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Reduced light and moderate water deficiency sustain nitrogen assimilation and sucrose degradation at low temperature in durum wheat

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ABSTRACT

The rate of carbon and nitrogen assimilation is highly sensitive to stress factors, such as low temperature and drought. Little is known about the role of light in the simultaneous effect of cold and drought. The present study thus focused on the combined effect of mild water deficiency and different light intensities during the early cold hardening in durum wheat (*Triticum turgidum* ssp. *durum* L.) cultivars with different levels of cold sensitivity.

The results showed that reduced illumination decreased the undesirable effects of photoinhibition in the case of net photosynthesis and nitrate reduction, which may help to sustain these processes at low temperature. Mild water deficiency also had a slight positive effect on the effective quantum efficiency of PSII and the nitrate reductase activity in the cold. Glutamine synthesis was affected by light rather than by water deprivation during cold stress. The invertase activity increased to a greater extent by water deprivation, but an increase in illumination also had a facilitating effect on this enzyme. This suggests that both moderate water deficiency and light have an influence on nitrogen metabolism and sucrose degradation during cold hardening. A possible rise in the soluble sugar content caused by the invertase may compensate for the decline in photosynthetic carbon assimilation indicated by the decrease in net photosynthesis. The changes in the osmotic potential can be also correlated to the enhanced level of invertase activity. Both of them were regulated by light at normal water supply, but not at water deprivation in the cold. However, changes in the metabolic enzyme activities and osmotic adjustment could not be directly contributed to the different levels of cold tolerance of the cultivars in the early acclimation period.

1. Introduction

In areas with a continental climate crops are exposed to very fluctuating weather conditions. Low temperature and water deficiency adversely affect the growth and development of cereal crops. These conditions are frequently experienced in late autumn if preceded by a dry summer. These two stressors have a prominent impact on the annual yield.

Low temperature induces a wide range of physiological and biochemical responses. Membrane rearrangement causes changes in the stability and mobility of proteins and a shift in redox poise which decreases enzyme activities. Changes in membrane structure and the additional effect of light energy often act as stress factors and cause an imbalance in light utilization compared to optimal temperature conditions (Ruelland et al., 2009). At low temperature, the overexcitation of the photosystems induces photoinhibitory conditions, which results in the accumulation of reduced components in the photosystems, a decrease in energy-containing substances such as ATP, and the build-up of free radicals (ROS), which degrades the light-harvesting complexes (Keren and Krieger-Liszkay, 2011). High levels of ROS inhibit the activity of RuBisCO and fructose-1,6-bisphosphatase (Hurry et al., 1994). Further, low temperature temporarily inhibits sucrose synthesis,

Abbreviations: Abs, absorptivity of incident light; *D*, mild water deficiency; ETR, apparent electron transport rate; Fv/Fm, maximal quantum efficiency of PSII; gs, stomatal conductance; GS, glutamine synthetase; *I*, normal irrigation; LL, low (reduced) light; NIR, near infrared light; NL, normal light; NPQ, nonphotochemical quenching parameter; NR, nitrate reductase; PAR, photosynthetically active radiation; Pn, net photosynthesis; PPFD, photosynthetic photon flux density; PSII, photosystem II; R, red light; ROS, reactive oxygen species; RWC, relative water content; Y(II), effective quantum yield of PSII.

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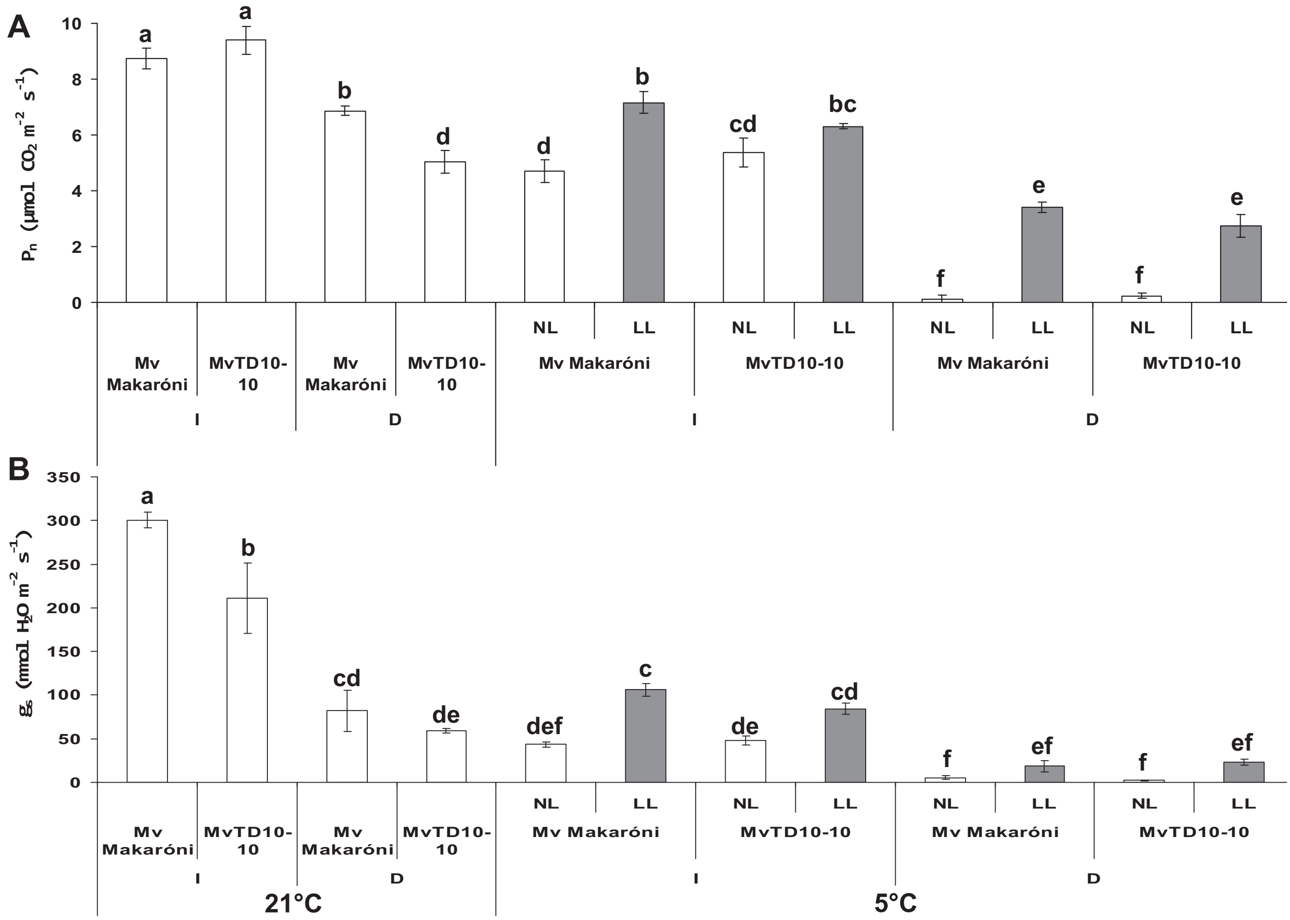

Fig. 1. Changes in the net photosynthesis (Pn) (A) and stomatal conductance (gs) (B) of the cold-tolerant Mv Makaróni and cold-sensitive MvTD10-10 durum cultivars determined at a common laboratory temperature. Plants were grown at 21 °C and hardening (5 °C) temperatures under normal irrigation (*I*), mild water deprivation (*D*), normal light (NL) and low light (LL) conditions. Data represent mean ± standard deviation of five plants per pot in each treatment. Different letters indicate statistically significant differences between the cultivars at $p \leq 0.05$, using Tukey's post hoc test.

Table 1
Relative water content (RWC) of the cold-tolerant Mv Makaróni and cold-sensitive MvTD10-10 durum cultivars at growth (21 °C) and hardening (5 °C) temperatures under normal irrigation (I), mild water deprivation (D), normal light (NL) and low light (LL) conditions. Data represent mean ± standard deviation of five plants per pot in each treatment. Different letters indicate statistically significant differences between the cultivars at $p \leq 0.05$, using Tukey's post hoc test.

	21 °C		5 °C			
	I	*D*	*I*		*D*	
			NL	LL	NL	LL
Mv Makaróni	93.62 ± 1.57 [a]	43.54 ± 3.51 [c]	90.06 ± 7.30 [a]	84.55 ± 3.18 [a]	47.72 ± 4.85 [c]	51.23 ± 5.61 [c]
MvTD10-10	92.62 ± 4.48 [a]	45.50 ± 3.64 [c]	91.17 ± 1.99 [a]	91.09 ± 1.22 [a]	63.44 ± 4.08 [b]	63.10 ± 2.56 [b]

which contributes to the depletion of ATP reserves via a low level of inorganic phosphate. The deceleration of ATP synthesis and the regeneration of ribulose-1,5-bisphosphate can be attributed to the limited capacity for CO_2 fixation and the consequent decline in photosynthetic sugar synthesis (Ensminger et al., 2006).

Low temperature limits net photosynthetic activity via photoinhibition, while water deprivation primarily induces stomatal closure, which also reduces the intercellular CO_2 concentration. The RuBisCO activity is also known to be affected by drought (Reddy et al., 2004). Thus, low temperature and water deficit may greatly impede sugar synthesis in the Calvin cycle, which triggers other metabolic pathways to compensate the sugar deficit and provide reducing agents for assimilation. One of these responses is the remobilization of sugars from carbohydrate reserves (Gupta and Kaur, 2005).

Besides CO_2 fixation and sugar synthesis, the uptake of nitrate and the incorporation of NH_4^+ into organic compounds are also important for adequate plant growth and development. The initial step, namely the conversion of inorganic nitrate to nitrite is catalysed by the enzyme nitrate reductase (NR). A further enzymatic reaction, the synthesis of glutamine catalysed by glutamine synthetase (GS), is pivotal in the conversion of inorganic ammonium to organic nitrogenous compounds, e.g., amino acids. Both NR (Campbell, 1999) and GS reaction greatly depends on light which directly modulates the GS activity in leaves at transcriptional (Oliveira and Coruzzi, 1999) via photorepector-mediated way and post-translational level via phosphorylation of the GS protein (Lima et al., 2006). The efficiency of photosynthesis is light-dependent and provide ATP and the carbon skeleton for amino acid synthesis. Beside light, the abundance of GS and RuBisCO showed a positive correlation with the severity of stress, including low temperature