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Photorespiration in D1 protein mutant weed biotypes with limited xanthophyll cycle capacities

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Adverse effects on the photosynthetic apparatus, such as photoinhibition and photooxidative damage, occur when the photoprotection capacity of the plant is exceeded. Dissipation of the excess energy absorbed by the plants is achieved by a combination of non-photochemical and photochemical quenching processes. Non-photochemical quenching processes dissipate the excess energy as heat via the xanthophyll cycle in the antenna of photosystem II (PS II). The photochemical quenching of the excess energy includes photorespiratory O_2 uptake via the Rubisco reaction and O_2 uptake via the Mehler ascorbate peroxidase reaction. As photorespiration is an energy-consuming process, it has been proposed that photorespiration may protect C_3 plants from photoinhibition (Ogren 1984; Kozaki and Takeba 1996).

Atrazine-resistant (AR) weeds are more sensitive to photoinhibition than are atrazine-susceptible (AS) biotypes, especially when the plants are grown at high-light levels. The difference in sensitivity to photoinhibition may be caused by differences in efficiency of the various photoprotective mechanisms. Different photoprotective strategies have been presumed in the wild and D1 protein mutant biotypes of *Erigeron canadensis* (Darkó et al. 2000).

The present work reports on an investigation of the photorespiration and the xanthophyll cycle capacity in the AS and AR biotypes of high-light-grown weeds such as *Chenopodium album, Epilobium adenocaulon*, *Erigeron canadensis* and *Solanum nigrum.*

Materials and Methods

Plant material. Seeds of AS and AR weeds were germinated and grown in soil containers under natural, high-light (maximum about 1650 µmol m^{-2} s^{-1} PAR) conditions. All experiments were performed on the youngest, fully-expanded intact leaves of the 40-45-day-old plants

Measurements of CO_2 fixation and photorespiration. The light response of CO_2 assimilation was measured with an LCA-3 infrared gas analyser (Analytical Development Co. Ltd, England) in an open gas-exchange system. The attached leaves were exposed for 10 min to white light of different light intensities (from 50 to 1800 µmol photons m^{-2} s^{-1}). Air with controlled CO_2 (340 ppm) and O_2 (21 or 1%) contents was passed through the chamber at 300 ml min^{-1}. The difference in CO_2 uptake in 21 and 1% O_2 is due to photorespiration. The assimilation rates were calculated according to the equations of von Caemmerer and Farquhar (1981).

Pigment analyses. Xanthophyll cycle pigments (violaxanthin (V), antheraxanthin (A), zeaxanthin: (Z)) were determined with a reversed-phase HPLC system. The light response of the xanthophyll cycle was studied on leaf discs floated on tap water and illuminated for 1 h with white light from halogen light sources. Samples were frozen in liquid nitrogen and then extracted with acetone/water (85/15, v/v). Pigment contents were calculated via the areas of the peaks recorded at 450 nm. The rate of interconversion was expressed in terms of the de-epoxidation of the xanthophyll cycle pigments, calculated as DEi=(Z+0.5A)/(V+A+Z), as used by Brugnoli et al. (1994).

Results and Discussion

The light response curves of the interconversion of zeaxanthin to violaxanthin are shown in Figure 1 as the index of de-epoxidation (DEi=(Z%+0.5A%)/100) for the AS and AR biotypes of *Chenopodium album* and *Solanum nigrum.* In both biotypes, the xanthophyll cycle responded to the light intensity, but a lower activity of the xanthophyll cycle was dectected in the AR biotype as compared to the AS biotype. Similar results was observed for the AS and AR biotypes of the other species. These observations suggest the lower contribution of the xanthophyll cycle to the dissipation of excessive absorbed energy as heat in the AR biotypes.

The changes in the light responses curves for CO_2 assimilation rates at O_2 concentrations of 21% and 1% are shown in Figure 2. There were no significant differences in photosynthesis between the AR and AS biotypes of *Chenopodium* (or *Epilobium adenocaulon, Erigeron canadensis and Senecio vulgaris*; results not shown), but the extent of photosynthesis was slightly lower in the AR biotype of *Solanum nigrum.*

The role of photorespiration in photoprotection can be conveniently assessed by varying the gas composition to inhibit the oxygenation reaction of Rubisco (Sharkey, 1988). Under photorespiratory conditions, when the O_2 concentration in the air was reduced to 1%, the stimulation of CO_2 fixation was approximately 40% for both biotypes of *Chenopodium* (and in fact for all the weed species investigated). Only the AR biotype of *Solanum nigrum* displayed a slightly higher rate of photorespiration (the stimulation of CO_2 fixation was approximately 50%).

It seems, that the greater sensitivity of the AR biotypes to photoinhibition as compared to the AS weeds is not caused

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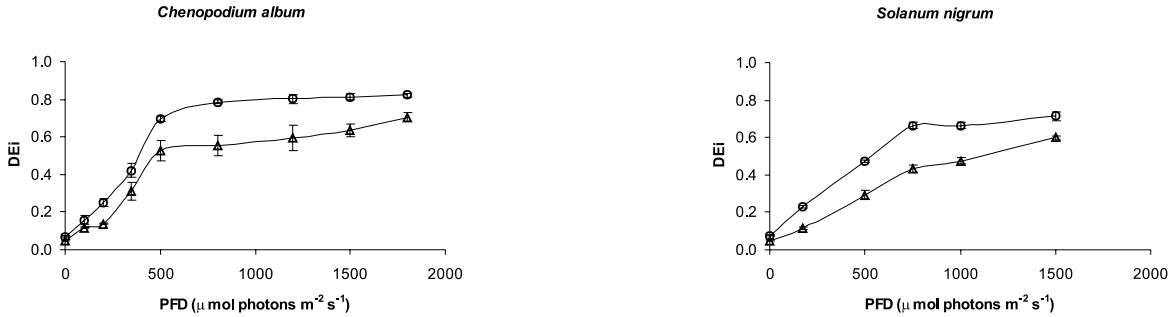

Figure 1. Light response curves of the de-epoxidation index in atrazine-resistant (triangles) and susceptible (circles) biotypes of high-light-grown *Chenopodium album* and *Solanum nigrum.* The results are means (SE from three independent experiments).

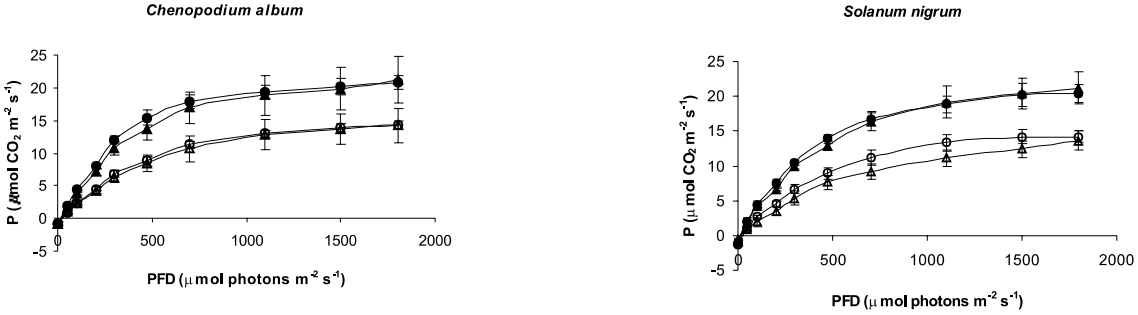

Figure 2. Light response curves of CO_2 assimilation rates of the atrazine-susceptible (circles) and atrazine-resistant (triangles) biotypes of high-light-grown *Chenopodium album* and *Solanum nigrum* at O_2 concentrations of 21% (open symbols) and on 1% (closed symbols). The results are means (SE from three independent experiments).

by a lower photorespiration capacity. This conclusion is supported by the observation that the leaves from the AR and AS weeds furnished similar light response curves for CO_2 fixation in atmospheres containing either 21% or 1% O_2.

We concluded that the photorespiration capacity affords equal protection against photoinhibition in the AR and AS biotypes and the enhanced susceptibility of the AR biotypes to excess light can be ascribed in part to a limited thermal deactivation (non-photochemical quenching) capacity of the excitation energy via the xanthophyll cycle in the antenna of PS II of the D1 protein mutant weeds.

Acknowledgement

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