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EXPERIMENTAL PAPERS

Pigment Apparatus in *Ajuga reptans* Plants as Affected by Adaptation to Light Growth Conditions

O. V. Dymova and T. K. Golovko

Institute of Biology, Komi Research Center, Ural Division, Russian Academy of Sciences, Kommunisticheskaya ul. 28, Syktyvkar, 167982 Russia;
fax: 7 (8212) 24-0163; e-mail: dymovao@ib.komisc.ru

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Abstract—Mechanisms of adaptation of the photosynthetic apparatus at the level of pigment complex in a shade-tolerant bugle plant (*Ajuga reptans* L.) grown at full solar irradiation in an open plot were studied. In "sun" plants, the content of photosynthetic pigments decreased markedly as compared to "shade" plants grown under a forest canopy at 5–10% of the full solar irradiation. In leaves of sun plants, the portion of β-carotene and lutein in the carotenoid spectrum was higher than in shade plant leaves, antheraxanthin and zeaxanthin were present, and de-epoxidation of violaxanthin was by an order of magnitude higher in sun plant leaves reaching 40%. The data obtained indicate the role of the violaxanthin cycle in the protection of photosynthetic apparatus in a shade-tolerant plant against destruction under excessive irradiation.

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Key words: Ajuga reptans - pigments - chlorophylls - carotenoids - violaxanthin - xanthophyll cycle - light stress

INTRODUCTION

Light is functionally essential for photosynthesizing organisms that transform and store solar energy in the form of chemical bonds of organic substances. At the same time, light is an aggressive factor capable of inducing the photodynamic destruction of the photosynthetic apparatus [1–3]. Excessive absorption of light energy may result in the damage of pigment–protein complexes of thylakoid membranes due to formation of active oxygen species. The pigment–protein complexes of photosystem II are most sensitive to photodamage [2, 4].

In the course of evolution, plants developed several means of defense against light stress at structural–functional and molecular-genetic levels. Chloroplast carotenoids play a special role in protection of reaction centers. These pigments can efficiently quench the triplet state of chlorophyll and free radicals which appear during irradiation [5]. Three carotenoids involved in the violaxanthin cycle (VC) regulate light harvesting in the pigment–protein complexes [6–9]. Xanthophylls located in the light-harvesting complexes (LHC) of all photosynthesizing organisms contribute to light harvesting and protection against photoinhibition [8, 10]. Zeaxanthin synthesized by violaxanthin de-epoxidation via antheraxanthin plays the principal role in protection of the photosynthetic apparatus against photodamage. Zeaxanthin is supposed to transform the excess light energy into heat thus preventing excitation energy transfer to the reaction center [1, 5]. Losses of energy of absorbed quanta as thermal radiation and/or quenching of chlorophyll excitations have been assigned to nonphotochemical fluorescence quenching (NPQ). The changes in NPQ and zeaxanthin content were shown to be proportional [11]. However, in some cases, no correlation between zeaxanthin accumulation and NPQ was found [12, 13].

Previously, we studied changes in anatomical and morphological as well as in physiological and biochemical leaf characteristics of a shade-tolerant bugle plant (*Ajuga reptans* L.) during adaptation to light conditions [14–16]. In sun plants grown in an open plot, the specific leaf weight (SLW) and maximal rate of net photosynthesis per unit leaf area increased by 2.3 times and 20–30%, respectively. The content of green pigments decreased 1.3–1.4-fold, the chlorophyll to carotenoid ratio was lower as well. The study of light response of CO_2 exchange in leaves of shade plants grown under a forest canopy showed that net photosynthesis was inhibited at intensity of photosynthetically active radiation (PAR) above 100 W/m^2. In some cases, we observed the same response in plants grown in an open plot.

Considering the fact that, in leaves of sun plants of *A. reptans*, the rate of net photosynthesis increased insignificantly when SLW increased more than twofold, we suggested that protective mechanisms were

Abbreviations: DEPS—de-epoxidation state of the violaxanthin cycle; LHC—light-harvesting complex; NPQ—nonphotochemical fluorescence quenching; PAR—photosynthetically active radiation; SLW—specific leaf weight; VC—violaxanthin cycle.

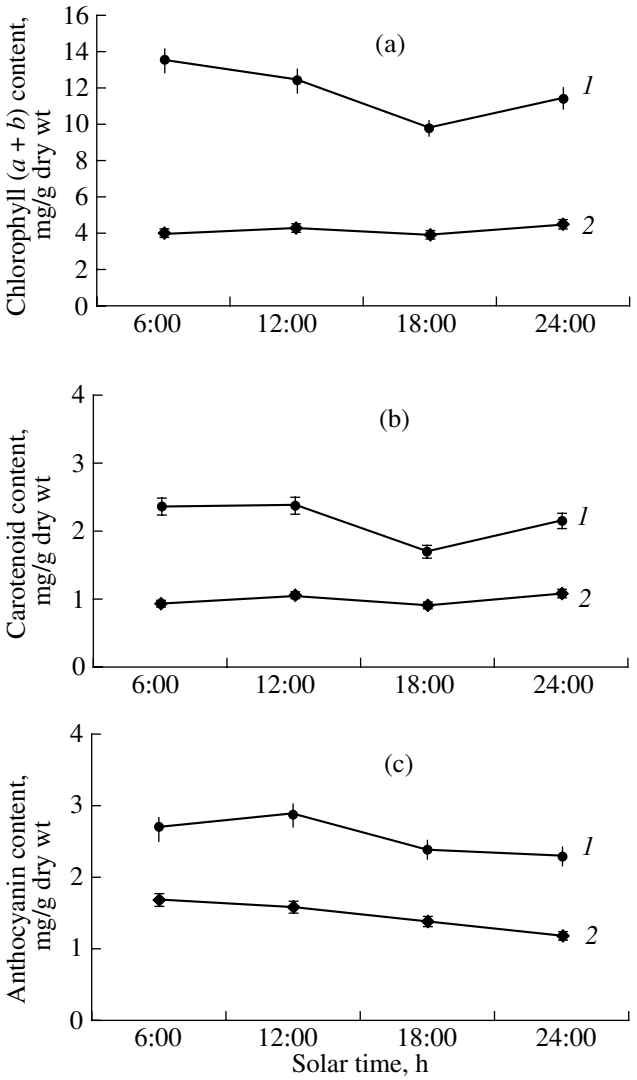

Fig. 1. Diurnal dynamics of the pigment content in leaves of (*1*) shaded and (*2*) sun *A. reptans* plants.
(a) Chlorophyll *a* + *b*; (b) carotenoids; (c) anthocyanins.

activated providing dissipation of excess absorbed energy.

The objective of this work was to study comparatively the pigment apparatus and evaluate the de-epoxidation state of the xanthophyll cycle pigments in leaves of sun and shade plants of *A. reptans*.

MATERIALS AND METHODS

Shade bugle plants (*Ajuga reptans* L.) grew under a canopy of mixed-herb spruce–aspen forest. In July, at the stage of maximum leafage area, irradiation was 5–10% of the full sunlight. To obtain sun plants, plants from the forest were transferred to an open plot in the tree nursery as described previously [14]. During experiments, full irradiance at the latitude of Syktyvkar at noon was 90 W/m^2. Experiments were carried out on August 11–12, 2004, one year after the plant transfer. Mature green leaves of summer generation developed during the current growing season were used in the experiments. Leaf samples were taken from 20–25 representative plants four times a day.

Photosynthetic pigments were extracted from 150–200 mg of fresh plant material with boiling 100% acetone [17]. The chlorophyll and carotenoid content was determined in acetone extracts with UV-1700 (Shimadzu, Japan) spectrophotometer from the absorption at 662 and 644 nm (chlorophylls) [18], and 470 nm (carotenoids) [19]. We calculated chlorophyll portion in LHC according to Lichtenthaler [20], assuming that practically all chlorophyll *b* was located in LHC and the chlorophyll *a*/*b* ratio in this complex was equal to 1.2. Anthocyanins were extracted with 1% HCl solution at 45°C for 20 min and measured spectrophotometrically at 510 nm [21].

A portion of leaf blades was dried between the sheets of filter paper in full darkness at room temperature and stored at –80°C. Pigments were separated by reverse phase HPLC (Jasco, Japan) according to modified method [13, 22]. Leaf blades were ground in solvent A (acetonitrile : methanol : water, 72 : 8 : 1) and centrifuged at 12000 *g* for 5 min. The supernatant was filtered and loaded (100 μl) on the Nucleosil C18 column (250 × 40 mm), particle size was 5 μm (Teknokroma, Spain). Pigments were eluted isocratically for 40 min with solvents A and B (methanol : ethyl acetate, 68 : 32, v/v) at a flow rate of 2 ml/min.

The de-epoxidation state (DEPS) was calculated according to [23] as a ratio [(Z + 0.5 An)/(V + An + Z)], where Z designates zeaxanthin, An is antheraxanthin, and V is violaxanthin. Coefficient 0.5 shows that An contains epoxy group in one of two β-ionone rings.

All measurements were replicated four to six times and all assays were repeated three times. Data in tables and figures represent means and their standard deviations. The significance of differences was evaluated using the Student's test.

RESULTS

Figure 1 shows diurnal dynamics of the chlorophyll, carotenoid, and anthocyanin content in green bugle leaves of summer generation grown under the forest canopy and in the open plot. In leaves of shade plants, the content of photosynthetic pigments and anthocyanins calculated per dry wt was significantly higher than in sun leaves. In the sum of chlorophylls *a* and *b*, shaded leaves exceeded sun leaves 2.5–3-fold, carotenoid content was nearly twice higher, and anthocyanin content was 1.5-fold higher, on average. In shade plants, daily changes in the pigment content were revealed. In the morning and at noon, the chlorophyll and carotenoid content in the leaves was higher by 20–25 and 28%, respectively, as compared to that in the evening.

Table 1. Pigment content in leaves of *A. reptans*, mg/dm^2

Solar time, h	Treatment	Chlorophyll *a*	Chlorophyll *b*	Chlorophyll (*a* + *b*)	Carotenoids
6:00	shaded	2.45 ± 0.06	0.94 ± 0.06	3.39 ± 0.18	0.62 ± 0.03
	sun	1.71 ± 0.09*	0.61 ± 0.05*	2.32 ± 0.13*	0.54 ± 0.03
12:00	shaded	1.93 ± 0.09	0.72 ± 0.07	2.65 ± 0.15	0.49 ± 0.02
	sun	1.43 ± 0.05*	0.46 ± 0.02*	1.89 ± 0.09*	0.43 ± 0.01
18:00	shaded	2.19 ± 0.09	0.92 ± 0.04	3.11 ± 0.10	0.54 ± 0.03
	sun	1.62 ± 0.09*	0.61 ± 0.04*	2.23 ± 0.13*	0.50 ± 0.02
24:00	shaded	2.29 ± 0.08	0.85 ± 0.03	3.14 ± 0.05	0.59 ± 0.02
	sun	2.10 ± 0.15	0.66 ± 0.09	2.76 ± 0.23	0.66 ± 0.09

Note: $n = 5$.
* The differences are significant at $P \le 0.05$.

Table 2. Characteristics of the photosynthetic apparatus in leaves of *A. reptans*

Solar time, h	Treatment	SLW, g/dm^2	Chlorophyll *a*/*b* ratio	Percentage of chlorophyll in LHC, %	Chlorophyll/carotenoid ratio
6:00	shaded	0.28 ± 0.01	2.6 ± 0.1	61	5.5 ± 0.1
	sun	0.57 ± 0.01*	2.8 ± 0.1	58	4.3 ± 0.1*
12:00	shaded	0.21 ± 0.01	2.7 ± 0.1	60	5.4 ± 0.1
	sun	0.42 ± 0.01*	3.1 ± 0.1*	54	4.4 ± 0.1*
18:00	shaded	0.25 ± 0.01	2.4 ± 0.1	65	5.8 ± 0.2
	sun	0.55 ± 0.01*	2.7 ± 0.1	60	4.4 ± 0.1*
24:00	shaded	0.26 ± 0.01	2.7 ± 0.2	60	5.3 ± 0.1
	sun	0.59 ± 0.01*	2.8 ± 0.2	53	4.2 ± 0.2*

Note: $n = 5$.
* The differences are significant at $P \le 0.05$.

The differences in chlorophyll content between shaded and sun leaves remained evident when the pigment content was calculated per unit leaf area (Table 1). The smaller difference between compared values was due to the twofold increase in SLW in sun leaves as compared to shaded ones (Table 2). In shaded and sun leaves, the daily changes in SLW were revealed, the lowest SLW value was found at noon.

As seen from Table 2, in leaves of shade plants, a tendency to lower chlorophyll *a*/*b* ratio and higher chlorophyll portion attributed to LHC was observed. In sun plants, the ratio of green and yellow pigments was reliably lower indicating a relatively high carotenoid content in the pool of photosynthetic pigments.

Chromatographic determination of pigments revealed changes in the relative content of components of the pigment apparatus in leaves of sun and shade plants (Fig. 2). In the carotenoid spectrum of sun plants, antheraxanthin and zeaxanthin were present. In this case, the portion of zeaxanthin increased in the evening while that of antheraxanthin was higher in the morning. In leaves of shade plants, zeaxanthin and antheraxanthin were found in trace quantities. In leaves of sun plants, β-carotene and lutein portion was higher, while the neoxanthin content was higher in the leaves of shade plants.

Evaluation of violaxantin de-epoxidation state (DEPS) using the ratio [(Z + 0.5An)/(V + An + Z)] showed that the de-epoxidation of the xanthophyll cycle pigments was significantly higher (by an order of magnitude) in sun plants as compared to shade plants (Fig. 3). Although de-epoxidation of VC pigments in sun plants remained comparatively high over 24-h cycle, maximum DEPS values were observed during afternoon hours.

DISCUSSION

Environmental conditions, especially light, influence the functional activity of plants greatly, thus affecting their pigment apparatus. The pigment content and ratio are controlled by many external and internal factors. Integrated action of these factors determines the activities of pigment biosynthesis and degradation. Our data showed that the pigment content was lower in plants grown under high irradiance as compared to

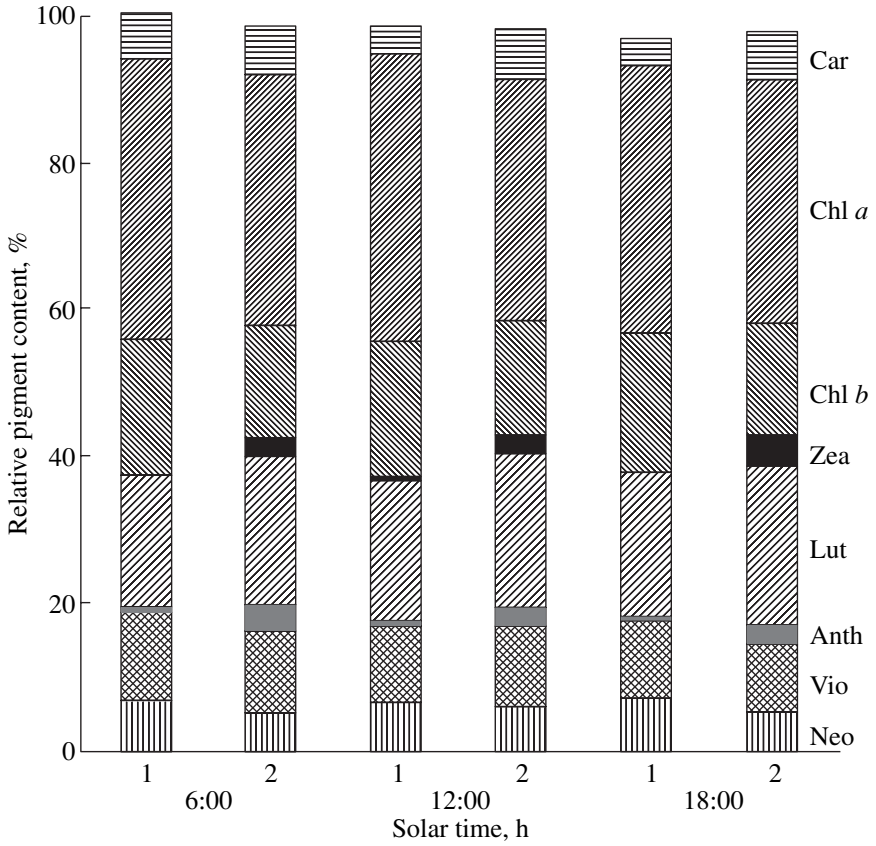

Fig. 2. Portion of different chlorophylls and carotenoids in the total pool of photosynthetic pigments in leaves of (1) shaded and (2) sun *A. reptans* plants.

Neo—neoxanthin; Vio—violaxanthin; Anth—antheraxanthin; Lut—lutein; Zea—zeaxanthin; Chl *b*—chlorophyll *b*; Chl *a*—chlorophyll *a*; Car—β-carotene.

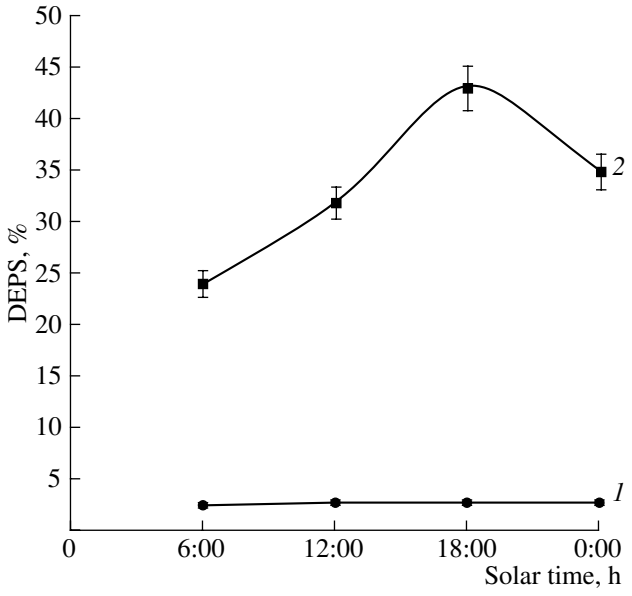

Fig. 3. Diurnal dynamics of the violaxanthin de-epoxidation state (DEPS, %) in leaves of (*1*) shaded and (*2*) sun *A. reptans* plants.

plants under a forest canopy (Fig. 1). In this case, the accumulation level of green and yellow pigments did not change over 24-h cycle indicating that the rate of their formation de novo and degradation was balanced.

In plants grown under a forest canopy, daily changes in the content of photosynthetic pigments were revealed: in the afternoon, the pigment concentration in leaves was reliably lower than in the morning. Chlorophyll turnover in leaves is known to be as high as 5–10% a day depending on species and growth condition [24]. In the leaves of shade plants, a decrease in the content of green and yellow pigments may be related to endogenous physiological rhythms and/or may be due to exogenous factors. In the morning hours and at noon, solar radiation is enriched in infrared and red light [25] which seems more effective for biosynthesis of green pigments, especially chlorophyll *a* and carotenoids. A comparison of daily changes in the pigment content and photosynthetic rate in the shade plant leaves showed that the maximum content of chlorophyll and carotenoids during daytime corresponded to the highest CO_2 assimilation rate (2–3 mg CO_2/dm^2 h) under natural irradiance (data not shown).

During adaptation of bugle leaves to high irradiance, the decrease in the total content of photosynthetic pigments was accompanied by the reduction of LHC, typical of C_3 species, as evidenced by a decline in the chlorophyll portion attributed to LHC (Table 2).

As follows from the data on chlorophyll/carotenoid ratio, the higher relative content of yellow pigments was found in sun plants (Table 2). In other words, under full irradiance, the carotenoid pool decreased to a lesser degree than that of green pigments. Among carotenoids, xanthophylls fulfill a protective function during adaptation of plant photosynthetic apparatus to excessive irradiation. After long-term adaptation to high irradiance, plants are characterized by larger xanthophyll pool and zeaxanthin formation [26–28]. De-epoxidation in the light includes transformation of epoxyxanthophyll (violaxanthin) to epoxy-free zeaxanthin and changes in the content of the intermediate, antheraxanthin (5,6-monoepoxyzeaxanthin).

Zeaxanthin is known to be accumulated in light and formed from the so-called "active" violaxanthin pool. The more reduced the plastoquinone pool, the higher is accessibility of violaxanthin for de-epoxidation. According to Strzalka et al. [29], violaxanthin transformation to zeaxanthin takes place within the lipid matrix. It was shown that in plants *Urtica dioica* and *Ranunculus acris* vegetating in summer at high insolation, zeaxanthin formation increased and its content reached 60% of xanthophyll pool of VC [30]. Herbaceous perennial plants as well as ephemers can transform up to 85% of the VC pigment pool to zeaxanthin in the light. Zeaxanthin is able to capture the excessive energy from excited chlorophyll and rapidly dissipate it to heat, faster than energy is transferred to the reaction center [1]. The mechanism of excessive energy dissipation by zeaxanthin is not clearly established so far. It was suggested that zeaxanthin indirectly affected the processes of energy dissipation facilitating the allosteric changes in the pigment–protein complexes resulting in an increase in NPQ [10, 31]. However, available literature presents limited data on the involvement of this cycle in the process of adaptation of shade-tolerant plants to excessive radiation [26].

Our results show that in shade-tolerant bugle plants, the de-epoxidation state of the VC components increased significantly during adaptation to full sunlight. Full light induced transformation of violaxanthin to zeaxanthin (via antheraxanthin). Leaves of sun plants grown in an open plot were able to dissipate the excess absorbed energy with a high rate. Energy dissipation in VC is likely to play essential role in the protection of photosynthetic apparatus of shade-tolerant plants during adaptation to full light. Apparently, this may explain the previously established fact [14] that in the plants grown in open plots, the maximum photosynthetic rate did not differ markedly (by 20–30%) from that in plants grown under a forest canopy.

We showed that the content of nonphotosynthetic pigments—anthocyanins absorbing light at 500–590 nm—was higher in shade plants as compared to sun plants. According to Shakhov [32], anthocyanins affect the intracellular light regime and facilitate the effective use of solar radiation under unfavorable conditions. Close and Davidson suggested that anthocyanin accumulation in the leaves of *Eucalyptus nitens* reflected a long-term "strategy" of seedling adaptation to photoinhibitory conditions (long-term flooding, low irradiation) [33]. The role of anthocyanins in the protection of cells against harmful UV radiation is particularly emphasized in the literature [34]. However, a hypothesis for anthocyanin role in the protection of *Syzygium* juvenile leaves against UV radiation was not confirmed [35]. We propose that increased content of anthocyanin pigments in the bugle leaves grown under a forest canopy was related to their protective function against sunflecks. This is in line with the hypothesis that anthocyanins provide protection of shaded chloroplasts against bright sunflecks penetrating a canopy [36]. The fact that we have not observed increased anthocyanin accumulation in the bugle leaves grown under full sunlight may be explained by the induction of more efficient protective mechanisms. Our data showed that one of such mechanism was the activation of violaxanthin cycle, which provided thermal dissipation of excess excitation energy.

Thus, we revealed adaptive reactions of a shade-tolerant bugle plant at the level of pigment apparatus. In leaves exposed to excessive irradiance, the content of green pigments and LHC-bound chlorophylls decreased, while the de-epoxidation of the VC pigments increased.

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