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Increased Photoinhibition in Dehydrated Leaves of Hot Pepper (*Capsicum annuum* L.) Is Not Accompanied by an Incremental Loss of Functional PSII

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We examined the photosynthetic responses to photoinhibition in dehydrated leaves of hot pepper (*Capsicum annuum* L.). Stress was induced by immersing the roots of whole plants in Hoaglands solution containing polyethylene glycol (PEG) under high light (900 μmol photons $m^{-2} \cdot s^{-1}$). This PEG-treatment lowered the leaf water potential and the maximal rate of photosynthetic O_2 evolution (Pmax) linearly, in a time-dependent manner, to about 50% inhibition after 6 h. Pmax also decreased linearly as the period of high-light treatment lengthened. That inhibitory response was not as extreme, showing about 30% inhibition after 6 h. However, when the treatments of dehydration and high light were simultaneously administered, Pmax decreased more rapidly, in a synergistic fashion, showing about 90% inhibition within 2 h. Dehydration, in contrast to the light treatment, did not lower the maximal photochemical efficiency (Fv/Fm). Furthermore, this decline in Fv/Fm for light-treated, dehydrated leaves was almost identical to the response of photoinhibited leaves that were not dehydrated. Similar changes were observed in the number of functional PSII complexes. The decrease in Pmax and the amount of functional PSII was linearly correlated in photoinhibited leaves, but not in dehydrated leaves, regardless of light treatment. Therefore, we have demonstrated that exacerbated photoinhibition in dehydrated leaves occurs without an incremental loss of functional PSII.

Keywords: chlorophyll fluorescence, dehydration, functional PSII, photoinhibition

Light is an essential component for harnessing photosynthesis, but excessive levels can be detrimental to the photosynthetic apparatus (Powles, 1984; Barber and Andersson, 1992). In nature, plants more often than not encounter light intensities that exceed their photosynthetic capacity (Ort, 2001). Under those conditions, photosynthetic activities are inhibited, leading to less efficient photosynthesis and, ultimately, reduced growth. This phenomenon, known as photoinhibition or photoinactivation (Kok, 1956; Powles, 1984), results from the reception of more light than plants can utilize for their photochemistry, and depends on the rate of absorption (Jones and Kok, 1966; Anderson et al., 1997). However, the amount of light considered excessive for a given plant varies over awide range of irradiance levels, and according to environmental conditions (Ort, 2001). Thus the deteriorative effect of photoinhibition often increases when plants are growing under stresses (Björkman and Powles, 1984; Ben et al., 1987; Gamon and Pearcy, 1990).

Other factors influence photoinactivation of PSII, including light dose or photon exposure. In fact, given certain circumstances, a particular combination of irradiance and duration of illumination that provides the same amount of photon exposure may not cause the same level of photoinactivation (Park et al., 1995, 1996; Lee et al., 1999). Therefore, photoinhibition is not just an inevitable result of sustained excessive illumination, but may also occur under limited light (Park et al., 1995; Ort, 2001).

In addition to excess light, plants are adversely affected by other environmental factors that cause multiple stresses, such as water deficit and temperatures out of the optimal range. The susceptibility of plants to photoinhibition at a given light intensity also varies with their genetic adaptation, physiological

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Abbreviations: Chl, chlorophyll; Fm, maximal chlorophyll fluorescence after dark-adaptation; Fm', maximal chlorophyll fluorescence during illumination; Fo, initial chlorophyll fluorescence; Fv, variable chlorophyll fluorescence; NPQ, nonphotochemical quenching of chlorophyll fluorescence; PEG, polyethylene glycol; PFR, photon fluence rate; Pmax, maximal photosynthetic rate of O_2 evolution; PS, photosystem; qP, photochemical quenching of chlorophyll fluorescence; Φ_{PSII}, quantum yield of PSII

state, and life history (Powles, 1984). Photoinhibition is enhanced if high light is combined with other environmental stresses, namely, low or high temperature, drought, or CO_2 deficiency (Ludlow and Björkman, 1984; Boyer et al., 1987; Cornic et al., 1989). For example, at low water potential, plants show closed stomata and inhibited photorespiration, leading to reduced CO_2 availability and assimilation (Powles and Osmond, 1979; Osmond, 1981; Cornic and Briantais, 1991; Cornic, 1994). This response can cause damagingly high levels of excitation energy, even under otherwise favorable PFR (Ludlow and Powles, 1988; Gamon and Pearcy, 1990).

In *Nerium oleander*, chloroplast activities (i.e., electron transport activity and variable fluorescence yield) are inhibited more when low leaf potential develops in full sunlight than in shade, and photoinhibition is most severe when gas exchange is eliminated by complete stomatal closure (Björkman and Powles, 1984). Moreover, when low light-grown leaves are exposed to full illumination, both the light-saturated rate (Pmax) and the photon yield of photosynthesis are reduced, as well as PSII-driven electron transport activity (Powles and Critchley, 1980). Therefore, it is likely that these direct effects of water deficits on chloroplast function increase the susceptibility to photoinhibitory injury. However, PSII is highly resilient to water stress even though it is the targeting site for photoinhibition. Furthermore, it has been demonstrated that degree of susceptibility in plants to photoinhibition under water stress was independent of light intensity (Sharp and Boyer, 1986). What is more, increased photoinhibition is observed only under severe water stress or low CO_2 and O_2 concentrations (Ögren and Öquist, 1985; Sharp and Boyer, 1986; Cornic and Briantais, 1991). Nevertheless, despite some contradictory reports, it is generally agreed that photoinhibition is increased in plants experiencing water stress, but that the origin of increased susceptibility is unknown, as is any direct involvement by PSII.

Our primary objective in this study was to estimate the contribution of functional PSII to this exacerbated photoinhibition under water stress by directly assessing PSII functionality, which is best represented by the number of functional PSII complexes that are actually involved photochemically when light is absorbed (Chow et al., 1989). For our experimental materials, we selected hot pepper (*C. annuum* L.), a major crop in Korea, because its growing season often coincides with periods of drought often combined with high light intensities.

MATERIALS AND METHODS

Plant Material

Hot pepper plants (*C. annuum* L.) were grown for 4 to 5 weeks in pots containing Bioplug #2 soil (Hungnong Seeds Co, Ltd., Korea) in a growth chamber maintained at 25±1×C with a 16-h photoperiod. Light was provided from four banks of True-lite II fluorescent lamps (Durotest, USA) at the intensity of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Plants were grown under low light level to induce an increased susceptibility to the photoinhibitory treatment.

Photoinhibitory and Dehydration Treatments

Photoinhibitory and dehydration treatments were conducted as described by Lee et al. (1998, 1999). For the photoinhibitory treatment, detached leaves were floated in a water bath and directly illuminated on their adaxial sides with a tungsten halogen lamp (Itami Protex Co. Ltd., Japan) at 900 μmol photons$\cdot m^{-2} \cdot s^{-1}$ for up to 6 h. A glass container filled with running water was placed above the water bath to dissipate the heat. For the dehydration treatment, plants of the same age were carefully taken from their pots and washed in running water to remove the soil without damaging the roots. The roots were then immersed in various PEG-6000 solutions (2 to 30%; w/v) for zero to 6 h, either in the dark or under light (900 $\mu mol \cdot m^{-2} \cdot s^{-1}$) prior to the leaves being sampled. Leaves located perpendicular to the incident light and at the same height to receive an equal intensity were chosen for subsequent measurements.

Measurement of Water Potential

Water potential was measured psychrometrically at room temperature (Boyer and Knipling, 1965), using a dewpoint microvoltmeter (HR-33T) connected to a C-52 sample chamber (Wescor, USA). Leaf discs (0.7 cm diam.) were held in the chamber for at least 15 min to reach equilibrium, then cooled for 45 s before recording the voltage. Water potential was calculated from the voltage values, and corrected for temperature.

Measurement of O_2 Evolution and Chl Fluorescence

O_2 evolution and Chl fluorescence were measured simultaneously at 25°C, using 3.5-cm-diam. leaf discs

in a Hansatech LD2 leaf disc chamber (Kings Lynn, UK), a Walz PAM Chl fluorometer (Effeltrich, Germany), and a Clark type electrode connected to a Hansatech O_2 electrode control box (Delieu and Walker, 1983). Following either the dehydration or the photoinhibitory treatment, the samples were dark-adapted for 15 min. The leaf discs were first selected to have approximately equal Chl contents, as measured with a Minolta Chl meter (SPAD-502, Minolta, Japan); any differences were normalized. Our measurements of Chl content with a SPAD-502 matched reliably with those obtained conventionally via the acetone extraction method (Jun et al., 2001). Values for Fv/Fm (maximal photochemical efficiency), NPQ (non-photochemical quenching; Fm/Fm'-1), and qP (photochemical quenching; Fm'-F/Fm'-Fo') were calculated as described by Schreiber et al. (1994). Φ_{PSII} (quantum yield of PSII; $\Delta F/Fm'$) was calculated according to Genty et al. (1989).

Determination of Functional PSII Content

The number of functional PSII complexes was determined by the O_2 evolution of the leaf discs, according to the method of Chow et al. (1989). After the discs were dark-adapted for 15 min in a Hansatech O_2 electrode chamber, we applied repetitive single-turnover, saturating xenon flashes (10 Hz, 2.5 s full width at half-peak height) from a xenon flash lamp (Stroboslave type 1539-A) for 4 min, followed by 4 min of darkness. Subsequent cycles of flashes and darkness were the same. Background far-red light (approx. 1 $\mu mol \cdot m^{-2} \cdot s^{-1}$, 700 to 730 nm), which induced no appreciable oxygen evolution, was given during flash illumination to minimize the limitation of linear electron transport by PSI. The number of PSII complexes was expressed on a Chl basis, and was normalized to the control samples. Chl content was measured with a Minolta Chl meter.

RESULTS

Changes in Water Potential by PEG Treatment

To induce dehydration, whole plants of hot pepper were immersed for several hours in nutrition media containing various concentrations of PEG-6000. This treatment caused gradual wilting of the leaves. Under both light and dark experimental conditions, leaf water potential decreased linearly as the duration of the PEG treatment lengthened (Fig. 1). Although the degree of dehydration was dependent on concentration of the solution, a level of 5% (w/v) PEG gave rise to fast and sufficient dehydration, and thus was chosen as the optimal condition for subsequent procedures. Water potential in the leaf dropped linearly, from 0.75 MPa to 1.11 MPa, during 6 h of PEG treatment in the dark; nearly identical results were seen under high light (Fig. 1). Treatments of longer than 8 h caused no further decrease in potential, but permanent wilting was achieved (data not shown).

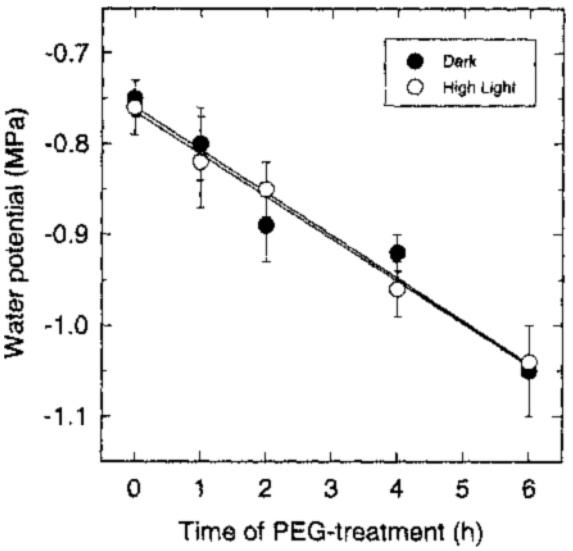

Figure 1. Changes in leaf water potential by 5% (w/v) PEG treatment. Dehydration was induced either in the dark or under high light (900 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Data are mean values ± SE (n= 2).

Changes in Pmax

Pmax of O_2 evolution decreased linearly as time increased for the PEG- or photoinhibitory treatments. The rate of inhibition induced by dehydration was faster than that caused by photoinhibition, i.e., 50% and 30% inhibition in Pmax, respectively, after 6 h of treatment (Fig. 2). However, when both stresses were administered simultaneously, Pmax decreased more rapidly and synergistically, showing 60% and 92% inhibition after only 1 h and 2 h, respectively (Fig. 2). Therefore, the adverse effect of photoinhibition was apparently exacerbated in the dehydrated pepper leaves.

Changes in Chl Fluorescence Parameters

Because PSII is the primary site affected by photoin-

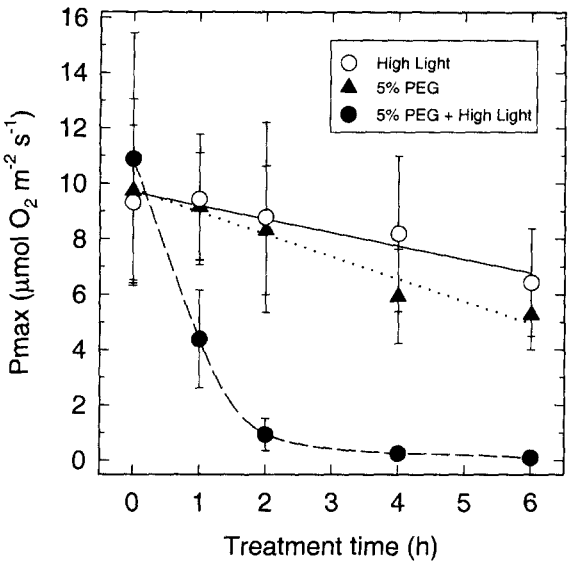

Figure 2. Changes in maximal photosynthetic O_2 evolution (Pmax) after high-light, PEG, or simultaneous treatment. Data are mean values ± SE (n=5).

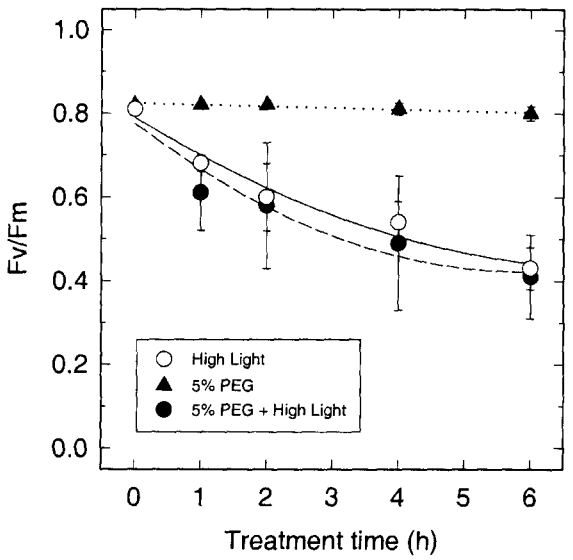

Figure 3. Change in maximal photochemical efficiency of PSII (Fv/Fm) after high-light, PEG, or simultaneous treatment. Data are mean values ± SE (n=5).

hibition (Powles and Critchley, 1980; Powles, 1984; Barber and Andersson, 1992; Barber, 1995), it is likely that the synergistic effect of photoinhibition in dehydrated leaves comes from the incremental damage to PSII or additional lesion sites caused by dehydration. The Chl fluorescence parameters of Fo and Fv/Fm are often used to assess PSII function (Renger and Schreiber, 1986). In our study, Fo was not influenced much by either dehydration or photoinhibitory treatments of up to 6 h, although that value was slightly lowered by simultaneous stress applications (data not shown). Similarly, Fv/Fm was little changed by the lowered water potential in the leaves (Fig. 3), but was greatly decreased, in a time-dependent mode, by the photoinhibitory treatment and by simultaneous treatment of dehydration and high light (Fig. 3). Even after that combined treatment, no further decrease was produced (Fig. 3). Therefore, Fv/Fm was decreased only to the extent imposed by photoinhibition alone. Based on these results, it appears that synergistic inhibition of Pmax by simultaneous treatments of high light and dehydration does not arise from incremental damage in PSII.

Changes in Functional PSII Content

Fv/Fm is often used as a dependable indicator for PSII functionality. However, the functional PSII content is a more direct parameter for estimating PSII damage. Although tedious and time-consuming, especially with a large sample size, the measurement of O_2 yield per single-turnover flash is a straightforward method for estimating the number of functional PSII complexes in leaf discs (Chow et al., 1989). In this study we instead tested the feasibility of using a more convenient Chl fluorescence parameter, 1/Fo - 1/Fm, to describe functional PSII content under our experimental conditions. This value was previously used in pea and hot pepper grown under moderate and high light intensities (Park et al., 1995, 1996; Lee et al., 1999, 2001). Thus (1/Fo - 1/Fm) was replotted against O_2 yield to examine the relationship between the two. Functional PSII content ranged from 30 to 100%, and was also linearly correlated with the values obtained from low light-grown (100 $\mu mol \cdot m^{-2} \cdot s^{-1}$) plants (data not shown). Consequently, we chose to use this alternative parameter for measuring the relative content of functional PSII complexes.

Functional PSII content remained stable after the dehydration treatment, but decreased gradually following the photoinhibitory stress (Fig. 4). However, no additional decrease in content was observed when photoinhibition was administered with dehydration compared with the results from our photoinhibition-only experiment (Fig. 4). Therefore, it is evident that the synergistic inhibition of high light in dehydrated leaves does not originate from additional damage to functional PSII, but arises elsewhere. Our plotting of the Pmax value against the number of functional PSII plainly demonstrated a linear relationship between

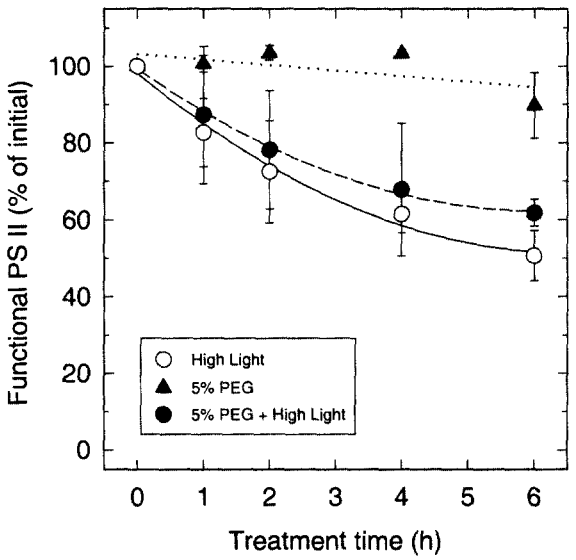

Figure 4. Change in number of functional PSII complexes after high-light, PEG, or simultaneous treatment. Data are mean values ± SE ($n=5$).

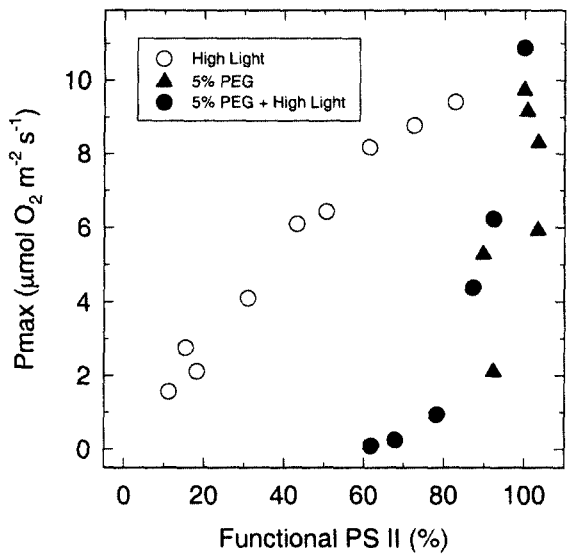

Figure 5. Relationship between Pmax and relative functional PSII content after high-light, PEG, or simultaneous treatment.

Pmax and the functional PSII content in photoinhibited leaves. However, in dehydrated leaves and in leaves that were simultaneously stressed, this linear relationship disappeared (Fig. 5). It was clear that the decline in Pmax was caused by factors other than the decrease in the number of functional PSII complexes and that dehydration, even when combined with photoinhibition, did not cause any more damage to PSII.

Changes in Chl Fluorescence Quenching Parameters

Changes in the Chl fluorescence quenching parameters are good indicators of photosynthetic electron flow and ΔpH formation (Schreiber et al., 1994). After the onset of illumination, maximal Chl fluorescence declines as the photosynthetic reaction proceeds due to the photosynthetic electron flow, qP, and nonradiative energy dissipation, NPQ (Genty et al., 1989). Therefore, we monitored these quenching parameters to estimate the contribution of those processes toward exacerbated photoinhibition. Photoinhibitory treatment substantially increased qP, but this value remained stable upon dehydration for the initial 2 h, and was only moderately decreased thereafter (Fig. 6). In contrast, qP continuously decreased when photoinhibition was given together with dehydration (Fig. 6). Φ_{PSII} ($\Delta F/Fm'$) was not significantly changed by dehydration, but was substantially decreased by photoinhibitory treatment (Fig. 6). That decrease was even more dramatic under simultaneous stresses, implying that PSII photochemistry efficiency was more severely hampered (Fig. 6). In contrast, NPQ was decreased to a similar extent by either the photoinhibitory or the simultaneous treatment (Fig. 7), indicating that thermal dissipation was not further increased in the dehydrated leaves.

DISCUSSION

Photoinhibition is manifested as a decline in photosynthetic activity when plants are exposed to excessive inputs of light energy, thereby causing the photoinactivation of PSII (Chow, 1994; Park et al., 1995; Anderson et al., 1997). Consequently, when photosynthetic activities are somehow hindered, the deteriorating effect of photoinhibition is often magnified, especially when plants are under stressed conditions (Björkman and Powles, 1984; Ludlow and Björkman, 1984; Ludlow and Powles, 1988; Gamon and Pearcy, 1990). Therefore, plants that experience water stress are more susceptible to photoinhibition (Björkman and Powles, 1984; Ludlow and Powles, 1988; Cornic et al., 1989; Cornic, 1994). However, the origin of this enhanced susceptibility and the contribution of functional PSII, a primary site of photoinhibition, to that effect are not yet thoroughly understood.

We investigated this matter using hot pepper plants subjected to simultaneous administration of high light

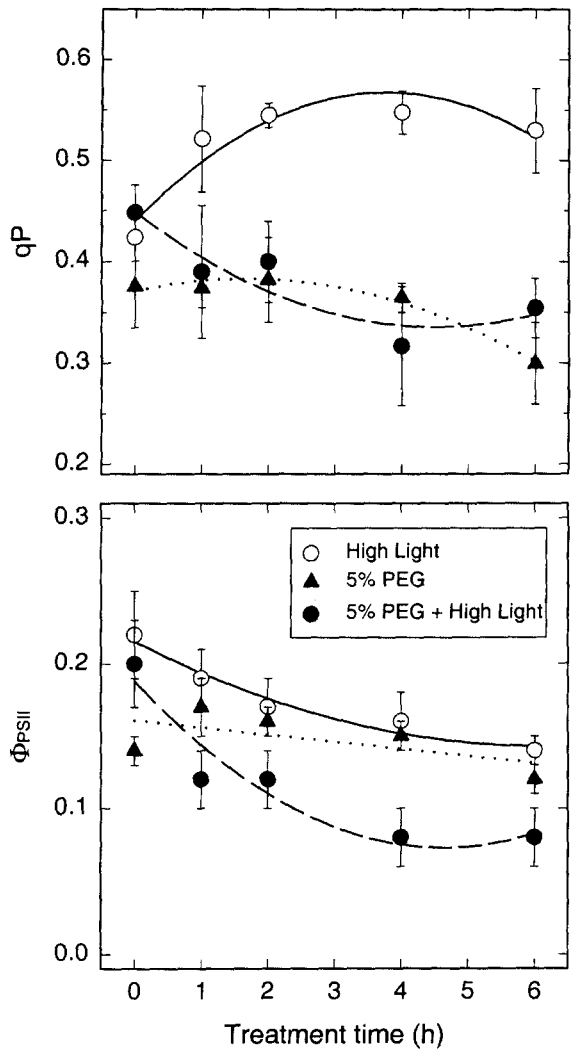

Figure 6. Change in PSII quantum yield (Φ_{PSII}) and photochemical quenching (qP) after high-light, PEG, or simultaneous treatment. Data are mean values ± SE ($n=5$).

and dehydration. Although limiting the water supply is the easiest and most common way to induce water deficit, actual field conditions can vary depending on soil water content, relative humidity, etc. Therefore, to provide more uniform and physiologically relevant conditions, we induced dehydration by immersing plants in a nutrition medium containing chemically inert PEG-6000 (Jackson, 1962; Lawlor, 1970; Michel, 1970). Our PEG treatment was useful in consistently lowering leaf water potential regardless of the amount of available light (see Fig. 1).

Whereas independent treatments with PEG or high light intensities decreased Pmax, the inhibitory effect was even more dramatic when both were administered together. Dehydration greatly enhanced the plants susceptibility (Fig. 2), with photoinhibition in the dehydrated leaves occurring not only more rapidly but also to a several-fold-higher degree than that without accompanying photoinhibition. Photoinhibition is accompanied with a loss in PSII function, which is often manifested by a rise in Fo and a decline in Fv/Fm (Renger and Schreiber, 1986). Our light treatment significantly decreased both Fm and Fv/Fm, reflecting substantial PSII damage (Fig. 3). In contrast, after dehydration, Fv/Fm showed little change, indicating no hindrance in PSII function. Nevertheless, although Pmax did decrease more under that condition than when photoinhibition was applied alone (see Fig. 3). Thus, PSII activity seems to be highly resistant to water stress, as previously reported (Björkman and Powles, 1984; Ögren and Öquist, 1985; Lee et al., 1998). Instead PSII activity was hampered only under severe water deficit conditions or when combined with photoinhibition (Nir and Poljakoff-Mayber, 1967; Keck and Boyer, 1974; Ögren and Öquist, 1985; Cornic et al., 1989; Havaux, 1992).

Jun et al. (1995) reported that direct measurement of PSII function using thylakoid membranes from wheat leaves after 24-h dehydration in PEG solution shows little reduction in PSII activity. It is questionable, however, whether PSII is damaged to the same extent by a combined stress treatment as it is when only photoinhibition is applied. Because photoinhibition results from PSII damage, it is possible that the increased susceptibility might originate from further damage to PSII. If photoinhibition under water stress does increase deterioration of PSII, Fv/Fm value would be expected to decline even more when photoinhibition is applied simultaneously with dehydration. However, our results proved otherwise (Fig. 3). Therefore, we believe it is very unlikely that the higher degree of inhibition in Pmax under the combined stresses resulted from further damage to PSII.

The number of functional PSII complexes is a reliable indicator of PSII functionality. A direct measurement of this parameter, though not difficult, is tedious. As an alternative, a Chl fluorescence parameter of (1/Fo - 1/Fm) was suggested to reflect function (Havaux et al., 1991; Walters and Horton, 1993). This parameter has already been used to describe functional PSII content in pea and hot pepper under various growing conditions (Park et al., 1995; Lee et al., 2001). Likewise, we found a linear relationship between (1/Fo - 1/Fm) value and PSII activity in our low light-grown pepper plants (data not shown), which allowed us to use this parameter for assessing

the number of functional PSII. The decrease in Pmax after photoinhibitory treatment was closely related with that seen with the decline in functional PSII content (Fig. 4). Even when photoinhibition was applied with dehydration, functional PSII contents decreased to the same extent as when the photoinhibitory treatment was given alone (Fig. 4). This was demonstrated by the existence of a linear relationship between Pmax and functional PSII content in photoinhibited leaves, but was lacking for either the dehydration-only leaves and or those treated with simultaneous stresses (see Fig. 5). It is evident that Pmax was further reduced by factors other than a greater decrease in the number of functional PSII. Therefore, we conclude that dehydration when combined with photoinhibition causes no additional damage to PSII, and that PSII is harmed only up to the level that results from exposure to high light, even when the two stresses are applied together.

Our measured NPQ values did not differ significantly between the photoinhibitory-only and the simultaneous treatments (Fig. 7). Therefore, it is unlikely that any incremental photodamage to PSII under the simultaneous treatment was due to increased thermal dissipation from the dehydrated leaves. It is possible, however, that nonfunctional PSII neighbors may have protected the remaining fraction of active PSII, as has also been suggested by Öquist et al. (1992). On the contrary, the decrease in qP and a more prominent drop in Φ_{PSII} under the combined stresses indicate that electron transport was hampered to a greater degree after the simultaneous treatment (see Fig. 6). Under water deficit conditions, PSII-driven electron transport activities are lower than normal (Björkman and Powles, 1984; Sharp and Boyer, 1986). In addition, both ATP content and ATP synthase activity are involved in water stress induced decrease in photosynthesis (Terzara et al., 1999). Thus, it is possible that, in leaves where dehydration and photoinhibition occur together, the hampered electron transport, along with a lowered ATP content induced by dehydration may be responsible for the additional decrease in Pmax as well as the lower measure of functional PSII content brought on by photoinhibition.

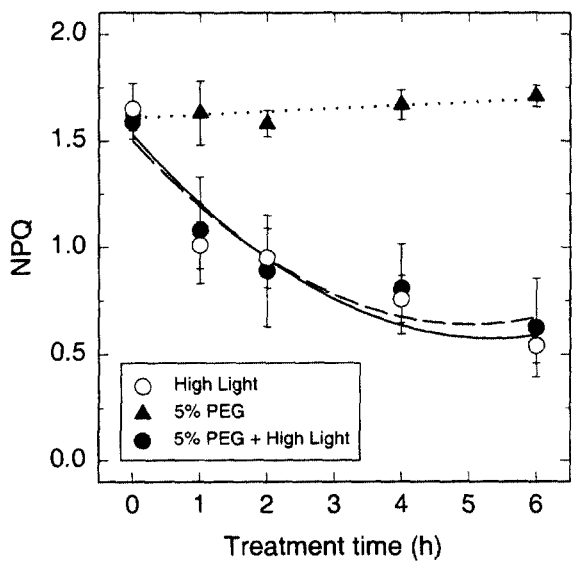

Figure 7. Change in nonphotochemical quenching (NPQ) after high-light, PEG, or simultaneous treatment. Data are mean values ± SE ($n=5$).

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