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BRIEF COMMUNICATION

Low night temperature effects on photosynthetic performance on two grapevine genotypes

M. BERTAMINI*, L. ZULINI*, K. MUTHUCHELIAN** and N. NEDUNCHEZHIAN*[1]

*IASMA Research Center, Agricultural Resources Department, via E. Mach, I-38010 San Michele all'Adige, Italy** *School of Energy, Environment and Natural Resources, Madurai Kamaraj University, Madurai-625021, India***

Abstract

The functional activities of the photosynthetic apparatus of two grapevine genotypes (*Vitis vinifera* L. cvs. Müller-Thurgau and Lagrein) were investigated after low night temperature (LNT) treatment for 7 d. LNT caused important reductions of the net photosynthetic rate (P_N) of Lagrein plants due to non-stomatal components. These non-stomatal effects were not evident in Müller-Thurgau. At LNT treatment, the contents of photosynthetic pigments decreased significantly in Lagrein, but in Müller-Thurgau the contents of chlorophyll (Chl) remained unchanged whereas the contents of carotenoids (Car) increased. An increase and decrease of Chl *a*/*b* was shown in Müller-Thurgau and Lagrein stressed plants, respectively. RuBPC activity and content of soluble proteins were also significantly reduced in Lagrein. Under LNT treatment, photosystem (PS) 2 was markedly more inhibited in Lagrein than in Müller-Thurgau. The decrease in PS 2 activity in Lagrein was mostly due to the marked loss of D1, 47, 43, 33, 28-25, 23 and 17 kDa proteins determined by immunological and SDS-PAGE studies.

Additional key words: carotenoids, chlorophyll fluorescence, electron transport, RuBPC.

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 photosynthetic rate (Ebrahim *et al*. 1998). The photosystems are the primary targets for chilling-induced photoinhibition (Cavaco *et al*. 2003). In some chilling-sensitive plant species inhibition of photosynthetic electron transport can occur, despite relatively minimal reductions in variable to maximal fluorescence ratio (F_v/F_m) due to photoinactivation of photosystem (PS) 1 rather than PS 2 (Sonoike 1999, Hendrickson *et al*. 2004) when leaf temperature drops to around 10 °C.

Low temperature-induced stress has been shown to limit growth of grapevine (Buttrose 1969). However, grapevine leaves in the field remain relatively resilient to low temperature-induced photoinactivation of PS 2 based on sustained, high F_v/F_m (Flexas *et al*. 1999, 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 irradiance.

Chilling temperatures can limit photosynthesis *via* stomatal closure, inhibition of thylakoid electron transport and photophosphorylation, RuBPC inactivation, inhibition of key enzymes in sucrose and starch biosynthesis, and phloem loading (Allen and Ort 2001, Huang and Guo 2005). When low temperature events physically and metabolically restrict the demand for carbon, supply exceeds demand and photosynthesis is down regulated to correct this balance. This down regulation is affected by reduced RuBPC activity or reduced rate of RuBPC regeneration.

The D1 protein in the PS 2 reaction center is a primary target for oxidative damage by reactive oxygen

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Abbreviations: Car - carotenoids; Chl - chlorophyll; DCBQ - 2,6-dichloro-*p*-benzoquinone; F_0 - minimal fluorescence; F_m - maximum fluorescence; F_v - variable fluorescence; g_s - stomatal conductance; LNT - low night temperature; MV - methyl viologen; P_N - net photosynthetic rate; PS - photosystem; ΦPS 2 - efficiency of open reaction center in light; RuBPC - ribulose-1,5-bisphosphate carboxylase.

[1] Corresponding author, present address: Govt. Higher Secondary School, Vellimedupettai-604207, Tindivanam, India; fax: (+91) 4147 222512, e-mail: nedu1963@yahoo.com

species (Aro *et al*. 1990). Plants which 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 proteo-lysis is decreased, 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. In the present study, the effects of low night temperature (LNT) on leaf pigments, ribulose-1,5-bisphosphate carboxylase and photosynthetic efficiency of two grapevine genotypes (*Vitis vinifera* L. cv. Müller-Thurgau and Lagrein) were determined. Based on this physiological comparison, insight in to the mechanism responsible for differences in tolerance low temperature should be possible.

Plants of two grapevine (*Vitis vinifera* L.) cultivars Müller-Thurgau and Lagrein were grown in pots with silica sand and daily irrigated and fertilized with half-strength Hoagland's nutrient solution. Plants were grown in controlled glasshouse at 12-h photoperiod, irradiance of 400 μmol m^{-2} s^{-1}, relative humidity of 55 % and day/night temperature of 25/20 °C. One group of plants was continuously grown at 25/20 °C (control), while the other group of plants were subjected to low night temperature (LNT) treatment of 5 °C by transferring the pots to the walk-in growth chamber (*Lab line*, 104 A, IL, USA) and treatment was given for 12 h daily (each night from 18:00 to 06:00) for 7 d. During daytime, the plants were given under glasshouse condition as described above.

Measurements of leaf net photosynthetic rate (P_N) and stomatal conductance (g_s) of leaves were taken at 11:00 with a portable photosynthesis system (*Li-6200, LI-COR*, Lincoln, USA). The contents of chlorophyll (Chl) and carotenoids (Car) were determined spectrophotometrically by the method of Lichtenthaler (1987). Modulated Chl fluorescence in leaves was measured on leaf discs using a *PAM 2000* fluorometer (*H. Walz,* Effeltrich*, G*ermany). F_o was measured by switching on the modulated irradiation of 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 6 000 μmol m^{-2} s^{-1} of "white light". Efficiency of the open reaction center in light [$\Phi PS\ 2 = F_v'/F_m' = (F_m'-F_o)/F_m'$)] was calculated according to Bilger and Björkman (1990). Soluble proteins and RuBPC activity were determined by the method of Nedunchezhian and Kulandaivelu (1991). Electrolyte leakage was determined according to the method of Lafuente *et al*. (1991).

Thylakoid membranes were isolated from the leaves as described by Berthhold *et al.* (1981). Whole chain electron transport (H_2O → MV) and partial reactions of photosynthetic electron transport mediated by PS 2 (H_2O → DCBQ) and PS1 ($DCPIPH_2$ → MV) were measured as described by Nedunchezhian *et al*. (1997). Thylakoid membrane proteins and crude leaf extracts of RuBPC were separated using the polyacrylamide gel system of Laemmli (1970). The relative content of D1 protein was determined immunologically by Western blotting (Nedunchezhian *et al*. 1997).

The net photosynthetic rate (P_N) measured immediately after the LNT period was significantly reduced (38 %) in treated plants of Lagrein, while Müller-Thurgau plants showed no such modifications after the stress (Table 1). Under this stress condition, there was no evidence of stomatal conductance (g_s) influencing the inhibition of net photosynthetic rate in Lagrein plants (Table 1). The increase in the g_s observed in treated Lagrein plants indicated that the reduction in P_N during the stress was not limited by stomatal closure, but by alterations on mesophyll capacity .

The contents of Chl and Car were strongly reduced in LNT stressed Lagrein plants (Table 1). The reduction in Chl contents was largely exhibited through the reduction of both Chl *a* and Chl *b* and LNT stress probably enhanced the chlorophyllase activity in Lagrein leaves. Similar results was observed in LNT treated wheat (Lidon *et al*. 2001) and rubber (Sunder and Ramachandra Reddy 2000). The increase of the Chl *a*/*b* ratio and the decrease of the Chl/Car ratio in stressed Müller-Thurgau plants suggest that these relationships could be used as an indicator of stress tolerance (Loggini *et al*. 1999, Jatimliansky *et al*. 2004).

To obtain information on PS 2 activity, F_v/F_m, which reflects the potential quantum yield of PS 2 photochemistry (Krause and Weis 1991), was determined *in vivo* using leaves which had been dark-adapted for 30 min. LNT treatment modified the Chl fluorescence emission in stressed Lagrein plants (Table 1). The initial fluorescence (F_o) increased, while variable fluorescence F_v were reduced at the end of the LNT treatment in relation to control plants (Jatimliansky *et al*. 2004). Maximum photochemical efficiency of PS 2, expressed as F_v/F_m, as well as the efficiency of open reaction center of light, expressed as ΦPS 2, were reduced in the stressed plants of Lagrein at the end of the LNT treatment indicating that an important portion of the PS 2 reaction center was damaged (Klimov *et al*. 1980). Müller-Thurgau plants showed no modifications of any of the fluorescence parameters during the LNT treatment (Table 1).

The analysis of various electron transport activities measured in thylakoids isolated from control and LNT treated both genotypes, showed an inhibition of the whole chain of electron transport activity by over 30 % in LNT treated Lagrein plants and only 6 % in LNT treated Müller-Thurgau plants (Table 1). However, the PS1 activity was much less diminished in both genotypes (Table 1). A marked inhibition of PS 2 activity was observed only in LNT treated Lagrein plants (Table 1). Similar large reduction in PS 2 activity has been reported in chilling stressed plants (Sundar and Ramachandra Reddy 2000, Lidon *et al*. 2001).

Table 1. Changes in contents of leaf pigments, soluble proteins, RuBPC activity, gas exchange, chlorophyll fluorescence, electron transport activities, electrolyte leakage, and D1 protein in leaves of control and LNT treated plants of cvs. Müller-Thurgau and Lagrein. Means ± SE of 5 replicates of each experiment.

Parameters		Lagrein control	LNT	Müller-Thurgau control	LNT
Leaf pigments [g kg^{-1}(f.m)]	Chl *a*	1.52 ± 0.16	1.70 ± 0.11	1.71 ± 0.13	0.95 ± 0.09
	Chl *b*	0.44 ± 0.03	0.48 ± 0.02	0.52 ± 0.02	0.30 ± 0.01
	Chl *a*+*b*	1.96 ± 0.12	2.18 ± 1.10	2.23 ± 1.21	1.25 ± 0.07
	Car	0.45 ± 0.02	0.53 ± 0.24	0.52 ± 0.25	0.33 ± 0.01
	Chl *a*/*b*	3.34 ± 0.14	3.74 ± 0.17	3.28 ± 0.17	3.06 ± 0.15
	Chl/Car	4.35 ± 0.21	3.75 ± 0.16	4.28 ± 0.21	4.20 ± 0.22
Soluble proteins [g kg^{-1} (f.m)]		52.90 ± 2.03	52.80 ± 2.40	59.20 ± 2.80	41.40 ± 2.20
RuBPC [mmol(CO_2) kg^{-1}(prot.) s^{-1}]		50.60 ± 2.60	50.50 ± 2.30	53.10 ± 2.90	39.80 ± 1.90
Gas exchange	P_N [μmol m^{-2} s^{-1}]	13.40 ± 0.90	13.20 ± 0.70	18.80 ± 0.90	12.31 ± 0.61
	g_s [mmol m^{-2} s^{-1}]	610.1 ± 31.0	608.0 ± 32.0	560.2 ± 29.4	728.1 ± 37.4
Chl fluorescence	F_0	0.409 ± 0.02	0.400 ± 0.02	0.429 ± 0.03	0.469 ± 0.02
	F_v	1.364 ± 0.05	1.362 ± 0.07	1.471 ± 0.07	1.110 ± 0.05
	F_v/F_m	0.768 ± 0.03	0.763 ± 0.04	0.774 ± 0.04	0.693 ± 0.03
	ΦPS 2	0.700 ± 0.03	0.690 ± 0.03	0.660 ± 0.04	0.540 ± 0.02
Electron transport activities	H_2O → MV	161.3 ± 8.30	151.6 ± 7.20	157.5 ± 7.90	102.3 ± 5.80
[mmol (O_2) kg^{-1}(Chl) s^{-1}]	H_2O → DCBQ	178.2 ± 8.40	169.1 ± 8.40	167.6 ± 8.90	113.9 ± 5.40
	$DCPIPH_2$ → MV	324.5 ± 17.0	317.1 ± 16.7	322.8 ± 16.5	305.9 ± 15.5
Electrolytic leakage [%]		19.00 ± 0.90	17.10 ± 0.91	26.00 ± 1.40	39.00 ± 1.90
D1 protein [%]		100.0 ± 5.40	97.0 ± 4.80	100.0 ± 5.10	70.0 ± 4.20

The changes in photosynthetic electron transport activities could be caused primarily by the changes or reorganization of thylakoid components, *e.g.,* the thylakoid membrane polypeptide profiles (Fig. 1). A marked loss of 47, 43, 33, 28-25, 23 and 17 kDa polypeptides was noticed in LNT treated Lagrein plants while no changes in Müller-Thurgau plants. The extrinsic proteins of 33, 23 and 17 kDa associated with the lumenal surface of the thylakoid membranes are required for optimal functioning of the oxygen evolving machinery (Enami *et al*. 1994). Our results indicate that the loss of 33, 23 and 17 kDa polypeptide could be one of the reasons for loss of PS 2 activity in Lagrein plants after LNT treatment. LNT treatment induced not only the loss of extrinsic proteins but also a marked loss of 47, 43 and 28 - 25 kDa polypeptides in thylakoid membranes which may be due to greater disruption of the PS 2 complex in Lagrein plants. The relative content of D1 protein decreased to 30 % in LNT treated Lagrein plants while no changes in Müller-Thurgau stressed plants (Table 1). The decrease of the D1 protein demonstrates that the PS 2 rapidly degraded under LNT stress in Lagrein plants. A similar phenomenon has already been observed by Salonen *et al*. (1998) in pumpkin plants treated cold stress.

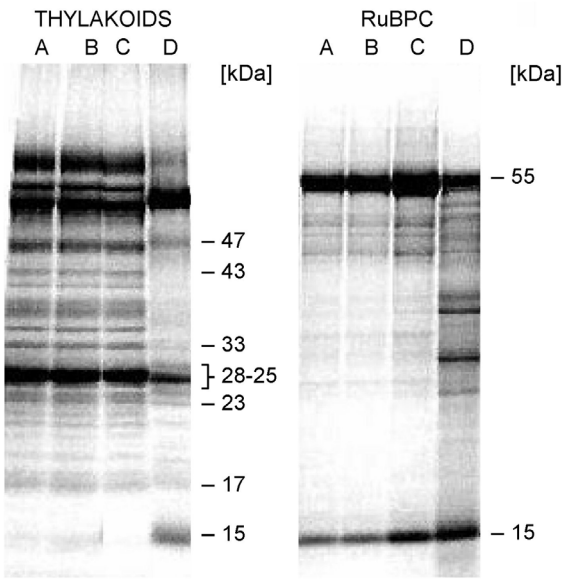

Fig. 1. Coomassie brilliant blue stained polypeptide profiles of thylakoid membranes and crude leaf extracts of RuBPC isolated from in leaves of control and LNT stressed plants of cvs. Müller-Thurgau and Lagrein. *Lane A* - control of Müller-Thurgau, *lane B* - LNT stressed Müller-Thurgau; *lane C* - control of Lagrein; *lane D* - LNT stressed Lagrein. Gel lanes were loaded with equal amount of protein (100 μg).

The content of soluble proteins and RuBPC activity were decreased markedly in LNT stressed Lagrein plants (Table 1). This concurs with similar reports (Sundar and Ramachandra Reddy 2000). The marked loss of RuBPC activity was mainly due to an inhibition of protein synthesis. This is supported by SDS-PAGE analysis of crude leaf extracts of RuBPC proteins shown by the significant loss of 55 kDa polypeptide in LNT treated Lagrein plants (Fig. 1). This loss of 55 kDa polypeptides

is one of the reasons for the loss of RuBPC activity in LNT stressed Lagrein plants.

The functioning of the membrane was altered by LNT stress. An increase in electrolyte leakage was observed in LNT stressed Lagrein plants (Table 1), indicating alterations in the permeability of the membranes. However, in Müller-Thurgau, the permeability of the membrane was not modified by LNT treatment, indicating the maintenance of its functioning. Inefficient functioning of the membranes have been found in different species and under several stress condition (Karim *et al*. 1999, Jatimliansky *et al*. 2004).

To the best of our knowledge, for the first time the comparison of two grapevine genotypes permitted determining that the tolerance or sensitivity to low night temperature was clearly manifested throughout the photosynthetic activity. The exposure to LNT provoked important reductions in photosynthesis in Lagrein, while Müller-Thurgau was not affected. This reduction in the CO_2 assimilation rate observed in Lagrein was generated by affection in the PS 2 functioning. We propose that the pigments content of the light harvesting complex is an important aspect related to the tolerance of grapevine plants to LNT. The loss of integrity of the membranes was also associated with the chilling tolerance of grapevine plants. From the results we conclude that Lagrein plants are sensitive and Müller-Thurgau plants are tolerance against the chilling stress.

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Saito, K., De Kok, L.J., Stulen, I., Hawkesford, M.J., Schnug, E., Sirko, A., Rennenberg, H. (ed.): **Sulfur Transport and Assimilation in Plants in the Post Genomic Era. -** Backhuys Publishers, Leiden 2005. 270 pp. ISBN 90-5782-166-4.

This book contains the invited (8) and contributed (47) papers of the 6th International Workshop on Plant Sulfur Metabolism hosted at the Kazusa Akademia Center, Kisarazu, Chiba, Japan from May 17 to 21, 2005. It covers a various aspects of sulfur metabolism in plants as the previous volumes of this sulfur series do, and as we are living in a post-genomic era it is not surprising that the emphasis is put on the comprehensive analysis termed "omics" approach. The reader can see how the understanding of sulfur metabolism is rapidly progressing in the past few years, particularly at a molecular level.

The book is divided into four sections each of them consists of one to three papers that present comprehensive reviews of the subject and number of short contributions to the subject. The first section dedicated to "Transport and distribution of sulfur-containing compounds" starts with paper that highlights some historical aspects of sulfate transport, presents some of the important biological processes involved, identifies gaps in our knowledge and poses a number of important questions that need to be addressed. The second review provided us a complete set of sulfate transporter gene family in *Arabidopsis*, which consists of 14 isoforms showing homology to one another. The kinetic properties, expression patterns and functional characteristics together with localization data of individual groups of sulfate transporters are discussed. Third paper is more specialized and concerns with the role and importance of sulfur distribution and redistribution in cereal growth and development, especially at low levels of S nutrition. Following 7 short contributions demonstrate transport activities of sulfate transporters and their regulation, techniques that can be used to identify characteristic sulfur groups in natural samples and *in vivo* imaging of glutathione.

The second section "Reduction and metabolism of sulfur", the largest ones is introduced by paper giving comprehensive review on open questions of sulfur metabolism, identifying research areas, which have been neglected or altogether overlooked during last 14 years. This especially concerns areas related to regulation and areas outside of the mainstream. The next review summarizes progress on the regulation of the gene for cystathionine γ-synthase in *Arabidopsis*. The following group of 9 short papers summarizes recent progress on the regulation, the level of expression and functional analysis of the genes for the key-step enzymes of sulfur assimilatory metabolism and structural and biochemical characteristics of these enzymes. Five last short papers are more special, they deal with divergence of the myrosinase gene among *Brassica* species, alliinase among *Allium* species, with the impact of H_2S exposure on sulfur metabolism in onion and effects of S-deprivation on sulfolipid metabolism in *Chlamydomonas reinhardtii*.

The third section devoted to "Sulfur omics" contains the papers evaluating effect of sulfur availability on *Arabidopsis thaliana* primary metabolism, the response of the transcriptome and metabolome to sulfur nutrition especially to sulfur deprivation and analysis of molecular signaling in response to S-deficiency. The last three short papers present the new analytical technology for comprehensive analysis of metabolites (METABOLIX), mathematical model of sulfur metabolism in higher plants, and database system for searching relationships between metabolites and species (KNApSAcK).

The last section "Sulfur metabolism under stress" is concentrated on improved phytoremediation of contaminated soils by changes in sulfur metabolism, molecular analysis of sulfur-based defense reactions in plant-pathogen interactions, the effects of abiotic stresses on the sulfate assimilation pathways and involvement of S-containing compounds in cadmium- or herbicide-tolerance. The final paper of the book is a chronicle of sulfur research with the special view to agricultural production during the past 25 years.

The book is well arranged and produced. All papers written by leading scientists are well arranged and include many tables, figures and schemes. Helpful are also author index and detailed subject index. Photo of participants and "Chiba Sulfur Song 2005" composed by J.W. Anderson are supplemented.

This stimulating book will be certainly enjoyed by all plant physiologists and molecular biologists especially those working in physiology of mineral nutrition.

O. GAŠPARÍKOVÁ (*Bratislava*)