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Functional Plant Biology, 2003, **30**, 515–524

Response of *chlorina* barley mutants to heat stress under low and high light

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Abstract. Barley plants (*Hordeum vulgare* L.) of wild type and two *chlorina* mutants, *chlorina 126* and *chlorina* f_2, were subjected to 42°C for 5 h at light intensities of 100 and 1000 µmol photons m^{-2} s^{-1}. The exposure of plants to heat stress at a light intensity of 100 µmol m^{-2} s^{-1} induced enormous proline accumulation, indicating that the effect of heat stress was stronger when it was combined with low light intensity. The functional activity of PSII, O_2 evolution and flash-induced thermoluminescence B-band amplitude were strongly reduced when plants were exposed to heat at low light intensity. The results clearly showed that high light intensity had a protective effect on photosynthetic activity when barley plants were treated with high temperature. Comparison of the thermosensitivity of wild type plants and *chlorina* mutants revealed that O_2 evolution in *chlorina 126* and, especially, in *chlorina* f_2 was more sensitive to heat than in wild type.

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J. Plant Physiol. 160. 205–208 (2003)

http://www.urbanfischer.de/journals/jpp

JOURNAL OF PLANT PHYSIOLOGY

Short Communication

Response of barley seedlings to UV-B radiation as affected by NaCl

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Received February 15, 2002 · Accepted July 5, 2002

Summary

The response of barley seedlings, subjected to 150 mmol/L NaCl for 4 days at different light regimes (4 d in the light, 4 d in darkness and a 12 h light/dark cycle) before UV-B radiation was investigated. NaCl treatment resulted in a decrease of total chlorophyll content and an increase in H_2O_2, free proline and lipid peroxidation, as quantified by measurement of malondialdehyde. Significantly more proline was accumulated in the light than in darkness. The combination of UV-B and NaCl treatment produced an additive effect on most of the parameters studied. UV-B radiation reduced the chlorophyll/carotenoids ratio and photochemical efficiency of PSII as estimated by chlorophyll fluorescence. NaCl pre-exposure decreased H_2O_2 generation and lipid peroxidation and alleviated the inhibitory effect of UV-B on PSII activity. Proline accumulated under salt stress conditions might be one of the reasons for the observed tolerance of barley seedlings to UV-B radiation.

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BIOLOGIA PLANTARUM 47 (4): 549-554, 2003/4

Response of barley seedlings to UV-B radiation as affected by proline and NaCl

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Abstract

Barley (*Hordeum vulgare* L. cv. Alfa) seedlings were treated for 4 d before UV-B irradiation with 0.05 mM proline or 150 mM NaCl. UV-B exposure induced synthesis of yellow coloured compounds with maximum absorbance at 438 nm. The content of these compounds was increased in proline-treated and decreased in NaCl-treated plants. UV-B radiation reduced chlorophyll/carotenoids ratio, oxygen evolution rate and photochemical efficiency of PS 2 as estimated by chlorophyll fluorescence and increased proline accumulation, H_2O_2 generation and lipid peroxidation. Exogenous proline had no effect on the parameters studied and did not change the response of plants to UV-B radiation. NaCl inhibited photochemical efficiency of PS 2, reduced oxygen evolution and increased H_2O_2 concentration and lipid peroxidation. The combination of NaCl and proline treatment led to lowering the inhibitory effect of NaCl in non UV-B irradiated seedlings. There was not relationship between the level of UV-B-induced compounds and UV-B tolerance of barley seedlings.

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Photosynthesis Research (2005) 85: 191–203

Regular paper

Comparative study on the changes in photosynthetic activity of the homoiochlorophyllous desiccation-tolerant *Haberlea rhodopensis* and desiccation-sensitive spinach leaves during desiccation and rehydration

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Received 18 November 2004; accepted in revised form 14 February 2005

Abstract

The functional peculiarities and responses of the photosynthetic system in the flowering homoiochlorophyllous desiccation-tolerant (HDT) *Haberlea rhodopensis* and the non-desiccation-tolerant spinach were compared during desiccation and rehydration. Increasing rate of water loss clearly modifies the kinetic parameters of fluorescence induction, thermoluminescence emission, far-red induced P700 oxidation and oxygen evolution in the leaves of both species. The values of these parameters returned nearly to the control level after 24 h rehydration only of the leaves of HDT plant. PS II was converted in a non-functional state in desiccated spinach in accordance with the changes in membrane permeability, malondialdehyde, proline and H_2O_2 contents. Moreover, our data showed a strong reduction of the total number of PS II centers in *Haberlea* without any changes in the energetics of the charge recombination. We consider this observation, together with the previously reported unusually high temperature of B-band ($S_2Q_{B^-}$) emission of *Haberlea* to reflect some specific adaptive characteristics of the photosynthetic system. As far as we know this is the first time when such adaptive characteristics and mechanism of the photosynthetic system of a flowering HDT higher plant is described. These features of *Haberlea* can explain the fast recovery of its photosynthesis after desiccation, which enable this HDT plant to rapidly take advantage of frequent changes in water availability.

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IV. Alps-Adria Scientific Workshop Portoroz, Slovenia 2005.

SOME RESPONSES OF THE HOMOIOCHLOROPHYLLOUS DESICCANT-TOLERANT DICOT *HABERLEA RHODOPENSIS FRIV.* TO DESICCATION AND REHYDRATION

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Introduction

Desiccation-tolerant (DT) plants can survive the loss of 80–95% of their cell water and after a shorter or longer period in the desiccated state, they revive and resume normal metabolism when they are remoistened. DT plants may be subdivided into homoiochlorophyllous (HDT) and poikilochlorophyllous (PDT) types. The HDTs retain their chlorophyll on desiccation, whereas in PDTs desiccation results in the loss of chlorophyll, which must be resynthetized following rehydration (Tuba et al, 1998). Although the majority of the DT plants are homoiochlorophyllous, we still do not have enough information about the HDT ones, especially information on flower DT plants are needed.

Net CO_2 assimilation (Pn) in *Haberlea rhodopensis* was characterized using data from measurements of CO_2 gas exchange, the kinetics of chlorophyll fluorescence (variable Chl fluorescence ratio, Fv/Fm) in various hydration conditions. The development of pigment accumulation, thylakoid function and photosynthetic CO_2 assimilation were fully recovered after rehydration. Long-term experiments would be needed to make a confident forecast of the responses of desiccation tolerant plants to the global environmental changes.

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Proceedings of the 8th Hungarian Congress on Plant Physiology and the 6th Hungarian Conference on Photosynthesis, 2005

Volume 49(1-2):173-174, 2005
Acta Biologica Szegediensis
http://www.sci.u-szeged.hu/ABS

Investigation of the homoiochlorophyllous desiccation-tolerant dicot *Haberlea rhodopensis* Friv. during dessication and rehydration

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ABSTRACT In this study the recovery of the photosynthetic activity during rehydration following dry stage was examined in the case of a homoiochlorophyllous desiccation-tolerant (HDT) plant, *Haberlea rhodopensis*. Although the majority of the DT plants are homoiochlorophyllous, we still do not have enough information about the HDT ones, especially information on flower DT plants are needed. Net CO_2 assimilation (Pn) in *Haberlea rhodopensis* was characterized using data from measurements of CO_2 gas exchange, the kinetics of chlorophyll fluorescence (variable Chl fluorescence ratio, Fv/Fm) in various hydration conditions. The pigment accumulation, thylakoid function and photosynthetic CO_2 assimilation were fully recovered after rehydration. Long-term experiments would be needed to make a confident forecast of the responses of desiccation tolerant plants to the global environmental changes.
Acta Biol Szeged 49(1-2):173-174 (2005)

KEY WORDS

desiccation
rehydration
CO_2 gas exchange
chlorophyll fluorescence

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Environmental and Experimental Botany 54 (2005) 182–191

Environmental and Experimental Botany

www.elsevier.com/locate/envexpbot

UV-B-induced compounds as affected by proline and NaCl in *Hordeum vulgare* L. cv. Alfa

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Accepted 8 July 2004

Abstract

From the leaves of barley seedlings (*Hordeum vulgare* L. cv. Alfa) UV-B induced compounds, with maximum absorbance at 438 nm (A_{438}) were extracted. The relationship between the level of UV-B induced compounds and UV-B tolerance of barley seedlings was investigated. The level of these compounds depended on the time of UV-B irradiation. They increased 4 h after UV-B treatment, reached maximum after 24 h and then declined. Contrary, the syntheses of UV-absorbing compounds extracted in acidified methanol continued for a long period after UV exposure and after 120 h the values of A_{300} are higher. The content of UV-induced compounds enhanced in the plants treated with proline before UV-B irradiation and decreased as a result of NaCl pretreatment in a concentration depending manner. A physiological response to UV-B irradiation was evaluated by measuring the oxygen evolution rate, chlorophyll fluorescence and chlorophyll/carotenoids ratio. No correlation was found between the level of A_{438} and UV-B tolerance of barley seedlings. It is possible these compounds to play a subtle role in plant UV-B protection than simple UV-B screening or to serve as stress markers.

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Available online at www.sciencedirect.com

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Environmental and Experimental Botany 56 (2006) 225–230

Environmental and Experimental Botany

www.elsevier.com/locate/envexpbot

Effect of pretreatment of barley seedlings with different salts on the level of UV-B induced and UV-B absorbing compounds

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Accepted 14 February 2005

Abstract

The relationship between the level of UV-B-induced and/or UV-B-absorbing compounds and stress tolerance of barley seedlings (*Hordeum vulgare* L. cv. Alfa) was investigated. A physiological response to UV-B irradiation was evaluated by measuring the oxygen evolution rate and chlorophyll fluorescence. UV-B irradiation led to an increase of the amount of UV-B absorbing compounds, including flavonoids, measured in acidified methanol extract at 300 nm and of UV-B induced compounds, with maximum absorbance at 438 nm, extracted in 0.1% trichloracetic acid. The content of free proline, malondialdehide and H_2O_2 increased as a result of 4 days treatment with 150 mM NaCl, KCl or $NaNO_3$. Salt pretreatment resulted in considerable decrease of the level of UV-induced and UV-B absorbing compounds measured 24 h after UV-B irradiation. In the meantime chlorophyll fluorescence parameters and oxygen evolution in salt pretreated seedlings were less affected by UV-B in comparison to the control. Damaging effect of UV-B measured by the MDA and H_2O_2 generation and electron transport activity corresponded to the increased levels of UV-B induced and UV-B absorbing compounds. We do not necessarily exclude UV-inducing compounds from an important role in overall UV-B protection but the data presented here showed that the accumulation of these compounds could be a consequence of stress-induced damage to the cells and probably they may serve as stress markers.

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Thermostability and Photostability of Photosystem II of the Resurrection Plant *Haberlea rhodopensis* Studied by Chlorophyll Fluorescence

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Z. Naturforsch. **61 c,** 234–240 (2006); received August 23/September 27, 2005

The stability of PSII in leaves of the resurrection plant *Haberlea rhodopensis* to high temperature and high light intensities was studied by means of chlorophyll fluorescence measurements. The photochemical efficiency of PSII in well-hydrated *Haberlea* leaves was not significantly influenced by temperatures up to 40 °C. F_0 reached a maximum at 50 °C, which is connected with blocking of electron transport in reaction center II. The intrinsic efficiency of PSII photochemistry, monitored as F_v/F_m was less vulnerable to heat stress than the quantum yield of PSII electron transport under illumination (ΦPSII). The reduction of ΦPSII values was mainly due to a decrease in the proportion of open PSII centers (qP). *Haberlea rhodopensis* was very sensitive to photoinhibition. The light intensity of 120 μmol m^{-2} s^{-1} sharply decreased the quantum yield of PSII photochemistry and it was almost fully inhibited at 350 μmol m^{-2} s^{-1}. As could be expected decreased photochemical efficiency of PSII was accompanied by increased proportion of thermal energy dissipation, which is considered as a protective effect regulating the light energy distribution in PSII. When differentiating between the three components of qN it was evident that the energy-dependent quenching, qE, was prevailing over photoinhibitory quenching, qI, and the quenching related to state 1-state 2 transitions, qT, at all light intensities at 25 °C. However, the qE values declined with increasing temperature and light intensities. The qI was higher than qE at 40 °C and it was the major part of qN at 45 °C, indicating a progressing photoinhibition of the photosynthetic apparatus.

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PHOTOSYNTHETICA 44 (4): 569-578, 2006

Photosynthetic response of different pea cultivars to low and high temperature treatments

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Abstract

The thermo-sensitivity of two new pea (*Pisum sativum* L.) cultivars—Afila (mutant in the gene transforming leaves into mustaches) and Ranen (mutant for early ripening)—as compared to the control cultivar Pleven-4 to either low (4 °C, T_4) or high temperature (38 °C, T_{38}) was investigated by means of chlorophyll (Chl) fluorescence kinetics. The low temperature treatment decreased the photosynthetic activity, measured *via* a decline of the Chl fluorescence decrease ratios $R_{Fd}690$ and $R_{Fd}735$, and this was mainly due to a decline of the Chl fluorescence decrease parameter F_d and maximum Chl fluorescence F_m. In the new cv. Ranen the R_{Fd} ratios at first decreased and increased again after 24-h exposure to 4 °C, indicating its good acclimation ability to low temperature. The cold-induced changes in the photosynthetic performance of all cultivars were reversed after transferring plants back to 23 °C for 48 h. In the Chl and carotenoid (Car) contents no or little changes occurred during the T_4 treatment, except for a slight but clear increase of the ratio Chl *a/b* and a decrease in the ratio Chl/Car. In contrast to this, the T_{38} treatment for 72 h decreased the R_{Fd} ratios more strongly than the T_4 exposure did. In fact, an irreversible injury of the photosynthetic apparatus was caused in the control pea cv. Pleven-4 by a 48-h T_{38} exposure and for the new cv. Afila after a 72-h T_{38} exposure. In contrast, the cv. Ranen was less and little sensitive to the T_{38} exposure. In the heat-sensitive cvs. Pleven-4 and Afila, the decrease in R_{Fd} values at T_{38} was associated with a strong decline of the Chl *a+b* and total Car contents. The Chl *a+b* decline could also be followed *via* an increase of the Chl fluorescence ratio F_{690}/F_{735}. Parallel to this, a strong decline of Chl *a/b* from *ca.* 3.0 (range 2.85–3.15) to *ca.* 1.9 (range 1.85–1.95) occurred indicating a preferential decline of the Chl *a*-pigment proteins but not of the Chl *a/b*-pigment protein LHC2. In the relatively heat-tolerant cv. Ranen, however, the ratio Chl *a/b* declined only partially. After the T_4 treatment the stress adaptation index Ap was higher in cv. Ranen than in controls and reached in heat-treated Ranen plants almost the starting value indicating a cold and heat stress hardening of the treated plants. The Chl fluorescence parameters and pigment contents were influenced by T_{38} and T_4 treatments in various ways indicating that the mechanisms of low and high temperature injury of the photosynthetic apparatus are different. The new cv. Ranen exhibited a cross tolerance showing a fairly good acclimation ability to both T_4 and T_{38}, hence it is a very suitable plant for outdoor growth and for clarification of the acclimation mechanisms to unfavourable temperatures.

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Egypt. J. of Appl. Sci., 21 (12A) 2006 17-29

EFFECT OF CHLORAMPHENICOL AND CYCLOHEXIMIDE ON THE LEVEL OF UV-B INDUCED COMPOUNDS IN BARLEY SEEDLINGS

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Key Words: Chlorophyll fluorescence; Flavonoids; *Hordeum vulgare*; Oxygen evolution; UV-B; UV-B absorbing compounds

Abbreviations used: CHL, chloramphenicol; CHI cyclohexymide; F_0, chlorophyll fluorescence in dark-adapted state; F_m, maximal fluorescence yield in dark-adapted state; F_m', maximal fluorescence yield in light-adapted state; F_v, variable chlorophyll fluorescence; PPFD, photosynthetic photon flux density; PSII, photosystem II; TCA, trichloracetic acid.

ABSTRACT

Barley seedlings (*Hordeum vulgare* L., cv. Alfa) were treated with 25-µg ml^{-1} cyclohexymide (CHI) or with 100-µg ml^{-1} chloramphenicol (CHL) for 3 h and 24 h and then were irradiated with UV-B at the rate of $49 KJ.m^{-2}.d^{-1}$ for 30 min. Both antibiotics had no effect on the level of UV-B induced compounds (A_{438}) and flavonoids in non-irradiated seedlings. In UV-B irradiated seedlings antibiotics had some non-specific stimulating effect on the content of A_{438} and did not alter the level of UV-absorbing compounds. CHI and CHL acts as a stress factors and induced proline accumulation both in control and irradiated plants. The photochemical efficiency of PSII was not influenced by CHI and CHL treatment but the oxygen evolution rate was decreased. UV-B irradiation reduced both PSII activity and oxygen evolution in non-treated barley seedlings and no synergic effect in antibiotics-treated seedlings was detected.

The data showed that UV-B induced compounds are not proteins and their accumulation is not related with protein synthesis. It is possible for these compounds to accumulate as a result of UV-B cell damage.

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BIOLOGIA PLANTARUM 51 (4): 699-706, 2007

UV-B response of green and etiolated barley seedlings

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Abstract

7-d-old etiolated and green barley seedlings (*Hordeum vulgare* L. cv. Alfa) were irradiated with UV-B for 30 min and then kept for 24 h in light or darkness. Chlorophyll (Chl) synthesis was inhibited by about 30 % as a result of UV-B irradiation, but there were no significant changes in photochemical activity measured by variable to maximum fluorescence ratio (F_v/F_m), quantum yield (Φ_{PS2}) and oxygen evolution rate. Electron transport of etiolated seedlings was similar to that of green ones, nevertheless, the Chl content was more then 2-fold lower. Ribulose-1,5-bisphosphate carboxylase/oxygenase large and small subunits were diminished as a result of UV-B irradiation in etiolated and green plants, especially in those kept in the darkness. Catalase activity decreased and total superoxide dismutase activity increased in green and etiolated plants following UV-B treatment. When benzidine was used as a substrate, an isoform located between guaiacol peroxidases 2 and 3 (guaiacol peroxidase X) appeared, which was specific for UV-B treatment. As a result of irradiation, the contents of UV-B absorbing and UV-B induced compounds increased in green seedlings but not in etiolated seedlings.

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Planta (2007) 225:955–964
DOI 10.1007/s00425-006-0396-8

ORIGINAL ARTICLE

Photosynthetic activity of homoiochlorophyllous desiccation tolerant plant *Haberlea rhodopensis* during dehydration and rehydration

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Received: 12 June 2006 / Accepted: 22 August 2006 / Published online: 16 September 2006

Abstract The functional state of the photosynthetic apparatus of flowering homoiochlorophyllous desiccation tolerant plant *Haberlea rhodopensis* during dehydration and subsequent rehydration was investigated in order to characterize some of the mechanisms by which resurrection plants survive drought stress. The changes in the CO_2 assimilation rate, chlorophyll fluorescence parameters, thermoluminescence, fluorescence imaging and electrophoretic characteristics of the chloroplast proteins were measured in control, moderately dehydrated (50% water content), desiccated (5% water content) and rehydrated plants. During the first phase of desiccation the net CO_2 assimilation decline was influenced by stomatal closure. Further lowering of net CO_2 assimilation was caused by both the decrease in stomatal conductance and in the photochemical activity of photosystem II. Severe dehydration caused inhibition of quantum yield of PSII electron transport, disappearance of thermoluminescence B band and mainly charge recombination related to $S_2Q_A^-$ takes place. The blue and green fluorescence emission in desiccated leaves strongly increased. It could be suggested that unchanged chlorophyll content and amounts of chlorophyll–proteins, reversible modifications in PSII electron transport and enhanced probability for non-radiative energy dissipation as well as increased polyphenolic synthesis during desiccation of *Haberlea* contribute to drought resistance and fast recovery after rehydration.

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PHOTOSYNTHETICA 46 (2): 208-215, 2008

Responses of the resurrection plant *Haberlea rhodopensis* to high irradiance

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Abstract

The effect of high irradiance (HI) during desiccation and subsequent rehydration of the homoiochlorophyllous desiccation-tolerant shade plant *Haberlea rhodopensis* was investigated. Plants were irradiated with a high quantum fluence rate (HI; 350 µmol m^{-2} s^{-1} compared to *ca.* 30 µmol m^{-2} s^{-1} at the natural rock habitat below trees) and subjected either to fast desiccation (tufts dehydrated with naturally occurring thin soil layers) or slow desiccation (tufts planted in pots in peat-soil dehydrated by withholding irrigation). Leaf water content was 5 % of the control after 4 d of fast and 19 d of slow desiccation. *Haberlea* was very sensitive to HI under all conditions. After 19 d at HI, even in well-watered plants there was a strong reduction of rates of net photosynthesis and transpiration, contents of chlorophyll (Chl) and carotenoids, as well as photosystem 2 activity (detected by the Chl fluorescence ratio R_{Fd}). Simultaneously, the blue/red and green/red fluorescence ratios increased considerably suggesting increased synthesis of polyphenolic compounds. Desiccation of plants in HI induced irreversible changes in the photosynthetic apparatus and leaves did not recover after rehydration regardless of fast or slow desiccation. Only young leaves survived desiccation.

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Acta Physiol Plant (2008) 30:561–567
DOI 10.1007/s11738-008-0155-5

ORIGINAL PAPER

NaCl induced cross-acclimation to UV-B radiation in four Barley (*Hordeum vulgare* L.) cultivars

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Received: 8 May 2007 / Revised: 13 February 2008 / Accepted: 19 February 2008 / Published online: 11 March 2008

Abstract The effect of pre-treatment with 200 mM NaCl on the response of four barley cultivars (*Hordeum vulgare* L. cv. Bülbül-89, Kalaycı-97, Tarm-92 and Tokak-157/37) to UV-B radiation was investigated. Salt stress as well as UV-B irradiation led to a decrease of the total chlorophyll (chl) content in all cultivars, except in Kalaycı-97. While carotenoids are almost not affected by NaCl treatment, UV-B irradiation caused an increase by 5–20% of carotenoid content of all cultivars. UV-B induced damages of photosynthetic apparatus were estimated by the rate of photosynthetic electron transport measured by chl fluorescence and the rate of oxygen evolution, the latter being more affected. Pre-treatment with NaCl alleviated harmful effect of UV-B irradiation on F_v/F_m and ETR, but not on oxygen evolution. UV-B-induced and UV-B-absorbing compounds with absorption at 300 and 438 nm increased as a result of UV-B treatment. The level of stress marker proline increased considerably as a result of NaCl treatment, while UV-B irradiation resulted in a pronounced increase of the level of H_2O_2. MDA enhanced in the seedlings subjected to salt and UV-B stress. Established cross-acclimation to UV-B as a result of salt treatment could be due to the increased free proline and the level of UV-B absorbing compounds in barley seedlings subjected to NaCl.

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Volume 52(1):115-117, 2008
Acta Biologica Szegediensis
http://www.sci.u-szeged.hu/ABS

ARTICLE

Root respiration in whole Haberlea rhodopensis Friv. plants during desiccation and rehydration

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ABSTRACT The current study investigated changes in root respiration connection with root relative water content in whole Haberlea rhodopensis Friv. plant during desiccation and recovery phases. Whole plant was examined during full hydrated, 72 h dehydration and 96 h rehydration period every 6 and 24 hours continuously. Root respiration rates decreased during water stress while it has exceeded the starting values after rehydration. There was a linear relationship between relative water content and root respiration. H. rhodopensis whole plants were able to maintain root respiration for the whole desiccation period. The root respiration rate was linearly related to root tissue relative water content. **Acta Biol Szeged 52(1):115-117 (2008)**

KEY WORDS

desiccation tolerance,
root respiration,
relative water content

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Acta Biologica Hungarica 60 (2), pp. 195–210 (2009)
DOI: 10.1556/ABiol.60.2009.2.7

UV-B RESPONSE OF GREENING BARLEY SEEDLINGS

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(Received: June 3, 2008; accepted: July 29, 2008)

The relationship between the greening stage of barley seedlings and their response to UV-B irradiation was studied. Etiolated barley seedlings (*Hordeum vulgare* L., cv. Alfa) greened 12, 24 and 48 h were exposed to UV-B irradiation (312 nm) for 5 h. As a result of UV-B treatment the rate of CO_2 fixation and chlorophyll contents decreased but flavonoids, UV-B-induced compounds and carotenoids increased. The inhibition of photosynthesis in green plants was lower in comparison to greening ones. The 12 h greening plants were more sensitive to UV-B treatment than the plants greening 24 h and particularly 48 h, estimated by the quantum efficiency of PSII photochemistry and the oxygen production rate. The levels of flavonoids and UV-B induced compounds enhanced with increasing the greening time. Activity of antioxidant enzymes catalase, peroxidase and superoxide dismutase increased during the seedlings greening and as a result of UV-B irradiation, but the pattern of isoforms remained similar to those found in the controls. UV-B preferentially induced Cu,Zn-superoxide dismutase. Increase of UV-B induced synthesis of antioxidant enzymes is in line with their important role in the plant response to UV-B stress. Data presented show that the response of barley seedlings to UV-B irradiation is related to the development stage of photosynthetic apparatus.

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Journal of Plant Physiology 166 (2009) 1520—1528

Available online at www.sciencedirect.com

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JOURNAL OF PLANT PHYSIOLOGY

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Changes in some thylakoid membrane proteins and pigments upon desiccation of the resurrection plant *Haberlea rhodopensis*

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Received 5 November 2008; received in revised form 2 March 2009; accepted 24 March 2009

KEYWORDS
Desiccation-tolerant plant;
LHC;
Photosystems;
Zeaxanthin

Summary

The changes in some proteins involved in the light reactions of photosynthesis of the resurrection plant *Haberlea rhodopensis* were examined in connection with desiccation. Fully hydrated (control) and completely desiccated plants (relative water content (RWC) 6.5%) were used for thylakoid preparations. The chlorophyll (Chl) a to Chl b ratios of thylakoids isolated from control and desiccated leaves were very similar, which was also confirmed by measuring their absorption spectra. HPLC analysis revealed that β-carotene content was only slightly enhanced in desiccated leaves compared with the control, but the zeaxanthin level was strongly increased. Desiccation of *H. rhodopensis* to an air-dried state at very low light irradiance led to a little decrease in the level of D1, D2, PsbS and PsaA/B proteins in thylakoids, but a relative increase in LHC polypeptides. To further elucidate whether the composition of the protein complexes of the thylakoid membranes had changed, we performed a separation of solubilized thylakoids on sucrose density gradients. In contrast to spinach, *Haberlea* thylakoids appeared to be much more resistant to the same solubilization procedure, i.e. complexes were not separated completely and complexes of higher density were found. However, the fractions analyzed provided clear evidence for a move of part of the antenna complexes from PSII to PSI when plants became desiccated. This move was also confirmed by low temperature emission spectra of thylakoids.

Overall, the photosynthetic proteins remained comparatively stable in dried *Haberlea* leaves when plants were desiccated under conditions similar to their natural habitat. Low light during desiccation was enough to induce a rise in the xanthophyll zeaxanthin and β-carotene. Together with the extensive leaf shrinkage and some leaf folding, increased zeaxanthin content and the observed shift in antenna proteins from PSII to PSI during desiccation of *Haberlea* contributed to the integrity of the photosynthetic apparatus, which is important for rapid recovery after rehydration.

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J. Agronomy & Crop Science (2009) ISSN 0931-2250

MISCELLANEOUS

Methyl Jasmonate Counteract UV-B Stress in Barley Seedlings

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Keywords
antioxidant enzymes; chlorophyll fluorescence; flavonoids; methyl jasmonate; oxygen evolution; ultraviolet B radiation

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Accepted December 17, 2008

doi:10.1111/j.1439-037X.2008.00358.x

Abstract

The role of exogenously applied phytohormone methyl jasmonate (MeJA) in counteracting the ultraviolet B (UV-B) stress in barley seedlings was investigated. Barley seedlings (*Hordeum vulgare* L., cv. Alfa) 4 days old were supplied with 5×10^{-5} M MeJA through the roots for 3 days and then exposed for 2 days for 5 h per day to UV-B (312 nm, biological effectiveness of UV-B radiation 28.8 kJ $m^{-2}day^{-1}$). The rate of $^{14}CO_2$ fixation, PSI and PSII activities and chlorophyll content decreased, but flavonoids, H_2O_2, malondialdehyde, proline and UV-B induced compounds increased after UV-B treatment. The rate of photosynthetic oxygen evolution was more strongly inhibited by UV-B-irradiation than PSI and PSII efficiency. MeJA itself increased the content of free proline, which acts as a stress protector due to its radical scavenging ability. Increased superoxide dismutase, catalase and peroxidase (POX) activities in the leaves and in the roots and the POX isoforms induction revealed the MeJA involvement in plant tolerance to oxidative stress caused by UV-B irradiation. It was shown that pre-treatment with MeJA counteracted UV-B stress. Therefore, it was suggested that MeJA could acts as a mediator in plant defense responses to UV-B irradiation by enhancing the activity of antioxidant system and free radical scavenging capability of plant cells.

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CHANGES IN SOME ANTIOXIDANT ENZYME ACTIVITIES IN *HABERLEA RHODOPENSIS* DURING DESICCATION AT HIGH TEMPERATURE

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ABSTRACT

Haberlea rhodopensis (Gesneriaceae) is endemic plant in a very small group of poikilohydric angiosperms that are able to survive in an almost complete dehydrate state. Upon watering the plants rapidly revive and are restored to their former state. H. rhodopensis belongs to the homoiochlorophyllous type of desiccation tolerant plants that keep their chlorophyll content during drying. The high amount of chlorophyll molecules retained during desiccation could be a source for potentially harmful singlet oxygen production. That is why it was important to investigate the changes in the activity of some antioxidant enzymes during dehydration of Haberlea. Plants were desiccated at optimal (23 °C) and high (38 °C) temperature as drought stress is frequently accompanied by high temperatures under field conditions. The results showed that superoxide dismutase (SOD; EC 1.15.1.1) activity gradually decreased, whereas catalase (EC 1. 11. 1. 6) activity significantly increased during desiccation of Haberlea plants under both optimal and high temperature. Exposure of plants to high temperature reduced the activity of these enzymes. The enhanced activity of ascorbate peroxidase (APX; EC 1.11.1.11) and guaiacol peroxidase (GPX; EC 1.11.1.7) was observed under moderate water stress, after which they declined. High temperature stress applied alone did not influence the APX and GPX activity.

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General and Applied Plant Physiology – 2009, Volume 35 (3–4), pp. 111–116
©2009 ISSN 1312-8183 Published by the Institute of Plant Physiology – Bulgarian Academy of Sciences
Available online at http://www.bio21.bas.bg/ipp/

Special Issue (Part I) – Proceedings of the XI National Conference on Plant Physiology
18–19 November 2009, Sofia, Bulgaria

LIGHT DEPENDENCE OF PHOTOSYNTHETIC OXYGEN EVOLUTION OF *HABERLEA RHODOPENSIS* DESICCATED AT HIGH TEMPERATURE

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Received: *26 January 2010* Accepted: *22 February 2010*

Summary. The effect of light on the rate of oxygen evolution of *Haberlea* leaves desiccated at optimal (23°C) and high (38°C) temperatures was investigated. The maximum rate of photosynthesis (A_{max}) decreased in the course of desiccation and this effect was stronger at high temperature. Activation of alternative electron sinks (AES) was found in *Haberlea* plants desiccated to 50% RWC at high temperature as compared to those desiccated at optimal temperature, as well as after their rehydration. Due to more active dark respiration light compensation was reached more slowly in plants desiccated at high temperature. The enhancement of AES together with increased dark respiration provided energy necessary for the reparatory processes which was important for overcoming the stress.

BIOLOGIA PLANTARUM 54 (3): 571-574, 2010

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BRIEF COMMUNICATION

UV-B induced stress responses in three rice cultivars

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Abstract

UV-B responses of three rice (*Oryza sativa* L.) cultivars (Sasanishiki, Norin 1 and Surjamkhi) with different photolyase activity were investigated. Carbon dioxide assimilation data support that Sasanishiki was less sensitive to UV-B than Norin 1 and Surjamkhi. UV-B radiation sharply decreased the content of Rubisco protein in Surjamkhi and has no effect in Sasanishiki. The photochemical activities of photosystem (PS) 1 and PS 2 was slightly affected by UV-B treatment. The content of H_2O_2 and the activities of antioxidant enzymes, catalase (CAT), peroxides (POX) and superoxide dismutase (SOD) were enhanced after UV-B treatment. The activities of CAT and POX isoenzymes in Sasanishiki were more enhanced by UV-B radiation than those in Norin 1 and Surjamkhi.

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Annals of Botany **105**: 117–126, 2010
doi:10.1093/aob/mcp274, available online at www.aob.oxfordjournals.org

ANNALS OF BOTANY Founded 1887

Protection of thylakoids against combined light and drought by a lumenal substance in the resurrection plant *Haberlea rhodopensis*

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Received: 12 June 2009 Returned for revision: 10 August 2009 Accepted: 1 October 2009 Published electronically: 13 November 2009

• *Background and Aims* *Haberlea rhodopensis* is a perennial, herbaceous, saxicolous, poikilohydric flowering plant that is able to survive desiccation to air-dried state under irradiance below 30 µmol m^{-2} s^{-1}. However, desiccation at irradiance of 350 µmol m^{-2} s^{-1} induced irreversible changes in the photosynthetic apparatus, and mature leaves did not recover after rehydration. The aim here was to establish the causes and mechanisms of irreversible damage of the photosynthetic apparatus due to dehydration at high irradiance, and to elucidate the mechanisms determining recovery.
• *Methods* Changes in chloroplast structure, CO_2 assimilation, chlorophyll fluorescence parameters, fluorescence imaging and the polypeptide patterns during desiccation of *Haberlea* under medium (100 µmol m^{-2} s^{-1}; ML) irradiance were compared with those under low (30 µmol m^{-2} s^{-1}; LL) irradiance.
• *Key Results* Well-watered plants (control) at 100 µmol m^{-2} s^{-1} were not damaged. Plants desiccated at LL or ML had similar rates of water loss. Dehydration at ML decreased the quantum efficiency of photosystem II photochemistry, and particularly the CO_2 assimilation rate, more rapidly than at LL. Dehydration induced accumulation of stress proteins in leaves under both LL and ML. Photosynthetic activity and polypeptide composition were completely restored in LL plants after 1 week of rehydration, but changes persisted under ML conditions. Electron microscopy of structural changes in the chloroplast showed that the thylakoid lumen is filled with an electron-dense substance (dense luminal substance, DLS), while the thylakoid membranes are lightly stained. Upon dehydration and rehydration the DLS thinned and disappeared, the time course largely depending on the illumination: whereas DLS persisted during desiccation and started to disappear during late recovery under LL, it disappeared from the onset of dehydration and later was completely lost under ML.
• *Conclusions* Accumulation of DLS (possibly phenolics) in the thylakoid lumen is demonstrated and is proposed as a mechanism protecting the thylakoid membranes of *H. rhodopensis* during desiccation and recovery under LL. Disappearance of DLS during desiccation in ML could leave the thylakoid membranes without protection, allowing oxidative damage during dehydration and the initial rehydration, thus preventing recovery of photosynthesis.

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BIOLOGIA PLANTARUM 55 (3): 581-585, 2011

BRIEF COMMUNICATION

Fatty acid content during reconstitution of the photosynthetic apparatus in the air-dried leaves of *Xerophyta scabrida* after rehydration

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Abstract

Desiccation of *Xerophyta scabrida* caused considerable damage of chloroplast ultrastructure together with a complete loss of chlorophyll. Upon rehydration, the relative water content of the pale-green leaves almost reached that of the dark-green ones, however, the Chl content and photosynthetic activity remained lower. The process of reconstitution of the photosynthetic apparatus in the re-greening leaves was accompanied by changes in fatty acid (FA) content. The amount of the FA methyl esters was more than 2-fold higher in the green leaves as compared to the dry ones and slightly increased after rehydration in the pale-green leaves. Among the three main fatty acids in the leaves, oleic, palmitic and linoleic acid, the latter increased more than 3-fold during rehydration. This acid is concentrated mainly in the glycolipids and this was an indirect indication for the restoration of the photosynthetic apparatus. Our results showed that rehydration of *X. scabrida* led to a decrease of the saturated FA in parallel with an increase of the unsaturated FA, thus indicating increased membrane permeability. The observed changes in the lipid content can be considered as a characteristic feature of *X. scabrida* and most probably of other poikilochlorophyllous species.

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Photosynth Res (2011) 108:5–13
DOI 10.1007/s11120-011-9644-2

REGULAR PAPER

Desiccation of the resurrection plant *Haberlea rhodopensis* at high temperature

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Received: 27 January 2010 / Accepted: 28 February 2011 / Published online: 12 March 2011

Abstract *Haberlea rhodopensis* plants, growing under low irradiance in their natural habitat, were desiccated to air-dry state at a similar light intensity (about 30 μmol m^{-2} s^{-1}) under optimal (23/20°C, day/night) or high (38/30°C) temperature. Dehydration of plants at high temperature increased the rate of water loss threefold and had a more detrimental effect than either drought or high temperature alone. Water deficit decreased the photochemical activity of PSII and PSI and the rate of photosynthetic oxygen evolution, and these effects were stronger when desiccation was carried out at 38°C. Some reduction in the amount of the main PSI and PSII proteins was observed especially in severely desiccated *Haberlea* leaves. The results clearly showed that desiccation of the homoiochlorophyllous poikilohydric plant *Haberlea rhodopensis* at high temperature had more damaging effects than desiccation at optimal temperature and in addition recovery was slower. Increased thermal energy dissipation together with higher proline and carotenoid content in the course of desiccation at 38°C compared to desiccation at 23°C probably helped in overcoming the stress.

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DOI: 10.1007/s11099-011-0020-4 PHOTOSYNTHETICA 49 (1): 119-126, 2011

Changes in chloroplast morphology of different parenchyma cells in leaves of *Haberlea rhodopensis* Friv. during desiccation and following rehydration

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Abstract

The size, shape, and number of chloroplasts in the palisade and spongy parenchyma layers of *Haberlea rhodopensis* leaves changed significantly during desiccation and following rehydration. The chloroplasts became smaller and more rounded during desiccation, and aggregated in the middle of the cell. The size and number of chloroplasts in the palisade parenchyma cells were higher than in spongy parenchyma. The good correlation observed between the size or number of chloroplasts and the cross-sectional area of mesophyll cells, the cross-sectional width of the leaf and its water content suggested that the palisade cells were more responsive to water availability than the spongy cells. Changes in chloroplast number during desiccation and rehydration process are characteristic features for desiccation-tolerant plants (especially in homoiochlorophyllous strategy).

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Effect of light on the photosynthetic activity during desiccation of the resurrection plant *Haberlea rhodopensis*

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Abstract: The effect of light during desiccation of the resurrection plant *Haberlea rhodopensis* on the photosynthetic activity and some morphological parameters was evaluated using plants growing at low or high irradiance in natural habitat. Chlorophyll content was not only lower in sun plants compared to shade plants, but it declined to a higher extent when desiccation was carried out at high light irradiance. Regardless of lower chlorophyll content in sun plants their photosynthetic activity (P_N) was about 30% higher compared to shade plants. However, during dehydration P_N declined more rapidly in sun plants. The mean leaf thickness of fully hydrated leaves from sun plants was larger when compared with shade plants, which was due to higher thickness of the mesophyll. Following rehydration plants rapidly recovered and P_N was higher by about 70% in sun than in shade plants. The results showed that the sun-exposed *Haberlea* plants exhibited good adaptation to desiccation under high irradiance.

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Effect of desiccation of the resurrection plant *Haberlea rhodopensis* at high temperature on the photochemical activity of PSI and PSII

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Abstract: Changes in the photochemical activity of the homoiochlorophyllous poikilohydric plant *Haberlea rhodopensis* under dehydration at high temperature was investigated. Plants, growing under low irradiance in their natural habitat, were desiccated to air-dry state at a similar light intensity (about 30 μmol m^{-2} s^{-1} PPFD) under optimal (23°C/ 20°C) or high (38/30°C) day/night temperature. Water deficit reduced photochemical activity of PSII and PSI. The results showed that desiccation of *Haberlea rhodopensis* at high temperature had more limiting effects than desiccation at optimal temperature. However, the damage was limited to a level where repair was still possible and thus plants fully recovered after 7 days of rehydration.

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CHARACTERIZATION OF ENERGY TRANSFER PROCESSES AND FLASH OXYGEN YIELDS OF THYALAKOID MEMBRANES ISOLATED FROM RESURRECTION PLANT *HABERLEA RHODOPENSIS* SUBJECTED TO DIFFERENT EXTENT OF DESICCATION

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Abstract: The resurrection plants are unique with their extra desiccation tolerance. The physico-chemical properties of photosynthetic apparatus are of crucial importance for survival of plants upon water stress. In present work the effect of different extent of desiccation on the energy transfer properties and oxygen evolving capacity of isolated thylakoid membranes from resurrection plant *Haberlea Rhodopensis* are investigated. The plants from different habitats in Bulgaria are compared. Energy distribution and spillover between both photosystems are studied by means of 77K chlorophyll fluorescence. The dependence of fluorescence ratio F735/F685 on the degree of desiccation of plants was also followed. Functionality of PSII and especially of oxygen-evolving apparatus under water deficit was estimated by flash oxygen yields and initial oxygen burst of thylakoid membranes isolated from plants desiccated up to 50% and 8% relative water content (RWC). Population of S_i states as well as the misses and the double hits were calculated according non-cooperative Kok's model and compared for plants from different habitats and different RWC. The results are discussed in terms of involvement of "fast" and "slow" centers from grana and stroma regions in oxygen evolution and alteration of their contribution as a result of desiccation.

Turkish Journal of Agriculture and Forestry

The role of short-term high temperature pre-treatment on UV-B tolerance of barley cultivars

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Abstract: The impact of pre-treated with high temperature (45 °C for 45 min) on UV-B tolerance of four barley cultivars (*Hordeum vulgare* L. cv. Bülbül-89, Kalaycı-97, Tarm-92 and Tokak-157/37) was examined. The response of plants to treatments was evaluated by measuring the pigment content, chlorophyll *a* fluorescence, oxygen evolution, the fraction of oxygen evolving complex, proline content, UV-B absorbing compounds (A_{535} and A_{300}) and stress markers (malondialdehyde, H_2O_2 and UV-B marker). Regardless of high temperature pre-treatment, UV-B irradiation decreased photosynthetic pigment content, photosystem II activity, the oxygen evolution and the fraction of oxygen evolving complex in almost all the barley cultivars. UV-B treatment significantly increased the proline content, UV-B absorbing compounds and the stress markers. According to the findings, it can be deduced that short-term high temperature pre-treatment might not provide a cross-tolerance to UV-B irradiation in four barley cultivars, even if it aggravates the responses. In addition, although plants substantially accumulated the UV-B absorbing compounds, the photosynthetic process might not be adequately protected from the UV-B radiation.

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Acta Physiol Plant
DOI 10.1007/s11738-011-0891-9

ORIGINAL PAPER

Differences in physiological adaptation of *Haberlea rhodopensis* Friv. leaves and roots during dehydration–rehydration cycle

Evelin R. Péli · Gergana Mihailova · Snejanka Petkova · Zoltán Tuba · Katya Georgieva

Received: 4 April 2011 / Revised: 12 September 2011 / Accepted: 31 October 2011

Abstract The ecophysiological responses of the homoiochlorophyllous desiccation-tolerant (HDT) plant *Haberlea rhodopensis* showed that this plant could tolerate water deficit and both leaves and roots had high ability to survive severe desiccation. The changes and correlation between CO_2 assimilation, stomatal conductance, contents of photosynthetic pigments, root respiration and specific leaf area during dehydration–rehydration cycle were investigated. The physiological activity of leaves and roots were examined in fully hydrated (control) plants and during 72 h of dehydration, as well as following 96 h of rehydration every 6 and 24 h. After 6 h of dehydration, the stomatal conductance declined and the intercellular CO_2 concentration increased. The reduction in CO_2 assimilation rate was observed after 54 h of dehydration. There was a good correlation between the root respiration and water content. Our results showed that the plasticity of adaptation in leaves and roots were different during extreme water conditions. Roots were more sensitive and reacted faster to water stress than leaves, but their activity rapidly recovered due to immediate and efficient utilization of periodic water supply.

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Plant Growth Regulation

Response of sun- and shade-adapted plants of *Haberlea rhodopensis* to desiccation

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Abstract

The variabilities in some morphological and physiological characteristics of sun- and shade-adapted *Haberlea rhodopensis* plants were compared. Changes in the photosynthetic activity, electrolyte leakage from leaf tissues, malondialdehyde content and leaf anatomy were studied at different degrees of desiccation as well as after rehydration of plants. The malondialdehyde (MDA) content in well-watered sun *Haberlea* plants was higher compared to shade plants suggesting higher lipid peroxidation, which is commonly regarded as an indicator of oxidative stress, but desiccation of plants at high light did not cause additional oxidative damage as judged by the unaffected MDA content. The electrolyte leakage from dried leaves (8% RWC) from both shade and sun plants increased 4-fold indicating similar membrane damage. However, the recovery after rehydration showed that this damage was reversible. Well-watered sun plants had higher photosynthetic activity probably due to the higher thickness of the mesophyll layer. On the other hand, desiccation at high light reduced strongly CO_2 assimilation which was in accordance with the stronger reduction of stomatal conductance. Stomata were visible only on the abaxial side of sun leaves having also higher abundance of non-glandular trichomes. Increased trichomes density and epicuticular waxes and filaments upon desiccation could help plants to increase reflection, reduce net radiation income, slow down the rate of water loss and survive adverse conditions.

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Comptes rendus **de l'Academie bulgare des Sciences**

PHOTOCHEMICAL EFFICIENCY OF PHOTOSYSTEM II DURING DESICCATION OF SHADE- AND SUN-ADAPTED PLANTS OF *HABERLEA RHODOPENSIS*

Katya Georgieva, Gergana Mihailova, Snejana Petkova

Abstact

The changes in photochemical activity of PSII and energy dissipation during dehydration of shade and sun *Haberlea rhodopensis* plants from different habitats were examined. The photochemical activity of sun plants was higher compared to shade plants during desiccation to relative water content (RWC) of 50%. Further water loss sharply decreased the photochemical activity. The increase in the thermal energy dissipation, expressed as non-photochemical quenching, had a major role in preventing photoinhibition upon desiccation up to 50% RWC and 20% RWC of shade and sun plants, respectively, while at extremely low RWC other mechanisms may become important to avoid photodamage.