Published on *Plants in Action* (http://plantsinaction.science.uq.edu.au/edition1)

2.2.1??Evolution of the C4 mode

Approximately 85% of all terrestrial plant species are C_3 plants, while about 10% are CAM plants and are usually found in highly xeric sites (deserts, epiphytic habitats). The remainder are C_4 plants, and these become more dominant with aridity. Naively, we could conclude that evolution of C_4 photosynthesis was a response to selection by high temperature and low water availability. More likely, a decline in atmospheric CO_2 concentration during past millennia provided an initial impetus.

One hundred million years ago (Mid-Cretaceous), atmospheric CO_2 was between 1500 and 3000 µL L^{-1}, or four to ten times postindustrial levels. Given such a large concentration of CO_2 at that time, photorespiration of C_3 plants was inhibited (Section 2.3) so that photosynthetic ef?ciency was higher than it is now. In addition, maximum photosynthetic rates were double twentieth century values, and the energy cost of photosynthesis would have been around three ATP and two NADPH per molecule of CO_2 ?xed. However, as atmospheric CO_2 concentrations declined to approximately 250–300 µL L^{-1}, photosynthetic rates were halved, photo-respiration increased substantially, photosynthetic ef?ciency declined and the energetic costs of photosynthesis increased to approximately ?ve ATP and 3.2 NADPH per CO_2 molecule ?xed. Such events would have generated a strong selection pressure for genetic variants with increased carboxylation ef?ciency and increased photosynthetic rates.

Angiosperms have a higher relative speci?city of Rubisco for CO_2 than ferns and mosses (see examples of other less evolutionarily advanced species in Figure 2.2). Such differences imply minor evolution in this highly conserved molecule of Rubisco and there is little variation between species of vascular plants. Consequently, alteration of Rubisco in response to a changing atmospheric CO_2 concentration has not been an option.

By contrast, evolution of a new photosynthetic pathway (C_4) has occurred independently and on several occasions in diverse taxa over 50 to 60 million years as CO_2 levels declined. The oldest identi?able fossils with pronounced bundle sheath layers are seven million years old, although necessary metabolic pathways could have evolved earlier, prior to this adaptation in anatomy. C_4 plants are known to differ from C_3 plants in their discrimination against atmospheric $^{13}CO_2$, and shifts in the stable carbon-isotope signature of soil carbonate layers that reflect emergence of C_4 plants have been dated at 7.5 million years bp. By inference, C_4 photosynthesis evolved in response to a signi?cant decline in atmospheric CO_2 concen-tration, from 1500–3000 µL L^{-1} to about 300 µL L^{-1}. By evolving a CO_2-concentrating mechanism, C_4 plants presented their Rubisco with an elevated partial pressure of CO_2 despite lower atmospheric CO_2. As a consequence, photorespiration was inhibited, maximum photosynthetic rates increased and energetic costs reduced.

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