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The Ecology of Photosynthetic Pathways

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Plants have evolved three photosynthetic pathways, each in response to distinct environmental conditions, resulting in differences in their ecological patterns of growth and distribution.

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Plant fitness revolves around the ability to gain carbon for growth and reproduction. Photosynthetic carbon is used to build structures for the acquisition of nutrients and water (roots), to compete for light (stems, leaves), and for defense against enemies (toxins, spines, etc.). Other factors being equal, greater photosynthetic carbon gain should lead to higher

growth rates and reproductive output.

Photosynthetic carbon assimilation (A) can be viewed as a diffusion process whereby a concentration gradient in carbon dioxide (CO_2) is multiplied by the conductance to CO_2 (g_{CO_2}):

$$A = g_{\text{CO}_2} (C_a - C_i)$$

The concentration gradient is the difference in concentration between the CO_2 in the surrounding air (C_a) and inside the leaf (C_i) (Figure 1). CO_2 concentration inside an illuminated leaf is less than the concentration outside the leaf because of the biochemical fixation of carbon into carbohydrates during photosynthesis. Hence CO_2 will diffuse down this concentration gradient into the leaf. The conductance to CO_2 (g_{CO_2}) is a composite term made up of the rate of diffusion through the stomata, diffusion across the intercellular air spaces into the chloroplasts, and the rate of enzymatic fixation of carbon.

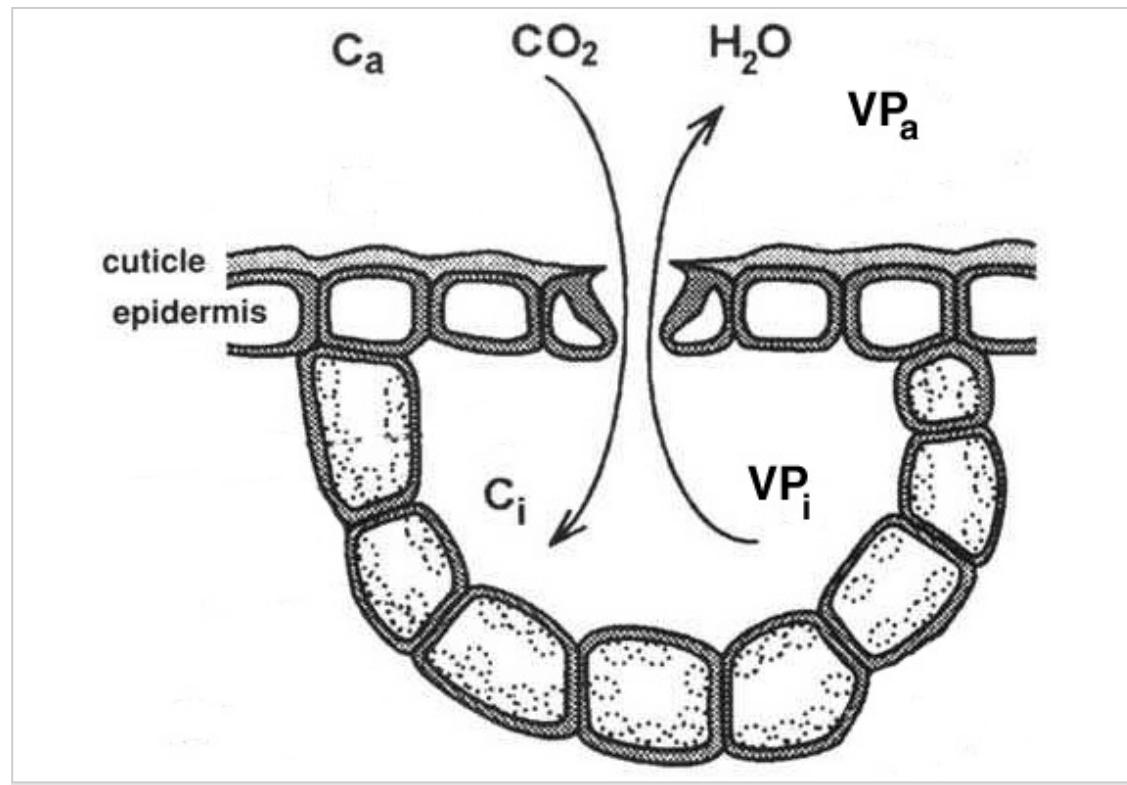


Figure 1: The diffusion pathway for CO_2 from the surrounding air through the stomata and into a leaf and for water vapor from inside the leaf to the outside air

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One way to maximize photosynthesis is to maximize g_{CO_2} . There are two ways plants can achieve this. First, they can minimize the resistance to diffusion of CO_2 through the stomata (i.e., have lots of large, open stomata). Second, they can maximize the biochemical rate of fixation (i.e., have high concentrations of photosynthetic enzymes).

However, there are tradeoffs to maximizing the rate of photosynthesis. First, photosynthetic enzymes require nitrogen, which is often a limiting resource. So there are limits to how much carboxylating enzyme plants can make. Second, transpiration — the evaporation of water from the inside of the leaf to the surrounding air — also involves diffusion

through the stomata (Figure 1). Transpiration can be expressed in much the same way as photosynthesis (where E = transpiration rate, 1.6 = the ratio of the diffusivity of water to CO_2 , VP_a = water vapor pressure of the air outside the leaf, and VP_i = water vapor pressure inside the leaf):

$$E = 1.6 \text{ gCO}_2 (\text{VP}_a - \text{VP}_i)$$

The air inside of leaves is saturated with water vapor, making VP_i much higher than VP_a and causing water to diffuse from inside the leaf to the outside. Maximizing gCO_2 thus maximizes transpiration as well as photosynthesis. In dry habitats, this could result in dehydration and death. Terrestrial plants, therefore, face an evolutionary dilemma: how to gain carbon for growth and reproduction without first losing so much water that they dehydrate and die?

One measure of a plant's success in solving this dilemma is transpiration efficiency, the ratio of photosynthesis to transpiration (A/E). Transpiration efficiency can be calculated by combining the first two equations:

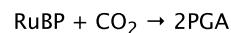
$$A/E = (C_a - C_i)/1.6 (\text{VP}_a - \text{VP}_i)$$

This equation highlights the point that transpiration efficiency is partially determined by the environment ($\text{VP}_a - \text{VP}_i$) — the larger the gradient between vapor pressure inside the leaf and in the surrounding air, the lower A/E will be. The difference between VP_a and VP_i is largest when temperatures are high and the air is dry. Thus, it is difficult for plants to achieve high A/E in such environments. Plants show a variety of adaptations to hot, dry conditions, such as vertical leaf angles and white, reflective leaves that help to decrease midday leaf temperatures. In addition, many plants reduce water loss through thick, waxy cuticles covering their leaf epidermis as well as by stomatal closure.

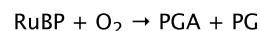
Transpiration efficiency is also a function of the CO_2 concentration gradient, $C_a - C_i$. Ambient CO_2 concentrations (C_a) are relatively constant, but the intercellular CO_2 concentration (C_i) is determined by the balance between CO_2 supply through the stomata, and CO_2 uptake by photosynthesis. Thus, plants can change C_i through their physiological responses to the environment. The more stomata restrict the diffusion of CO_2 , the lower C_i will be, leading to higher A/E (all other factors being equal). So high C_i is associated with low A/E and low C_i is associated with high A/E , at constant vapor pressure differences. There are also tradeoffs with photosynthesis implied by this relationship. Restricting CO_2 diffusion will limit photosynthesis as well as transpiration, so often high A/E in plants is associated with slow growth and low photosynthetic rates.

C₃ Photosynthetic Pathway

The first photosynthetic pathway that was biochemically characterized is called the C₃ pathway because the initial products of carbon fixation are 3-carbon compounds (phosphoglyceric acid, PGA) (Figure 2). CO_2 is combined with a 5-carbon sugar, ribulose bisphosphate (RuBP), using the enzyme ribulose bisphosphate carboxylase/oxygenase (rubisco):



Rubisco is the most common soluble protein in the world and can account for 50% of a leaf's nitrogen content. Rubisco also catalyzes a second reaction, that of oxygen with RuBP (Figure 3):



This reaction leads to no net gain of carbon for the plant. One of the products of this reaction, 2-phosphoglycolate (PG) is further metabolized in the photorespiratory carbon oxidation cycle, which leads to the release of CO_2 in the light, a process called photorespiration.

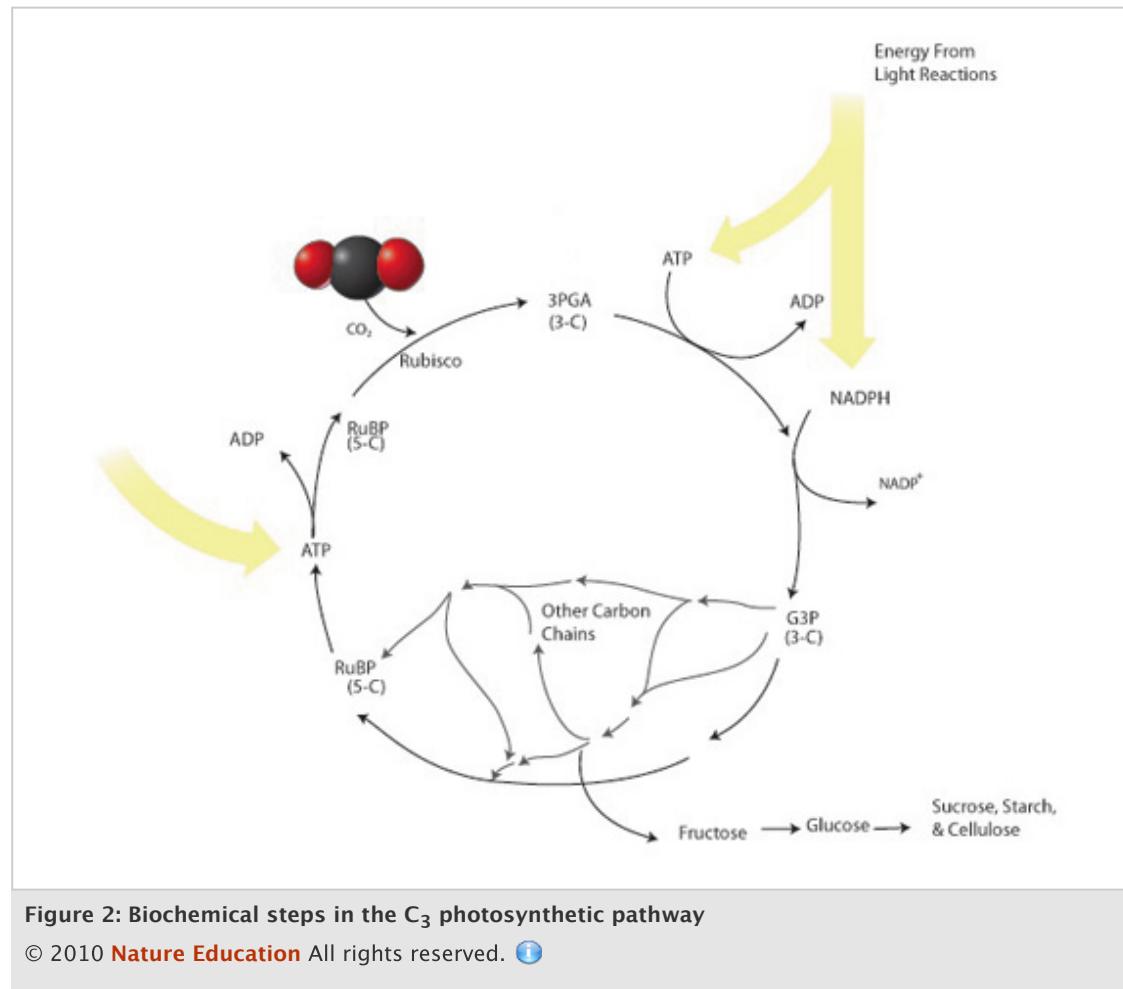
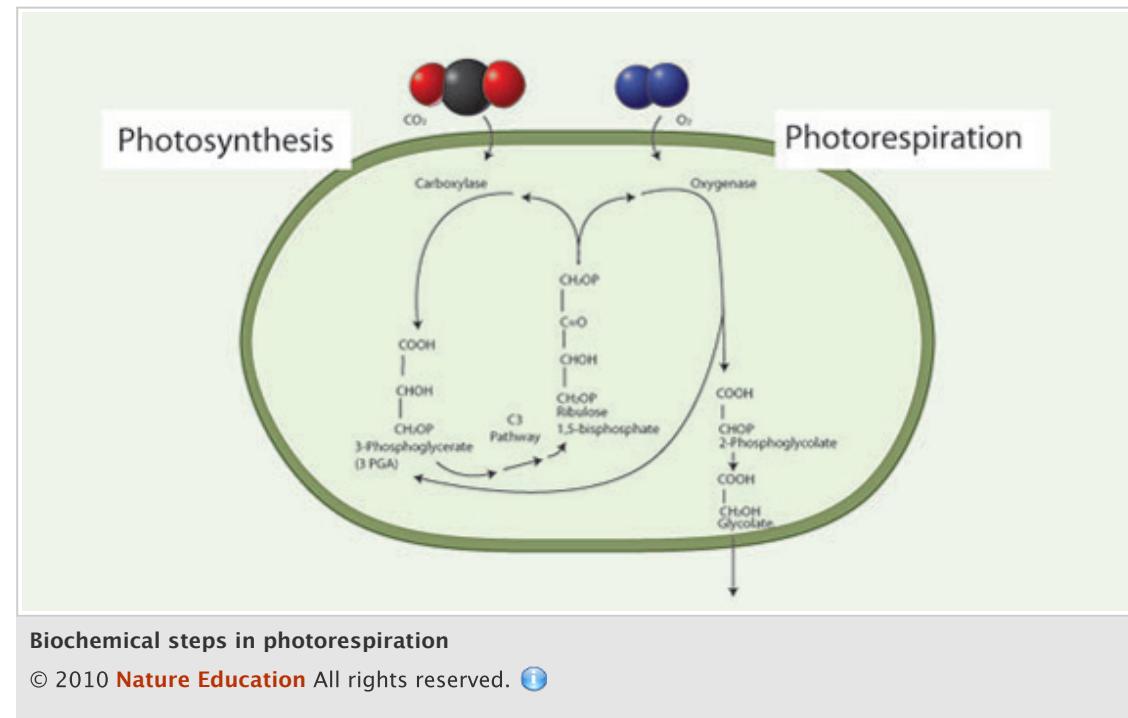


Figure 2: Biochemical steps in the C₃ photosynthetic pathway

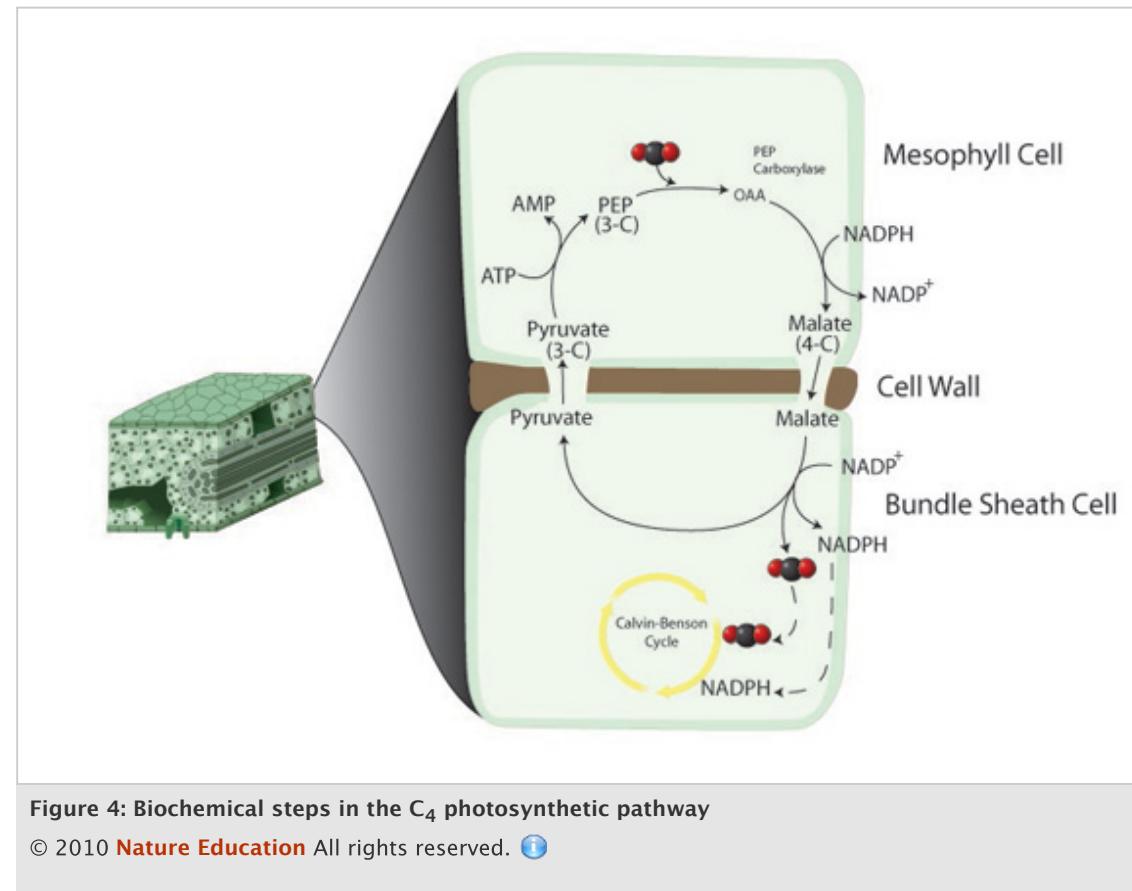
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Photorespiration reduces net photosynthesis in two ways. First, there is a competition between O₂ and CO₂ for the active site of rubisco. Those active sites that take up O₂ cannot take up CO₂. Second, there is the release of CO₂ in the PCO cycle. These two mechanisms can reduce net photosynthesis between 35–50% depending upon environmental conditions. Photorespiration increases with increasing temperature due to the fact that the solubility of O₂ decreases more slowly than the solubility of CO₂ with increasing temperature. When environmental conditions lead to stomatal closure and lower C_i, O₂ will gain a competitive binding advantage over CO₂. Thus, warm and arid habitats lead to greater photorespiration. Scientists view this as a primary selective force in the evolution of alternative photosynthetic pathways.



C₄ Photosynthetic Pathway

The C₄ photosynthetic pathway differs from the C₃ pathway in its initial carboxylating enzyme and initial products (Figure 4). The primary carboxylating enzyme in C₄ plants is phosphoenolpyruvate (PEP) carboxylase. This enzyme has a higher affinity for CO₂ than rubisco and has no oxygenase activity. The enzyme catalyzes the reaction of CO₂ with PEP, forming a 4-carbon acid. C₄ plants still have C₃ biochemistry; however, there is a physical separation of enzymes. The outer, mesophyll cells have PEP carboxylase and few chloroplasts while rubisco and many chloroplasts are located in bundle sheath cells, a jacket of cells surrounding the xylem and phloem (Figure 5).



The physical separation of biochemical activities acts as a CO₂ concentrating mechanism for rubisco. After CO₂ is combined with PEP, the C₄ acid is transferred to the bundle sheath cells, where it is decarboxylated. CO₂ is released next to rubisco in the bundle sheath cells, providing it with a competitive advantage over O₂. C₄ plants show no photorespiration in intact leaves, although their rubisco still has oxygenase activity. Any CO₂ that is released in the bundle sheath cells is fixed by PEP carboxylase in the mesophyll cells before it can diffuse out of the leaf.

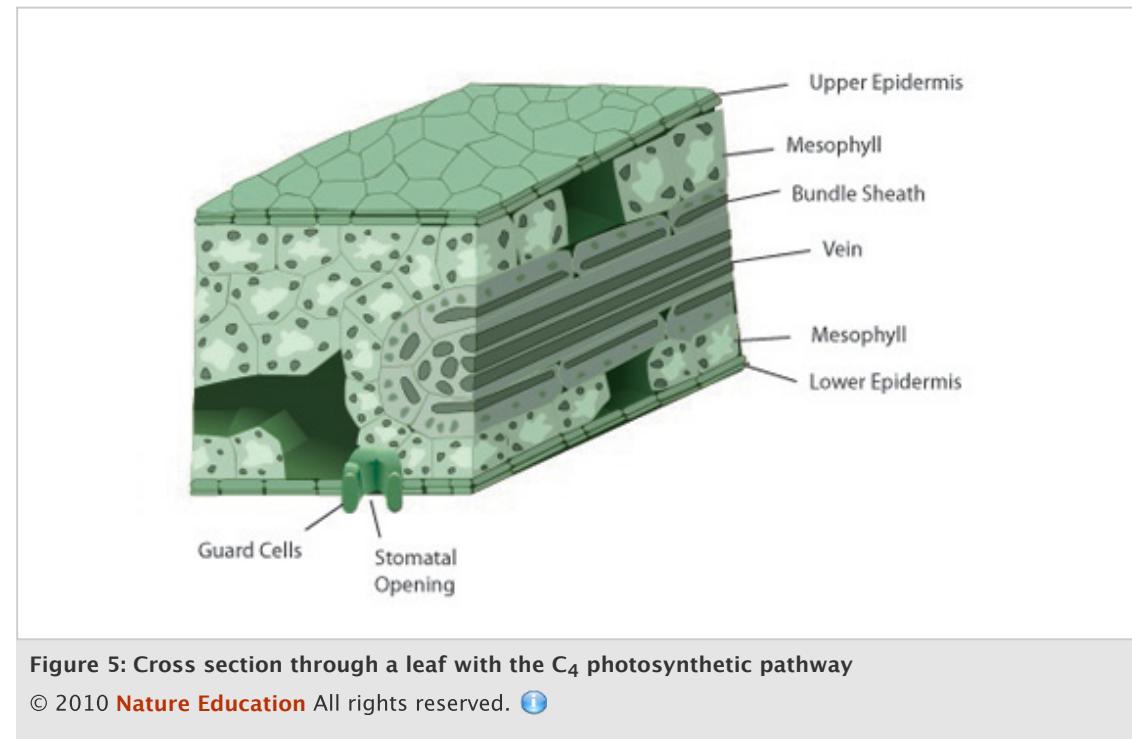


Figure 5: Cross section through a leaf with the C₄ photosynthetic pathway

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Reduced photorespiration gives a photosynthetic advantage to C₄ plants relative to C₃ plants in conditions where photorespiration is high (i.e., in low CO₂ concentrations and/or in high temperatures). Because PEP carboxylase has a higher affinity for CO₂, it can work efficiently at low intercellular concentrations of CO₂. Thus, for a given photosynthetic rate, stomatal conductance can be lower, decreasing transpiration and increasing transpiration efficiency.

Crassulacean Acid Metabolism (CAM) Photosynthesis

The biochemistry of the CAM photosynthetic pathway is similar to that of C₄ plants. However, rather than a physical separation of biochemistry, enzyme activities are separated in time (Figure 6). In this pathway, stomata open at night, which allows CO₂ to diffuse into the leaf to be combined with PEP and form malate. This acid is then stored in large central vacuoles until daytime. During the day, malate is released from the vacuoles and decarboxylated. Rubisco then combines the released CO₂ with RuBP in the C₃ pathway. In CAM plants, photosynthesis is proportional to vacuolar storage capacity, so CAM plants usually have thick and fleshy water-storing leaves or stems (i.e., they are succulents).

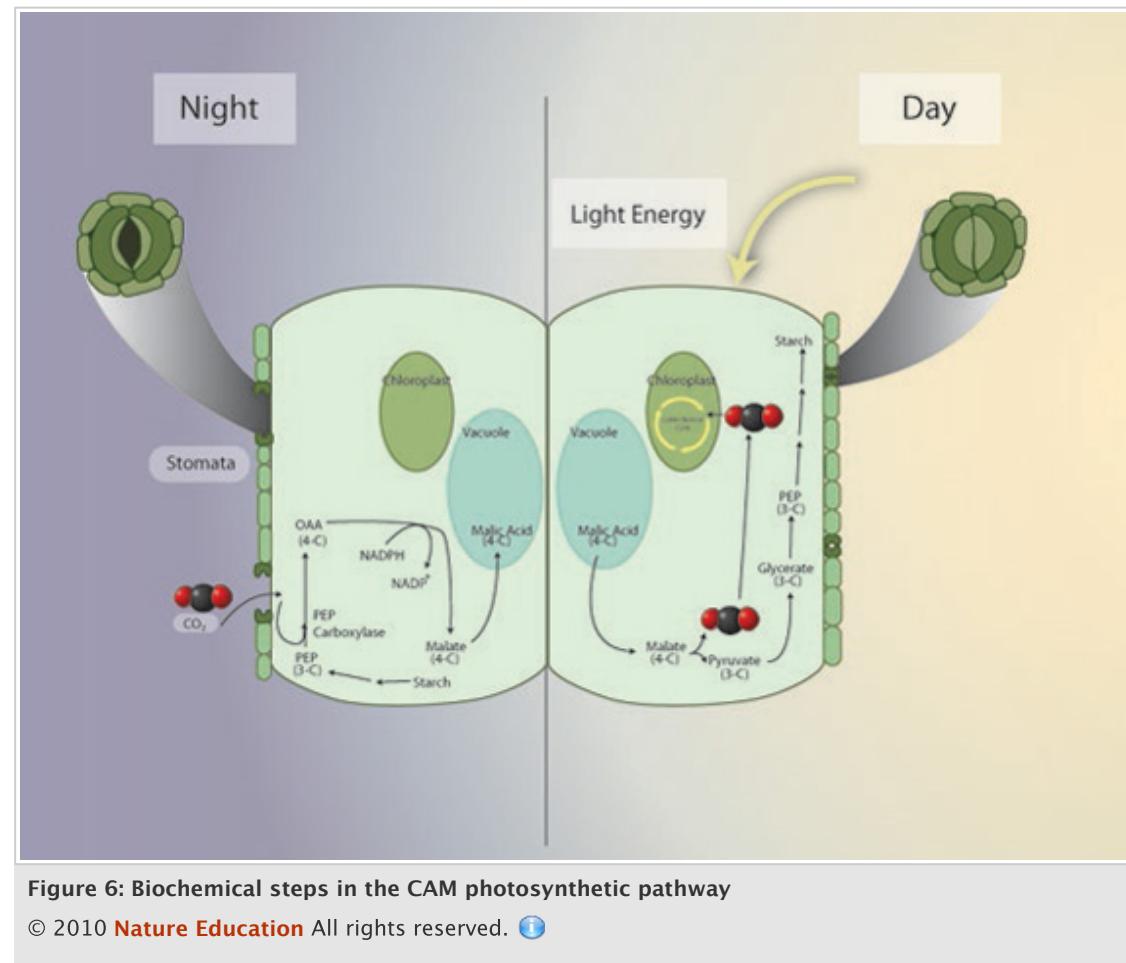


Figure 6: Biochemical steps in the CAM photosynthetic pathway

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Ecological Significance Of Pathway Variation

Because of the biochemical and morphological differences among the three photosynthetic pathways, each has its own unique set of advantages and disadvantages. These differences result in differential performance in different environments.

The C₃ pathway is the oldest (originating around 2,800 million years ago) and is also the most widespread, both taxonomically and environmentally. C₃ plants can be found in the warmest deserts and the coldest arctic habitats.

C₄ photosynthesis has evolved independently approximately fifty times but is most widespread in grasses where about 50% of the species are C₄ photosynthesizers (Edwards and Smith 2010). C₄ photosynthesis occurs in 3% of vascular plant species, but accounts for 25% of terrestrial photosynthesis (Sage, 2004). It is thus a relatively recent innovation, with the earliest appearances occurring during the low atmospheric CO₂ levels that occurred in the mid-Oligocene (approximately thirty million years ago). C₄ plants reach their peak of productivity in high-light and warm climates with summer rains (Figure 7), dominating tropical and subtropical grasslands and savannas whereas C₃ grasses dominate cooler, temperate grasslands. Because C₄ photosynthesis is saturated at lower CO₂ concentrations and allows lower stomatal conductance for a given photosynthetic

rate, C₄ plants also perform well in saline and dry habitats. Edwards and Smith (2010) found that eighteen of twenty evolutionary origins of C₄ grasses were correlated with reductions in mean annual precipitation, consistent with a shift out of tropical forests into open, high-light tropical savannas as the global climate became drier in the Oligocene. Australia is now one of the driest continents in the world, and a survey of over a thousand grass species found that C₄ grasses dominate 80–85% of the continent (Hattersley 1983). But even within Australia there are differences in pathway distribution, with C₄ species being most numerous where the summer is hot and wet while C₃ species are most common where the spring is cool and wet (extreme southern Australia and Tasmania). Studies along environmental gradients of temperature and precipitation have often highlighted differences between C₃ and C₄ species. For example, Tieszen *et al.* (1979) used an altitudinal gradient to show that the percent of grass species with the C₃ pathway in African savannas increased with altitude as precipitation increased and temperature decreased. Cabido *et al.* (1997) found a similar pattern in the temperate grasslands of Argentina (Table 1).

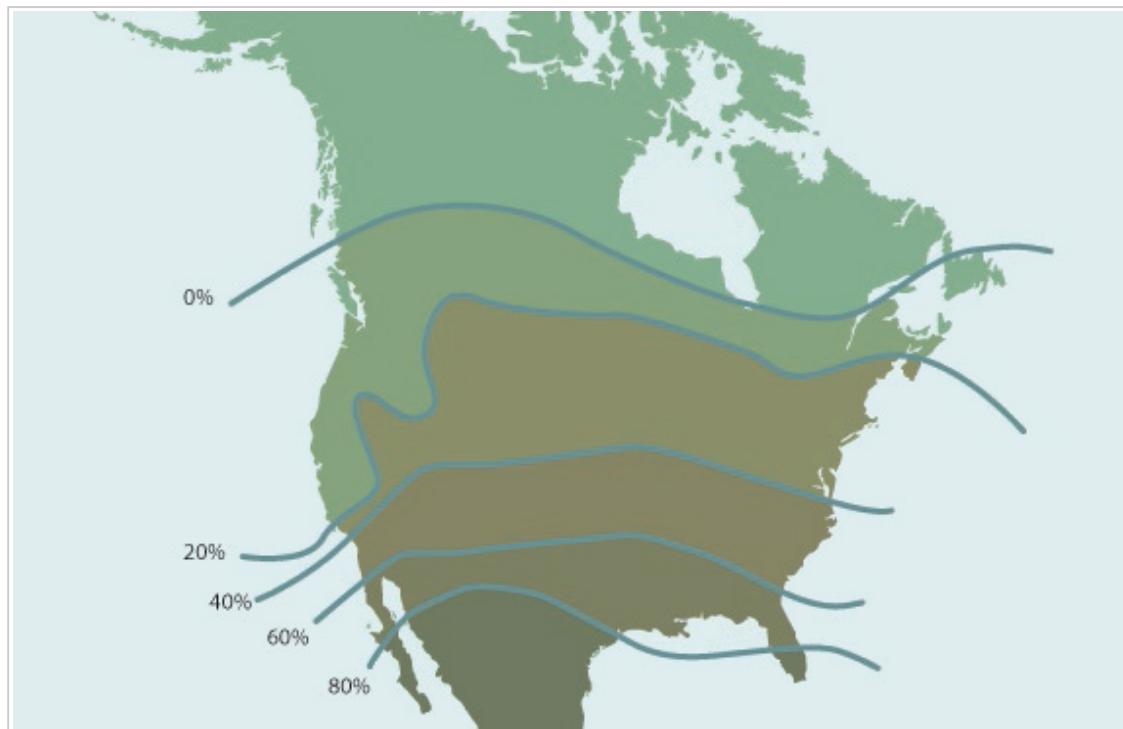


Figure 7: The percentage of grass flora made up of C₄ plants in the grasslands of North America

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C₄ plant species also have a potential advantage over C₃ species in low-nutrient habitats. Rubisco can account for 25–30% of leaf nitrogen in C₃ plants, but C₄ plants contain three to six times less rubisco. The higher affinity of PEP carboxylase for CO₂ means that C₄ plants don't need as much enzyme, so overall leaf nitrogen is often less than half that found in C₃ plants. However, this reduction in leaf nitrogen does not result in lower maximal photosynthetic rates; thus, C₄ plants have higher photosynthetic–nitrogen-use efficiency (ratio of photosynthesis to leaf nitrogen) than C₃ plants. This gives them an advantage in high-light, low-nutrient environments.

Altitude (m)	350	600	1,000	1,400	1,600	1,800	1,900	2,100
% of C ₃ species	2.3	10.0	35.8	39.2	60.6	65.6	69.2	80.0

% of C ₄ species	97.7	90.0	64.2	60.8	38.2	34.4	30.8	20.0
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Table 1: The percentage of C₃ and C₄ grass species at different elevations in central Argentina

Source: Cabido *et al.* 1997

Despite the advantages outlined above for C₄ species, there are several disadvantages to this form of photosynthesis. For example, the regeneration of PEP in the C₄ pathway (Figure 4) leads to higher costs for ATP than in the C₃ pathway. ATP for photosynthetic biochemistry is supplied by the light reactions. The extra cost of C₄ biochemistry is a disadvantage where low light occurs, as found in inner-canopy competitive situations in cool, wet forests. It is rare to find C₄ plants in such environments.

CAM photosynthesis is found in more than 7% of vascular plant species, and has evolved independently several times. Due to their stomata being open at night when the vapor pressure differences between the leaf and the surrounding air are lowest (reducing transpiration), CAM photosynthetic plants have higher transpiration efficiencies than either C₃ or C₄ plants. Distribution patterns for CAM plants reflect this and are dominated by habitat aridity. Water storing cacti are adapted to enduring long periods with no precipitation. This is because they close their stomata, even at night during prolonged periods of drought and can refix CO₂ lost in respiration before it diffuses out of the leaf or stem. Consequently, some cactus species lose very little biomass over months without rain.

An interesting aspect of CAM distribution is the high number of CAM species found in tropical environments. Epiphytes are plants that do not have their roots in the ground but instead grow on other plants (primarily trees). Thus, they frequently lack a ready supply of liquid water. Many epiphytic species in tropical and subtropical regions, such as orchids and bromeliads, therefore exhibit the CAM pathway.

A disadvantage for CAM plants is that they often have low photosynthetic capacity, slow growth, and low competitive abilities because their photosynthetic rates are limited by vacuolar storage capacity and by greater ATP costs, similar to those for C₄ species. However, there is great plasticity in the expression of CAM photosynthesis. Many CAM plants can function in a C₃ mode with stomata open during the day when water is available, so low photosynthetic and growth rates are not always limiting factors.

An interesting example that illustrates another advantage for the nighttime activity of CAM photosynthesis is found in aquatic plants such as *Isoetes howellii*. This plant is found in temporary vernal ponds in the western United States in which CO₂ is depleted on warm, sunny days by other submerged aquatic plants. Since CO₂ diffuses very slowly in water and its solubility decreases with increasing temperature, these habitats can easily become CO₂ depleted. *Isoetes howellii*, with its CAM photosynthesis, takes advantage of higher CO₂ concentrations in the water at night when other plants are releasing CO₂ through respiration. In a similar fashion, the advantage of C₄ photosynthesis in low CO₂ conditions is illustrated by some submerged aquatic plants, such as *Hydrilla verticillata*. *Hydrilla* uses C₄ photosynthesis to cope with the reduced CO₂ concentrations that occur in warm, high-light aquatic environments in the summer.

Photosynthetic Pathway Plasticity

There are many plants that can switch between a C₃ mode and a CAM mode. This is called facultative CAM. For example, *Mesembryanthemum crystallinum* (the ice plant) is an annual plant that switches photosynthetic mode in response to water and/or salt stress. It starts life using the C₃ pathway but then switches to CAM later during flowering or under stress. This plant is native to Mediterranean type climates with cool, wet springs and hot, dry summers. This plasticity allows facultative CAM species to utilize the C₃ pathway when water is available, which increases photosynthetic rates and growth, and then increase their stress tolerance during drier time periods through the CAM pathway.

In summary, there is considerable variety in the biochemistry of photosynthesis in the plant kingdom. Plants have evolved multiple photosynthetic pathways in response to low CO₂ concentrations, high temperatures, and limitations in the availability of water. This physiological variation is combined with many other morphological and anatomical adaptations to allow plants to exploit a wide variety of aquatic and terrestrial habitats around the world.

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