Photoinhibition is exacerbated in the dehydrated leaves of green pepper

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Introduction

Light, an essential component to harness photosynthesis, can be detrimental to the photosynthetic apparatus when excessive. Resultantly, decline in photosynthetic activities defined as photoinhibition or photoinactivation is ensued (Kok 1956; Powles 1984). Moreover, photoinhibition as a physiological phenomenon is dependent on other environmental conditions besides light (Björkman and Powles 1984; Ben et al. 1987). In particular, photoinhibition is enhanced if high light is combined with other environmental stresses such as low or high temperature, drought, or CO₂ deficiency (Powles and Osmond 1979; Boyer et al. 1987; Cornic et al. 1989; Gamon and Pearcy 1990). In spite of some contradictory reports, it is generally accepted that photoinhibition is augmented in the plants experiencing water stress. At low water potential, it has been suggested that if stomata were closed and photorespiration was inhibited, the availability of CO₂ would decrease and the reduction of CO₂ would be lessened (Powles and Osmond 1979; Cornic and Briantais 1991). It is also possible that direct effects of water deficits on chloroplast function increase the susceptibility to photoinhibitory injury (Sharp and Bover 1986). The purpose of present study is to estimate the role of changes in PSII functionality for the increased susceptibility to high light when photoinhibition is given under water stress. We demonstrate here that exacerbated photoinhibition in the dehydrated plants is accompanied with no incremental damage to PSII.

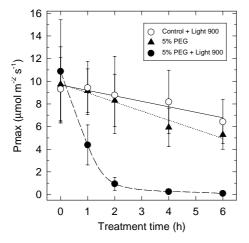
Materials and methods

Green pepper (*Capsicum annuum* L.) plants were grown for 4 to 5 weeks in a growth chamber maintained at 25±1°C with a diurnal cycle of 16 h-light and 8 h-dark under the light intensity of 100 μmol·m⁻²·s⁻¹. Photoinhibitory and dehydration treatment was done either by exposing the detached leaves directly to the light of 900 μmol·m⁻²·s⁻¹ supplied by halogen lamp or by immersing the roots in the Hoagland solution containing 5% (W/V) PEG-6000. Water potential of leaf was measured using dewpoint microvoltmeter (HR-33T, Wescor, USA). O₂ evolution and Chl fluorescence was simultaneously measured using a leaf disc (diameter 3.5 cm) in Hansatech (Kings Lynn, UK) LD2 leaf disc chamber with Clark type electrode and Walz PAM Chl fluorometer (Effeltrich, Germany). Each leaf disc was chosen to have approximately equal Chl content, when measured by Minolta Chl meter (SPAD-502, Minolta, Japan) and normalized to the control. The number of functional PSII was determined by O₂ evolution of leaf discs induced by repetitive flashes (Chow *et al.* 1989) and was expressed on Chl basis.

Results and discussion

Changes in Pmax and Chl fluorescence.

Green pepper plants subjected to PEG-treatment exhibited gradual wilting with concomitant decrease of water potential in the leaf, which was in linearity with increasing time of PEG-treatment. Water potential in the leaf prior to PEG-treatment was observed to be -0.75 ± 0.06 MPa, and was linearly dropped to -1.11 ± 0.16 MPa for the initial 6 h of PEG-treatment (not shown). Pmax of O_2 evolution was linearly decreased in relation to the increased time of PEG-treatment and photoinhibitory treatment. The pace of inhibition caused by dehydration was faster than by photoinhibition exhibiting roughly 50% and 30% inhibition, respectively, after 6 h of each treatment. When photoinhibition was given together with dehydration, decrease in Pmax was exacerbated to 60% inhibition after 1 h and near complete inhibition after 2 h (Fig. 1).



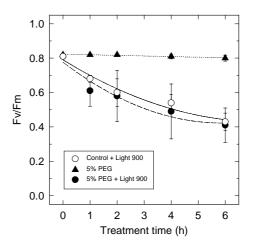


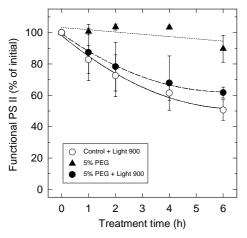
Fig. 1. Changes in Pmax by PEG, photoinhibitory, and simultaneous treatment.

Fig. 2. Changes in Fv/Fm by PEG, photoinhibitory, and simultaneous treatment.

Generally, PSII is the primary site mostly affected by photoinhibition. The synergistic effect of photoinhibition in the dehydrated leaves may come from incremental damage to PSII or additional lesion sites caused by dehydration. Fv/Fm, an indicator for PSII functionality, was little changed by the lowered water potential in the leaves. However, Fv/Fm was hyperbolically decreased by increasing time of photoinhibitory treatment. Moreover, there was no further decrease in Fv/Fm when photoinhibition was given together with dehydration. Fv/Fm was decreased to the similar extent by photoinhibition alone or photoinhibition along with dehydration (Fig. 2). Therefore, it appeared that synergistic inhibition in Pmax by the simultaneous treatment of high light and dehydration did not come from incremental damage to PSII.

Changes in functional PSII contents.

The Chl fluorescence parameter of [1/Fo - 1/Fm] was previously shown to represent functional PSII content in pea and green pepper (Park *et al.* 1995; Lee *et al.* 2001), and was proved to be valid in low light (100 µmol·m⁻²·s⁻¹) grown pepper in moist air containing 1% CO₂ used for this study (not shown). Functional PSII contents remained stable after dehydration treatment, but decreased by photoinhibitory treatment. When photoinhibition was given together with dehydration, functional PSII contents were similarly decreased as in photoinhibitory treatment alone (Fig. 3). Plotting of Pmax against the number of functional PSII yielded a linear relationship between these two parameters in the photoinhibited leaves. However, in the dehydrated leaves and simultaneously treated leaves, the linear relationship was disappeared



Control + Light 900 10 5% PEG + Light 900 Pmax (µmol m⁻² s⁻¹) 8 00 6 0 4 0 2 0 0 20 40 60 80 Functional PS II (%)

Fig. 3. Changes in the number of functional PSII by photoinhibitory, PEG, and simultaneous treatment.

Fig. 4. Relationships between Pmax and functional PSII in the leaves after PEG, photoinhibitory, and simultaneous treatment.

В

6

5

Changes in Chl fluorescence quenching parameters.

Chl fluorescence quenching parameters are indicative of photosynthetic electron flow and ΔpH formation. Upon dehydration, qP was slightly decreased while NPQ was slightly increased (Fig. 5). However, qP was more significantly decreased by photoinhibitory treatment, and further decreased by simultaneous treatment (Fig. 5A). Changes in Φ_{PSII} showed similar pattern as qP (not shown). On the other hand, NPQ was similarly decreased after photoinhibitory treatment alone or simultaneous treatment (Fig. 5B). Recently, decrease in ATP synthase activity and ATP content was shown to be involved in water stress induced decrease in photosynthesis (Tezara *et al.* 1999). It is possible that, in the leaves where dehydration and photoinhibition were given together, the lowered ATP content induced by dehydration may be responsible for the additional decrease in Pmax along with decrease in functional PS II contents induced by photoinhibition.

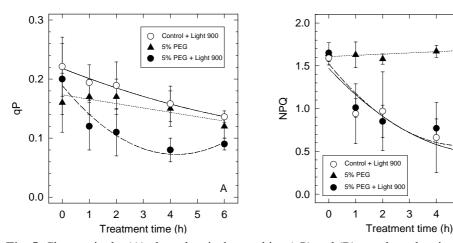


Fig. 5. Changes in the (A) photochemical quenching (qP) and (B) nonphotochemical quenching (NPQ) by PEG, photoinhibitory, and simultaneous treatment.

Conclusion

Exacerbated photoinhibition was observed in the dehydrated leaves, but without incremental damage to PSII as evidenced by no further reduction in both Fv/Fm and functional PSII contents. Deviation from linearity between Pmax and functional PSII contents in the dehydrated leaves under high light in contrast to photoinhibited leaves further demonstrates that incremental damage to PSII is not involved in the increased susceptibility. Magnified inhibition may come from additional lesion sites including partially hindered electron transport.

Acknowledgments

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