Photosynthesis but not CAM responded flexibly to changes in irradiance in *Plectranthus marrubioides* (Lamiaceae)

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Abstract

Well-watered plants of *Plectranthus marrubioides* Benth., a crassulacean acid metabolism (CAM) species naturally inhabiting sun exposed succulent places, were grown at photosynthetically active photon flux densities (PPFD) of either 150 (LL) or 300 (HL) µmol m\(^{-2}\) s\(^{-1}\) in a controlled environment. Photosynthesis of LL plants was saturated by irradiance of ca. 500 µmol m\(^{-2}\) s\(^{-1}\) while in HL plants saturation was not reached up to 1200 µmol m\(^{-2}\) s\(^{-1}\) and photosynthetic capacity was nearly 50% higher than in the LL plants. However, maximum photon yield was 55% lower and compensation irradiance was 25% higher in LL plants. The former also had larger, more succulent leaves, i.e., they were morphologically more sun adapted. On the other hand, nocturnal accumulation of malic and citric acid, nighttime CO\(_2\) gain, and the low relative carbon recycling were independent of the prevailing PPFD. Furthermore, photosynthetic performance was flexibly and reversibly adjusted in HL plants after transfer to 600 or 150 µmol m\(^{-2}\) s\(^{-1}\) while nocturnal CO\(_2\) uptake was not influenced. Photosynthesis showed a high acclimation potential to high PPFD and patterns of gas exchange became more C\(_3\)-like the higher the irradiance was, without a direct effect on CAM in *P. marrubioides*.

Additional key words: Crassulacean acid metabolism; gas exchange; irradiance response; malic acid accumulation.

Introduction

Early research on crassulacean acid metabolism (CAM) was done on relatively few, selected species mainly native to extreme desert habitats (Kluge and Ting 1978,

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Osmond 1978). So, the opinion elicited that CAM was a rather static metabolic adaptation of very specialized plants to long-term drought periods. Meanwhile, it has become clear that CAM is much more widespread among plants from very different habitats, including submerged water plants (Keeley 1996). The phenomenon of CAM can dynamically cover large diversity of expression and combinations of gas exchange patterns (Griffiths 1988b) in many species from many families (Smith and Winter 1996). These plants optimize their carbon metabolism and gas exchange very flexibly in response to changes in environment. Thus, the mode of photosynthesis can reversibly and quickly be changed from approximately that of a C3 plant to an exclusive nighttime CO2 uptake within very few days with or without greatly affecting nocturnal accumulation of malic acid (Winter and Smith 1996).

One of the species showing a high plasticity of CAM is P. marrubioides (Herppich 1989, Herppich and Herppich 1996). Plectranthus is a genus in the large family Lamiaceae, widespread in the Old World tropics and subtropics but also occurring in Asia, Australia, New Zealand and even Hawaii (Jacobsen 1981). It includes most of the relatively few succulent species in the Lamiaceae (Jacobsen 1981) and the only five CAM taxa described up to now in this family (Kluge and Ting 1978, Herppich and Herppich 1998).

In P. marrubioides, which is native to the East African Highlands and the western Higher Escarpment in Yemen (Deil 1988), patterns of CAM and diurnal gas exchange respond very flexibly to a variety of environmental stimuli (Herppich et al., unpublished). This taxon is preferentially found sun exposed or semi-shaded on shallow soils in rocky grassland and dry secondary succulent highland places up to an altitude of more than 2200 m (Deil 1988). Its natural habitats are characterized by high mean annual temperatures (~20 °C), frequent mist and dew fall in the early morning hours and the evening and high, periodic rainfalls (annual mean > 600 mm, Deil 1988). Therefore, besides episodic droughts and high temperatures, pronounced short and long-term changes in irradiance ranging from very high incident irradiation to low PPFD during prevailing mist may be the major environmental constraints affecting CAM and photosynthesis.

Only very limited information about photosynthetic performance and CAM in the genus Plectranthus is available (Herppich and Herppich 1996). Therefore, controlled environment experiments with the high mountain CAM species P. marrubioides were done to elucidate the functional interrelationships between irradiance and photosynthesis, CAM and gas exchange patterns.

**Material and methods**

Plants of *Plectranthus marrubioides* Benth., collected in Yemen (Deil 1988), were propagated from cuttings in plastic pots containing sandy soil. During greenhouse growth in a semi-controlled environment (day: temperature (TD) = 27±5 °C, relative humidity (RH_D) = 50±15 %; night: TN = 15±5 °C, RH_N = 85±10 %), plants were abundantly watered every third day. Mean integrated daily irradiance (400-700 nm) was 12±3 mol(photon) d⁻¹, as derived from measurements of PPFD with a LI-190 S