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Low-night temperature increased the photoinhibition of photosynthesis in grapevine (*Vitis vinifera* L. cv. Riesling) leaves

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Abstract

Photoinhibition of photosynthesis is a process by which excessive light radiation, which is absorbed by the leaves, results in the inactivation and/or impairment of the chlorophyll-containing reaction centers of the chloroplasts, thus inhibiting photosynthesis. The susceptibility of leaves to photoinhibition is known to be enhanced by additional stress factors, which coincide with the light. In this work, we have studied photoinhibition of photosynthesis in control and low-night temperature (LNT) leaves of grapevine (*Vitis vinifera* L. cv. Riesling) under controlled conditions (irradiation of detached leaves to about 1900 $\mu mol\, m^{-2}\, s^{-1}$). The degree of photoinhibition was determined by means of the ratio of variable to maximum chlorophyll (Chl) fluorescence (F_v/F_m) and electron transport measurements. The potential efficiency of PSII, F_v/F_m declined, F_0 increased significantly in high light (HL) irradiated LNT leaves than in control leaves. In isolated thylakoids, the rate of whole chain and PSII activity markedly decreased in HL irradiated more in leaves of LNT than in leaves of control. A smaller inhibition of PSI activity was also observed in both leaves. The artificial exogenous electron donors DPC, NH_2OH and Mn^{2+} failed to restore the HL induced loss of PSII activity in control leaves, while DPC and NH_2OH were restored in LNT leaves. It is concluded that HL in LNT leaves inactivates both acceptor and donor side of PSII whereas it does at the acceptor side only in control leaves. Quantification of the PSII reaction center protein D1 and 33 kDa protein water splitting complex following HL exposure of leaves showed pronounced differences between control and LNT. The marked loss of PSII activity in HL irradiated LNT leaves were due to the marked loss of D1 and 33 kDa proteins. The high degree of photoinhibition observed in LNT leaves probably represents a dynamic regulatory process protecting the photosynthetic apparatus from severe damage by excess light.

Keywords: Acceptor side; Chlorophyll fluorescence; Electron transport; Photosystem

1. Introduction

Light is essential for plant growth and development. However, too much of it may become harmful. The term photoinhibition relates to light-induced inhibition of the light reactions of photosynthesis. It results from the absorption of light energy in excess of the leaf capacity to utilize it for productive electron transport. Photoinhibition is a wide term, ranging from a protective, readily reversible regulatory mechanism of PSII centers, to the accumulation of irreversible photodamage (Kyle and Ohad, 1986; Aro et al., 1993). The photoinactivation and impairment of electron transport occurs at the acceptor and donor sides of PSII, although inactivation of the acceptor side may be the main mechanism for the impairment of electron transport (Eckert et al., 1991; Aro et al., 1993).

Low temperature is a major factor limiting the geographical locations suitable for crop growth and periodically accounts for significant losses in plant production. Short term exposure of plants to low temperature usually inhibits net photosynthesis due to accumulation of soluble sugars and reduced orthophosphate cycling from the cytosol back to

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the chloroplast and therefore limits ATP synthesis needed for Rubisco regeneration (Ebrahim et al., 1998; Hurry et al., 1998). The photosystems are the primary targets for chilling-induced photoinactivation. In some chilling-sensitive plant species inhibition of photosynthetic electron transport can occur, despite relatively minimal reductions in F_v/F_m due to net photoinactivation of PSI rather than PSII (Tjus et al., 1998; Sonoike, 1999).

Low temperature-induced stress has been shown to limit growth of grapevine (Buttrose, 1969), which is an economically important C_3 crop in many parts of the world. However, grapevine leaves in the field remain relatively resilient to low temperature-induced net photoinactivation of PSII based on sustained, high variable chlorophyll fluorescence (Hendrickson et al., 2003, 2004). This implies one or more highly efficient energy dissipation mechanism(s) are induced in grapevine leaves by the combination of low temperature and high light.

The damage resulting from excess light absorption may also be extenuated by other environmental factors. Essentially any perturbation, which decreases the rate of photosynthesis, will lead to an increased susceptibility to excess light absorption. It is well documented that exposure to the combination of low temperature and light irradiance produces large decreases in both the maximal rate quantum yield of carbon assimilation (Long et al., 1983; Ortiz-Lopez et al., 1990). Low temperature affects photoinhibition at several levels. It shows down the enzymatic reactions of electron transport and carbon metabolism, as well as the stroma-grana lateral diffusion and protein synthesis involved in repair of damaged PSII centers. Chilling in the light enhances photoinhibition in both chilling-sensitive and chilling tolerant plants, and the basic mechanism of photoinhibition, in so far as PSII is involved, appears to be the same (Aro et al., 1990).

The D1 reaction center protein of PSII is a target of light-induced damage to the PSII complex; turnover of the D1 protein is accelerated by increasing irradiance (Aro et al., 1993). The hypothesis that degradation of D1 protein may regulate the functioning of the PSII repair cycle under photoinhibitory conditions has arisen from experiments with higher plants acclimated to different growth irradiances. It was suggested that, like in cold-acclimated spinach, the D1 protein is stabilized in young canopy leaves and in D1 inactivation, and that turnover takes little part in photoinhibition and recovery. Plants that are capable of sustaining high rates of replacement of damaged D1 protein are likely to show little reduction in quantum efficiency of O_2 evolution or F_v/F_m (Andersson and Aro, 2001). However, it has been found in higher plants that D1 repair is generally limited at low temperatures because D1 proteolysis is showed down, thus preventing the integration of newly synthesized D1 protein and consequently increasing photoinhibitory damage (Aro et al., 1990). For grapevine leaves, Chaumont et al. (1995) demonstrated that 80% of initial D1 pool size was retained during a 5 °C and 1500 μmol m^{-2} s^{-1} treatment over several hours, suggesting that the rate of repair is still considerable at low temperatures in contrast to the results of other C_3 plants.

In the work presented here we have focused on the photoinhibitory responses in control and LNT leaves of grapevine (*Vitis vinifera* L. cv. Riesling). The effect of photoinhibition was analyzed with respect to photosynthetic oxygen evolution and potential efficiency of PSII (F_v/F_m) function by fluorescence. The amount of D1 and 33 kDa proteins were also analyzed in relation to the functional properties of PSII after photoinhibition.

2. Materials and methods

2.1. Plant material and low-night temperature treatment

One-year-old cuttings of *Vitis vinifera* L. cv. Riesling were grown in 10 L pots under natural photoperiod. The maximum irradiance avilable at the top of the plant was 1500 μmol m^{-2} s^{-1} on a clear day. Daily maximum and minimum air temperatures were 26–29 °C and 20–22 °C, respectively. Light intensity and temperature were measured as in Iacono et al. (1995). The plants were watered regularly with nutrient solution.

Low-night temperature (LNT) treatment was carried out as follows: plants were transferred in the evening into walk-in growth chamber (Lab line, 104 A, IL, USA) for overnight (18:00–06:00) exposure in the dark. Control plants were treated similarly, except for overnight incubation at 28 °C rather than 5 °C. On the following morning they were equilibrated for 1 h at ambient temperature in the shade (PAR = 30–100 μmol m^{-2} s^{-1}) then exposed leaves to HL under controlled environmental chamber.

2.2. Photoinhibition and recovery under controlled conditions

Detached control and LNT leaves were placed into a controlled-environment chamber equipped with a 24 V/250 W metal-halide lamp (H. Walz, Effeltrich, FRG). The upper leaf surface was exposed to a photon flux density (PFD) of 1900 μmol m^{-2} s^{-1}. Air temperature was 20 °C and relative humidity 66 ± 5%. The PPFD was measured with quantum sensor (LI-Cor, Lincoln, Neb., USA). Leaf temperatures, recorded with thermocouple attached to the lower surface were between 27 and 29 °C. Discs of 1.6 cm^{-2} area were punched from the leaf blades after specified times of high-light (HL) exposure and placed on moist filter paper in petri dishes (temperature 25–27 °C). The leaf discs were darkened for 5 min before the degree of photoinhibition was determined by fluorescence measurement.

2.3. Modulated chlorophyll fluorescence in leaves

Chlorophyll fluorescence was measured on leaf discs using a PAM 2000 fluorometer (H. Walz, Effeltrich, FRG).

Before the measurements, the leaves were dark adapted for 30 min. F_0 was measured by switching on the modulated light 0.6 kHz; PPFD was less than 0.1 μmol m^{-2} s^{-1} at the leaf surface. F_m was measured at 20 kHz with a 1 s pulse of 6000 μmol m^{-2} s^{-1} of white light.

2.4. Activities of electron transport

Thylakoid membranes were isolated from the leaves as described by Berthhold et al. (1981). Whole chain electron transport ($H_2O \rightarrow MV$) and partial reactions of photosynthetic electron transport mediated by PSII ($H_2O \rightarrow DCBQ$; $H_2O \rightarrow SiMo$) and PSI ($DCPIPH_2 \rightarrow MV$) were measured as described by Nedunchezhian et al. (1997). Thylakoids were suspended at 10 μg Chl ml^{-1} in the assay medium containing 20 mM Tris–HCl, pH 7.5, 10 mM NaCl, 5 mM $MgCl_2$, 5 mM NH_4Cl and 100 mM sucrose supplemented with 0.5 mM DCBQ and 0.2 mM SiMo.

2.5. DCPIP photoreduction

The rate of DCPIP photoreduction was determined as the decrease in absorbance at 590 nm using a Hitachi 557 spectrophotometer. The reaction mixture (3 cm^3) contained 20 mM Tris–HCl, pH 7.5, 5 mM $MgCl_2$, 10 mM NaCl, 100 mM sucrose, 0.1 mM DCPIP and thylakoid membranes equivalent to 20 μg of Chl. Where mentioned, the concentration of $MnCl_2$, DPC and NH_2OH were 5, 0.5, and 5 mM, respectively.

2.6. Immunological determination of thylakoid proteins

The relative contents of certain thylakoid proteins/mg chlorophyll were determined immunologically by western blotting. Thylakoids were solubilized in 5% SDS, 15% glycerine, 50 mM Tris–HCl (pH 6.8) and 2% mercaptoethanol at room temperature for 30 min. The polypeptides were separated by SDS-PAGE as described by Laemmli (1970) and proteins were then transferred to nitrocellulose by electroblotting for 3 h at 0.4 A. After saturation with 10% milk powder in TBS buffer (pH 7.5). The first antibody in 1% gelatine was allowed to react overnight at room temperature. After washing with TBS containing 0.05% Tween-20, the secondary antibody [Anti-rabbit IgG (whole molecule) Biotin Conjugate, Sigma] was allowed to react in 1% gelatine for 2 h. For detection of D1 protein a polyclonal antiserum against spinach D1 protein was used (kindly provided by Prof. I. Ohad, Jerusalum, Israel), and the antibody against the 33 kDa protein of the water-splitting system was a gift from Dr. Barbato, Padova, Italy. The densitometry analysis of western blots was performed with a Bio-Image analyser (Millipore Corporation, MI, USA).

2.7. Statistical analysis

The physiological responses were tested using a three-way analysis of variance (ANOVA) if the data met the assumptions of normality and homoscedasticity. Significant differences were determined by the student's *t*-tests criterion. All the statistical procedures were performed with SPSS 10.0 for Windows (SPSS Inc., Chicago, IL, USA).

3. Results

In order to compare the susceptibility to photoinhibition between control and LNT leaf samples were subjected to HL exposure in a controlled-environment chamber. The PSII potential efficiency, measured as F_v/F_m of leaves at 0 min high light, was 0.798 and 0.781 for control and LNT leaves, respectively (Fig. 1). For leaves measured at 60 min HL treatment, the F_0 increased significantly in LNT leaves, while F_0 slightly increase in control leaves. The F_v/F_m ratio also decreased around 0.630 in control and 0.429 in LNT leaves.

Photosynthetic electron transport activities were measured in thylakoids isolated from HL irradiated control and LNT leaves are shown in Fig. 2. After 60 min, photosynthetic electron transport from $H_2O \rightarrow DCBQ$ and $H_2O \rightarrow SiMo$ was

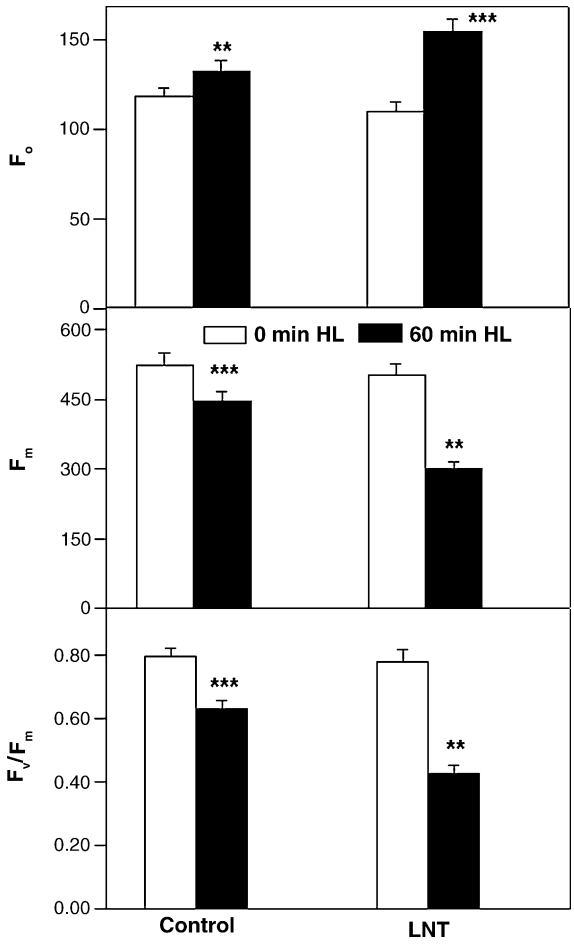

Fig. 1. Changes the relative levels of fluorescence emitted as minimal fluorescence (F_0), maximal fluorescence (F_m) and the ratio of variable to maximal fluorescence (F_v/F_m) of control and LNT leaves irradiated with 60 min high light (HL). Means ± S.E. are shown ($^{***}P < 0.001$, $^{**}P < 0.01$).

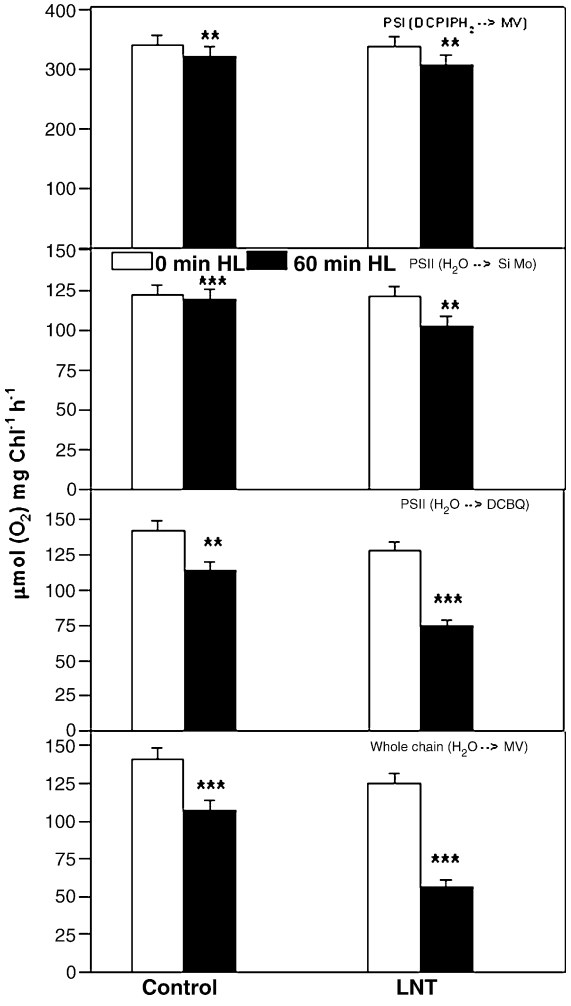

Fig. 2. Changes in the rates of whole chain ($H_2O \rightarrow MV$), PSII ($H_2O \rightarrow$ DCBQ; $H_2O \rightarrow$ SiMo) and PSI ($DCPIPH_2 \rightarrow MV$) electron transport activities in thylakoids isolated from HL (HL) irradiated in control and LNT leaves. Means ± S.E. are shown ($^{***}P < 0.001$, $^{**}P < 0.01$).

reduced by 20 and 2% in control, and 41 and 15% in LNT leaves, respectively. A significant reduction of PSII activity noticed when DCBQ and SiMo were used electron acceptor in LNT leaves but not inhibited when SiMo was used electron acceptor in control leaves (Fig. 2). A small inhibition of PSI activity was also observed in both control and LNT leaves (Fig. 2).

To locate the possible site(s) of inhibition in the PSII reaction, we followed the DCPIP photoreduction supported by various exogenous electron donors in thylakoids isolated from 60 min HL irradiated control and LNT leaves. Wydrzynski and Govindjee (1975) have shown that $MnCl_2$, DPC, NH_2OH and HQ could donate the electrons in the PSII reaction. Fig. 3 shows the electron transport activity of PSII in the presence and absence of three of the above compounds. The PSII activity was reduced to about 22 and 52% in control and LNT leaves, when water served as electron donor. A similar trend was also found using DPC, NH_2OH and $MnCl_2$ as

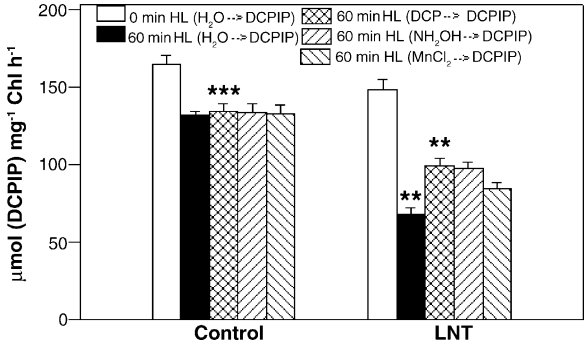

Fig. 3. Effect of various exogenous electron donors on PSII activity ($H_2O \rightarrow$ DCPIP) in thylakoids isolated from 60 min high light (HL) irradiated control and LNT leaves. Means ± S.E. are shown ($^{***}P < 0.001$, $^{**}P < 0.01$).

donor in control leaves. In contrast, the loss of PSII activity was restored using DPC and NH_2OH in LNT leaves (Fig. 3).

Photoinhibition of PSII is known to induce breakdown of the D1 protein (Andersson and Styring, 1991; Prasil et al., 1992). In systems without protein biosynthesis this can be seen directly as a loss in D1 protein content. In intact plant the correlation between D1 protein content and activity of PSII is more complex (Smith et al., 1990; Lutz et al., 1992). Photoinhibition induced inhibition of PSII activity in thylakoids of control and LNT leaves was compared with changes in the relative content of D1 and 33 kDa proteins as determined by western blotting (Fig. 4) followed by quantification by the bio-image apparatus (Fig. 4). The relative content of D1

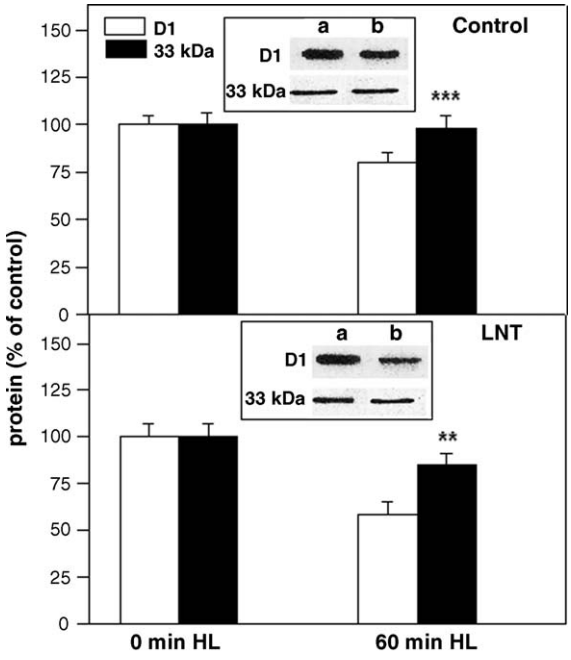

Fig. 4. Contents of D1 and 33 kDa protein as determined by western blotting in high light (HL) irradiated control and LNT leaves. Lane a, 0 min HL; and lane b, 60 min HL. Each lane loaded with equal amounts of Chl (5 μg). The protein amounts obtained from the densitiometrical evaluation of the western blots. Means ± S.E. are shown ($^{***}P < 0.001$, $^{**}P < 0.01$).

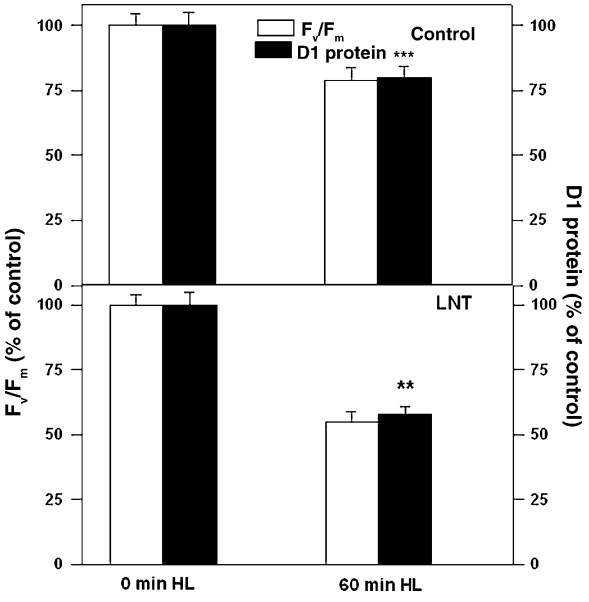

Fig. 5. Quantification of D1 protein and degree of photoinhibition in control and LNT leaves irradiated with high light (HL). Data are given in % of non-photoinhibited controls. Means ± S.E. are shown ($^{***}P < 0.001$, $^{**}P < 0.01$).

and 33 kDa protein decreased to 20 and 2% in control, and 42 and 15% in LNT leaves irradiated with 60 min high light, respectively.

In Fig. 5, relative D1 protein contents and F_v/F_m ratios are compared after photoinhibitory treatments of control and LNT leaves. In the control leaves, D1 degradation could be attributed to the action of photoinhibitory light, when the F_v/F_m ratios had decreased to 20–21%. The LNT leaves showed a strong decrease in D1 protein content together with the decline of F_v/F_m ratio about 45% (Fig. 5).

4. Discussion

Many plants are tolerant to HL levels and their photosynthetic capacity is inhibited only when HL accompanied by additional stress such as the absence of sufficient CO_2 (Morot-Gaudry et al., 1986). A combination of water stress and HL caused decrease in PSII efficiency in *Nerium oleander* (Demmig-Adams et al., 1988). Similarly, in our results exposure to chilly nights and followed by HL induced severe inhibition of photosynthetic activity and potential efficiency of PSII (F_v/F_m) in grapevine leaves.

The decline in F_v/F_m indicates a reduction in potential PSII efficiency. In many studies, a close correlation of the F_v/F_m ratio with the quantum yield of photosynthetic O_2 evolution or CO_2 assimilation under light limiting conditions has been reported (Krause and Weis, 1991; Krause et al., 1995). The reduction of F_v/F_m in HL irradiated LNT leaves were mainly caused by a decline in F_m. It has been proposed that an increase in F_0 may be induced by the inactivation of part of PSII reaction centers (Critchley and Russell, 1994; Yamane et al., 1997). Our experimental results from LNT leaves are in accordance with this idea. When F_0 increased in LNT leaves under high light, some PSII reaction centers lost their photochemical activity as indicated by a marked decline in the photochemical efficiency of PSII (F_v/F_m). Similar depressions in F_v/F_m ratio have been already reported for several plant species (Demming-Adams and Adams, 1992; Iacono et al., 1994; Chaumont et al., 1995).

In thylakoids isolated from HL irradiated LNT leaves, the oxygen evolution was inhibited markedly when the electron acceptor used were DCBQ and SiMo. This is mainly due to HL inactivate both in the reducing side and donor side of PSII. This is also supported by our chlorophyll fluorescence studies where F_0 was markedly increased and F_v markedly decreased (Asada et al., 1992; Endo et al., 1998). In contrast, thylakoids isolated from control leaves, the rate of PSII activity observed with DCBQ is lower than the one observed with that SiMo. This is due to acceptor side is more impaired than the donor side of PSII (Allakhverdiev et al., 1987; Setlik et al., 1990). A relationship between F_v/F_m and PSII electron transport activity in thylakoids isolated from photoinhibited leaves has also been shown (Somersalo and Krause, 1990; Schnettger et al., 1994).

To locate the possible site of inhibition in the PSII reaction, we followed the DCPIP photoreduction supported by various exogenous electron donors in thylakoids isolated from 60 min HL irradiated both control and LNT leaves. Among the artificial electron donors tested DPC donates electrons directly to the reaction center (Wydrzynski and Govindjee, 1975). Addition of DPC and NH_2OH restored in HL induced loss of PSII activity in LNT leaves. This is due to water-oxidizing system is sensitive to HL in LNT leaves. In contrast, using either DPC or NH_2OH in control leaves did not restore the loss of PSII activity. It is clear that HL induced changes only on the acceptor side of PSII in control leaves (Eckert et al., 1991; Aro et al., 1993).

The loss of PSII activity could only partially be ascribed to functional inhibition of PSII since F_v/F_m was reduced by about 21 and 45% in control and LNT leaves, respectively. We, therefore, assume that it was mainly due to loss of PSII centers on a chlorophyll basis. This could be confirmed by the immunological determination of the PSII reaction center protein of D1 and 33 kDa protein of water splitting complex. It is often thought that photoinhibition is a result of loss of D1 protein in control leaves, while marked loss of D1 and 33 kDa protein in LNT leaves. So it occurs only when the rate of damage to D1 protein exceeds the rate of its repair (Kyle et al., 1984; Barber, 1995). Moreover, the decrease in F_v/F_m under photoinhibitory conditions is often attributed to the loss of D1 protein. The extrinsic protein of 33 kDa associated with the lumenal surface of the thylakoid membranes are required for optimal functioning of the oxygen evolving machinary (Millner et al., 1987; Enami et al., 1994). Our immunological results indicate that the loss of 33 kDa protein could be one of the reasons for the marked loss of O_2 evolution (PSII) capacity in LNT leaves.

However, as shown by D1 protein quantification, strong photoinhibition of LNT leaves does seem to be related to inactivation and degradation of the D1 protein in the PSII reaction center. We found good relation between photoinhibition of photosynthesis and loss of the D1 protein when LNT leaves irradiated with HL were compared. D1 protein repair is also a highly important process at low temperature in grapevine leaves. This is surprising given that the D1 repair process has been reportedly suppressed by low temperature in Capsicum (Lee et al., 1999) and even completely inhibited at 4 °C in pumpkin (Salonen et al., 1998). Cold acclimation of plants includes a desaturation of glycerolipids within the thylakoid membrane that accelerates the processing of precursor D1 protein (Murata and Nishiyama, 1998). It is therefore expected that cold-acclimated grapevines would have an even greater resilience to photoinactivation at low leaf temperatures (Hendrickson et al., 2004).

From the results we conclude that the high degree of photoinhibition in the LNT leaves indicated by a strong decrease in the F_v/F_m ratio probably reflects a dynamic regulator response of the photosynthetic system to excess absorbed light energy. The observed photoinhibition is possibly associated with some loss of productivity but might protect photosynthetic pigments and the electron transport apparatus from destruction. Our results also suggest that photoinactivation of PSII is correlated with loss of D1 protein, and photoinhibition represents the formation of inactive centers (Smith et al., 1990; Flexas et al., 2001). We have found that low-night temperature markedly enhance photodamage in grapevine leaves. Low-night temperature cause sub-optimal photosynthetic performance even when no visual symptoms are observed. The non-destructive measurements of chlorophyll fluorescence and electron transport measurements are most useful to detect such conditions. Low-night temperature damage might result indirectly from a secondary factor such as sunlight. For agricultural purposes, it might be easier to avoid the secondary factor rather than the primary one. Further studies are in progress to know the molecular mechanism(s) in photosynthetic machinery by HL exposed to LNT leaves.

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