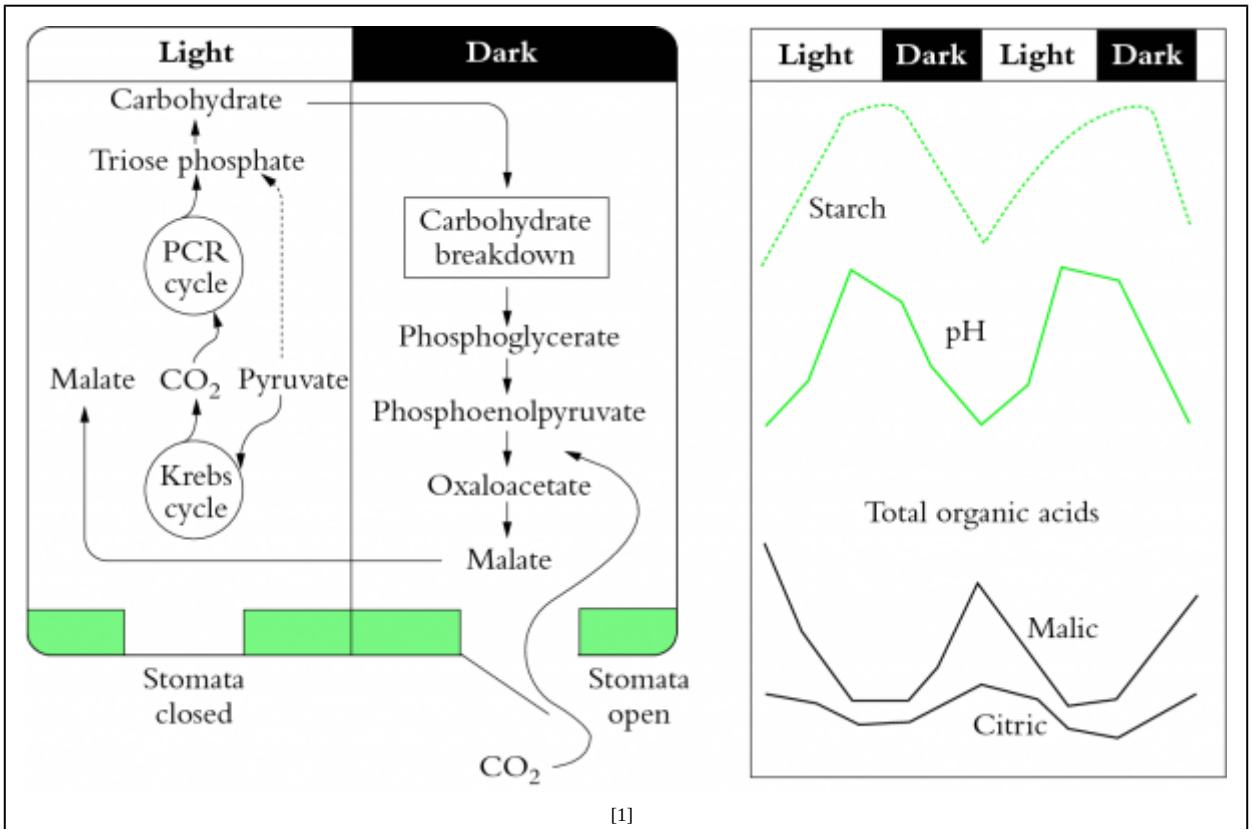
2.1.6??Crassulacean acid metabolism (CAM)

A further adaptation to high temperature and in particular arid conditions is crassulacean acid metabolism (CAM) photo-synthesis. Compared with the anatomical specialisation and *spatial* separation of biochemical function in C_4 plants, CAM photosynthesis does not require anatomical differentiation but instead involves a *temporal* separation of an *in situ* biochemical function. CAM is essentially an adaptation to reduce water loss through stomata by *reversing* the diurnal rhythm of CO_2 ?xation. Typically, CAM plants are equipped with fleshy assimilatory organs (commonly phyllodes or cladodes) and include the majority of cacti and orchids as well as many salt-tolerant succulents (such as the ice plant *Mesembryanthemum crystallinum*) and pineapple. Whereas C_4 plants have a biochemical CO_2 pump, CAM plants operate more like a biochemical storage battery. During the night-time when heat load is low and atmospheric water vapour pressure relatively high, stomata open, admitting CO_2, which is ?xed by PEP carboxylase in much the same way as in C_4 photosynthesis. The C_4 product (usually malate) is stored in vacuolar compartments of these fleshy organs until the daytime. Malate is then decarboxylated to provide CO_2 for Rubisco (reviewed by Winter 1985). This tight cycle of malic acid storage and breakdown, often called ‘acidi?cation’ and ‘deacidi?cation’, is shown schematically in Figure 2.7 along with a simpli?ed version of the CAM pathway.



[1]

Figure 2.7 Crassulacean acid metabolism (CAM) is a photosynthetic adaptation to dry conditions and represents a 'survival option'. Stomata open at night-time allowing CO_2 entry and incorporation into a malate pool in mesophyll vacuoles.The next day, malate is metabolised to release CO2 which is refixed by Rubisco while stomata remain closed (Based on Walker 1992)

Historically, the discovery of CAM plants can be attributed to this cyclical acidi?cation/deacidi?cation. In a letter to the Linnean Society in 1813 Benjamin Heyne wrote 'the leaves of the…plant called by Mr Salisbury *Bryophyllum calycinum*, which on the whole have an herbaceous taste, are in the morning as acid as sorrel, if not more so. As the day advances, they lose their acidity and are tasteless about noon…' (a more detailed account appears in Walker 1992). *B. calycinum* is, of course, a CAM plant and the acid taste is due to the build up of malic acid at night. However, despite these early observations, it took another 150 years to unravel the complexities of the CAM pathway.

Because the primary steps of carbon ?xation by CAM plants occur in darkness, PEP synthesis and energy supply (in the form of ATP and reducing power) are closely linked to respiration plus breakdown of stored carbohydrates made during the previous photoperiod. Simpli?ed in Figure 2.7, the CAM pathway relies on starch as a 'storage battery' of light-derived energy for subsequent PEP carboxylation in darkness. Malate stored in vacuolar compartments from night-time ?xation is a carbon store that yields CO_2 in daytime.

Unlike C_4 plants, which have some of the highest growth rates of all land plants (Hatch 1988), CAM plants achieve rather meagre rates of photosynthesis and suffer a yield penalty as a result. Moreover, their modi?ed pathway of photosynthesis with temporal separation of photochemical and biochemcial functions incurs an energetic cost of between 5.5 and 6.5 ATP and two NADPH per CO_2 ?xed (Walker 1992). Compare this with a requirement of only three ATP (and two NADPH) per CO_2 ?xed during C_3 photosynthesis in low O_2.

Table 2.1 Photosynthesis and leaf conductances in C_3, C_4 and CAM plants. Tr ratio (transpiration ratio) is expressed as mass of water transpired per unit mass of CO_2 assimilated

Mode	Photosynthesis µmol CO_2 m^{-2} s^{-1}	Stomatal mol m^{-2} s^{-1}	Mesophyll mol m^{-2} s^{-1}	Tr ratio $H_2O\uparrow/CO_2\downarrow$
C_3	12.5–25.0	0.8–0.08	0.13–0.04	450–600
C_4	18.5–50.0	0.5–0.25	0.40–0.20	250–350
CAM light	1.85–12.5	0.06–0.04	0.02–0.01	150–600
dark	6.25–9.25	0.20–0.04	0.40–0.20	25–150

(Derived from generalised values of Szarek and Ting 1975)

Restrictions on inward diffusion of ambient CO_2 via sparse stomata and slow progress between decarboxylation and ?xation sites through an extensive liquid phase of assimilatory tissue would place further constraints on carbon gain. Some relativities for C_3, C_4 and CAM gas exchange are summarised in Table 2.1. Potentially greater rates of assimilation by C_4 plants put that group at an advantage in terms of biomass gain and water use ef?ciency in daytime. For a given stomatal conductance, transpiration by C_3 and C_4 would be comparable, but the greater CO_2-scavenging capacity of C_4 plants makes them more water ef?cient (greater inward flux of CO_2 for a given outward flux of H_2O). At night, CAM plants achieve further improvement in water use ef?ciency because CO_2 uptake is then combined with much reduced transpiration.

Table 2.1 emphasises adaptive features of C_3, C_4 and CAM photosynthesis. Light-saturated rates of photosynthesis in C_4 plants can be up to twice those in C_3, even though maximum stomatal conductance is commonly somewhat lower. By contrast, C_4 plants achieve much higher mesophyll conductance (a consequence of their remarkable CO_2-scavenging ability), and water use ef?ciency during photosynthesis is consequently enhanced (i.e. transpiration ratio is lower). Daytime assimilation by CAM plants can occur when moisture is abundant, and is analogous to C_3 photosynthesis with maximal rates comparable to lower values of C_3 plants. C_3 engagement by CAM plants diminishes as moisture stress intensi?es, and in full CAM mode night-time assimilation assumes prominence. In that condition, PEP carboxylase is responsible for initial ?xation with mesophyll conductance comparable to that of a C_4 plant. Water use ef?ciency is, however, much greater due to lower evaporative demand. Under extreme conditions, the night-time transpiration ratio in CAM plants can be an order of magnitude lower than in C_4 plants (right-hand column, Table 2.1).

Notwithstanding stomatal restrictions on CO_2 assimilation, frugal use of water rather than high rates of carbon gain would have been the primary driving variable for evolution of CAM plants. In this context, CAM photosynthesis is more of a ‘survival option’ where slow assimilation is an acceptable trade-off for a water-retentive physiology. The spectacular success of CAM photosynthesis in arid zones and dry habitats worldwide con?rms this principle.

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