

The xanthophyll cycle is induced by light irrespective of water status in field-grown lavender (*Lavandula stoechas*) plants

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The water relations, the photosynthetic capacity and the pigment content of leaves, i.e. chlorophylls, carotenes and xanthophylls, were analysed during the summer drought and recovery after autumn rainfalls in lavender (*Lavandula stoechas* L.) plants grown in Mediterranean field conditions. Summer drought caused photoinhibition of photosynthesis and significant decreases in chlorophylls (by ca 75%), β -carotene (by ca 65%), and lutein and neoxanthin (by ca 50%), although their contents remained unaltered between predawn and midday, suggesting a progressive decrease in response to drought. In contrast, the levels of violaxanthin decreased from predawn

to midday, giving rise to enhanced formation of zeaxanthin and antheraxanthin in high light. Zeaxanthin and antheraxanthin formation was not induced by water deficit. Although the levels of photosynthetic pigments were severely affected by water deficit, carotenoids decreased less than chlorophylls, which resulted in increased levels of carotenoids per unit of chlorophyll. We conclude that the enhanced formation of zeaxanthin in high light and the increased levels of carotenoids per unit of chlorophyll observed in water-stressed plants may help to avoid photoinhibitory damage to the photosynthetic apparatus.

Introduction

Although the reactions that convert solar energy into chemical energy are remarkably efficient, the capacity of these reactions is limited. Therefore, plants often absorb more light energy than they use for photosynthesis. In addition, many environmental stresses, including water deficit, can further limit the ability of plants to use light energy. It is well known that water deficit can predispose plants to photoinhibition (Björkman and Powles 1984, Ludlow and Björkman 1984), especially in Mediterranean field conditions, where plants are exposed to a combination of both water deficit and high-light stress during summer.

The term 'photoinhibition' has been used to include not only damage to the photosynthetic apparatus but also certain photoprotective mechanisms, which reduce the efficiency of photosynthetic energy conversion as a result of high-light treatments (Chow 1994). One of the mechanisms by which plants avoid photoinhibitory damage during water deficit is radiationless dissipation of excess energy by the

xanthophyll cycle (Niyogi 1999). In this cycle, the excess of excitation energy in the pigment bed induces the formation of zeaxanthin by de-epoxidation of violaxanthin, via the intermediate antheraxanthin. Zeaxanthin, and perhaps also antheraxanthin, is believed to be able to trap the surplus energy present in the pigment bed of the light harvesting complexes, and dissipate it harmlessly as heat. In low light the reaction is reversed and violaxanthin is formed (Eskling et al. 1997).

The photoprotective role of the xanthophyll cycle in plants has been extensively studied (Demmig-Adams and Adams 1996). However, it has been shown that the xanthophyll cycle may not necessarily function in photoinhibitory conditions (Ederli et al. 1997) and that other carotenoids, such as lutein, may contribute to non-photochemical quenching of chlorophyll fluorescence (Casper-Lindley and Björkman 1998, Bungard et al. 1999). Carotenoids, including xanthophylls, are also essential components of the light-

Abbreviations – A, antheraxanthin; β -Car, β -carotene; Chl, chlorophyll *a* + *b*; DPS, de-epoxidation state of the xanthophyll cycle; DW, dry weight; ϕ_{PSII} , relative efficiency of PSII photochemistry; F_v/F_m , intrinsic efficiency of PSII photochemistry; L, lutein; N, neoxanthin; PPF, photosynthetically-active photon flux density; PSII, photosystem II; qP, photochemical quenching of chlorophyll fluorescence; RWC, relative leaf water content; V, violaxanthin; Z, zeaxanthin.

harvesting complex and play a critical role in oxidative stress by quenching triplet chlorophyll, scavenging singlet oxygen and lipid peroxy radicals and inhibiting lipid peroxidation (Winston 1990, Pogson et al. 1996, Deltoro et al. 1998).

The aim of this work was to study the influence of water deficit and high light in the endogenous levels of photosynthetic pigments in lavender (*Lavandula stoechas* L.) plants growing in Mediterranean field conditions. Emphasis is given to the photoprotective role of carotenes and xanthophylls during drought and recovery.

Materials and methods

Plant material and growth conditions

Lavender (*L. stoechas* L.) plants were grown at the Experimental Fields of the University of Barcelona (Barcelona, NE Spain) for 3 years before the experiment began. For measurements, fully developed young leaves of 16 plants were collected at predawn (1 h before sunrise) and midday (at maximum incident photosynthetically active photon flux density [PPFD]) on a sunny day each month from June to October 1998. Plants grew in natural Mediterranean field conditions throughout the experiment. Before the experiment started, plants were watered with 20 mm on 2, 11 and 18 May. Thereafter, plants received water exclusively from rainfall. From June to August a very severe drought occurred and plants received less than 20 mm of water in 3 months. Heavy rain during September and October allowed us to study drought recovery (Fig. 1). PPFD and precipitation were measured throughout the experiment using a Quantum Sensor (Li-Cor, Lincoln, NB, USA) and a standard rain-gauge, respectively.

Plant water status and photosynthesis

Plant water status was determined by measuring the relative water content (RWC) of 6 fully developed young leaves as

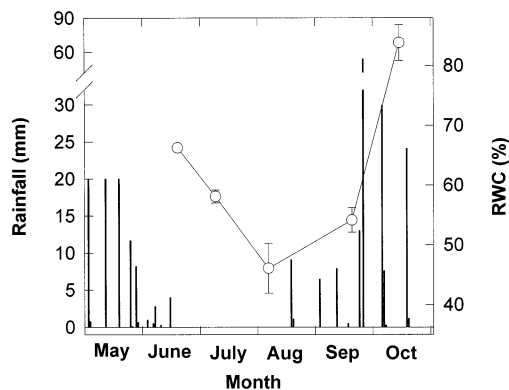


Fig. 1. Rainfall pattern (closed bars) at the Experimental Fields of the University of Barcelona (NE Spain) and predawn RWC (open circles) of *L. stoechas* plants. Plants were watered with 20 mm on 2, 11 and 18 May before the experiment began. Thereafter, plants received water exclusively from rainfall. Note the severe drought during the summer and heavy storms in autumn, typical of the Mediterranean climate. Data corresponding to RWC are the means \pm SE of 6 independent replicates.

$RWC = (FW - DW)/(TW - DW) \times 100$ where FW is the fresh weight, TW is the turgid weight after rehydrating the samples for 24 h and DW is the dry weight after drying the samples to constant weight in an oven at ca 85°C.

The photosynthetic capacity of leaves was determined by measuring the leaf gas exchange rates and modulated chlorophyll fluorescence of leaves as described previously (Munné-Bosch and Alegre 1999). Leaf gas exchange rates of 6 10-cm apical non-woody shoots were measured with an LI-6200 portable measuring system (Li-Cor) using the equations developed by von Caemmerer and Farquhar (1981). Steady-state modulated chlorophyll fluorescence of 6 fully developed young attached leaves was measured using a portable fluorimeter (mini-PAM, Walz, Effeltrich, Germany) with a far-red light source adapter. This adapter consisted of a KL1500 lamp (halogen lamp, Schott, Mainz, Germany) connected with a fiberoptics, which had 2 optical filters attached to the end (type RG-9 and BG-39, Schott, Germany). The fiberoptics was adjusted to an angle of 60° 8 mm from the leaf surface when measuring F'_o (minimum fluorescence yield in the light adapted state). This device gave a signal of $8 \mu\text{mol m}^{-2} \text{s}^{-1}$ of far-red light (700–750 nm) and together with the mini-PAM portable fluorimeter permitted measurements of the chlorophyll fluorescence parameters that depend on F'_o . A close correlation between the F'_o measured and the F'_o calculated from the equation developed by Oxborough and Baker (1997) was observed. The relative and the maximum efficiency of PSII photochemistry (ϕ_{PSII} , F_v/F_m), the intrinsic efficiency of PSII photochemistry (F'_v/F'_m), the photochemical quenching of chlorophyll fluorescence (qP) and the non-photochemical quenching of chlorophyll fluorescence (NPQ) were estimated from chlorophyll fluorescence data according to Genty et al. (1989).

Pigment analysis

Leaves were collected at predawn (1 h before sunrise) and midday (at maximum incident PPFD), immediately frozen in liquid nitrogen and stored at -38°C until analysis. The extraction and analysis of pigments were carried out essentially as described by Thayer and Björkman (1990).

Leaves (500 mg) were ground in a mortar in liquid nitrogen and extracted with cold 85% (v/v) acetone using ultrasonication (Vibra-Cell Ultrasonic Processor, Sonics & Materials Inc., Danbury, CT, USA). The extract was centrifuged for 3 min at 3°C and 1000 g and the pellet was re-extracted 3 times in 100% acetone. The supernatants were combined and filtered through a $0.20 \mu\text{m}$ syringe filter prior to analysis.

Pigments were separated on a Dupont non-encapped Zorbax ODS-5 μm column ($250 \times 4.6 \text{ mm}$, 20% C, Teknokroma, St. Cugat, Spain) at 30°C for 38 min at a flow rate of 1 ml min^{-1} . The solvents consisted of (A) acetonitrile/methanol (85:15) and (B) methanol/ethyl acetate (68:32). The gradient used was: 0–14 min 100% A, 14–16 min decreasing to 0% A, 16–28 min 0% A, 28–30 min increasing to 100% A, and 30–38 min 100% A. Detection was carried out at 445 nm (Spectralphotometer 430 Kontron, Zurich, Switzerland).

Table 1. CO₂ assimilation (A), relative efficiency of PSII photochemistry at natural incident PPFD (ϕ_{PSII}), maximum efficiency of PSII photochemistry after dark adaptation for 10 min (F_v/F_m), intrinsic efficiency of PSII photochemistry (F'_v/F'_m), photochemical quenching of chlorophyll fluorescence (qP), non-photochemical quenching of chlorophyll fluorescence (NPQ) and chlorophyll *a* to chlorophyll *b* ratio (Chl *a/b*) in *L. stoechas* plants grown under the Mediterranean climate. Values correspond to measurements made at midday, PPFD values during the measurements are also given. Data are the means \pm SE of 6 independent replicates.

Day	PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	ϕ_{PSII}	F_v/F_m	F'_v/F'_m	qP	NPQ	Chl <i>a/b</i>
June	1 970	4.2 \pm 0.5	0.29 \pm 0.02	0.79 \pm 0.03	0.58 \pm 0.02	0.50 \pm 0.02	1.41 \pm 0.06	2.39 \pm 0.05
July	1 898	2.0 \pm 0.6	0.20 \pm 0.03	0.73 \pm 0.04	0.50 \pm 0.04	0.40 \pm 0.02	1.38 \pm 0.09	2.41 \pm 0.03
August	1 755	1.1 \pm 0.1	0.18 \pm 0.02	0.72 \pm 0.05	0.46 \pm 0.03	0.39 \pm 0.03	1.80 \pm 0.16	2.43 \pm 0.09
September	1 544	2.1 \pm 0.1	0.25 \pm 0.03	0.76 \pm 0.04	0.60 \pm 0.05	0.42 \pm 0.03	0.75 \pm 0.03	2.52 \pm 0.03
October	1 210	8.1 \pm 0.4	0.36 \pm 0.04	0.79 \pm 0.02	0.70 \pm 0.05	0.52 \pm 0.04	0.39 \pm 0.05	2.38 \pm 0.07

Purified standards of chlorophyll *a* and chlorophyll *b* were purchased from Fluka (Buchs, Switzerland), and lutein, zeaxanthin and β -carotene were provided by Hoffmann-La Roche (Basel, Switzerland). Neoxanthin, violaxanthin and antheraxanthin were identified by their spectra in hexane (Almela et al. 1990) and ethanol (Britton 1985). The conversion factors from peak area units to pmol/injection were: chlorophyll *a* (167), chlorophyll *b* (163), lutein (359), zeaxanthin (359), β -carotene (283), neoxanthin (344), violaxanthin (400) and antheraxanthin (372), which were in agreement ($r^2 = 0.9996$) with those used by Thayer and Björkman (1990). Extraction and analytical procedures were run in duplicate.

Results

L. stoechas plants showed a significant decrease in the RWC during the summer, reaching minimum values below 50% during August (Fig. 1). Despite these low RWCs, plants recovered completely after autumn rainfalls, reaching values above 80%. These values were significantly higher than those observed during June, which indicates that plants were under stress at the beginning of the measuring period (Fig. 1).

Water deficit caused a large decrease in CO₂ assimilation rates in *L. stoechas*, which decreased by ca 70% from June to August. Maximum rates were observed during October, 2-fold higher than those observed during June (Table 1). The maximum efficiency of PSII photochemistry (F_v/F_m) at predawn was maintained unaltered at ca 0.8 throughout the experiment but the relative efficiency of PSII photochemistry (ϕ_{PSII}) at midday decreased during the summer by ca 40% at maximum incident PPFD in the field. This depletion of ϕ_{PSII} at midday was completely reversible. Leaves were dark-adapted for 10 min and values not significantly different (ANOVA, $P < 0.05$) from those measured at predawn were obtained. Besides, midday ϕ_{PSII} values ($= \text{qP} \times F'_v/F'_m$) recovered during autumn to values higher than those observed during the summer. Both F'_v/F'_m and qP were responsible for the variations observed in ϕ_{PSII} (Table 1). The F'_v/F'_m at midday decreased by ca 20% in water-stressed plants from June to August, and maximum levels were observed during October, when plants showed maximum RWC and the maximum incident PPFD was lower than during the summer. Accordingly, the non-photochemical quenching of chlorophyll fluorescence (NPQ) was at its

highest in water-stressed plants during August, and minimum values were observed during autumn. The Chl *a/b* was maintained unchanged throughout the study period (Table 1).

The chlorophyll *a* + *b* (Chl) content of leaves decreased by up to 75% during the summer and recovered after autumn rainfalls. Chl levels during June and October were not significantly different (Fig. 2), despite the differences in plant water status and PPFD (Fig. 1, Table 1). Besides, the increase in PPFD at midday did not give rise to variations in the Chl content of leaves throughout the experiment. These results indicate that Chl degradation was induced at RWC below 60% in *L. stoechas* and that this degradation occurred progressively under water deficit. The same was observed for lutein, β -carotene and neoxanthin, although the decreases observed in response to water stress were smaller than those observed for Chl (up to 65% for β -carotene and up to 50% for lutein and neoxanthin, Fig. 2).

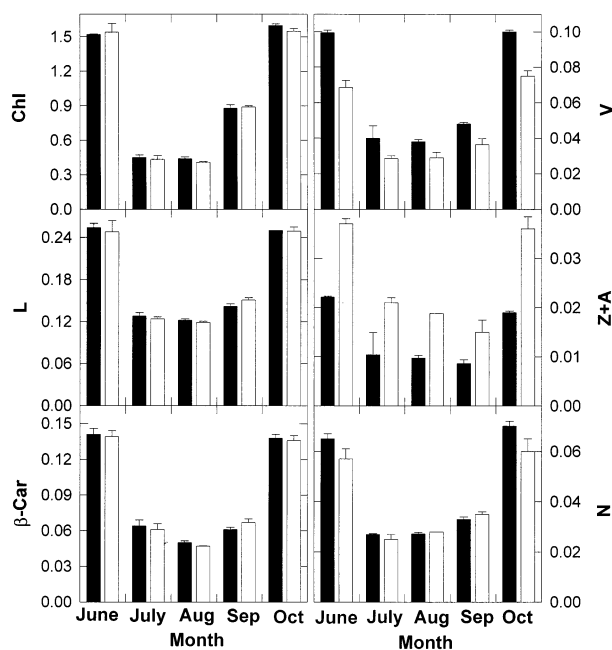


Fig. 2. Chlorophyll *a* + *b* (Chl), lutein (L), β -carotene (β -Car), violaxanthin (V), zeaxanthin and antheraxanthin (Z + A) and neoxanthin (N) content (mg g^{-1} DW) of *L. stoechas* leaves from June to October 1998. Predawn (closed bars) and midday (open bars) values are given. Note the large depletion of photosynthetic pigments during the summer and their recovery in autumn, as well as the differential variation of individual pigments at midday. Data are the means \pm SE of 4 independent replicates.

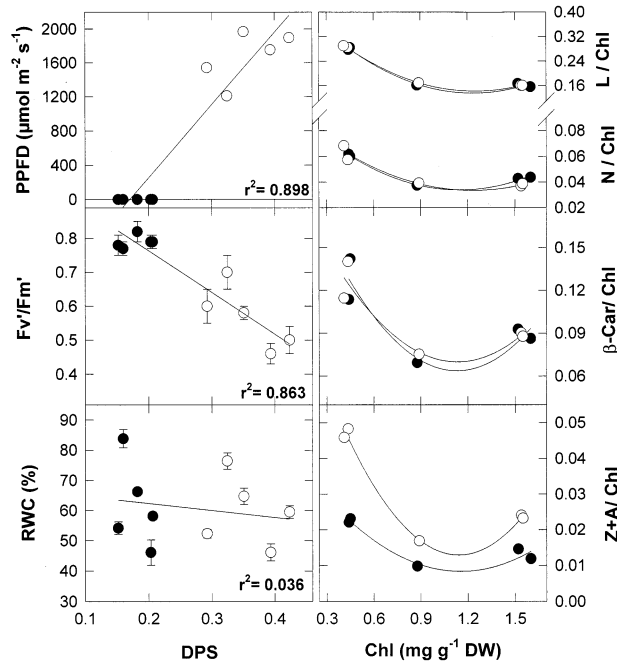


Fig. 3. Relationship between the de-epoxidation state of the xanthophyll cycle (DPS, calculated as $(Z + A)/(V + Z + A)$) and incident PPFD, intrinsic efficiency of PSII photochemistry (F_v/F_m) and RWC; and relationship between chlorophyll loss and the levels of lutein (L), neoxanthin (N), β -carotene (β -Car), zeaxanthin and antheraxanthin (Z + A) per unit of chlorophyll $a + b$ (Chl) in *L. stoechas* plants grown under the Mediterranean climate. Predawn (closed symbols) and midday (open symbols) values are given. Data are the means \pm SE of 4 independent replicates.

Violaxanthin (V), zeaxanthin (Z) and antheraxanthin (A) followed a similar pattern to that observed for the other photosynthetic pigments. However, their concentrations were also affected by light (Fig. 2). The xanthophyll pool ($V + Z + A$) at predawn decreased by ca 60% in response to water deficit. Decreases in violaxanthin and consequent increases in zeaxanthin and antheraxanthin were observed in response to high light at midday irrespective of plant water status. The decreases in V corresponded to the increases in (Z + A) observed at midday, which indicates that the de-epoxidation of violaxanthin was induced by light irrespective of water status in *L. stoechas*. However, the decreases in violaxanthin in response to water deficit measured at predawn did not lead to increases in zeaxanthin and antheraxanthin (Fig. 2).

Although the xanthophyll pool ($V + Z + A$) decreased in water-stressed plants, the de-epoxidation state of the xanthophyll cycle (DPS), calculated as $(Z + A)/(V + Z + A)$, increased at midday. The de-epoxidation of violaxanthin to zeaxanthin and antheraxanthin was induced by light but not by water deficit, as indicated by the relationship between the DPS and the PPFD and RWC (Fig. 3). Variations in the DPS were well correlated ($r^2 = 0.898$) with variations in PPFD and no significant correlation ($r^2 = 0.036$) was observed with the RWC. Thus, part of the variation observed in ϕ_{PSII} that was caused by changes in F_v/F_m is explained by the de-epoxidation of violaxanthin to zeaxanthin and antheraxanthin.

Although the levels of photosynthetic pigments were severely affected by water deficit, carotenoids decreased less than chlorophylls, which resulted in significant increases in the levels of carotenoids per unit of chlorophyll (Fig. 3). Thus, the capacity of leaves for photoprotection (given by the amount of carotenoids) per amount of light intercepted (given by Chl) was enhanced in stressed *L. stoechas* plants.

Discussion

Lavender (*L. stoechas* L.) plants were subjected to severe drought during the Mediterranean summer, which led to a significant decrease in the relative water content of leaves, showing values below 50%. In these conditions the capacity to assimilate carbon dioxide was reduced and photoinhibition of photosynthesis, measured as a decrease in the relative efficiency of PSII photochemistry, was observed, in agreement with previous studies (Munné-Bosch et al. 1999). This photoinhibition was caused by decreases in the photochemical capacity of PSII (given by qP) and by a limitation of PSII photochemistry by competition with thermal decay processes (given by F_v'/F_m).

F_v'/F_m and NPQ followed a similar trend in *L. stoechas* plants grown under Mediterranean climate. Changes in F_v'/F_m and NPQ have been associated with the dissipation of excess absorbed light energy as heat, in which the acidification of the thylakoid lumen and the conversion of violaxanthin to antheraxanthin and zeaxanthin seem to play a key role (Demmig-Adams and Adams 1996). Therefore, in many cases the photoinhibition of photosynthesis shown by plants exposed to water deficit has been at least partly attributed to the photoprotection conferred by the xanthophyll cycle (Adams et al. 1987, Björkman 1987, Demmig et al. 1988).

In *L. stoechas*, the de-epoxidation of violaxanthin to zeaxanthin was induced by high light but not by water deficit. The decreases in violaxanthin at predawn observed in water-stressed plants did not result in increased levels of zeaxanthin or antheraxanthin. Zeaxanthin and antheraxanthin did not accumulate at predawn in water-stressed plants, associated with the high levels of F_v/F_m observed at predawn in this species (Adams et al. 1994). The decreases of violaxanthin at predawn in water-stressed plants did correlate with those observed for neoxanthin. Thus, violaxanthin was partly de-epoxidised to antheraxanthin and zeaxanthin in high light, but in water-stressed plants it could also give rise to other carotenoids (Bungard et al. 1999).

The decreases observed in ϕ_{PSII} at midday were completely reversible within a few minutes of dark adaptation, which indicates that the photoinhibition observed in this species was due to photoprotective processes and not to photoinhibitory damage. Thus, the lack of induction of the xanthophyll cycle in response to water deficit did not adversely affect water-stressed leaves in *L. stoechas* plants growing in Mediterranean field conditions. Other processes for the protection of the photosynthetic apparatus, i.e. photorespiration and scavenger systems for the removal of reactive oxygen species, could also operate in this species and contribute to avoid photoinhibitory damage in water-stressed plants (Foyer et al. 1994, Asada 1996).

Chlorophyll loss could also significantly contribute to the avoidance of photoinhibitory damage. Chlorophyll loss is a negative consequence of stress. However, it can also be considered an adaptation to prolonged drought, since it reduces the amount of light intercepted by leaves and increases the capacity to dissipate excess excitation energy per amount of light intercepted (Maslova and Popova 1993, Kyprisiss et al. 1995, Munné-Bosch and Alegre 1999). In this study, the amount of carotenoids decreased under water deficit, but less than Chl, which resulted in an increase in the ratio of carotenoids to Chl. Thus, the capacity to dissipate excess excitation energy as heat, to scavenge singlet oxygen and lipid peroxy radicals and to inhibit lipid peroxidation (functions carried out by carotenoids) was enhanced per amount of light intercepted in stressed leaves.

We conclude that the enhanced formation of zeaxanthin by de-epoxidation of violaxanthin in high light and the increased levels of carotenoids per unit of chlorophyll observed in water-stressed plants may help to avoid photoinhibitory damage to the photosynthetic apparatus in *L. stoechas* plants growing in Mediterranean field conditions.

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