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Protection of photosynthesis in coastal salt marsh plants *Aster tripolium* and *Hydrocotyle vulgaris* in conditions of increased soil salinity

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Abstract

The aim of the present study was to investigate if plants native to habitats with fluctuating soil salinity levels induce a higher level of photosynthesis protection in conditions of elevated salinity. Two plant species from a coastal salt marsh were used in the experiments – *Aster tripolium* and *Hydrocotyle vulgaris*. Changes in photosystem II photochemistry and protection under the effect of NaCl at different light intensities were characterized by chlorophyll *a* fluorescence and ascorbate peroxidase activity. NaCl-treated *A. tripolium* plants grown at moderate light tended to have higher maximum quantum use efficiency of photosystem II (F_v/F_m) over the control level. Relative electron transport rate (ETR) decreased in NaCl-treated plants. In contrast, thermal dissipation of excess energy measured as non-photochemical quenching (NPQ) increased. Treatment with 25 mM NaCl led to relatively small changes in F_v/F_m in *H. vulgaris* plants at all light intensities. At 100 mM NaCl a pronounced decrease of F_v/F_m was evident, which was more severe at moderate and high light. NaCl significantly inhibited ETR at both low and moderate light. However the decrease of ETR was only temporal. Similary, the treatment caused an increase of NPQ. Concentration-dependent increase of ascorbate peroxidase activity was found in leaves of *A. tripolium* treated with NaCl. In contrast, ascorbate peroxidase activity decreased in leaves of *H. vulgaris*. The data are discussed in respect to different strategies of adaptation of salt marsh plants to high soil NaCl.

Key words: *Aster tripolium*; *Hydrocotyle vulgaris*; light; photochemistry of photosynthesis; salinity.
Abbreviations: ETR, relative electron transport rate; F_v/F_m, maximum quantum use efficiency of photosystem II in the dark adapted state; NPQ, non-photochemical quenching of chlorophyll fluorescence; PAR, photosynthetically active radiation; PSI, photosystem I; PSII, photosystem II.

Introduction

Pronounced spatial and temporal variability of both resources and abiotic factors create major environmental constraints in coastal habitats (Ievinsh 2006). Fluctuation of soil salinity mostly affect plants of coastal meadows and salt marshes. Plants native to these habitats evidently possess adaptive morphological and biochemical characteristics that allow successful growth and reproduction in conditions of high salinity. Most importantly, to maintain plant fitness, photosynthetic machinery must be protected against any environmental extremes, as photosystem II (PSII) is highly sensitive to these changes (Vass et al. 2007).

It is commonly accepted that NaCl treatment results in decrease of photosynthesis in a wide variety of plant species (Sudhir, Murthy 2004). However, the photosynthetic apparatus of chloroplasts in plants seems to be relatively tolerant against increased tissue concentration of NaCl. Even in studies with glycophyte species (e.a. *Gossypium hirsutum*), no decrease in photochemical efficiency of PSII due to NaCl up to 200 mM has been found, while the rate of net photosynthesis was strongly inhibited, probably through the decrease of the stomatal conductance (Meloni et al. 2003). Similarly, a study on four wheat genotypes with contrasting degrees of Na^+ accumulation showed no significant effect of 150 mM NaCl on chlorophyll fluorescence parameters within 30 days after the application (Rivelli et al. 2002).

It was proposed earlier that the degree of NaCl tolerance might be reflected to degree of protection of the photosynthetic system. However, in comparative studies using both halophyte and glycophyte species, it was shown that there are no fundamental differences in PSII characteristics between these species (Ball, Anderson 1986). Therefore, it can be proposed that high accumulation of ions in the chloroplasts of plants, irrespective of their salt tolerance, will result in damage to PSII, especially in high light conditions. While there is no evidence that Na^+ or Cl^- can accumulate in chloroplasts, high soil salinity (400 mM) can damage thylakoid membranes, causing disturbance or inhibition of photochemical reactions (Barhoumi et al. 2007).

Thermal energy dissipation and antioxidant systems collectively protect photosynthetic tissues from harmful effects of excess light absorption (Logan et al. 2006). To prevent oxidative stress in suboptimal environmental conditions, photogenerated reactive oxygen species must be captured at the site of formation by means of the enzymatic antioxidative system. Among them, chloroplastic ascorbate peroxidase is crucial for scavenging of H_2O_2 produced in chloroplasts. In addition, ascorbate peroxidase activity can be used as an indicator of the capacity of the Mehler reaction putatively participating in oxygen-dependent quenching of excessive energy (Logan et al. 2006).

In the present paper we address the following question: do plants native to saline environments induce any means of protection of PSII photochemistry in conditions of increased NaCl? More specifically, we hypothesised that true halophytes have higher maximum potential quantum yield of PSII when grown at optimal salinity levels. Two rare and protected plant species in Latvia from a coastal salt marsh of the Baltic Sea were used in the present experiments. *Aster tripolium* is a perennial true halophyte species frequently found on European seashores, especially in salt marshes with fluctuating high levels of soil salinity within a growth season (EC 7.90 to 11.95 mS cm^{-1}; Ievinsh et al., unpublished data). *A. tripolium* is known to have broad genetic plasticity, allowing it to use different physiological adaptations in response to changes in the respective environment (Brock et al. 2007). In addition, *A. tripolium* has emerged as a model halophyte species in salinity tolerance studies (Shennan et al. 1987). *Hydrocotyle vulgaris* plants grow in habitats with different light regimes (from deep tree canopy shade to full sunlight) and moderate fluctuations of soil salinity within a season (EC 0.57 to 3.32 mS cm^{-1}) that are seawater inundation-dependent (Ievinsh et al., unpublished data). No data on salt tolerance of *H. vulgaris* have been published so far.

Putative changes in PSII photochemistry and protection in *A. tripolium* and *H. vulgaris* plants under the effect of NaCl at different light intensities were characterized by chlorophyll *a* fluorescence and ascorbate peroxidase activity.

Materials and methods

Plant material and growth conditions

Aster tripolium L. plants were propagated by tissue culture from shoot apical explants (Klavina et al. 2006). Plants representing genetically identical material with four to five leaves were transferred to plastic pots (12 × 12 cm, 15 cm deep) filled with a commercial neutralized (pH 5.5 – 6.3) peat with mineral nutrients (NPK 14-16-18).

Stock plant material of *Hydrocotyle vulgaris* L. was introduced in laboratory culture from one genet of naturally growing plants during summer of 2005. For experiments, plants were propagated during early spring of 2006 and 2007. They represented genetically identical clonal material.

As starting material, five small plants with three ramets each was planted in a 30 × 40 cm plastic trays filled with a commercial neutralized peat with mineral nutrients (NPK 14-16-18).

Three light regimes were used in the present experiments for *H. vulgaris*: (i) 120 μmol m^{-2} s^{-1} of photosynthetically active radiation at the plant level provided by three fluorescent lamps in a growth chamber; (ii) simulated canopy shade provided by a green plastic filter by using the same three lamps, with a photon flux density of 45 μmol m^{-2} s^{-1} at the plant level in a growth chamber; and (iii) high light intensity provided by natural sunlight in greenhouse with an average photon flux density at midday of 600 to 800 μmol m^{-2} s^{-1} at the plant level. Only 120 and 600 to 800 μmol m^{-2} s^{-1} regimes were used for experiments with *A. tripolium*.

Plants were watered three times a week with tap water or tap water with different concentrations of NaCl. To avoid osmotic shock salt was added in steps of 50 mM per day.

Separate experiments with respective controls were performed for *A. tripolium* and *H. vulgaris* in greenhouse conditions. Experiments were repeated two or three times, for laboratory and greenhouse conditions, respectively. Only data from a representative experiment are shown.

Measurement of chlorophyll a *fluorescence*

Chlorophyll fluorescence was measured with a pulse amplitude modulated portable fluorometer (PAM 2100, Walz, Germany) and leaf clip holder (2030-B, Walz, Germany) with an integrated micro quantum-temperature sensor. A laptop computer (Fujitsu Siemens Lifebook S7110) equipped with an appropriate software (DA-2000, Walz, Germany) was used to drive the measurements. Leaves were dark adapted for 30 min. The minimal fluorescence level (F_0) was measured by low modulated light and the maximal fluorescence level (F_m) was determined by a saturating pulse on dark-adapted leaves. The ratio F_v/F_m was calculated, where F_v is the difference between the maximum fluorescence and the minimum fluorescence level F_0. The steady-state fluorescence (F_s) was recorded after 6-min light adaptation and then the maximal fluorescence level in the light-adapted state (using a saturating pulse, F_m') and the minimal fluorescence level (using far-red light, F'_0) were measured.

Maximum apparent electron transport rate through PSII (ETR) was calculated on the basis of measured overall photochemical quantum yield ($\Delta F / F_m'$; where $\Delta F = F_m' - F_s$) and of PAR according to the equation: $ETR = \Delta F / F_m' \times PAR \times 0.5 \times 0.84$; assuming that transport of one electron requires absorption of two quanta (factor 0.5) and that 84 % of the incident quanta are absorbed by the leaf (factor 0.84).

The chlorophyll *a* fluorescence parameter F_v/F_m measured after a dark adaptation period reflects the

potential quantum yield of PSII and thus is indicative of photoinhibition (Maxvell, Johnson 2000). The fluorescence induction curve with quenching analysis at 10 ms p^{-1} was recorded using a built-in standard procedure of DA-2000. Non-photochemical quenching (NPQ) was calculated according to the equation: NPQ = F_m – F_m') / F_m'. NPQ estimates the part of non-photochemical quenching reflecting heat dissipation of excitation energy in the antenna system.

Nondestructive chlorophyll *a* fluorescence measurement was performed three times a week for *A. tripolium* and once a week for *H. vulgaris* plants. Three fully-grown middle leaves per plant were measured at every time point for *A. tripolium*, three plants per experimental treatment. For *H. vulgaris*, five leaves per tray were measured at every time point, three trays per experimental treatment.

Measurement of ascorbate peroxidase activity

For measurement of enzyme activity, leaves were rinsed with deionized water, frozen in liquid nitrogen and stored at –80 °C until analysis. For extraction of enzymes, leaf tissues were ground in liquid nitrogen and extracted with 25 mmol L^{-1} HEPES (pH 7.2) containing 1 mM EDTA, 1 mM sodium ascorbate, and 3% insoluble polyvinylpolypyrrolidone for 15 min at 4 °C. The homogenate was filtered through nylon cloth and centrifuged at 15 000 g_n for 15 min. Ascorbate peroxidase activity was determined in a supernatant according to Nakano and Asada (1987) The assay was performed in a final volume of 1 mL, containing 50 mM sodium phosphate buffer (pH 7.0), 1 mM NaEDTA, 1 mM Na ascorbate, and 100 ml of supernatant. The reaction was started by the addition of 0.5 mL 3 mM H_2O_2. The decrease in absorbance at 290 nm was recorded.

Statistical analysis

Significance of differences between means were analyzed by the Tukey-Kramer test, determining the minimum significant difference at the $\alpha = 0.05$ level.

Results

A. tripolium plants were grown at two light intensities designated as moderate (120 μmol m^{-2} s^{-1}) and high (natural daylight, 600 to 800 μmol m^{-2} s^{-1} at midday). Light conditions significantly affected photochemical characteristics of *A. tripolium* plants grown without NaCl. In general, plants had higher maximum potential quantum yield of PSII (F_v/F_m) in high light conditions, compared to the moderate light conditions (Fig. 1). In plants grown in high light conditions, the relative electron transport rate through PSII (ETR) was significantly higher (Fig. 2) and nonphotochemical quenching (NPQ) was significantly lower (Fig. 3), in comparison to moderate light conditions. Decrease of F_v/F_m (Fig. 1A) followed by a decrease of ETR (Fig. 2B) was evident in all experimental treatments of greenhouse-grown *A. tripolium,* which coincided with an increase of day-time temperature in the greenhouse starting from day 4.

NaCl-treated *A. tripolium* plants grown at moderate light intensity tended to have higher F_v/F_m over the control level, starting from day 12 (Fig. 1A). The differences were statistically significant for high NaCl concentrations (100 mM and above). In contrast to conditions of moderate light intensity, there were no significant differences in F_v/F_m between treatments within 15 days of the experiment for *A. tripolium* grown in the greenhouse at high light intensity (Fig. 1B).

A. tripolium plants treated with NaCl had a tendency to have lower photosynthetic quantum yield of PSII, as represented by ETR, compared to control plants (Fig. 2). The effect was statistically significant only for plants grown at high light intensity (Fig. 2B).

Thermal dissipation of excess energy measured as NPQ increased in *A. tripolium* plants treated with NaCl (Fig. 3). In moderate light conditions the effect did not depend on concentration of NaCl used for the treatment (Fig. 3A). In contrast, in high light conditions a pronounced concentration-dependent effect of NaCl on NPQ was evident. The stimulative effect of NaCl on NPQ was highest 10 days after the start of the treatment for both light intensities.

In addition to moderate (120 μmol m^{-2} s^{-1}) and high light (natural sunlight, 600 to 800 μmol m^{-2} s^{-1}), *H. vulgaris* plants were grown also at low light conditions (45 μmol m^{-2} s^{-1}) resembling canopy shade in natural habitats. The light conditions significantly affected photochemical characteristics of control plants. Control levels of F_v/F_m were significantly lower in *H. vulgaris* grown at high light intensity in comparison to low and moderate light (Fig. 4). In contrast, ETR levels increased with higher light intensities (Fig. 5). However NPQ was significantly lower in high light conditions (Fig. 6).

Treatment with 25 mM NaCl led to relatively small changes in F_v/F_m in *H. vulgaris* plants in all light intensities used (Fig. 4). Treatment with 100 mM NaCl caused a pronounced decrease of F_v/F_m which was more severe at moderate (Fig. 3B) and high light (Fig. 3C) intensities. Photosynthetic yield of photosystem II expressed as ETR was significantly inhibited by both concentrations of NaCl at low and moderate light intensity (Fig. 5). However the decrease of ETR was only temporal and returned to control levels 6 and 5 weeks after the start of the treatment, for low and moderate light intensity, respectively. No changes in ETR were caused by NaCl at high light intensity (Fig. 5C). A similar trend of NaCl effect was found for NPQ, where the treatment caused increase of the parameter only at low and moderate light intensities (Fig. 6). In addition, the effect was more short-lived at increased light intensity.

A clear concentration-dependent increase in ascorbate peroxidase activity was found in leaves of *A. tripolium*

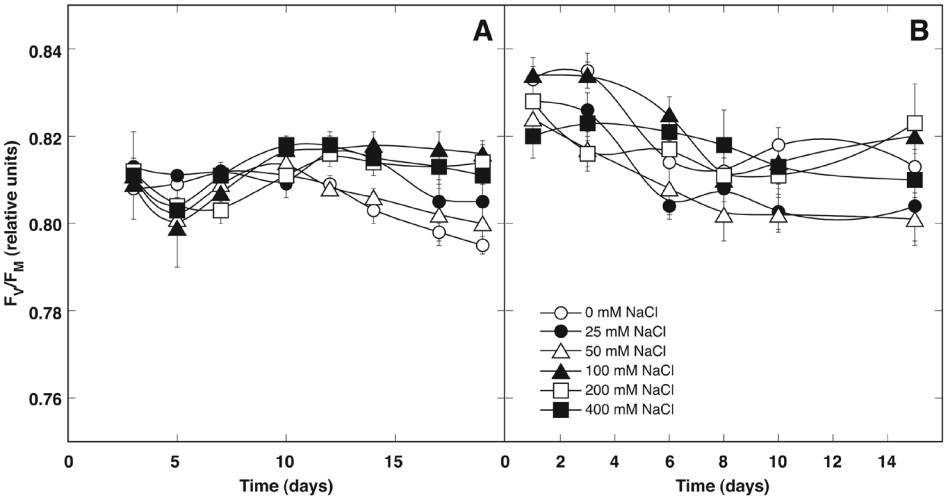

Fig. 1. Changes of maximum quantum efficiency of photosystem II photochemistry (F_v/F_m) under the effect of various concentrations of NaCl in leaves of *Aster tripolium* grown at 120 μmol m^{-2} s^{-1} (A) and 600 to 800 μmol m^{-2} s^{-1} (B) of PAR.

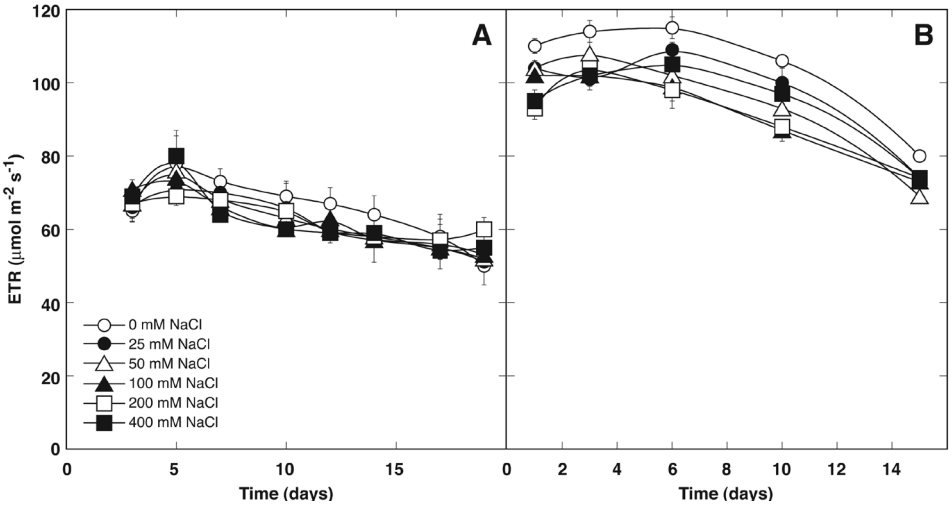

Fig. 2. Changes of relative electron transport rate through photosystem II (ETR) under the effect of various concentrations of NaCl in leaves of *Aster tripolium* grown at 120 μmol m^{-2} s^{-1} (A) and 600 to 800 μmol m^{-2} s^{-1} (B) of PAR.

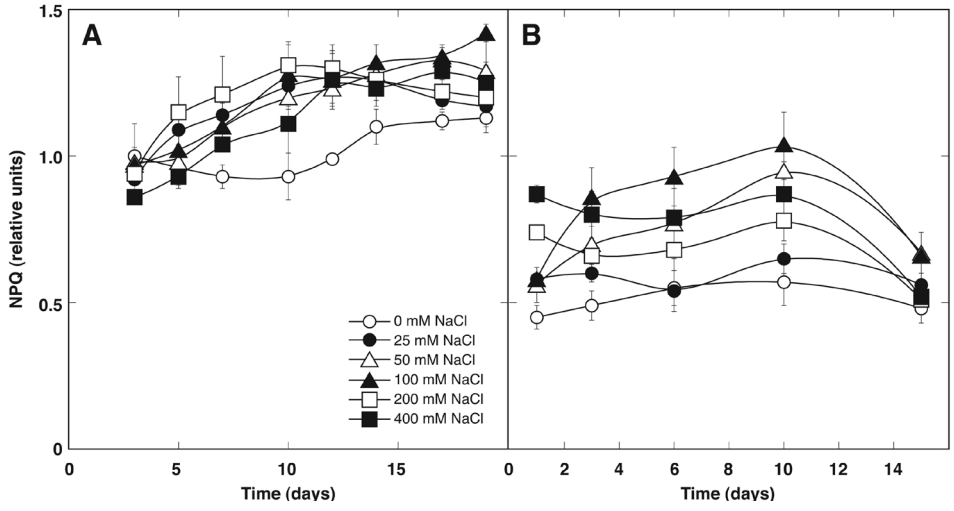

Fig. 3. Changes of non-photochemical quenching (NPQ) under the effect of various concentrations of NaCl in leaves of *Aster tripolium* grown at 120 μmol m^{-2} s^{-1} (A) and 600 to 800 μmol m^{-2} s^{-1} (B) of PAR.

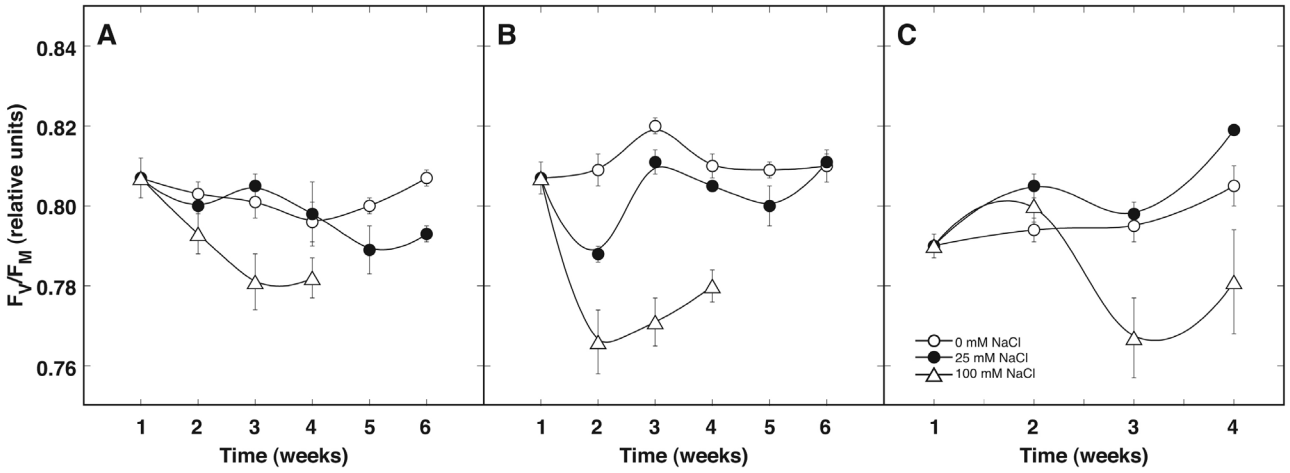

Fig. 4. Changes of maximum quantum efficiency of photosystem II photochemistry (F_v/F_m) under the effect of various concentrations of NaCl in leaves of *Hydrocotyle vulgaris* grown at 45 μmol m^{-2} s^{-1} (A), 120 μmol m^{-2} s^{-1} (B) and 600 to 800 μmol m^{-2} s^{-1} (C) of PAR.

treated with NaCl, both in moderate (Fig. 7A) and high light conditions (Fig. 7B) throughout the experimental period. No changes in the activity were observed in leaf petiole tissues of *A. tripolium* (data not shown). In contrast to *A. tripolium*, ascorbate peroxidase activity decreased both in leaf petioles and leaf blades of NaCl-treated *H. vulgaris* plants at all three light intensities tested (Fig. 8).

Discussion

With an increase of soil salinity due to flooding by seawater and following stomatal closure, salt marsh plants are faced to a situation where the amount of excess captured light energy not usable for photochemistry is increasing. Therefore it is logical to propose that inducible mechanisms should exist to protect these plants from the excess energy-caused photoinhibition in conditions of high salinity. However, information on effects of salinity on photochemistry of photosynthesis of halophytic plants has been contradictory.

Decrease in photosynthesis in *A. tripolium* by NaCl was shown to be due to stomatal limitation without any effect on quantum yield of photosynthesis (Ueda et al. 2003). Therefore, it was proposed that *A. tripolium* might have some type of scavenging mechanism in the light reaction system of photosynthesis leading to dissipation of excessive energy in conditions of NaCl-induced partial stomatal closure (Ueda et al. 2003). The present data support this hypothesis, as it was shown that both intensity of thermal energy dissipation (measured as NPQ) and enzymatic antioxidative capacity (ascorbate peroxidase activity) increased in *A. tripolium* as a result of NaCl treatment. The main factor contributing to nonphotochemical fluorescence quenching in PSII complexes under conditions such as those in our experiments has been suggested to be thermal energy dissipation that involves the xanthophyll cycle (Kornyeyev et al. 2003). Thermal energy dissipation and a water-water cycle (of which ascorbate peroxidase is a constituent) are

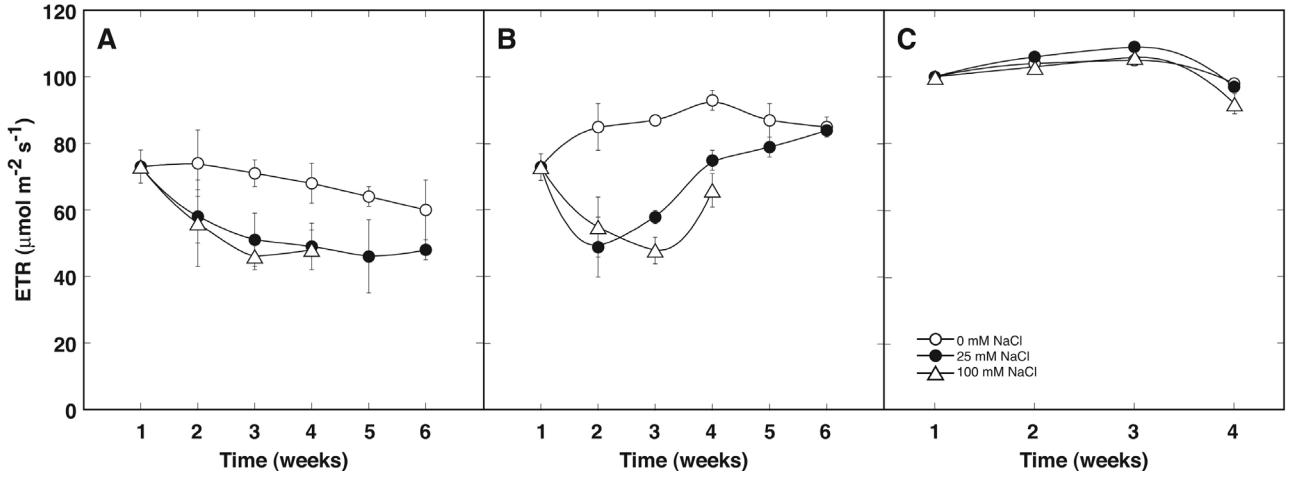

Fig. 5. Changes of relative electron transport rate through photosystem II (ETR) under the effect of various concentrations of NaCl in leaves of *Hydrocotyle vulgaris* grown at 45 μmol m^{-2} s^{-1} (A), 120 μmol m^{-2} s^{-1} (B) and 600 to 800 μmol m^{-2} s^{-1} (C) of PAR.

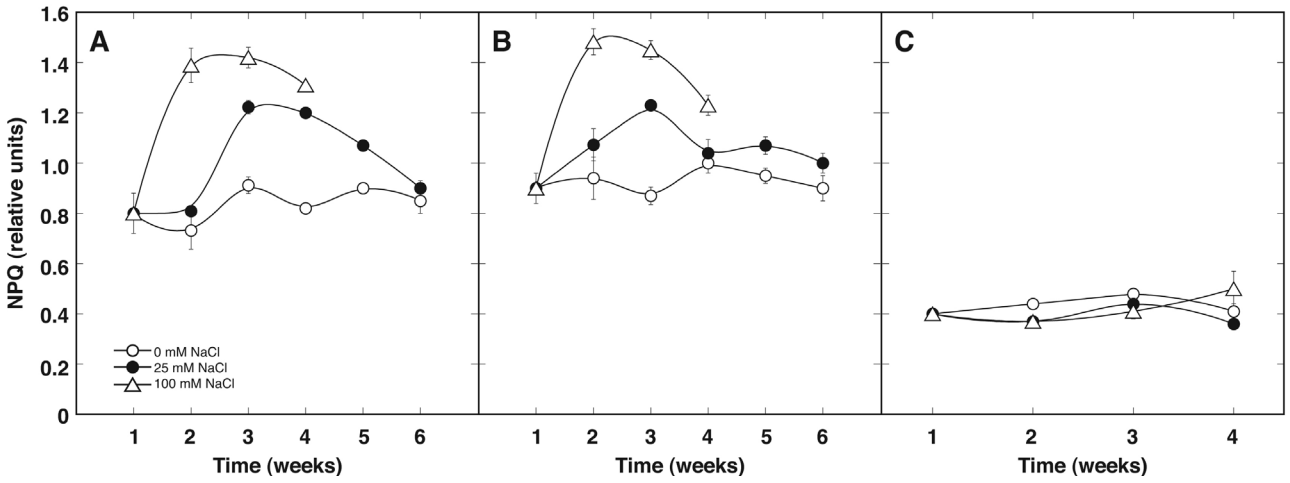

Fig. 6. Changes of non-photochemical quenching (NPQ) under the effect of various concentrations of NaCl in leaves of *Hydrocotyle vulgaris* grown at 45 μmol m^{-2} s^{-1} (A), 120 μmol m^{-2} s^{-1} (B) and 600 to 800 μmol m^{-2} s^{-1} (C) of PAR.

linked by complex and poorly understood interactions (Kornyeyev et al. 2003). It has been shown that most thermal energy dissipation is ΔpH-dependent (Demmig-Adams et al. 2006). On the other hand, chloroplastic ascorbate peroxidase activity contributes to maintenance of ΔpH (Neubauer and Yamamoto 1992; Ivanov, Edwards 2000). In support of the above conclusion, PSII quantum yields have been shown to be higher in stressed plants that are overexpressing chloroplastic ascorbate peroxidase (Kornyeyev et al. 2003). Thus, our experiments show that *A. tripolium* plants, in response to high NaCl, increase the capacity of protection of PSII through both thermal energy dissipation as well as O_2-dependent electron flow through ascorbate peroxidase. A linearly increasing capacity of NPQ with increasing NaCl concentration was shown previously for *A. tripolium* and another halophytic species, *Sesuvium portulacastrum* (Rammani et al. 2006).

In contrast to *A. tripolium*, in *H. vulgaris* plants NaCl treatment resulted in decrease of ascorbate peroxidase activity with a relatively small and only temporal increase of NPQ in low and moderate light conditions and no significant increase of NPQ in high light conditions Fig. 6). However, maximum quantum efficiency of PSII photochemistry (F_v/F_m) was significantly decreased in these conditions by NaCl treatment indicating photoinhibition of photosynthesis (Fig. 4). In contrast, observations made in the facultative halophyte *Mesembryanthemum crystallinum*, high salinity induced an increase of NPQ only in high light conditions while in low light conditions plus salinity it remained low (Broetto et al. 2007). These differences most probably reflect different strategies and/or degree of salt tolerance of these plants, as *H. vulgaris* is a relatively salt-sensitive species when growing in habitats with fluctuating levels of soil salinity (Ievinsh et al., unpublished results).

It appears that plants native to habitats with periodically fluctuating soil salinity may have at least two different

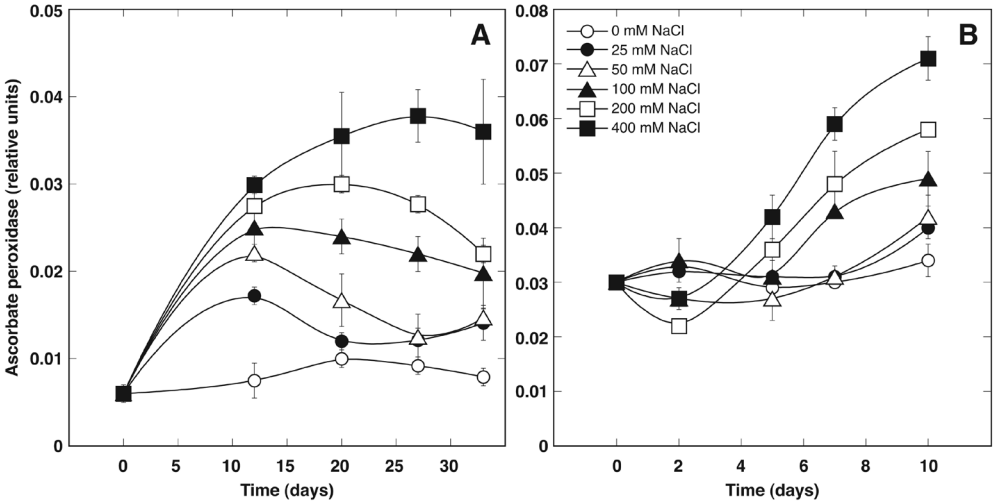

Fig. 7. Changes of ascorbate peroxidase activity as affected by different concentrations of NaCl in leaf blades of *Aster tripolium* grown at 120 μmol m^{-2} s^{-1} (A) and 600 to 800 μmol m^{-2} s^{-1} (B) of PAR.

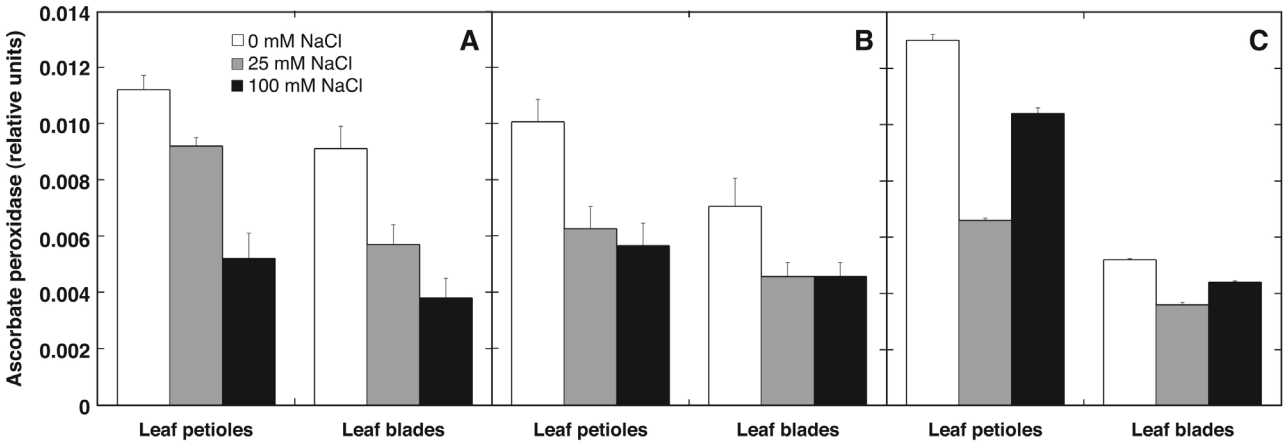

Fig. 8. Changes of ascorbate peroxidase activity as affected by different concentrations of NaCl in leaf petioles and leaf blades of *Hydrocotyle vulgaris* grown under 45 μmol m^{-2} s^{-1} (A), 120 μmol m^{-2} s^{-1} (B) and 600 to 800 μmol m^{-2} s^{-1} (C) of PAR. Enzyme activity was measured 4 weeks after the start of the treatment.

types of responses of photochemistry of photosynthesis to increased NaCl. Firstly, for plants that can induce an increase of NPQ and antioxidative system as a result of NaCl treatment, no decrease of F_v/F_m will appear, indicating that no photoinhibition of photosynthesis has occurred. Secondly, photoinhibition of photosynthesis will be visible in plants exhibiting no apparently increase of NPQ and capacity of the antioxidative system. In the present experiments, *A. tripolium* and *H. vulgaris* clearly correspond to the above two types, suggesting that the two mechanisms reflect different adaptive strategies in conditions of elevated soil salinity. Due to the dynamic nature of these adaptations both time after the start of the treatment as well as the concentration of NaCl are important. In addition, the degree of actual photoprotection mechanisms could strongly depend on ambient light conditions.

It was shown recently that coastal plant species exhibited no changes in F_v/F_m in conditions of elevated salinity, despite apparent visible signs of physiological stress, leading to a conclusion that thermal energy dissipation might protect PSII from excess energy in conditions of high salinity (Naumann et al. 2007). Surprisingly, in a series of experiments with different halophytes (*Artimisia anethifolia, Atriplex centralasiatica, Suaeda salsa*) no significant effect of NaCl on photochemistry of PSII was found, with the only exception of NPQ in *Atriplex centralasiatica*, where a significant increase of thermal dissipation was evident (Lu et al. 2002; Lu et al. 2003a; Lu et al. 2003b; Lu et al. 2003c; Qiu et al. 2003). In an extreme halophyte *Sarcocornia fruticosa,* quantum efficiency of PSII decreased due to NaCl treatment with little or no effect of salinity on photochemistry of PSII (Redondo-Gómez et al. 2006). Consequently, for plants that are highly tolerant to extreme NaCl concentrations, some other type of photosynthesis protection might be present. More likely, increased photorespiration and induction of cyclic electron transport are the means of photoprotection (Redondo-Gómez et al. 2006). It is known that cyclic electron flow associated with PSI is used for photoprotection of Antarctic plants (Pérez-Torres et al. 2007).

A causal relationship between salinity tolerance and components of the enzymatic antioxidative system has been described for different plant species (Sreenivasulu et al. 2000; Meloni et al. 2003; Sharma et al. 2005; Amor et al. 2006). In general, increased antioxidative capacity is thought to provide better protection against deleterious effects of salinity (Jithesh et al. 2006). Similar to our results, ascorbate peroxidase activity increased in leaves of the salt marsh halophyte *Plantago maritima* due to 200 mM NaCl treatment, in contrast to the salt sensitive species *Plantago media* where the treatment did not result in changes of the activity (Sekmen et al. 2007).

The following sequence of events during increased soil salinity can be proposed. Primary decrease in photosynthetic capacity in NaCl-treated plants is due to a stomatal limitation-associated decrease in tissue CO_2 concentration leads to lower need for ATP production. As a consequence, more captured light energy needs to be dissipated non-photosynthetically, which otherwise would lead to increased production of reactive oxygen species. The latter can stimulate a secondary decrease in photosynthetic capacity due to the photoinhibition if not captured by antioxidative systems. Thus, time of measurements of photosynthetic parameters in respect to the start of salinity treatment is crucial and differences in timing may lead to apparently different effects of NaCl on photochemical reactions described in the literature.

Our results suggest that, during acclimation to high NaCl, the system of excess energy dissipation protecting the photosynthetic machinery is modified. For maximum protection, both induced increase of appropriate duration in NPQ as well as activity of ascorbate peroxidase will be needed. When there is no increase of ascorbate peroxidase activity or even salinity-dependent decrease of the activity,

the increase in NPQ will be only temporal as in the case with *H. vulgaris*. However, prolonged induction of ascorbate peroxidase activity by NaCl is accompanied by a parallel increase in NPQ as in the case with *A. tripolium*.

High light in case of increased NaCl might lead to a higher degree of photoinhibition in comparison to low light conditions. Alternatively, a higher degree of photosynthesis protection in the form of thermal dissipation or other mechanisms might be present. However, it is difficult to interpret the differences in fluorescence parameters found in the present experiments for plants grown at different light intensities. Control plants of both *A. tripolium* and *H. vulgaris* had significantly lower NPQ when grown at high light intensity, in comparison to low light intensity (Fig. 3, 6). This is in contradiction with previously published data on thermal dissipation as a means of photosynthesis protection in high light conditions (Demmig-Adams, Adams 2006). The contradiction can be explained at least in part by the relatively low PAR levels used in the present experiments. In contrast, ascorbate peroxidase activity was higher in control plants in conditions of high light intensity (Fig. 7, 8), which is consistent with a role of chloroplastic ascorbate peroxidase in protection against high light-associated photoinhibition (Kornyeyev et al. 2003).

In conclusion, the data presented here indicate that one of the adaptive mechanisms of plants native to habitats with fluctuating soil salinity is an inducible increase of dissipation of absorbed light energy by means of thermal energy dissipation and ascorbate peroxidase activity. Both mechanisms were evident for the halophyte *A. tripolium*. However, *H. vulgaris* does not possess the latter mechanism. Our recent studies suggest that the clonal plant *H. vulgaris* is phenotypically highly plastic and relies on mechanisms of morphological adaptation to conditions of moderately fluctuating soil salinity (Ievinsh, unpublished data).

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