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Climate Change and the Evolution of C_4 Photosynthesis

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Plants assimilate carbon by one of three photosynthetic pathways, commonly called the C_3, C_4, and CAM pathways. The C_4 photosynthetic pathway, found only among the angiosperms, represents a modification of C_3 metabolism that is most effective at low concentrations of CO_2. Today, C_4 plants are most common in hot, open ecosystems, and it is commonly felt that they evolved under these conditions. However, high light and high temperature, by themselves, are not sufficient to favor the evolution of C_4 photosynthesis at atmospheric CO_2 levels significantly above the current ambient values. A review of evidence suggests that C_4 plants evolved in response to a reduction in atmospheric CO_2 levels that began during the Cretaceous and continued until the Miocene.

Plants possessing the C_3 photosynthetic pathway dominate most terrestrial ecosystems[1], and account for about 85% of all plant species. About 10% of the earth's flora possess CAM photosynthesis, and commonly grow in xeric sites, such as deserts and epiphytic habitats[2]. C_4 plants dominate warm to hot, open sites, but on a floristic basis comprise the lowest percentage of the terrestrial flora. Tropical and temperate grasslands, with abundant warm-season precipitation, are dominated by C_4 species.

C_4 plants have great economic significance, both as crops and weeds[3]. For this reason, C_4 plants have undergone much scrutiny since the discovery of the C_4 pathway in the mid-1960s. Although many aspects of C_4 metabolism are now well understood[4], questions remain about the initial evolution and subsequent expansion of C_4 plants. It is commonly thought that hot, arid conditions have favored their evolution[4]. However, while such environments have been common throughout the earth's history, the evolution of C_4 plants appears to be more recent (see below). The performance of C_4 plants relative to C_3 plants is highly dependent on levels of atmospheric CO_2: low CO_2 conditions favor C_4 species and high CO_2 levels favor C_3 species[5]. Geological evidence indicates that it has been only during the past 50 to 60 million years that CO_2 levels have declined to sufficiently low concentrations that C_4 photosynthesis has an advantage over C_3 photosynthesis[6]. Here we discuss the evidence that the primary selective factor influencing the evolution of C_4 photosynthesis was changes in the atmospheric CO_2 concentration, rather than aridity or high temperatures.

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Inefficiency of carboxylation in C_3 photosynthesis

Net carbon fixation in C_3 photosynthetic organisms is catalysed by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco)[7]. Rubisco normally catalyses the reaction between atmospheric CO_2 and RuBP to produce two three-carbon phosphoglycerate molecules (PGA), which are then further metabolized to the major end products of photosynthesis. However, Rubisco can also catalyse the oxygenation of RuBP to form one PGA and one phosphoglycolate, and further metabolism of phosphoglycolate results in the release of CO_2; these activities constitute photorespiration, a process that reduces the overall efficiency of net photosynthesis.

The oxygenase activity of Rubisco occurs, despite the physiological costs involved, because of particular aspects of the carboxylation reaction mechanism. During the carboxylation of RuBP, an intermediate is formed that is susceptible to reaction with oxygen[7]. Thus, the oxygenase activity of Rubisco may not have any useful function, but is simply an inevitable consequence of the reaction mechanism under aerobic conditions[7]. As oxygen in the atmosphere increased because of photosynthesis, the photorespiratory pathway evolved to process phosphoglycolate and recycle as much fixed carbon as possible. CO_2 and O_2 are competitive substrates, but Rubisco has a

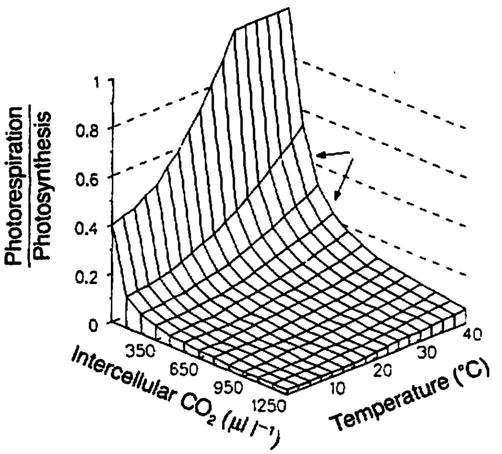

Fig. 1. Modelled CO_2 and temperature response of the ratio of photorespiration to the gross rate of photosynthesis in C_3 plants. Oxygen concentration was held constant at the current level of 21%. Arrows indicate the range of CO_2 concentrations typically occurring in leaves of C_3 plants under present atmospheric conditions. *Model derived from Ref. 11.*

much greater specificity for CO_2. Under current atmospheric conditions (350 $\mu l\ l^{-1}$ CO_2, 21% O_2, 78% N_2), however, the CO_2 concentration in the chloroplasts of C_3 leaves is approximately 1000 times less than that of O_2. This low CO_2:O_2 ratio allows a significant amount of photorespiration to occur, which reduces the efficiency of carboxylation during C_3 photosynthesis.

The ratio of photorespiration to photosynthesis is not fixed, but varies with environmental conditions. It is dependent on three factors: CO_2 concentration, O_2 concentration and leaf temperature. Increasing temperature reduces the specificity of Rubisco for CO_2 and decreases the concentration of CO_2 relative to O_2 within the chloroplast[8–10]. Using established equations[11], we can model the ratio of photorespiration to photosynthesis as a function of CO_2 and temperature, while keeping O_2 constant at current levels (Fig. 1). At either low temperature or high CO_2 concentration, photorespiration is minor. However, under present atmospheric CO_2 concentrations, photorespiration is a major component at moderate temperatures and becomes even greater as temperature is further increased. On the other hand, elevating CO_2 from the current ambient level of 350 $\mu l\ l^{-1}$ significantly reduces the rate of photorespiration. For example, a doubling of ambient CO_2, such as is anticipated to occur within the next 50–100 years, will result in approximately a 50% reduction in the rate of photorespiration. Increasing current atmospheric CO_2 levels five-fold would nearly eliminate photorespiratory activity in C_3 plants.

Benefits associated with C_4 photosynthesis

There are two mechanisms that can be used to improve the carboxylation:oxygenation ratio of Rubisco: increases in the CO_2/O_2 specificity of the enzyme and/or increases in the ratio of CO_2 to O_2 present at the enzyme's active site. There is evidence that the relative specificity of Rubisco for CO_2 is greater in angiosperms than in more primitive plant groups, but there is little variation in Rubisco's characteristics among vascular C_3 plants[7]. The most successful mechanism for reducing photorespiration and thus increasing carboxylation efficiency is the C_4 photosynthetic pathway.

In C_4 plants, atmospheric carbon is initially fixed in a reaction catalysed by phosphoenol pyruvate carboxylase (PEP carboxylase)[12]. This reaction takes place in mesophyll cells of C_4 plants where Rubisco is absent (Fig. 2). The resulting four-carbon organic acids are transported internally from the mesophyll to bundle sheath cells where they are decarboxylated to release CO_2. Chloroplasts in the bundle sheath cells contain Rubisco and fix the CO_2 released by C_4-acid decarboxylation using normal C_3 photosynthetic metabolism (Fig. 2). Since PEP carboxylase has a higher affinity for its substrate and a higher maximal velocity than Rubisco, the C_4 pathway acts as a CO_2-concentrating mechanism, increasing the CO_2 concentration within the bundle sheath cells. In plants using C_4 photosynthesis, mesophyll CO_2 concentrations are approximately 100 $\mu l\ l^{-1}$, whereas bundle sheath CO_2 concentration may be 10- to 20-fold higher[1]. The carboxylation efficiency of Rubisco is improved, therefore, and photorespiration becomes negligible in C_4 plants. Secondary improvements in water-use and nitrogen-use efficiencies will also occur in C_4 plants, associated with advantages of the CO_2-concentrating mechanism[1,13].

The presence of the C_4 photosynthetic pathway leads to a markedly different response of net photosynthesis to changes in atmospheric CO_2 or O_2 concentration than that found in C_3 plants[5,14]. While at low CO_2 concentrations C_4 plants typically have higher photosynthetic rates than C_3 plants, C_4 photosynthesis becomes saturated at concentrations above the current atmospheric levels, whereas C_3 photosynthesis does not (Fig. 3a). Also, because of Rubisco oxygenation and subsequent photorespiration, the quantum yield or light-use

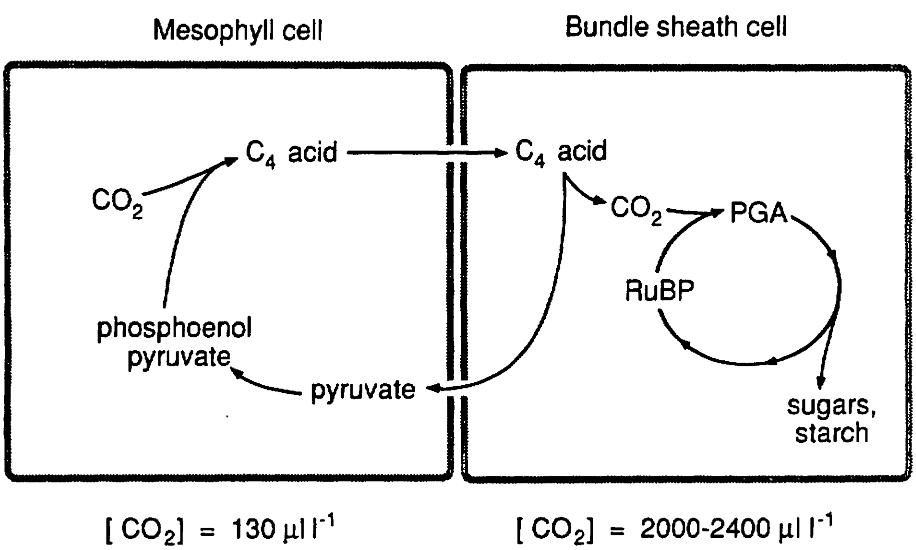

Fig. 2. Diagrammatic representation of C_4 photosynthesis. Atmospheric carbon is initially fixed inside leaf mesophyll cells in a reaction catalysed by phosphoenol pyruvate (PEP) carboxylase. The resulting C_4 acid is decarboxylated inside the bundle sheath cell, providing a source of CO_2 for ribulose-1,5-bisphosphate carboxylase (Rubisco) and the normal C_3 photosynthetic cycle. C_4 photosynthesis acts as a CO_2-concentrating mechanism. The CO_2 concentration inside the bundle sheath, where Rubisco functions, is 10- to 20-fold higher than the CO_2 concentration in the leaf mesophyll cells. PGA, phosphoglycerate; RuBP, ribulose bisphosphate.