C_3 plants

Given the potential advantages of the C_4 pathway, there has been much recent interest by agronomists and horticulturists in trying to breed C_4 photosynthesis into C_3 plants or trying to find C_3 plants with reduced photorespiration. The search for plants with reduced photorespiration has met with no success (46). On the other front, Björkman and his coworkers at the Carnegie Institution of Washington have attempted hybridization studies between C_3 and C_4 species of *Atriplex* (6). In their studies, *A. rosea* (C_4) was crossed with *A. triangularis* (C_3). The F_1 hybrid plants were highly uniform and intermediate between the 2 parents in leaf morphology. Chloroplasts were present in the bundle sheath cells of the hybrids, but photosynthesis was of the C_3 type even though a portion of the initial photosynthetic products were C_4 acids. Further crosses produced hybrid individuals with Kranz anatomy and the full complement of enzyme activities necessary for C_4 photosynthesis. However, all of the F_2 and F_3 hybrids possessed C_3 photosynthesis.

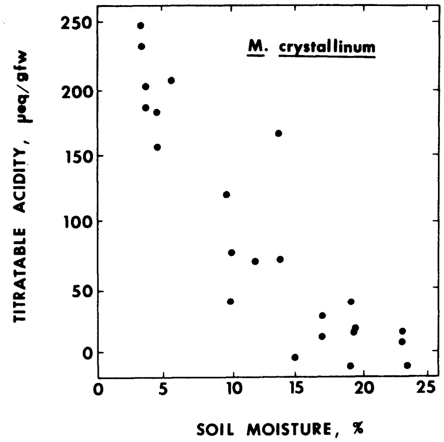

Fig. 5. Titratable acidity of leaf tissues of *Mesembryanthemum crystallinum* as a function of the soil moisture. Titratable acidity is a measure of how much CAM photosynthesis a plant is doing. Units of titratable acidity are micro-equivalents per gram fresh weight tissue. Based on data from Bloom (9).

Summary

Three photosynthetic pathways are known to exist in higher land plants. Two of the pathways (C_4 and CAM) are variations of the third and central pathway, C_3 photosynthesis. The operation of C_4 and CAM photosynthesis require morphological and enzymological changes from the C_3 pathway, but allow these plants competitive advantage in certain environments. C_4 and CAM photosynthesis overcome the problem of photorespiration found in C_3 plants. C_3 photosynthesis is most common in cool and moist habitats, C_4 photosynthesis in hot or salty habitats, and CAM photosynthesis in extremely arid habitats. Several species are known to be able to shift between pathways as the environmental conditions change. All attempts to produce C_4 plants from C_3 plants have failed.

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