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Treatment with methyl jasmonate alleviates the effects of paraquat on photosynthesis in barley plants

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Abstract

Twelve-day-old barley seedlings were supplied with 23 μM methyl jasmonate (MeJA) or 10 μM paraquat (Pq) *via* the transpiration stream and kept in the dark for 24 h. Then they were exposed to 100 μmol m^{-2} s^{-1} PAR and samples were taken 1, 2, 3, and 6 h after irradiation. Treatment of seedlings with MeJA alone resulted in decreased content of chlorophyll (Chl), and net photosynthetic (P_N) and transpiration rates. Pq treatment led to a decrease in Chl content and to a very strong inhibition of P_N, the effects were manifested by 1 h of irradiation. Pq treatment did not affect the activity of ribulose-1,5 bisphosphate carboxylase (RuBPC, EC 4.1.1.39) but increased the activity of the photorespiratory enzymes phosphoglycolate phosphatase (PGP, EC 3.1.3.18), glycolate oxidase (GO, EC 1.1.3.1), and catalase (EC 1.11.1.6). Pretreatment of seedlings with MeJA before exposure to Pq fully blocked the inhibitory effect of Pq on photosynthesis and protected against subsequent Pq-induced oxidative damage.

Additional key words: barley; catalase; chlorophyll; glycolate oxidase; *Hordeum vulgare;* methyl jasmonate; paraquat; phosphoglycolate phosphatase; photorespiration; ribulose-1,5 bisphosphate carboxylase; transpiration rate.

Introduction

Jasmonates (jasmonic acid, JA, and its methyl ester, MeJA) occur in many plant species and are involved in various physiological processes (reviewed in Sembdner and Parthier 1993, Creelman and Mullet 1997). When applied directly to plants or suspension culture, they produce effects such as induction of leaf senescence (Weidhase *et al.* 1987a,b), promotion of cell expansion (Takahashi *et al.* 1994), abscission, root formation, and synthesis of ethylene and β-carotene (Czapski and Saniewski 1985, Saniewski *et al.* 1998). In barley (*Hordeum vulgare* L.) plants exogenous treatment with JA or MeJA revealed changes in a number of photosynthetic parameters, such as a decrease in the rate of photosynthetic CO_2 fixation and in the activity of RuBPC. There were considerable increases in the rates of dark respiration and photorespiration, in the CO_2 compensation concentration, and in the stomatal resistance (Popova *et al.* 1988). A breakdown in the biosynthesis of RuBPC (Weidhase *et al.* 1987b, Popova and Vaklinova 1988), an inhibition of the Hill reaction activity, and some changes in the kinetic characteristics of the flash-induced O_2 evolution (Maslenkova *et al.* 1990) occur as a result of JA and MeJA treatments. Concomitant with this, considerable alterations in the chlorophyll (Chl) fluorescence parameters were reported in chloroplast membranes isolated from barley plants grown in the presence of increasing concentrations of JA (Ivanov and Kicheva 1993). Furthermore, jasmonates induce accumulation of a number of proteins (JIPs) in many plant species, including barley (Muller-Uri *et al.* 1988). Maslenkova *et al.* (1992) showed an induction of JIPs mainly belonging to the thylakoid-bounded polypeptides. Mostly of JA-induced polypeptides were identical to the ABA- and NaCl-induced ones, leading to the assumption that exogenously applied jasmonates act as stress agents.

The intensive research on plant response to various

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Abbreviations: Chl – chlorophyll; DTT – dithiothreitol; E – transpiration rate; g_s – stomatal conductance; GO – glycolate oxidase; MDA – malondialdehyde; MeJA – methyl ester of jasmonic acid; PGP – phosphoglycolate phosphatase; P_N – net photosynthetic rate; Pq – paraquat; RuBPC – ribulose-1,5-bisphosphate carboxylase; TCA – tricarboxylic acid.
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environmental stresses during the last years has revealed a role for jasmonates as signalling molecules or stress-modulating compounds. They are involved in plant response to wounding (Farmer and Rayan 1992), UV irradiation (Conconi *et al.* 1996), and pathogen infection (Creelman and Mullet 1997). Increased endogenous contents of jasmonates are in plants suffering drought and osmotic stress (Creelman and Mullet 1995), wounding (Creelman *et al.* 1992, Baldwin *et al.* 1997), after treatment with fungal elicitors (Gundlach *et al.* 1992), or upon pathogen attack (Farmer and Rayan 1992). In recent years jasmonates have been tested according to their ability to protect against salinity stress (Tsonev *et al.* 1998), UV irradiation (Mackerness *et al.* 1999), heavy metals (Maksymiec and Krupa 2002), or to increase freezing tolerance in bromegrass (Wilen *et al.* 1994). This suggests that jasmonates mediate the defence response to various environmental stresses. JA and MeJA act as part of a signalling pathway that is an important component of the plants' defences, although full details of the pathway have yet to be elucidated.

The common link among different stresses is that they all produce oxidative burst. Chloroplasts, a major source of activated O_2 in plants (Foyer *et al.* 1994a, Iturbe-Ormaetxe *et al.* 1998), and antioxidants, which prevent oxidative damage, are greatly affected by environmental stress (Bowler *et al.* 1994). The most of oxidative damages inhibit photosynthesis and growth as a result of the imbalance between production of activated O_2 and antioxidant defence system. Any perturbation in photosynthetic activity can cause the formation of reactive oxygen species: superoxide ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH), initiating either from photosystem 1 or 2, ferredoxin, or excited Chl. Other subcellular compartments of leaves, such as peroxisomes and mitochondria, are also potential generators of $O_2^{\cdot-}$ and H_2O_2 as a consequence of electron transport and enzymatic reactions. These active oxygen species are all very reactive and cause a cascade of lipoxidations resulting in Chl bleaching and breakdown of plastid and cytoplasmic membranes, DNA destruction, and hence extensive tissue damage (see Bowler *et al.* 1992 for review).

Bipyridyl herbicides such as paraquat (Pq) and diquat are non-selective contact herbicides that act by intercepting electrons from the photosynthetic electron transport chain at PS1. This reaction results in the production of bipyridyl radicals that readily react with O_2 to produce superoxide and then, through a series of reactions, produce H_2O_2 and the hydroxyl radical. These toxic oxygen species cause extensive lipid peroxidation (Babbs *et al.* 1989), Chl breakdown (Shaaltiel *et al.* 1988), loss of photosynthetic activity (Fedtke 1982), leakage of electrolytes (Harris and Dodge 1972), and loss in cell membranes integrity (Kunert and Dodge 1989). Cross-tolerances were found between oxidant generating herbicides and environmental oxidants in different plant biotypes constitutively tolerant to Pq, SO_2, and O_3 (Shaaltiel *et al.* 1988), to photoinhibition (Jansen *et al.* 1989), or drought stress (Malan *et al.* 1990). Survival under stress depends on the plant ability to perceive the stimulus, generate and transmit signals, and induce biochemical changes that adjust the metabolism accordingly (Enyedi *et al.* 1992).

In the present work we demonstrate that MeJA treatment protects photosynthesis against Pq stress in young barley plants, with special regard to changes in the activity of certain photosynthetic and photorespiratory enzymes, and to some typical parameters which are most affected by Pq treatment.

Materials and methods

Growth and treatment of seedlings: Barley plants (*Hordeum vulgare* L. cv. Alfa) were grown for 12 d in soil in a growth chamber. The soil was classified as *Eutric Fluvisol*, pH 5.75. The environmental conditions were: irradiance, 160 μmol m^{-2} s^{-1} PAR, 12 h-photoperiod, temperature of 24±2 °C, and relative humidity of 60±5 %. Twelve-day-old seedlings were cut at their basal end and incubated in solutions containing: distilled water (control), 23 μM MeJA (*Serva*), and 10 μM Pq (*Sigma*). They were kept for 24 h in the dark at room temperature. Thereafter, half of the MeJA-treated seedlings were transferred into a beaker containing 10 μM Pq and all variants were exposed to 100 μmol m^{-2} s^{-1} PAR, provided by cool-white fluorescent tubes and were sampled after 1, 2, 3, and 6 h.

Gas exchange measurements were performed by a portable photosynthesis system *Li-6000 (LI-Cor*, Lincoln, USA). Leaves of 5-6 plants (the first well-expanded leaf) were placed in a 250 cm^3 chamber. Quantum flux density was 160 μmol m^{-2} s^{-1} PAR, provided by a 500-W incandescent lamp fitted with reflector. Flow rate through the cuvette was 18-20 cm^3 s^{-1}, boundary layer resistance (r_a) was 0.8 cm^{-1}. Leaf temperature was 26±2 °C.

Enzyme extraction and assays: Leaf tissue without the major veins was ground in a mortar on ice at a ratio of 1 g fresh mass to 5 cm^3 cold extraction medium containing 0.33 M sorbitol, 0.05 M HEPES-NaOH, 0.002 M KNO_3, 0.002 M EDTA, 0.001 M $MnCl_2$, 0.001 M $MgCl_2$, 0.0005 M K_2HPO_4, 0.02 M NaCl, and 0.2 M Na-isoascorbate, pH 7.6. The homogenate was quickly filtered through four layers of cheesecloth and centrifuged at 20 000×*g* for 15 min. The supernatant was used directly for enzyme assay.

RuBPC (EC 4.1.1.39) activity was assayed in 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 $MgCl_2$, 1 μmol dithiothreitol (DTT), 20 μmol $NaHCO_3$ (containing 1.48 MBq, specific radioactivity 0.38 MBq μmol^{-1}), and enzyme extract equivalent to 0.3-0.4 mg protein. The reaction volume was 1 cm^3. Reactions, at 25±1 °C, were initiated by adding 2 μmol RuBP and stopped after 1-min reaction with 100 mm^3 of 6 M HCl. The amount of fixed $^{14}CO_2$ was measured in a liquid scintillation spectrometer (*Beckman LS 1801*, USA).

Activity of GO (EC 1.1.3.1) was measured as described by Popova *et al.* (1987). For enzyme extraction, 0.050 g of leaves was ground in a pre-chilled mortar with purified sea sand and 20 cm^3 of 1/15 M K/Na phosphate buffer, pH 8.0. The homogenate was filtered through four layers of cheesecloth and centrifuged at 20 000×*g* for 15 min. To 5 cm^3 of extracts 0.5 cm^3 of 0.1 M Na-glycolate (H_2O for the controls) was added. Reaction time was 15 min at 28±1 °C. At the end of the reaction, the extracts were precipitated with trichloracetic acid (TCA, final concentration 3 %) and a colour reaction with 0.3 % phenylhydrazine hydrochloride and 1.5 % $K_3Fe(CN)_6$ was carried out. The amount of glyoxylic acid was assayed spectrophotometrically at 530 nm (*Spekol 11*, *Carl Zeiss*, Jena, Germany).

PGP (EC 3.1.3.18) was extracted and assayed according to Randall *et al.* (1971). A 0.5-g fresh plant material was ground in a chilled mortar with 2 cm^3 of medium containing 20 mM cacodylate buffer and 1 mM EDTA at pH 6.3. The homogenate was squeezed through cheesecloth and the extract was centrifuged at 10 000×*g* for 10 min. The enzyme activity was assayed in the supernatant for 10 min at 28±1 °C using 10 μM substrate, 100 μM cacodylate buffer (pH 6.3), and 1 mM $MgCl_2$ in a final volume of 1.5 cm^3. The reaction was terminated by the addition of 0.5 cm^3 10 % TCA. The precipitate was removed by centrifugation and the release of phosphorus was measured by the method of Kondrashova *et al.* (1965).

Catalase (EC 1.11.1.6) activity was determined by measuring the rate of H_2O_2 conversion to O_2 at 25 °C using a Clark-type O_2 electrode (*DW1 Hansatech*, Norfolk, UK) as described by Del Rio *et al.* (1977) with small modifications. Approximately 250 mg of plant tissue was extracted in 10 cm^3 of 50 mM Tris- HCl buffer (pH 7.5) and 1 mM DTT, and then centrifuged at 10 000×*g* for 15 min. The rate of O_2 production was measured by adding 0.2 cm^3 of the supernatant to 50 mM Na_2HPO_4-KH_2PO_4 (pH 7.0) containing 33.5 mM H_2O_2 in a total volume of 3.0 cm^3.

Soluble protein content was determined by the method of Bradford (1976). Chl was extracted by acetone and measured spectrophotometrically according to Arnon (1949).

Determination of stress markers: The contents of some non-specific stress markers were measured. Fresh material (about 150 mg) was homogenised in 3 cm^3 of 0.1 % cold TCA. The homogenate was centrifuged at 15 000×*g* for 25 min. The supernatant obtained was used for the determination of both hydrogen peroxide and lipid peroxidation contents.

The endogenous hydrogen peroxide was measured spectrophotometrically (λ = 390 nm) by a reaction with 1 M KI according to Jessup *et al.* (1994). The results were calculated using the standard curve prepared with fresh hydrogen peroxide solutions.

Lipid peroxidation was measured with the method of Heath and Packer (1968) with slight modifications. 0.2-0.3 g of leaf material was homogenised in 3 cm^3 of 0.1 % TCA and centrifuged at 15 000×*g* and 4 °C for 30 min. To 0.5 cm^3 aliquot of the supernatant, 0.5 cm^3 of 50 mM K phosphate buffer (pH 7.0) and 1 cm^3 reagent (0.5 % thiobarbituric acid in 20 % TCA, m/v) were added. For a negative control, 0.5 cm^3 of 0.1 % TCA + 0.5 cm^3 of 50 mM K phosphate buffer (pH 7.0) and 1 cm^3 reagent were added. The test tubes were heated at 95 °C for 30 min and then quickly cooled in an ice bath. After cooling and centrifugation to give a clear supernatant the absorbance of the supernatant at 532 nm was read and the value for the non-specific absorption at 600 nm was subtracted. The amount of malondialdehyde (MDA) was estimated using the mM extinction coefficient of 155 mM^{-1} cm^{-1}.

The degree of membrane integrity in three plants of similar size also was assessed by measuring the leakage of electrolytes from those portions of each plant which were above ground. The plant explants (leaf segments) were carefully washed, blotted dry, weighed, and put in stopped vials filled with 30 cm^3 of bi-distilled and deionised water. The vials were than incubated for 20 h in the dark with continuous shaking. The amount of electrolyte leakage was measured conductometrically on a basis of leaf area according to Dexter *et al.* (1932).

Results

Chl and protein contents: Treatment of barley seedlings with 23 μM MeJA for 24 h in the dark followed by 6-h irradiation did not cause wilting or irreversible damage to photosynthesis. Our previous experiments demonstrated that concentrations of JA or MeJA ranging from 10 to 50 μM are relevant for physiological studies. They did not cause visible damage after long-term treatment (up to 7 d), but caused reproducible and reversible effects on photosynthesis, growth, and biochemistry of barley plants (Metodiev *et al.* 1996, Tsonev *et al.* 1998). In most experiments the effect of Pq on the studied physiological parameters was tested using Pq concentrations of 1, 10, and 100 μM. When seedlings were treated with 100 μM Pq for 24 h, they were wilted and had no measurable photosynthesis. On the other hand, 1 μM Pq had no effect on the studied parameters (values not shown).

Dark-treated barley seedlings with 23 μM MeJA did not show loss in Chl content, whereas 10 μM Pq-treated seedlings contained less Chl. Next irradiation led to a decrease in Chl content in both MeJA- and Pq-treated seedlings. Pre-treatment of plants with MeJA for 24 h before Pq application and irradiation for 6 h caused a slight protection against Pq-induced Chl loss (Fig. 1*A*).

Treatment of barley seedlings with MeJA or Pq did not affect significantly the leaf soluble protein contents. Only pre-treatment with MeJA before application of Pq led to increase in protein content (Fig. 1*B*).

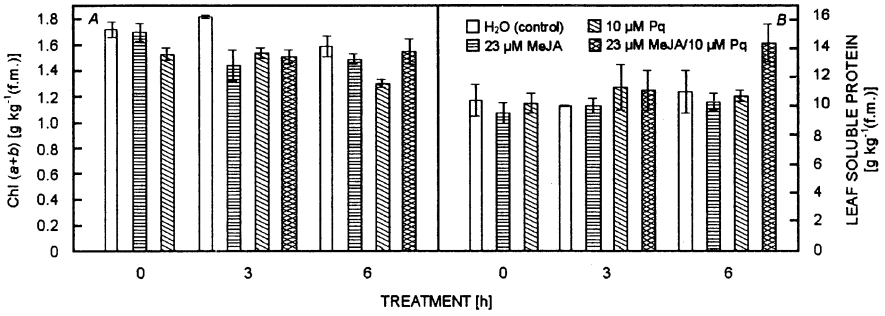

Fig. 1. Effect of MeJA and Pq on contents of chlorophyll (Chl) and leaf soluble protein in barley leaves. Cut ends of barley seedlings were incubated with distilled water (control), 23 μM MeJA, and 10 μM Pq for 24 h in the dark. Then half of the MeJA-treated seedlings were transferred into a beaker containing 10 μM Pq and all variants were exposed to 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR and sampled 3 and 6 h after irradiation, 0-24 h after dark treatment. Means ± S.E. of five replicate experiments.

Gas exchange: Treatment of barley seedlings with 23 μM MeJA for 24 h caused an inhibition in P_N. The effect was clearly expressed during the first hour of irradiation and then remained approximately constant. Incubation of seedlings with 10 μM Pq under the same experimental conditions led to a significant decrease in P_N in a time-dependent manner. After 2 h of irradiation P_N decreased by 62 % compared with the control values and reached approximately full suppression after 6 h of irradiation. P_N was fully recovered by pre-treatment of seedlings with MeJA for 24 h in the dark before the next exposure to Pq and irradiation (Fig. 2*A*).

Changes in the rate of transpiration (E) followed the tendency of P_N, the effect being better expressed during the first 3 h of irradiation (Fig. 2*B*). One hour after start of irradiation of barley seedlings the values for stomatal conductance (g_s) were very low in all variants, obviously due to stomata closure in the dark. After 3 and 6 h of irradiation they reached values measured in our other experiments with barley (Metodiev *et al.* 1996). We did not observe significant changes in the values of this parameter, leading to the suggestion than MeJA and Pq did not affect the stomata closure (Fig. 2*C*).

Effects of MeJA and Pq on activities of RuBPC, PGP, GO, and catalase: The *in vitro* RuBPC activity was almost unaffected when plants were treated for 24 h with 10 μM Pq and then irradiated for 6 h. Under the same experimental conditions, treatment with 23 μM MeJA or pre-treatment with MeJA before application of Pq led to a small decrease in the enzyme activity (Fig. 3*A*).

Treatment of plants with 23 μM MeJA alone influenced differently the activity of the photorespiratory enzymes. A slight decrease (approximately 15 %) was observed for the activity of GO, and an increase of 25 % in the activity of catalase. Pq treatment alone caused an almost 15 % increase in the activity PGP, and an approximately 30 % increase for GO and catalase activity, respectively. Pre-treatment of barley seedlings with 23 μM MeJA before exposure to 10 μM Pq caused a decline in the activity of the studied photorespiratory enzymes (Fig. 3*B-D*).

H_2O_2 content, lipid peroxidation, and electrolyte leakage: No major changes were observed in H_2O_2 content in plants treated with 23 μM MeJA. The respective values for Pq-treated or pre-treated with MeJA before exposure to Pq and irradiation were 40 % higher than in the control

(Fig. 4*A*).

Lipid peroxidation was assayed by monitoring MDA content in tissue extracts. Treatment with MeJA or Pq alone caused increases in MDA content to approximately 20 and 25 % of control. Pre-treatment with MeJA before exposure to Pq and irradiation also caused an increase in MDA content but to a lower extent (Fig. 4*B*).

Electrolyte leakage was much more pronounced in plants supplied with Pq than in those that were treated with MeJA. Pre-treatment with MeJA fully suppressed the values of Pq-induced increase in electrolyte leakage (Fig. 4*C*).

Discussion

Compounds that reduce the damaging effects of certain stresses, including herbicide stress, may be of great importance for both the theoretical and practical considerations. Hormones, including jasmonates, may mediate the acclimation of plants to environmental stress, and they may interact with other cellular metabolites and environmental factors in the regulation of stress responses (Parthier 1990).

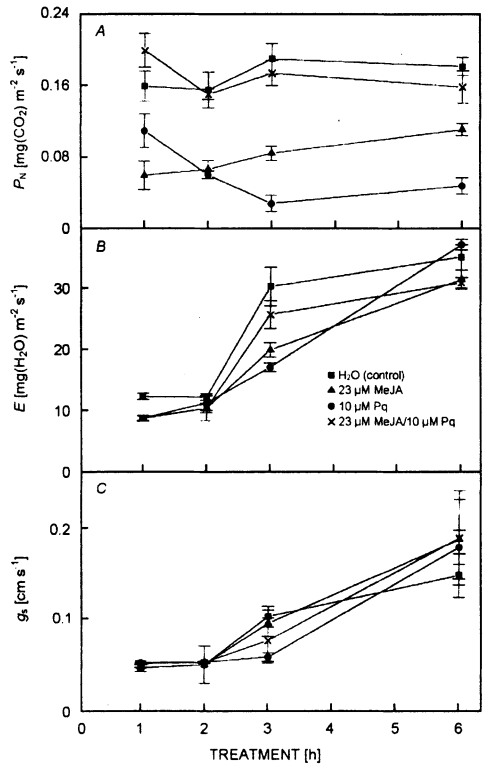

Fig. 2. Time-dependence of gas-exchange parameters in barley leaves treated with MeJA and Pq. P_N, net photosynthetic rate; E, transpiration rate; g_s, stomatal conductance. Variants and treatments as in Fig. 1. Means ± S.E. (n = 5).

The basic result of the present study is that exogenous pre-treatment of barley seedlings with MeJA for 24 h before exposure to Pq and irradiation protects photosynthesis (Fig. 2*A*). Treatment of barley seedlings with 10 µM Pq alone for 24 h in the dark followed by 6-h irradiation caused a strong decline in P_N in a time-dependent manner. P_N decreased and 3 h after the beginning of irradiation it was six-fold lower than in the control (Fig. 2*A*). A decrease in E also occurred but was less extent than the effect on P_N (Fig. 2*B*). A drop in the content of Chl (a+b) was found in Pq-treated plants (Fig. 1*A*). Pq-treatment did not affect the *in vitro* activity of RuBPC, while the activity of the photorespiratory enzymes PGP, GO, and catalase increased in treated plants (Fig. 3*A-D*). Relative to control plants, Pq-treated plants showed increases in the contents of H_2O_2, electrolyte leakage, and lipid peroxidation (Fig. 4*A-C*). All these results confirmed the well-known effect of Pq on photosynthesis, Chl breakdown, and on membrane integrity.

However, treatment of barley seedlings with 23 µM MeJA alone for 24 h in the dark followed by a 6-h irra-

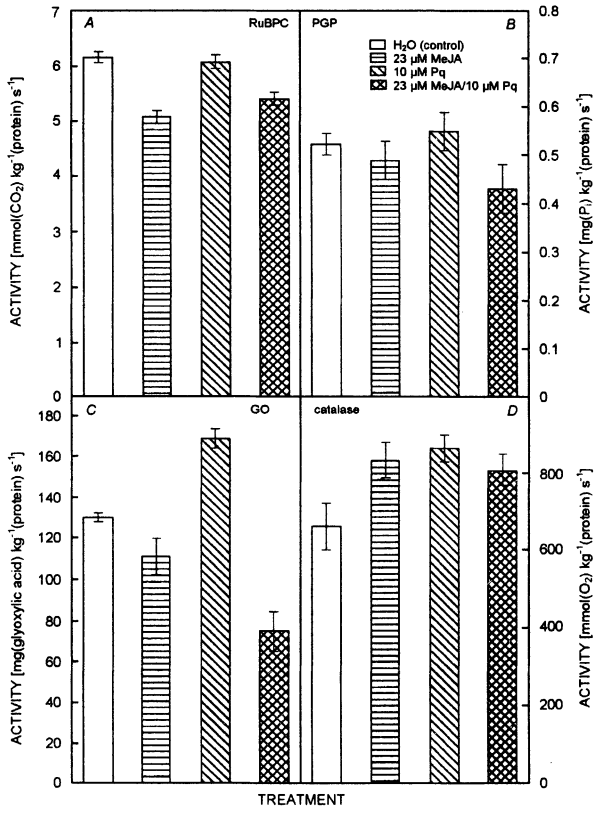

Fig. 3. Effect of MeJA and Pq treatment on the activity of RuBPC (*A*), PGP (*B*), GO (*C*), and catalase (*D*). Variants and treatments as described in Fig. 1. The activity of the enzymes was measured after 6 h of irradiation. Means from four separate experiments ± S.E.

diation also resulted in decrease in P_N and E. This agreed with our previous results: when barley seedlings were supplied with 10 μM JA through the transpiration stream for 24 h, P_N and g_s declined (Metodiev *et al.* 1996). Under our experimental conditions treatment with 23 μM MeJA caused a decrease in the activity of RuBPC (Fig. 3*A*). The electrolyte leakage and lipid peroxidation rate were higher in MeJA-treated plants than in the control (Fig. 4*B,C*).

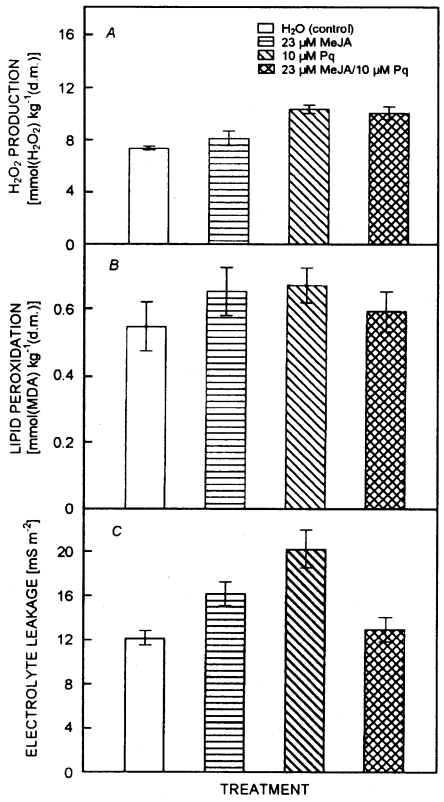

Fig. 4. Effect of MeJA and Pq treatment on H_2O_2 production (*A*), lipid peroxidation (*B*), and electrolyte leakage (*C*) in barley leaves. All measurements were done after 6 h of irradiation. Variants and treatments as described in Fig. 1. Means of four experiments ± S.E.

Many results suggest a connection between photosynthesis and jasmonates in plants (for review, see Creelman and Mullet 1997). In most of the cases, jasmonates protect photosynthesis against unfavourable conditions. For example, jasmonate-induced loss of Chl (Weidhase *et al.* 1987b, Popova *et al.* 1988) and the respective accumulation of anthocyanins (Franceschi and Grimes 1991) and β-carotene (Pérez *et al.* 1993) could protect against excess radiation. Jasmonate-mediated inhibition of the expression of photosynthetic genes, including those for the large and small subunits of RuBPCO and the light-harvesting Chl *a/b* binding protein, and other genes encoding proteins involved in photosynthesis (Reinbothe *et al.* 1993a,b), is consistent with the diminished need for photosynthates under high irradiance and excess carbon. Membrane stability may be a basic requirement for the maintenance of photosynthetic functions during unfavourable conditions. In this respect the modifications in composition and interaction of membrane components may be related not only to stress injury but also to an increase in stress tolerance. Maslenkova *et al.* (1990) established that exogenous treatment with JA led to inhibition of Hill reaction activity and to changes in the kinetic characteristics of flash-induced O_2 evolution. The modification of the stacking ability of thylakoid membranes could represent an adjustment to JA (Popova and Uzunova 1996). Some important changes in lipid composition (a decrease in the content of monogalactosyl-diacylglycerol and phosphatidylinositol) and in the extent of the fluidity of the membranes were related to biosynthesis of jasmonates and show that the plastid membranes are starting point for their synthesis. Under imbalance in the absorption and utilisation of photon energy, superoxide and hydroxyl radicals are generated. Antioxidant system is important in the protection against stress-induced damage in plants. As a part of this system, lipoxygenase and other enzymes that metabolise fatty acids may protect membranes from further damage by removing the oxy-radicals. The lipoxygenase-mediated generation of JA could induce changes in the cell that ameliorate further photochemical damage (Creelman and Mullet 1995).

The observed great activity of the photorespiratory enzymes and high H_2O_2 content in Pq-treated seedlings were most probably due to enhanced energy dissipation through photorespiration in stressed plants. Enhancement of photorespiration occurs during exposure of plants to salinity (Miteva and Vaklinova 1991) or after long-term treatment with ABA or JA (Popova *et al.* 1987, 1988). Despite the considerable loss of assimilated carbon as a result of photorespiration, photosynthesis benefits since photorespiration protects the photosynthetic membranes against photon-induced damage at time when carbon assimilation is limited (Heber *et al.* 1978, and for review see Foyer *et al.* 1994b).

In conclusion, we found that pre-treatment of barley seedlings with MeJA induced protection on photosynthesis against Pq stress. Many different causes may be considered in this respect: (*1*) MeJA could affect the photosynthetic light reactions leading to better adjustment of the rate of electron transport. (*2*) MeJA could activate the antioxidant enzymes (including lipoxygenase) in chloroplasts, which in turn increase Pq tolerance or trigger various defence-related genes. (*3*) The observed decrease in Chl and leaf protein breakdown in plants pre-treated with MeJA could prevent the further chloroplast destruction caused by Pq. The characterisation of specific

changes of the integrated antioxidant cell system to Pq and the role of jasmonates in protection of photosynthesis against Pq-induced oxidative damage requires further research.

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