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A salt–tolerant cultivar of wheat maintains photosynthetic activity by suppressing sodium uptake

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Abstract

The effects of NaCl treatment on the photosynthetic machinery in wheat (*Triticum aestivum* L.) cultivars differing in salt tolerance were investigated by comparison with iso-osmotic PEG treatment. Both cultivars similarly reduced the photosystem 2 (PS2) energy conversion efficiency (Φ_{PS2}) rapidly when plants were exposed to a 100 mM NaCl solution, though no decline was detected under the iso-osmotic PEG treatment. There was no correlation between the reduction of the leaf relative water content (RWC) and the Φ_{PS2} in the two iso-osmotic stress treatments. In contrast, a decline of Φ_{PS2} along with the increase of the leaf sodium content above 4 % dry matter was detected under the NaCl treatment, while no such correlation was detected with other cations. The recovery of Φ_{PS2} after photoinhibitory irradiation was repressed by the NaCl treatment as the increase of the duration of the treatment. Norin 61 subjected to the 100 mM NaCl treatment for 10 d showed a decline of the Φ_{PS2} after 1 h moderate irradiation of 400 µmol m^{-2} s^{-1} PPFD. Thus the concentrated Na^+ within a leaf under salinity treatments may decrease the stability of PS2 functions and lead to photochemical inactivation.

Additional key words: chlorophyll fluorescence; photochemical activity; photoinhibition; salt tolerance; *Triticum*.

Introduction

High concentrations of inorganic salts in the growing medium reduce the growth of most plants, and the decrease in plant productivity due to salinity is often associated with a decline in photosynthesis (Greenway and Munns 1980, Boyer 1982). In wheat, the effects of salinity on photosynthesis have been extensively studied (Delfine *et al.* 1998, Reddy *et al.* 1998, Shabala *et al.* 1998, Belkhodja *et al.* 1999, El-Shintinawy 2000). These studies showed that not only stomatal closure but also non-stomatal constraints such as inactivation of electron transport or photochemical enzymes could be a major cause of photosynthetic depression under salinity. In general, salinity involves the participation of both osmotic and ionic factors such as external water deficit and internal ion excess or deficit. These two factors lead to a reduction of photosynthetic activity in association or individually (Kawasaki *et al.* 1983, Matoh *et al.* 1986, Nagy and Galiba 1995, Nagy *et al.* 1995).

Under drought as well as under salinity, the photosynthetic depression due to both stomatal and nonstomatal factors has been often reported (Bethke and Drew 1992, Sharma and Hall 1992, Lutts *et al.* 1996, Delfine *et al.* 1998). However, some authors suggested that biochemical inactivation was only caused by severe dehydration (He *et al.* 1995, Calatayud *et al.* 1997, Basu *et al.* 1998, He *et al.* 1998). In our previous study, a rapid decline in the leaf net photosynthetic rate (P_N) and PS2 energy conversion efficiency (Φ_{PS2}) was only found under the 100 mM NaCl treatment, and not under the iso-osmotic PEG treatment (Muranaka *et al.* 2002). Thus, we assumed that severe photosynthetic depression under salinity was caused by the decline of the Φ_{PS2} due to ionic factors. Yet, the relation between photochemical inactivation and the changes in the water and ionic status within leaf tissues has not been elucidated.

Analysis of chlorophyll (Chl) *a* fluorescence emission has been used for the screening of salt tolerance (Smillie and Nott 1982, Belkhodja *et al.* 1994, Lutts *et al.* 1996, Jimenez *et al.* 1997, Belkhodja *et al.* 1999). However, details of the mechanisms that induce photochemical inactivation estimated by Chl fluorescence under salinity remain to be elucidated. If photochemical inactivation could account for the difference in salt tolerance, the analysis of Chl *a* fluorescence emission could become a suitable method for detailed investigations of salt tolerance. In the present study, we monitored and compared the changes in the activity of PS2 in relation to the water and ion status of two wheat cultivars differing in salt tolerance under the iso-osmotic NaCl and PEG treatments.

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Materials and methods

Plants and growth conditions: Two common wheat (*Triticum aestivum* L.) cvs. Norin 61 and Kharchia were used in these experiments. Seeds of Norin 61 were obtained from the Agricultural and Forestry Research Center, University of Tsukuba, Japan. Seeds of Kharchia were obtained from the USDA-ARS NSGRF (PI 322279). Seeds were germinated on a filter paper in Petri dishes with distilled water for 2 d. Germinated seeds were grown with an aerated modified Kasugaishi nutrient solution (pH 7.0) consisting of: 0.72 mM NH_4NO_3, 0.22 mM KH_2PO_4, 0.58 mM KCl, 0.71 mM $Ca(NO_3)_2$, 0.99 mM $MgSO_4$, 0.08 mM $FeC_6H_5O_7$, 46 µM H_3BO_3, 9.1 µM $MnCl_2$, 0.3 µM $CuSO_4$, 0.5 µM Na_2MoO_4, and 0.8 µM $ZnSO_4$ added to distilled water. At 10 d after sowing, when the 2nd leaves were fully expanded, four seedlings were transferred to a plastic pot (12 cm in diameter and 15 cm in depth) containing the aerated 1 000 cm^3 of nutrient solution. All the treatments and measurements were conducted in a growth chamber (*KG-50HLA*, *Koito*, Japan). The temperature was maintained at 22 and 20 °C during day and night, respectively. Relative humidity was about 70 %. The photoperiod was 12 h and PPFD at plant level was about 500 µmol m^{-2} s^{-1}.

Stress treatments: For the NaCl treatment solutions, 100 and 200 mM NaCl were added to the nutrient solution, respectively. By the addition of 12.1 % (m/v) polyethylene glycol (*PEG 6000*, *Nakarai Chemicals*, Japan) to the nutrient solution, the PEG treatment solution was prepared and adjusted to an iso-osmotic value (–0.58 MPa) with the 100 mM saline treatment solution. All the stress treatments were started when the plants were transferred to plastic pots containing each treatment solution. During the experimental period, water loss in each pot due to evapotranspiration was compensated by daily application of distilled water and all the treatment solutions were exchanged every 4 d.

Gas exchange and Chl *a* fluorescence emission: P_N was measured on the 2nd leaf blade of each plant, using a portable photosynthesis system (*LI-6400*, *LI-COR*, USA) every 2 d after the treatments. All the gas exchange measurements were conducted at 21-24 °C and PPFD 1 000 µmol m^{-2} s^{-1} on the leaf surface, and the air humidity ranged from 50 to 60 %.

Chl *a* fluorescence was measured with a portable chlorophyll fluorometer (*mini-PAM*, *Walz*, Effeltrich, Germany) in the centre of the leaf blades. After acclimation to darkness for 30 min using a dark leaf clip (*DLC-8*, *Walz*, Germany) to ensure that all components on the electron acceptor side of the PS2 complex were in an oxidised state, original (F_0) and maximal (F_m) fluorescence yields were monitored. The extent of the photoinduced decrease in the PS2 activity during the strong irradiation and during recovery under weak irradiance (F_v/F_m) was calculated as follows:

$$F_v/F_m = (F_m - F_0)/F_m$$

The maximum (F_m') and stationary (F_s) fluorescence emissions during irradiation were monitored under constant artificial radiation (PPFD 400 µmol m^{-2} s^{-1}). The efficiency of energy conversion in PS2 for different values of PFD (Φ_{PS2}; Genty *et al.* 1990) was calculated as follows:

$$\Phi_{PS2} = (F_m' - F_s)/F_m'$$

Relative water content (RWC): RWC was measured every 4 d after the treatment on the 1st and 2nd leaf blades of the plants subjected to the 100 mM NaCl treatment and iso-osmotic PEG treatment. Leaf segments, 4 cm in length, were taken from the centre of the leaf blade immediately after the measurements of Chl *a* fluorescence on each leaf. The leaf samples were immediately cut into two pieces and weighed to obtain their fresh mass (f.m.), then soaked in distilled water under dark conditions at 22 °C for 4 h. After the 4 h hydration period, the turgid leaf samples were rapidly blotted, dried, and weighed to obtain the turgid mass (t.m.). The leaf samples were then dried at 80 °C for 24 h and the dry mass (d.m.) was determined. Leaf RWC was calculated by the following formula:

$$\text{RWC [\%]} = [(\text{f.m.} - \text{d.m.})/(\text{t.m.} - \text{d.m.})] \times 100$$

Ion contents: Immediately after the measurement of photochemical activity, the 1st and 2nd leaf blades were detached from each plant under the low and high salinity treatments. For the measurement of the ion content, 4 leaf blades from 4 plants in the same pot were gathered to obtain a sufficient amount of sample. The leaf samples were dried at 80 °C for 48 h and then ground into a fine powder. Appropriate amounts were digested with 1 cm^3 of distilled water, 2 cm^3 sulphuric acid, and 6 cm^3 H_2O_2 (30 %) at 420 °C and the extracts were diluted to 100 cm^3. The contents of Na^+, K^+, Mg^{2+}, and Ca^{2+} were determined by atomic absorption spectrophotometry (*AA6400*, *Shimadzu*, Japan).

Photoinhibitory conditions: The apparatus for exposing leaves to various PPFD was composed of a high-luminance cold lighting device (*LA-150UX*, *Hayashi Watch-works*, Japan), a flexible fibre cable (*LGB(C)2-4L1000*, *Hayashi Watch-works*, Japan) and two condensing lenses (*SH-F16*, *Hayashi Watch-works*, Japan) in the growth chamber.

The 2nd leaves of each cultivar under the PEG and NaCl treatments were exposed for 3 h to a high PPFD (2 000 µmol m^{-2} s^{-1}). For the recovery phase after 3 h of high irradiance, the plants were placed in the chamber for an additional 3 h under low PPFD (80 µmol m^{-2} s^{-1}). During the 3-h high irradiance treatment and the 3 h recovery phase, the fluorescence parameter Φ_{PS2} was determined in the 2nd leaves.

To analyse the effect of irradiance on the photochemical activity, the 2nd leaves of the NaCl-treated plants were treated at various PPFD—400, 800, 1 200, 1 600, and 2 000 μmol m^{-2} s^{-1}—each for 1 h. Before and after the irradiation, the F_v/F_m ratio was determined by dark acclimation for 30 min.

Results

Fig. 1 shows the changes in P_N and Φ_{PS2} of the 2nd leaf under the 100 mM NaCl and iso-osmotic PEG treatments. Though the control plants in both cultivars maintained a constant and high P_N throughout the treatment period, the PEG and NaCl-treated plants showed a decline in P_N. Under the NaCl treatment, P_N in Norin 61 decreased rapidly during the 6-12 d period and became completely inactivated after the 14 d period while a rapid decline of P_N was only detected after the 12 d period in Kharchia. On the other hand, both cultivars showed a similar gradual decline in P_N only under the PEG treatment.

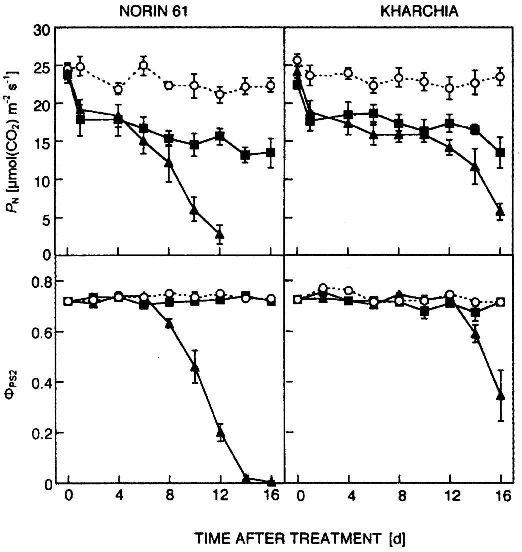

Fig. 1. Changes in net photosynthetic rate (P_N) and photosystem 2 energy conversion efficiency (Φ_{PS2}) of Norin 61 and Kharchia under control (○), PEG (■) and NaCl (▲) treatments. P_N was determined at PPFD of 1 000 μmol m^{-2} s^{-1}. Means ± SE (n = 4).

In Norin 61, the Φ_{PS2} decreased after the 6 d period of NaCl treatment, though Kharchia maintained a high Φ_{PS2} value until the 12 d period and the decline of the Φ_{PS2} was only detected after the 14 d period. However, the PEG-treated plants maintained a Φ_{PS2} as high as that of the control plants throughout the experimental period in both cultivars.

The control plants maintained a high RWC throughout the experimental period (Table 1). Under the PEG and NaCl treatments, the RWC decreased gradually to 77-84 % throughout the 12-d period. Though the RWC of the NaCl-treated plants was slightly lower than that of the PEG-treated plants, there was no significant difference in the RWC under the two stress treatments.

Table 1. Effects of PEG and NaCl treatments on leaf relative water content (RWC). Means (n = 4) followed by standard error.

Cultivar	Treatment	RWC [%] 4 d	8 d	12 d
Norin 61	control	99.0 ± 0.2	97.3 ± 0.4	97.7 ± 0.3
	PEG	89.1 ± 1.0	83.0 ± 1.7	83.8 ± 2.2
	NaCl	85.8 ± 1.9	84.1 ± 2.5	77.9 ± 5.2
Kharchia	control	97.6 ± 1.1	98.5 ± 0.2	97.2 ± 0.2
	PEG	87.1 ± 1.6	83.7 ± 2.4	82.9 ± 1.3
	NaCl	87.0 ± 0.3	81.3 ± 2.0	77.0 ± 6.2

Fig. 2 shows the changes in the Na$^+$ and K$^+$ contents within the 1st and 2nd leaf blades. In the plants subjected to 100 and 200 mM NaCl, the Na$^+$ contents of the 1st and 2nd leaf blades increased during the 12-d period. Under both 100 and 200 mM NaCl treatments, the Na$^+$ content in the 1st leaf blade was always higher than that in the 2nd leaf blade. In both the 1st and 2nd leaf blades, Norin 61 showed a higher increase of Na$^+$ content than Kharchia. Especially, the increase of the Na$^+$ content in the 2nd leaf blade of Norin 61 was particularly high during the 4-12 d period, so that the Na$^+$ content in the 2nd leaf blades finally reached similar values to those in the 1st leaf blade. In contrast, under both 100 and 200 mM NaCl treatments, Kharchia maintained a Na$^+$ content in the 2nd leaf blade below 5 % d.m. throughout the experimental period.

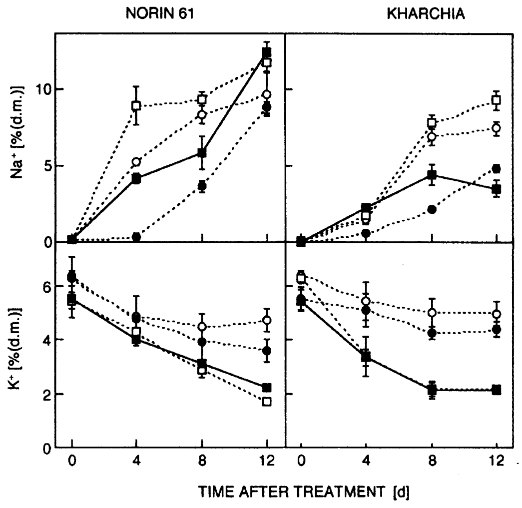

Fig. 2. Changes in the Na$^+$ and K$^+$ contents of the 1st (*open symbols*: ○, □) and 2nd (*closed symbols*: ●, ■) leaf blades under 100 (○, ●) and 200 (□,■) mM NaCl treatments. Means ± SE (n = 4).

Under the 200 mM salinity treatment, the K^+ content in the 1st and 2nd leaf blades decreased gradually, while no particular changes were detected under the 100 mM NaCl treatment. Under the PEG treatment which was iso-osmotic with the 100 mM NaCl treatment, no particular changes in the Na^+ and K^+ contents were recorded during the 12 d period (values not shown).

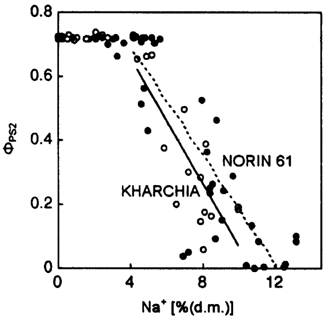

Fig. 3. Relation between the photosystem 2 energy conversion efficiency (Φ_{PS2}) and leaf Na^+ content in Norin 61 (○) and Kharchia (●) under NaCl treatments. Plots show all values of both 100 and 200 mM NaCl treatments ($n = 24$). The correlations were significant at 5 % level in both cultivars, Norin 61, $r = -0.859$; Kharchia, $r = -0.822$ above 4 % Na^+ content.

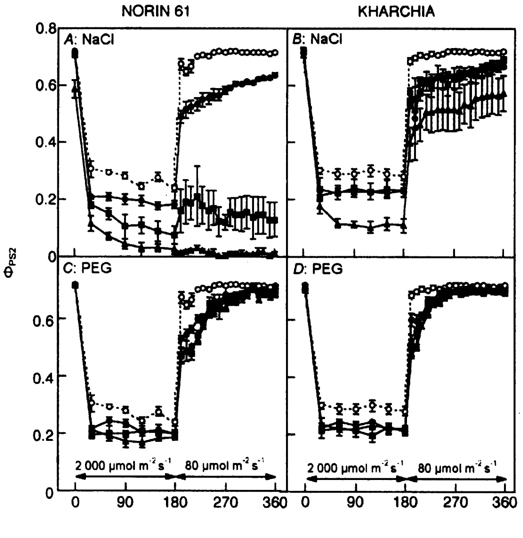

Fig. 4. Changes in the photosystem 2 energy conversion efficiency (Φ_{PS2}) during the photoinhibitory (PPFD 2 000 μmol m^{-2} s^{-1}) and recovery phases (PPFD 80 μmol m^{-2} s^{-1}). Norin 61 (*A*, *C*) and Kharchia (*B*, *D*) were treated with iso-osmotic NaCl (*A*, *B*) and PEG (*C*, *D*) solutions. Plots indicate 0 d (○), 2 d (●), 6 d (■), and 10 d (▲) after NaCl or PEG treatment. Means ± SE ($n = 4$).

Fig. 3 shows the relation between the Na^+ content and the Φ_{PS2} under the 100 and 200 mM NaCl treatments. While the Na^+ content was below 4 % d.m., no decline in the Φ_{PS2} was detected in any of the cultivars. However, when the Na^+ content was above 4 % d.m., the Φ_{PS2} also showed a rapid decline with the increase of Na^+ content and there was a significant correlation between the leaf Na^+ content and the Φ_{PS2} in both cultivars. Though the slope of the decline in the Φ_{PS2} of Norin 61 was less conspicuous than that of Kharchia, no differences among the cultivars were detected. On the other hand, no relationship was detected between the K content and Φ_{PS2} in either cultivar.

In the plants subjected to the 100 mM NaCl and iso-osmotic PEG treatments, the Φ_{PS2} decreased under photoinhibitory conditions regardless of the duration of the stress (Fig. 4). Under the 100 mM NaCl treatment, the decline in Φ_{PS2} was considerably enhanced by the increase of duration of the stress period, though no such change was detected in plants under the PEG treatment. Though the plants before the stress treatment showed a rapid recovery of Φ_{PS2} within 10 min under weak PPFD (80 μmol m^{-2} s^{-1}), the NaCl-treated plants did not display a sufficient recovery of Φ_{PS2} with the increase of duration of the NaCl treatment. Especially Norin 61 subjected to 6 and 10 d NaCl treatments did not show any recovery of Φ_{PS2} (Fig. 4*A*,*B*). Although the PEG treatment delayed the recovery of Φ_{PS2} during the recovery phase, the Φ_{PS2} recovered completely within 2 h regardless of the duration of the PEG treatment (Fig. 4*C*,*D*).

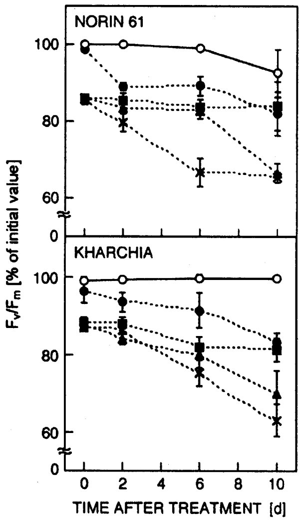

Fig. 5. Changes in the F_v/F_m ratio of Norin 61 and Kharchia after 1 h irradiation; PPFD 400 (○), 800 (●), 1 200 (■), 1 600 (▲), and 2 000 (x) μmol m^{-2} s^{-1} under NaCl treatment. The values represent the percentage of F_v/F_m after exposure to that of the initial F_v/F_m of the control (non-stressed) plants. Means ± SE ($n = 4$).

Fig. 5 shows the changes in F_v/F_m ratio in the 2nd leaf blades of plants subjected to 100 mM NaCl treatment after exposure to various PPFD for 1 h. The untreated plants showed a decline in F_v/F_m under high PPFD (1 200-2 000 μmol m^{-2} s^{-1}) in both cultivars, and the decline of F_v/F_m gradually increased with the increment of the duration of the NaCl treatment. In Kharchia, the F_v/F_m ratio did not decrease under moderate PPFD (400 μmol m^{-2} s^{-1}) which is equivalent to the irradiance for the growth conditions, regardless of the duration of the NaCl treatment, while Norin 61 which was subjected to the 10 d NaCl treatment showed a decline of F_v/F_m after exposure to a moderate PPFD (400 μmol m^{-2} s^{-1}).

Discussion

Our present results support the previous findings showing the contribution of photochemical inactivation to rapid decline of P_N under the 100 mM NaCl treatment (Muranaka *et al.* 2002). Although in the salt-tolerant Kharchia a relatively high P_N was maintained over a longer period of time than in the salt-sensitive Norin 61, the rapid decline in P_N coincided with the photochemical inactivation that was reflected by Φ_{PS2} under the NaCl treatment (Fig. 1). Thus, we assumed that the maintenance of a higher leaf P_N in the lower leaves of Kharchia enhanced the productivity of the whole plant and could have been associated with the salt-tolerance mechanism in Kharchia.

Throughout the treatment, the salt-tolerant Kharchia showed a lower leaf Na^+ content than the salt-sensitive Norin 61 (Fig. 2). Sharma (1996) reported a lower Na^+ uptake in a salt-tolerant cultivar than in a salt-sensitive one. He also reported a lower K^+ uptake in the salt sensitive cultivar than in the salt-tolerant cultivar and suggested the importance of the maintenance of physiological K^+ contents under salinity. However, we could not detect any differences in the leaf K^+ content and in the relationship between Φ_{PS2} and the leaf K^+ content in the two cultivars regardless of the difference in salt tolerance (Figs. 1 and 2). On the contrary, we detected a particular relation between Φ_{PS2} and the leaf Na^+ content (Fig. 3). The plants under the NaCl treatments showed a significant decline in Φ_{PS2} in both the 1st and 2nd leaf blades along with the increase of the leaf Na^+ content above 4 % d.m. This two-tier correlation between Φ_{PS2} and the Na^+ content was detected in both cultivars, while no such correlation between the Φ_{PS2} and the leaf ion content was detected for other cations. We suggest, therefore, that photochemical inactivation in wheat under the NaCl treatment was mediated by the direct damage to the PS2 core that was due to the accumulation in leaf tissues of excess Na^+ ion above 4 % d.m.

There have been contradictory reports on the relation between the accumulation of leaf Na^+ ion and photosynthetic depression in salt-stressed plants. Yeo *et al.* (1985) suggested that the accumulated Na^+ within the leaf tissues might cause a photosynthetic depression in rice. In contrast, Rawson *et al.* (1988) concluded that high leaf contents of Na^+ and chloride ions did not affect directly the rate of photosynthesis. Since the photosynthetic depression is a consequence of a combination of many physiological changes such as stomatal closure, Chl loss, and enzymatic inactivation, it may be difficult to find a clear relationship and it may be necessary to separate the effects of these limiting factors. In fact, Rawson *et al.* (1988) also suggested the existence of a correlation between bulk Na^+ or Cl^+ contents and P_N in the lower leaf.

The moderate photosynthetic depression without a decline of Φ_{PS2} at the beginning of the NaCl and iso-osmotic drought treatments was likely caused by a deficiency in the CO_2 supply to the assimilation site due to stomatal closure (Fig. 2). In contrast, the rapid photosynthetic depression detected only in the latter phase of the NaCl treatment was caused by excess ions that accumulated within the leaf tissues *via* photochemical inactivation. Drought tolerance of the photochemical activity decreased only under extreme dehydration conditions, such as 40 % decrease in RWC (He *et al.* 1995, Calatayud *et al.* 1997, Yordanov *et al.* 1999). In our study, the leaf RWC did not decrease below 40 % because the −0.58 MPa osmotic stress we imposed for the NaCl and PEG treatments was relatively moderate and insufficient to cause a severe decline of leaf RWC. Thus, the reduction in RWC could not be the main factor of the photochemical inactivation under the NaCl treatment.

Sharma and Hall (1991, 1992) reported that the combination of high irradiance and salinity reduced the PS2 energy conversion efficiency of isolated chloroplast, though no reduction was detected without strong irradiance. Excessive photon energy under high irradiance caused a decline of the photochemical activity due to the damage sustained by target molecules such as the D1 protein of PS2 centre (Anderson *et al.* 1998, Mattoo *et al.* 1999) or the PS1 centre (Gong *et al.* 1993, Terashima *et al.* 1998). Though Φ_{PS2} of the plants subjected to PEG treatment showed a rapid recovery during the recovery phase after the photoinhibitory irradiance, Φ_{PS2} could not recover in the plants subjected to NaCl treatment (Fig. 4). The fact that the recovery of Φ_{PS2} was more inhibited in Norin 61 than in Kharchia indicates that the leaf Na^+ content is closely related to the recovery from photo-inactivation of PS2. In both cultivars subjected to the NaCl treatment, Φ_{PS2} decreased under a moderate PPFD of 800 μmol m^{-2} s^{-1}. And, furthermore, in Norin 61 subjected to the 10-d period of NaCl treatment, Φ_{PS2} slightly decreased due to exposure to a weak PPFD of 400 μmol m^{-2} s^{-1} which was equivalent to the irradiance for the growth conditions. This is in agreement with the time when the Φ_{PS2} of Norin 61 started to decrease rapidly under the NaCl treatment (Figs. 1 and 5). These results suggest that the accumulation of Na^+ within a leaf lowered the tolerance to irradiance due to the inhibition of the recovery from photo-inactivation of PS2.

Little is known about the biochemical and biophysical mechanisms that inactivate the photosynthetic electron transport under either salinity or drought. In cyanobacteria, the extrinsic proteins of PS2, cytochrome c_{550} and PsbU, which stabilise the function of PS2, were easily dissociated in the presence of high contents of salts such as NaCl, $MgCl_2$, and $CaCl_2$ (Stewart *et al.* 1985, Shen *et al.* 1992, Nishiyama *et al.* 1999). In green algae and higher plants, the 23 and 17 kDa proteins appeared to share some common binding and functional features, though these proteins are apparently different from cytochrome c_{550} and PsbU (Shen *et al.* 1998). An increase in the intercellular content of Na^+ ions itself might lead to the dissociation of these proteins from the PS2 complex, causing a decrease in the rate of PS2-mediated electron transport. This hypothesis is substantiated by our results on Chl fluorescence where we did not observe a significant cultivar difference in the correlation between the Φ_{PS2} and the leaf Na^+ content. It could be a compatible statement about the mechanisms of the photochemical inactivation detected under severe drought stress. Allakhverdiev *et al.* (2000a,b) demonstrated that concentrated salts within the cyanobacterium cytosol due to dehydration also inactivated the photosynthetic electron transport of PS1 and PS2 under drought stress as well as salt stress. Thus severe drought, which may lead to a reduction of the leaf RWC below 40 %, could cause photochemical inactivation in common with salinity stress.

The results reported here show that photochemical inactivation in NaCl-treated wheat leaves was achieved by a combination of excessive photon energy and accumulation of excess Na^+ ions which reduced the stability of the PS2 function. In the salt-tolerant cultivar Kharchia, photosynthetic activity was maintained due to a higher suppression of root-leaf Na^+ translocation than in the salt-sensitive cultivar. However, the mechanisms underlying the photoinactivation of PS2 under salinity remain to be elucidated. It is difficult to exclude the effect of irradiance that is essential for the maintenance of life from the physiological changes under stress.

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Pasternak, D., Schlissel, A. (ed.): **Combating Desertification with Plants.** – Kluwer Academic/Plenum Publishers, New York – Boston – Dordrecht – London – Moscow 2001. ISBN 0-306-46632-5. 613 pp., € 137.00, USD 125.00.

The degradation of soil in drylands—desertification—is a phenomenon occurring in scores of countries around the globe. In semiarid regions, hundred millions of people are affected by the steady decline in the productivity of their lands. Biological treatments of this problem were discussed on a conference held in Beer Sheva, Israel, from 2-5 November 1999.

Proceedings of this conference—edited by Dov Pasternak and Arnold Schlissel from the International Program for Arid Land Crops, Ben-Gurion University of the Negev, Beer Sheva, Israel—present 43 papers prepared by 70 specialists from 27 countries [Australia (2), Belgium (1), Benin (1), Botswana (2), Burkina Fasso (2), Cameroon (1), China (3), France (1), Germany (1), Ghana (1), Indonesia (1), Israel (10), Italy (1), Kenya (2), Malavi (1), Niger (1), Nigeria (1), Palestinian National Authority (1), Russia (1), Senegal (1), Spain (1), Tanzania (2), Turkey (1), Uganda (2), USA (2), Zambia (1), and Zimbabwe (1)].

The book opens with two introductory papers dealing with global agricultural situation, and combating poverty with plants. Further papers are arranged in four parts. Part I (9 papers) is devoted to potential germplasm for arid lands (role of horticultural plants, mycorrhizal edible mushrooms, potential of traditional tuber crops, honeybees, and nectariferous plants as a factor to sustain modern agriculture, non-wood forest products, biodiversity prospecting in drylands, indigenous tree species).

Introduction, domestication, and dissemination of arid land plants are dealt with in 16 papers of the Part II (drought and salt tolerant plants for afforestation and landscaping in arid lands, screening of multipurpose tree species for agroforestry practices, desertification control in ciscaspian lowland, *Citrullus colocynthis* as a potential source of edible oil, *Euphorbia tirucalli* for high biomass production, *Boraginaceae* as potential source of γ-linolenic acid, role of roots in plant productivity, Australian acacias for human food, leaf diseases on wild indigenous fruit trees, cacti as vegetable crops in Israel, *Vigna radiata* for human and soil health, *Jatropha curcas* against desertification, *etc*.).

Part III (9 papers) discusses problems with land rehabilitation (combating desertification with *Hippophae* and *Tamarix*, bioreclamation of saline soils, natural regeneration of underground forest, sand dune stabilisation, large, herding ungulates against desertification, *etc*.).

Mechanisms of plant transfers are dealt with in 7 papers of Part IV (passive transfer, response to agroforestry intervention, FAO, plants and sustainable development in drylands, indigenous trees against desertification, *etc*.).

Although the book is focussed to more or less practical problems associated with combating degradation of soil and increasing production in drylands, it can provide readers of Photosynthetica some useful information (namely parameters of water relations, salt stress, and primary production). Besides, the volume presents information on hundreds of plants indigenous in semiarid and dry subhumid lands, or plants suitable for introduction in arid lands (*e.g.*, note comprehensive tables on pp. 126-147).

The book is accompanied with a short subject and plant index. References to relevant literature are included into individual papers (altogether almost 500 references). For those interested in arid zone research, let the book be one of the "weapons" for combating desertification with plants.

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