



Intra-species variation in transient accumulation of leaf anthocyanins in *Cistus creticus* during winter: Evidence that anthocyanins may compensate for an inherent photosynthetic and photoprotective inferiority of the red-leaf phenotype

Velissarios-Phaedon Kytridis, Panagiota Karageorgou, Efi Levizou, Yiannis Manetas*

Laboratory of Plant Physiology, Department of Biology, University of Patras, Patras GR-26500, Greece

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Summary

Leaf color in some individuals of *Cistus creticus* turns transiently to red during winter, while neighboring individuals occupying the same site remain green. We have examined whether anthocyanin accumulation can be associated with variations in photosynthetic and/or photoprotective characteristics between the two phenotypes, rendering the red phenotype more vulnerable to photoinhibition and, accordingly, needing additional protection in the form of anthocyanins. Towards this aim, maximum (pre-dawn) and effective (mid-day) PSII photochemical efficiencies, xanthophyll cycle pool sizes and leaf nitrogen contents were seasonably followed, encompassing both the green (spring, summer, autumn) and the red (winter) period of the year. Moreover, the distribution of the two phenotypes in exposed and shaded sites was assessed. The frequency of red individuals was considerably higher in fully exposed sites, pointing to a photoprotective function of leaf anthocyanins. Yet, the assumption was not corroborated by pre-dawn PSII yield measurements, since both phenotypes displayed similar high values throughout the year and a similar drop during winter. However, the red phenotype was characterized by lower light-saturated PSII yields, xanthophyll cycle pool sizes and leaf nitrogen, during both the green and the red period of the year. Based on this correlative

*Corresponding author. Tel./fax: +30 2610997411.
E-mail address: y.manetas@upatras.gr (Y. Manetas).

evidence, we suggest that winter redness in *C. creticus* may compensate for an inherent photosynthetic and photoprotective inferiority, possibly through a light screen and/or an antioxidant function of leaf anthocyanins.

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Introduction

Leaf is the organ optimized for photosynthesis, which starts with photon absorption by green chlorophyll (Chl). Yet, in some plants, under some circumstances, leaves may transiently turn red due to the accumulation of anthocyanins at levels enough to mask the green Chl reflectance. We may distinguish between developmentally and environmentally determined redness. In the first case, redness appears in young and/or senescing leaves of some species, while mature leaves are green. On the other hand, anthocyanin accumulation in mature leaves can be induced by a variety of biotic and abiotic agents like wounding (Bopp, 1959; Stone et al., 2001), pathogen attack (Hipskind et al., 1996), nutrient deficiency (Atkinson, 1973; Kumar and Sharma, 1999), UV-B radiation (Lindoo and Caldwell, 1978; Mendez et al., 1999) and high light combined with cold temperatures (Krol et al., 1995; Close et al., 2002; Pietrini et al., 2002). Since anthocyanins are not photosynthetic pigments, their presence should act antagonistically to Chl for photon absorption, thus reducing photosynthesis. Although this is disadvantageous for a healthy leaf under optimal conditions, it may become important under stress, when a reduction in excitation pressure of Chl is needed. Hence, one of the main hypotheses for the function of leaf anthocyanins is that of sunscreen against photoinhibition (for recent reviews on leaf anthocyanins and their possible functions see, Steyn et al., 2002; Close and Beadle, 2003; Gould, 2004; Manetas, 2006). This is reasonable to assume since the abiotic stresses inducing anthocyanins (high light combined with cold temperatures, nutrient deficiencies, etc.) also predispose leaves to photoinhibition of photosynthesis by perturbing the coordination between energy absorption and its utilization (Long and Humphries, 1994). One could speculate that when all the on-line flexible photoprotective safety measures are exceeded (xanthophyll cycle, Demmig-Adams et al., 1996; water-water cycle, Asada, 2000; C2 photorespiratory cycle, Tolbert, 1997; light-avoiding chloroplast movements, Williams et al., 2003; paraheliotropism, Pastenes et al., 2005), the transient formation of an anthocyanic umbrella would serve a sunscreen function until the withdrawal of the stress

factor(s). Alternatively (or in addition to the direct attenuation of incident light), anthocyanins may neutralize oxy-radicals through their powerful antioxidative capacity (Wang et al., 1997; Neill and Gould, 2003; Kytridis and Manetas, 2006).

Although the physiological background for the sunscreen/antioxidative hypothesis seems convincing, the experimental evidence is not conclusive. Thus, a positive correlation between the presence of anthocyanins and tolerance to photoinhibition was reported in some cases (Krol et al., 1995; Feild et al., 2001; Manetas et al., 2002; Pietrini et al., 2002) but not in others (Burger and Edwards, 1996). In the above-mentioned studies, the plants were grown in controlled environments or, if they were growing in the field, the photoinhibitory treatments were applied in the laboratory. In another study performed in a naturally lit glass-house with four *Syzygium* species bearing either green or red young leaves, the "red" species displayed greater chronic photoinhibition, yet their lower intrinsic photosynthetic capacities did not permit a firm conclusion for the possible photoprotective role of anthocyanins (Dodd et al., 1998; Woodall et al., 1998).

Apparently, the final criterion for the sunscreen hypothesis is whether anthocyanin accumulation affords any actual photoprotection in the field. However, Lee et al. (2003), in an extensive field survey with senescing leaves from 89 North American woody species, found no evidence for photoprotection by anthocyanins, as judged by pre-dawn measurements of PSII photochemical efficiency. Based on the same criterion, Manetas et al. (2003) came to the same conclusion for young red leaves of the Mediterranean tree *Quercus coccifera* and Kypris et al. (2007) for permanently red leaves of *Prunus cerasifera*. Yet, Liakopoulos et al. (2006) inferred a slight photoprotective function in young, developing leaves of *Vitis vinifera*. A corresponding field study with mature leaves turning red in winter is still lacking.

The present study was prompted by the observation that mature leaves of some individuals of the Mediterranean shrub *Cistus creticus* turn red by mid-winter and remain so up to mid-spring. Neighboring individuals, occupying the same habitat, remain green throughout the year. Consequently, a field of *C. creticus* during winter is a patch of green and red morphs. The red character

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