J Plant Growth Regul (1998) 17:153–159

Journal of
Plant
Growth
Regulation

A Possible Role for Jasmonic Acid in Adaptation of Barley Seedlings to Salinity Stress

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Received September 8, 1997; accepted May 19, 1998

Abstract. The changes caused by NaCl salinity and jasmonic acid (JA) treatment (8 days) on growth and photosynthesis of barley plants (*Hordeum vulgare* L., var. Alfa) have been studied. Gas exchange measurements and analysis of enzyme activities were used to study the reactions of photosynthesis to salinity and JA. Both 100 mM NaCl and 25 μM JA treatment led to a noticeable decrease in both the initial slope of the curves representing net photosynthetic rate vs intercellular CO_2 concentration and the maximal rate of photosynthesis. The calculated values of the intercellular CO_2 concentration, CO_2 compensation point, and maximal carboxylating efficiency of ribulose-1,5-bisphosphate carboxylase support the suggestion that biochemical factors are involved in the response of photosynthesis to JA and salinity stress. The activities of phosphoenolpyruvate carboxylase and carbonic anhydrase increased more than twofold. Pretreatment with JA for 4 days before salinization diminished the inhibitory effect of high salt concentration on the growth and photosynthesis. The results are discussed in terms of a possible role of JA in increasing salinity tolerance of the barley plants.

Key Words. Jasmonic acid—Salinity stress—Photosynthesis—Barley—*Hordeum vulgare* L.

Abbreviations: RuBPC, ribulose-1,5-bisphosphate carboxylase; PSII, photosystem II; ABA, abscisic acid; JA, jasmonic acid; CA, carbonic anhydrase; JA-ME, methyl ester of jasmonic acid; PEPC, phosphoenolpyruvate carboxylase; A, net CO_2 assimilation; Γ, CO_2 compensation point; L_s, stomatal limitation of photosynthesis; r'_s, stomatal resistance to CO_2; α, maximal carboxylating efficency; C_i, intercellular CO_2 concentration; C_a, ambient CO_2 concentration; RWC, relative water content; Tr, transpiration rate.

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Salinity is known to reduce the growth and development of glycophytes. The extent of this inhibition is correlated to the extent of NaCl salinity, the plant species sensitivity, and the environment.

Because plant productivity ultimately depends on the rate of photosynthesis, the effect of salinity on carbon assimilation has been studied frequently (Bethke and Drew 1992, Passera and Albuzio 1978). Much of the reported reduction of CO_2 assimilation can be attributed to the direct effect of salinity on the biochemical reactions of photosynthesis, e.g. reduced level and activity of ribulose-1,5-bisphosphate carboxylase (RuBPC) (Miteva et al. 1992, Seeman and Sharkey 1986), NaCl-induced alterations in the synthesis and distribution of photoassimilates, increase in both the rate of photorespiration and glycolate oxydase activity (Joshi and Nimbalkar 1984), inhibition of photosynthetic electron transport and PSII activity (Maslenkova et al. 1991, Mohanty and Saradhi 1992). Other have attributed the decline in photosynthesis caused by salinity to reduced photosynthetic surface area available for CO_2 assimilation, i.e. that the salinity effects on photosynthesis are mediated primarily via effects on leaf extension (Papp et al. 1983). Moreover, unavoidable uptake of specific ions by the plants and accumulation of these in the leaves are widely assumed to result in inhibition of photosynthesis (Robinson et al. 1983, Seemann and Critchley 1985).

To improve salt tolerance, nonhalophytic species have developed different strategies that allow plants to withstand salinity stress. The increase of salt resistance presumably involved a protection of cell membranes (Bewley 1979, Leopold and Willing 1984), including chloroplast membranes (Maslenkova et al. 1992), and from accumulation of some protector components (Clarkson and Hanson 1980, Greenway and Munns 1980).

The regulation of such complex plant responses suggests the existence of special signal transduction chain between stress signals and responses, where phytohormones are thought to be an integral part of the stress-

controlling mechanism in the plants (Parthier 1991, Zeevaart and Creelman 1988). Some of the phytohormones, such as abscisic acid (ABA), ethylene, or jasmonates, may act as stress modulators by suppressing or enhancing the stress responses of plants. Applied exogenously they can induce physiological changes identical with characteristic parts of the stress responses (La Rosa et al. 1985, Maslenkova et al. 1993, Popova et al. 1995, Skiver and Mundy 1990).

Exogenous treatment of barley seedlings with ABA and jasmonic acid (JA) reduced the rate of photosynthetic CO_2 fixation and the activity of RuBPC, increased the rate of photorespiration, and increased both the CO_2 compensation point and stomatal resistance (Popova et al. 1987, 1988). It has also been observed that barley seedlings treated with JA or grown on 50–100 mM NaCl have an increase in activity of carbonic anhydrase (CA), with a more pronounced effect on the cytoplasmically localized enzyme. It was suggested that the enzyme is involved in the plant's adaptation to osmotic stress as a possible biochemical mechanism (Popova et al. 1991). Maslenkova et al. (1989, 1990) have established that ABA and JA application to the growth medium of barley seedlings leads simultaneously to changes in photosynthetic light reactions connected with chloroplast thylakoid membranes. Treatment of barley leaf segments with ABA, JA, or JA-ME induced very similar patterns of specific proteins (Weidhase et al. 1987). Lehmann et al. (1995) demonstrated that application of ABA or JA-ME to barley segments or exposure to osmotic stress led to the synthesis of novel proteins that were identical with respect to immunological properties and molecular masses.

Our studies with salt-treated barley seedlings revealed significant changes in soluble and thylakoid membrane proteins which resemble to a great extent the specific changes in polypeptide profiles after exogenous JA application to the root medium (Maslenkova et al. 1992, Miteva et al. 1992).

The observed similarity in the photosynthetic responses of barley seedlings to salt stress and exogenous application of JA suggests that JA may play a specific role in the reaction of photosynthetic apparatus to salt stress. The assumption is that exogenously applied jasmonates, as presumed stressors, provoke alterations in photosynthetic responses which allow plants to increase their tolerance to unfavorable conditions. In this respect, we were interested in studying the importance of nonstomatal (biochemical) factors in the observed decline in photosynthesis. An important focus was to examine modification in the activities of phosphoenolpyruvate carboxylase (PEPC) and CA as one of the adaptive photosynthetic responses.

Different experimental approaches, namely long term stress treatment of barley seedlings with 100 mM NaCl and 25 μM JA, gradual application of low salt concentration, and JA pretreatment before salinization, allowed us to study the photosynthetic response to salt stress and the possible role of this plant growth substance in the process of stress adaptation.

Materials and Methods

Plants

Seeds of barley (*Hordeum vulgare* L., var. Alfa) were germinated for 2 days in two layers in moist filter paper in vermiculite at 25°C in the dark. Then they were transferred into Petri dishes containing 40 mL of distilled water or equal amounts of water solution at the required NaCl and JA concentrations (100 mM NaCl and 25 μM JA). During the experimental period the seedlings grew in a growth chamber under white fluorescent lamps (35 Wm^{-2}), with 12-h light/dark periods. Day/night temperatures were 25/20°C, and relative humidity was about 50%. To obtain NaCl stepwise-treated plants, the daily increase in NaCl concentration was 25 mM until 100 mM NaCl was reached. In the experiments with JA-pretreated plants 25 μM phytohormone was added to the growth medium of the seedlings for 4 days before salinization with 100 mM NaCl for the next 4 days.

Gas Exchange Measurements

Gas exchange measurements were performed by a portable photosynthesis apparatus (LI 6000, Li-Cor, Linkoln, NE). Leaves of five or six plants were placed into a 0.25-liter chamber. Quantum flux density was 830 μmol m^{-2} s^{-1} PAR, provided by a 500-W incandescent lamp (ZLN-500W, EVZ, Bulgaria) with reflector. Leaf temperature was 27 ± 2°C. The response of photosynthesis to leaf internal partial pressure of CO_2 (C_i) was determined as described by Davis et al. (1987).

Maximal carboxylating efficiency (α) was calculated as the initial slope of the curve relating net CO_2 assimilation (A) vs intercellular CO_2 concentration (C_i). The following function was fitted to the experimental data:

$$A = \frac{p_1 C_i}{p_2 + C_i} - p_3$$

where p_1, p_2, p_3 are parameters.

The stomatal limitation of photosynthesis (L_s) was calculated according to Farquhar and Sharkey (1982) as

$$L_s = \frac{A_0 - A}{A_0}$$

where A_0 is net photosynthetic rate at C_i = 350 μmol mol^{-1}, A is net photosynthetic rate at C_a = 350 μmol mol^{-1} (C_a is ambient CO_2 concentration).

Enzyme Extraction and Assays

Leaf tissue, without the major veins, was ground in a mortar on ice at a ratio of 1 g, fresh weight, to 5 mL of cold extraction medium containing 0.33 M sorbitol, 50 mM Hepes-NaOH, 2 mM KNO_3, 2 mM EDTA, 1 mM $MnCl_2$, 1 mM $MgCl_2$, 5 mM K_2HPO_4, 20 mM NaCl, and 0.2 M sodium isoascorbate (pH 7.6). The homogenate was quickly filtered through four layers of cheesecloth and centrifuged at 20,000 ×g for 15 min, and the supernatant was used directly for enzyme assay.

RuBPC (EC 4.1.1.39) and PEPC (EC 4.1.1.31) activities were assayed from the activated crude preparation by following the incorporation of $NaH^{14}CO_3$ into acid-stable products as described earlier (Popova et al. 1988).

The assay mixture for RuBPC contained in 50 mM Hepes-NaOH (pH 8.0): 20 μmol of $MgCl_2$, 1 μmol of dithiothreitol, 20 μmol of $NaHCO_3$ (containing 0.37 MBq of ^{14}C, specific radioactivity 1.48 MBq μmol^{-1}), and enzyme extract equivalent to 0.3–0.4 mg of protein. The reaction volume was 1 mL. Reactions, at 25°C, were initiated by the addition of 2 μmol of RuBP and stopped after 1 min reaction time with 6 N HCl.

The assay mixture for PEPC activity contained in 50 mM Hepes-NaOH (pH 8.0): 20 μmol of $MgCl_2$, 0.4 μmol of NADH, 20 μmol of $NaHCO_3$ (containing 0.37 MBq of ^{14}C, specific radioactivity 1.48 MBq μmol^{-1}), 1 μmol dithiothreitol, and enzyme extract equivalent to 0.3–0.4 mg of protein. Reaction volume was 1 mL. Reactions, at 30°C, were initiated by the addition of 3 μmol of PEP. Reaction time was 1 min.

The amount of fixed $^{14}CO_2$ was measured in a liquid scintillation counter.

Preparation of Leaf Extract for Assay of Carbonic Anhydrase (CA) (EC 4.2.1.1)

Leaf samples (1 g) were ground with pestle and mortar on ice-cold medium (10 mL) which contained 0.01 M Tris-glycine buffer (pH 8.3) and 5% sucrose. After centrifugation at 8,000 ×*g* for 20 min, the supernatant was removed and used for the enzyme assay.

CA was determined by following the time-dependent decrease in pH from 8.3 to 7.8. One unit of enzymatic activity (Willburg-Anderson) is defined as $10(t_0/t - 1)$, where t_0 and t represent the time required to change the pH of the buffer (0.05 M NaH_2PO_4, containing 5 mM cysteine and 1 mM EDTA) from 8.3 to 7.8 at 2°C after the addition of CO_2-saturated water in the presence and absence of the plant sample, respectively.

Relative Water Content

Relative water content (RWC) was measured as described by Morgan (1986) except that turgid mass was obtained after soaking the leaves for 2–3 h in distilled water. The RWC values were calculated according to the formula

$$\text{RWC} = \frac{\text{initial fresh mass} - \text{dry mass}}{\text{full turgid mass} - \text{dry mass}} \times 100.$$

Chlorophyll content extracted by acetone (80%, v/v) was measured according to Arnon (1949).

Soluble protein was determined according to Lowry et al. (1951) in aliquots of supernatants, with bovine serum albumin as the standard protein.

Chemicals

JA was purchased from Serva Chemical Corp. All other chemicals were obtained from Sigma (St. Louis, MO).

Results

Growth Responses and RWC

Treatment of barley seedlings with 100 mM NaCl or 25 μM JA for 8 days caused a significant decline in the rate of growth (Table 1). Although salinity had no effect on the rate on new leaf initiation, the initial rate of leaf extension and final leaf length each decrease in plants grown at 100 mM NaCl. Leaves were shorter in length and not well expanded. In contrast, when seedlings were exposed to stepwise changes in NaCl concentration, plant growth was only slightly affected. Pretreated seedlings with 25 μM JA before salinization were less affected by the next exposure to high NaCl concentration.

Table 1. Effects of NaCl and JA on the growth of barley seedlings and RWC of the leaves. The details are given under ''Materials and Methods.'' The means and S.E. of three different experiments with 20 seedlings each are reported.

Treatment	Length of the surface of the seedlings (cm)	RWC (%)
Control	9.94 ± 0.65	89.8 ± 0.9
100 mM NaCl	5.44 ± 0.39	49.6 ± 3.9
25–100 mM NaCl[a]	8.76 ± 0.81	81.0 ± 3.2
25 μM JA	6.93 ± 0.72	88.5 ± 2.7
25 μM JA + 100 mM NaCl	7.77 ± 0.58	62.0 ± 3.1

[a] Stepwise increased NaCl concentration from 25 to 100 mM within 8 days.

Leaf RWC of control plants was about 90%. Exposure of plants to 100 mM NaCl led to a strong decline in RWC. There were insignificant differences in the values of this parameter in JA-treated or stepwise NaCl-treated barley seedlings compared with the untreated control plants. The inhibitory effect of 100 mM NaCl on RWC was overcome to a significant extent during the JA pretreatment of the plants.

Gas Exchange

Changes in CO_2 assimilation rate (A) as a function of the calculated substomatal CO_2 concentration (C_i) were used to distinguish the role of stomatal resistance (r_s) in the limitation of A under salinity stress and JA treatment (Fig. 1). Treatment of barley seedlings with 100 mM NaCl for 8 days caused a very strong decline in the rate of A at normal C_a (350 μmol mol^{-1}). Long term treatment with JA also led to inhibition of A, but compared with the control the values of A were 2–2.5-fold lower. When seedlings were exposed to stepwise changes in NaCl concentration or pretreated with 25 μM JA for 4 days before salinization, the rate of photosynthesis was less inhibited (Fig. 1 and Table 2). All kinds of treatments led to a noticeable decrease in both the initial slope of the A/C_i curve (representing the maximal carboxylation efficiency (α) and the maximal A. In 100 mM NaCl-treated plants the value of α was almost tenfold lower compared with the control. The plants' exposure to 100 mM NaCl for 8 days resulted in a fourfold increase in the CO_2 compensation point (Γ). The values of Γ for the other variants were very similar to the control.

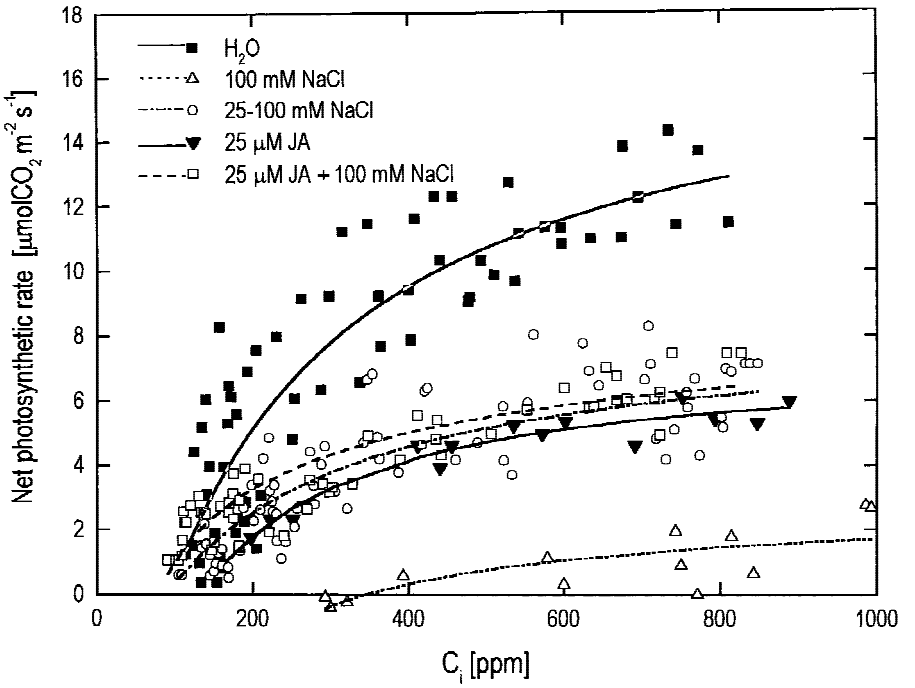

Fig. 1. Effect of NaCl and JA treatment on the response of net photosynthetic rate (A) to intercellular CO_2 concentration (C_i). Experimental data and regression lines fitted to the function $A = p_1 C_i/(p_2 + C_i) - p_3$ are presented.

Table 2. Leaf gas exchange characteristics of barley plants after treatment with NaCl and JA. α, carboxylating efficiency; Γ, CO_2 compensation point; A, net CO_2 assimilation; C_i, intercellular CO_2 concentration; L_s, stomatal limitation of photosynthesis; r'_s, stomatal resistance to CO_2; Tr, transpiration rate. The details are given under ''Materials and Methods.'' Values are means ± S.E. (n = 4).

Treatment	α (cm s^{-1})	Γ (μmol mol^{-1})	A (μmol CO_2 m^{-2} s^{-1})	L_s (%)	C_i/C_a (C_a = 350)	r'_s (s cm^{-1})	Tr (mgH_2O m^{-2} s^{-1})
Control	0.068	92.2	8.75	27.5	0.72	7.8 ± 0.5	29.5 ± 2.0
100 mM NaCl	0.007	345.3	0.05	41.2[a]	0.95[a]	48.8 ± 2.7	9.6 ± 1.4
25–100 mM NaCl[b]	0.033	87.2	4.20	42.1	0.64	18.5 ± 1.8	14.5 ± 1.2
25 μM JA	0.037	135.6	3.79	47.0	0.77	15.8 ± 0.2	19.8 ± 0.8
25 μM JA + 100 mM NaCl	0.054	77.7	4.71	39.7	0.69	17.5 ± 1.3	16.9 ± 0.9

[a] The data for L_s and C_i/C_a in the variant with 100 mM NaCl were calculated at C_a = 400 ppm because of greather Γ.
[b] Stepwise increased NaCl concentration from 25 to 10 mM within 8 days.

Long term treatment of barley seedlings with 100 mM NaCl or 25 μM JA resulted in manifold increase in r'_s. Pretreatment with JA or a progressive increase in NaCl concentration also caused an increase in r'_s but to much lower extent.

Transpiration rate (Tr) was decreased threefold in 100 mM NaCl-stressed plants. Pretreatment with JA or stepwise treatment with NaCl enhanced the values of this parameter.

Enzyme Activities, Chlorophyll and Protein Contents

RuBPC activity was reduced very strongly when plants were treated with 100 mM NaCl; the percentage of inhibition was approximately 65% of control (Fig. 2). JA also inhibited the activity of RuBPC but much slower; the inhibition was only 25%. It should be noted that stepwise treatment with NaCl or pretreatment with JA before salinization diminished the inhibitory effect of NaCl on the activity of RuBPC.

When barley plants were grown on 100 mM NaCl or 25 μM JA the activity of PEPC increased more than twice. Pretreatment with JA or a progressive increase in the NaCl concentration also caused an increase in the enzyme activity but to a lower extent.

CA activity was increased strongly when plants were treated long term with 100 mM NaCl or 25 μM JA (Fig. 2). The activity of the enzyme was increased by salinity stress to approximately 70%, by JA to 50% of control. The pretreatment with JA caused a much lower increase of CA activity. Stepwise treatment with NaCl did not affect the activity of the enzyme.

The chlorophyll (*a* and *b*) content decreased when seedlings were grown in the presence of NaCl. By con-

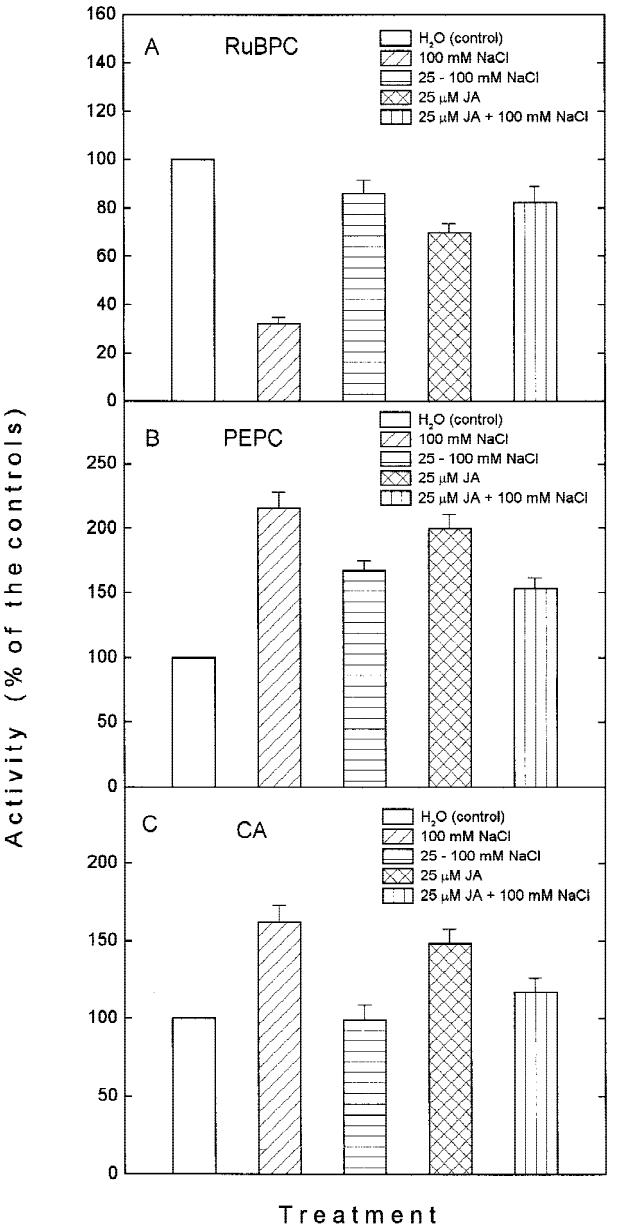

Fig. 2. Effect of NaCl and JA treatment on the activity of RuBPC (*A*), PEPC (*B*), and carbonic anhydrase (*C*) of barley leaves. Activity of the enzymes was determined as indicated under ''Materials and Methods.'' The activity of RuBPC was 0.384 μmol of CO_2 mg^{-1} protein min^{-1} in the control, for PEPC 0.064 μmol of CO_2 mg^{-1} protein min^{-1}, and for carbonic anhydrase 523.6 units mg^{-1} protein. Data are average of five experiments ± S.E.

trast, the long term treatment with 25 μM JA or pretreatment with JA before salinization did not affect the chlorophyll content (Table 3).

The leaf protein content was decreased in all treatments, the effect being more expressed in JA-treated seedlings (Table 3).

Table 3. Effects of NaCl and JA on chlorophyll content and leaf soluble protein. The details are given under ''Materials and Methods.'' Values are means ± S.E. (n = 7–9).

Treatment	Clorophyll (a + b) (mg Chl (g FW)$^{-1}$)	Leaf soluble protein (mg (g FW)$^{-1}$)
Control (H_2O)	2.30 ± 0.072	8.45 ± 1.012
100 mM NaCl	1.73 ± 0.047	6.11 ± 0.079
25–100 mM NaCl[a]	1.78 ± 0.052	5.32 ± 0.075
25 μM JA	2.43 ± 0.040	4.87 ± 0.042
25 μM JA + 100 mM NaCl	2.04 ± 0.069	5.28 ± 0.053

[a] Stepwise increased NaCl concentration from 25 to 100 mM within 8 days.

Discussion

The results presented here show that exogenous pretreatment of barley seedlings with jasmonic acid before salinization improved the growth and photosynthetic performance of the plants.

The growth of barley seedlings on water solution supplemented with 100 mM NaCl was reduced noticeably relative to untreated plants (Table 1). This is a typical response of nonhalophyte species. JA-stressed plants showed a low growth rate without any changes in the values of RWC. Our data indicated that a gradual low salt (25 mM) increase in NaCl concentrations had very low negative effect on the growth of the seedlings. More importantly, pretreatment of the seedlings with 25 μM JA diminished the inhibitory effect of high salinization on the plant growth. This was in agreement with our previously reported results for the similar effect of ABA pretreatment on the same plant species subjected to salinity stress (Popova et al. 1995).

The growth reduction of barley plants is likely to be a consequence of a number of different effects of both stress factors on plant processes, including effects on photosynthetic reactions. Actually, JA and especially high salt concentration have an inhibitory effect on the rate of photosynthesis when applied separately to the growth media.

The reduction in leaf chlorophyll concentration is a general phenomenon in sensitive plants subjected to salt stress (Robinson et al. 1983, Stiborova et al. 1987). In our experiments, the content of chlorophyll was decreased by NaCl to an extent approximately equal in all variants treated with NaCl (Table 3). Treatment with 25 μM JA for 8 days had no effect on the chlorophyll content; regardless of that, a decrease in the rate of photosynthesis was observed. The results showed that there was no correlation between the degree of inhibition of salt stress on the chlorophyll content and the intensity of photosynthesis. This indicates that the loss of chlorophyll is unlikely to be the primary cause of photosynthetic reduction for salinized barley plants.

The observed reduction in photosynthetic capacity resulting from salinity stress or exogenous application of JA could be discussed as a consequence of at least two main factors: 1) an indirect effect mediated by stomatal closure causing a reduction in CO_2 supply, or 2) a direct effect on the photosynthetic machinery independent of altered diffusion limitations. Although the role of stomata increased in all treated variants, the value of L_s (about 40%) shows that there are also biochemical constraints to photosynthesis. The suggestion that biochemical factors are involved in response in photosynthesis to salinity or JA is supported by the reduced rate of C_i-saturated photosynthesis, the occurrence of an increasing CO_2 compensation point, and the reduced values in the maximal carboxylating efficiency of RuBPC (α).

Reduction in photosynthetic capacity may result from a decrease in the rate at which RuBPC fixes CO_2 in the carboxylation reaction in vivo. This may be caused by reductions in either substrate concentration (CO_2 or RuBP) or in the activity of the enzymes that produce ATP and reducing equivalents. Actually, this suggestion is consistent with our data, indicating that high salinity and JA cause mainly alterations in the biochemical capacity of photosynthesis unrelated to the observed stomatal limitation (Maslenkova et al. 1990, Metodiev et al. 1996).

The inhibitory effect of 100 mM NaCl on photosynthesis was overcome to a significant extent after the stepwise NaCl treatment and by the JA pretreatment of the seedlings. The effect of NaCl salinity on photosynthetic capacity is also reflected by the inhibition of RuBPC activity. When the seedlings were exposed to stepwise changes in NaCl concentration or pretreated with JA before salinization, the RuBPC activity was approximately equal to the one of the control unstressed plants (Fig. 2).

Barley seedlings treated with JA or grown on 100 mM NaCl showed an increase in the activities of PEPC and CA (Fig. 2). We have made similar observations with barley plants treated with ABA or drought-stressed (Popova et al. 1996). An increase in PEPC activity has been reported after application of ABA to leaves of *Mesembryanthemum crystalinum* or exposure of plants to salt or drought stress. Evidence has been presented that the increases in PEPC activity are caused by an increase in the quantity of the enzyme protein (Chu et al. 1990).

CA catalyzes the reversible interconversion of HCO_3^- to CO_2. The majority of CA activity in leaves of C_3 plants resides within the stroma of the chloroplasts (Tsuzuki et al. 1985). It has often been suggested that chloroplast CA functions to ensure a continuous supply of CO_2 to RuBPC. It is quite possible that under different stress conditions (salinity, drought, or high levels of ABA and JA), when the supply of CO_2 is limited as a consequence of stomatal closure, the observed increase in PEPC and CA activities serves as an adaptive photosynthetic mechanism.

Experimental evidence has shown that photosynthetic organisms (mainly aquatic) have developed an inducible mechanism for the active transport of CO_2 as an adaptation to unfavorable conditions (Badger 1987). The CO_2-concentrating mechanism favors the carboxylation reaction catalyzed by RuBPC (for review, see Sultemeyer et al. 1993).

Here we observed that barley seedlings pretreated with JA or stepwise NaCl treated did not show an enhancement of CA activity. The activity of PEPC was slightly higher than in the control plants.

Ours and other previous data show that long term treatment of barley plants with JA or exposure to salt stress leads to increases in the rate of photorespiration and the activity of CA (Miteva and Vaklinova 1991, Popova et al. 1988). The results are consistent with those presented by Ramazanov and Cardenas (1992) who showed that in *Chlamydomonas* the integrity of the glycolate pathway is essential for the induction of CO_2 transport mechanism and CA activity.

In summary, we have shown that barley seedlings treated with a daily increasing NaCl concentration up to 100 μM or pretreated with JA before salinization had little decline in the growth and much lower inhibition of photosynthesis and RuBPC activity, indicating that barley plants are capable of tolerating a relatively high level of salinity, and probably JA is partially involved in the process of adaptation.

At present, we cannot explain the enhanced activities of PEPC and CA after JA treatment and salinity stress, but our suggestion is that this is part of the biochemical adaptation of photosynthesis to environmental stresses. However, the mechanism whereby JA can enhance the rate of adaptation or tolerance of barley to NaCl needs further study.

Acknowledgment. This research was supported by Grant K-511 from the National Fund for Scientific Investigations, Bulgaria.

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