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Photosynthetic acclimation to light of the three taxa of a *Primula vulgaris* x *P. veris* hybrid zone in the Bakony mountains

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ABSTRACT The effects of light on the habitat choice of *Primula vulgaris*, *P. veris* and their spontaneous interspecific hybrids were studied. Photosynthetic performance (CO_2 fixation) and composition of the photosynthetic pigments were measured on plants grown under semi-shaded conditions (control) and under natural high light condition for 20 days (HLG). Assimilation rates of *P. veris* were better than those of *P. vulgaris* at all light intensities. Hybrids photosynthesised similarly well as *P. veris* at lower light intensities, and presented intermediate photosynthetic performance between the parent species at higher light intensities. Total chlorophylls, chlorophyll a/b ratio, xanthophyll cycle pool, and the ratio of total carotenoids to total chlorophylls were higher in *P. veris* than in *P. vulgaris*, and these parameters, with the exception of the last one, showed considerable similarity of hybrids to *P. vulgaris*. Contrasting with the parent species, hybrid plants were able to increase the xantophyll cycle pool significantly after an intensive light exposure. The HLG treatment revealed that the extent of the photoinhibition was lower in *P. veris* than in the other two taxa. These results explain the difference between the habitat preferences of the parent species, and the ability of hybrids to occupy more open sites than *P. vulgaris* can.

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KEY WORDS

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Spontaneous hybrids of *Primula vulgaris* Huds. and *P. veris* L. (Primulaceae) occur in several points of the Bakony and Keszthelyi mountains in Hungary. *P. vulgaris* is generally associated with shady mesophil woodland formed mainly by *Fagus sylvatica* and *Carpinus betulus*, while *P. veris* can be found mainly in sunnier xerotherm forests of *Quercus* species in Hungary (Soó 1970). The *P. vulgaris* populations, taking place usually in the moist and humid valleys, and the *P. veris* populations, occurring generally on the dryer mountain ridges, meet and create hybrids typically on slopes (Cservenka 2004).

Acclimation of plants to different light environments involves changes in the photosynthetic capacity to utilize light and in the capacity of photoprotection. The later prevents the absorption of light energy and facilitates the heat dissipation through the xanthophyll cycle in excess of that required for photosynthetic processes, which would otherwise increase the probability for long-term damage to photosynthetic apparatus. Sun-grown leaves tend to have a higher photosynthetic capacity, higher light-saturated photosynthetic rates (A_{max}) and a higher saturated light intensity than do shade leaves, and are less prone to accumulate excessive excitation energy when exposed to high light.

The goal of the present study was to reveal the effects of light on the habitat choice of the parent species and the hybrids. Investigations included the analysis of the light response curves and the photosynthetic pigment composition on plants grown under semi-shaded conditions (control) and after a 20-day long high light treatment (HLG).

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Materials and Methods

Plant material

Primula vulgaris, *P. veris* and interspecific hybrid plants originating from a spontaneous hybrid zone (Bakony mountains, Hungary; Kálmán et al. 2003, 2004) were grown in well-watered pots in the Botanical Garden of the University of Szeged. Investigations were carried out on plants grown under natural semi-shaded conditions in May 2004 (control plants). The youngest fully developed leaves of 11-16 plants of each taxa were used for the measurements. The plants were kept at low (about 100 μmol $m^{-2}s^{-1}$) photosynthetically active photon flux density (PPFD) in the laboratory for 18 h before CO_2 assimilation measurements. After finishing the measurements, five plants of each taxa were exposed to natural high light (HLG) conditions for 20 days, then all measurements were repeated.

Pigment analysis

Chlorophyll *a*, chlorophyll *b* and total carotenoids were measured and calculated according to Lichtenthaler (1987), and xanthophyll cycle components were determined by means of HPLC according to Váradi et al. (2003). Measurements were made in five repetition from four leaf discs originating from different plants. Light response of the xanthophyll pigments

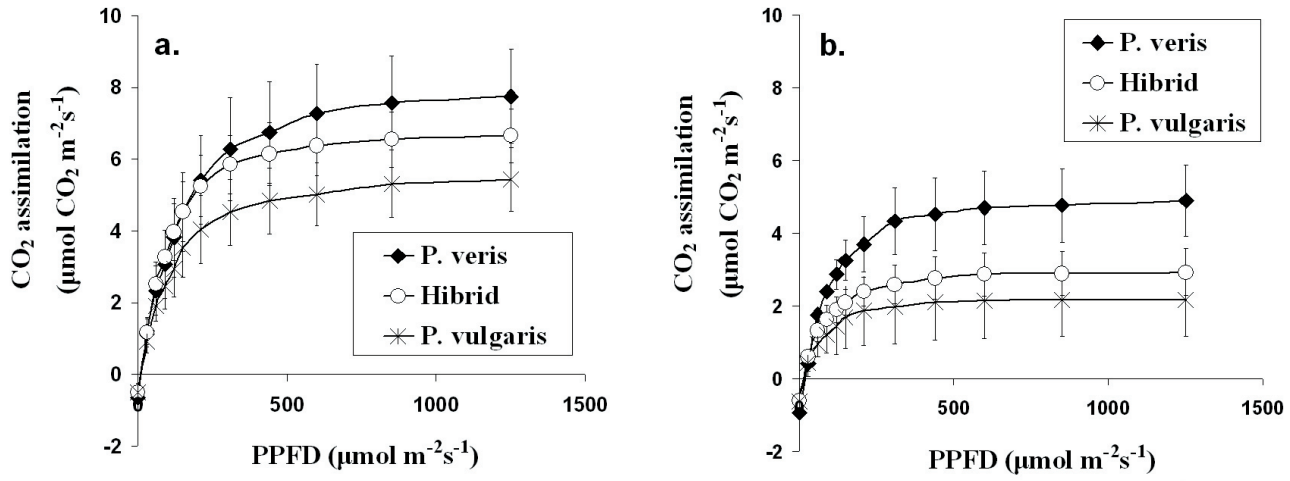

Figure 1. Light response of the CO_2 assimilation in the leaves of *Primula vulgaris*, *P. veris* and their hybrid in the control (a) and the HLG plants (b).

was determined by measuring them in dark-adapted and in illuminated leaves (1h, 1500 µmol $m^{-2}s^{-1}$ PPFD).

Photosynthetic performance

CO_2 assimilation measurements followed Váradi et al. (2003; LCA-3 infrared gas analyser (ADC, England), 340 ppm CO_2, 21% (v/v) O_2, 27°C, RH ≅ 50%). Readings were taken 6 min after each step of increasing PPFD, from 0 to 1250 µmol $m^{-2}s^{-1}$ PPFD in 12 steps.

Results and Discussion

Total chlorophylls, Chl a/b ratio, the ratio of total carotenoids to total chlorophylls, and the dark-adapted leaves' xanthophyll cycle pool were higher in control *P. veris* than in control *P. vulgaris* (Table 1). Plants growing in more exposed locations tend to present higher values of these parameters, so our results are consistent with the shade association of the two parent species: *P. veris* takes place usually on the sunnier patches in drier forests, while *P. vulgaris* grows in more shady and humid forests. Light response curves also confirm these habitat preferences, since the assimilation rates of control P. veris were higher than those of P. vulgaris at all light intensities, P. veris presented higher maximum photosynthetic performance (7.75 vs. 5.43 µmol CO_2 $m^{-2}s^{-1}$), and higher saturated light intensity (310 vs. 210 µmol $m^{-2}s^{-1}$ PPFD) than P. vulgaris did (Fig. 1a).

Total chlorophyll content was lower in hybrids than in the parent taxa, Chl a/b ratio and the xanthophyll cycle pool in hybrids were similar to those in P. vulgaris, and the ratio of total carotenoids to total chlorophylls did not differ between hybrids and P. veris (Table 1). Hybrids photosynthesised similarly well as P. veris at lower light intensities up to 310 µmol $m^{-2}s^{-1}$ PPFD, but they presented intermediate photosynthetic performance between the two parent species at higher light intensities (A_{max}: 6.65 µmol CO_2 $m^{-2}s^{-1}$; Fig. 1a). Pigment composition of the control plants does not explain the considerable difference between P. vulgaris and the hybrids

Table 1. Pigment composition of *Primula vulgaris*, *P. veris* and their interspecific hybrid in control and HLG plants. Three types of comparisons were performed by two-way ANOVAs: comparisons among the control plants of each taxa and among the HLG plants of each taxa were indicated by different lower case letters, while comparisons between control and HLG plants within each taxa were indicated by different capital letters if the differences were significant at $P < 0.05$.

	Primula veris		Hibrid		*Primula vulgaris*	
	Control	HLG	Control	HLG	Control	HLG
Chl a+b (µmol/m2)	223 ± 10 ^{a,A}	98 ± 20 ^{a,B}	158 ± 19 ^{b,A}	97 ± 16 ^{a,B}	197 ± 17 ^{a,A}	74 ± 5 ^{a,B}
Chl a/b	2.8 ± 0.07 ^{a,A}	2.66 ± 0.16 ^{ab,A}	2.47 ± 0.12 ^{b,A}	2.82 ± 0.14 ^{a,B}	2.33 ± 0.03 ^{b,A}	2.56 ± 0.11 ^{b,B}
Car/chl	0.458 ± 0.017 ^{a,A}	0.784 ± 0.057 ^{a,B}	0.426 ± 0.033 ^{ab,A}	0.753 ± 0.109 ^{a,B}	0.310 ± 0.007 ^{b,A}	0.689 ± 0.071 ^{a,B}
Xanthophyll cycle pool DA (rel. unit)	576 ± 86 ^{a,A}	614 ± 120 ^{a,A}	414 ± 21 ^{b,A}	526 ± 55 ^{ab,A}	368 ± 35 ^{b,A}	404 ± 73 ^{b,A}
Xanthophyll cycle pool HL (rel. unit)	299 ± 71 ^{a,A}	715 ± 38 ^{a,B}	537 ± 133 ^{b,A}	679 ± 36 ^{a,A}	196 ± 47 ^{a,A}	545 ± 42 ^{b,B}

in photosynthetic performance. Nevertheless, exposing the leaves to intensive light for an hour, the xanthophyll cycle pool decreased in the parent species, while the hybrid plants were able to increase it considerably (Table 1), which can provide a partial explanation for the better performance of the hybrids compared to *P. vulgaris*.

The 20-day long HLG treatment equalized the differences between the hybrids and the parent species concerning the total chlorophyll content and the Chl a/b ratio (Table 1). The ratio of total carotenoids to total chlorophylls was significantly lower in *P. vulgaris* than in the other two taxa, which indicates the least effective photoprotection of *P. vulgaris* among the three taxa and explains why the hybrid plants are able to occupy more open areas than *P. vulgaris* can. The photosynthetic CO_2 assimilation rates decreased in all the three taxa of the hybrid zone (Fig. 1b), but the extent of the photoinhibition was lower in *P. veris* than in the other two taxa: rise of the initial part of the light response curve and the A_{max} decreased less in *P. veris* (15.6%, 36.8%) than in *P. vulgaris* (44.3%, 60%) and in the hybrids (48.3%, 56%). The highest CO_2 assimilation rates of *P. veris* among the three taxa also support the better acclimation to higher light intensities of *P. veris*.

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