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Growth, lipid peroxidation and photosynthesis in two tall fescue cultivars differing in heat tolerance

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Abstract

Seedlings (70-d-old) of two tall fescue (*Festuca arundinacea* Schreb.) genotypes, heat-tolerant Jaguar 3 and heat-sensitive TF 66, were exposed to a high temperature stress of 35/30 °C (day/night) for 20 d and both light-saturated and CO_2-saturated leaf stomatal conductance decreased, especially in TF 66. Higher reductions of quantum efficiency, carboxylation efficiency and maximum photochemical efficiency of photosystem 2 in dark adapted leaves (measured as F_v/F_m) occurred in TF 66 than in Jaguar 3. High temperature stress increased photorespiration in the two plants, but more in TF 66. Moreover, high temperature stress also reduced the growth, chlorophyll content and caused cell membrane injuries in the two cultivars, the changes were again more pronounced in TF 66 than in Jaguar 3.

Additional key words: chlorophyll fluorescence, *Festuca arundinacea*, high temperature stress, carboxylation efficiency, stomatal conductance.

Introduction

High temperature stress is one of the major factors limiting the use of cool-season grasses in transitional and warm climatic regions (Beard 1997). Photosynthesis, one of the most heat sensitive processes may be reduced at high temperatures by both stomatal limitation and non-stomatal limitation in *Annona herimola* (Higuchia *et al*. 1999), while being mainly reduced by non-stomatal limitation in *Lycopersicon esculentum* (Camejo *et al*. 2005), *Colobanthus quitensis* and *Deschampsia antarctica* (Xiong *et al*. 1999). Non-stomatal limitations to photosynthesis in heat stressed plants might be related to enhanced dark respiration rate and oxidative damage of chloroplast ultrastructure, photosystem 2 (PS 2) center, pigments and proteins (Xu *et al*. 1995, Xiong *et al*. 1999, Karim *et al*. 2003). Chloroplasts are the main sites for generating ROS under both stressed and unstressed conditions, and it is one of the organelles in leaf tissues of plants most sensitive to high temperature stress (Xu *et al.* 1995, Sun *et al*. 2002). The chloroplasts of plants containing a reduced level of trienoic fatty acids and an elevated level of dienoic fatty acids were resistant to high temperatures (Murakami *et al*. 2000, Sohn and Back 2007). High temperatures could limit photosynthesis by changing the structural organization of the thylakoids, thus altering the energy distribution, changing the activity of the Calvin cycle and other metabolic processes such as photorespiration, and the stability of various carbon metabolism enzymes (Karim *et al*. 2003). PS 2 is the most heat-sensitive component of the photosynthetic system (Murakami *et al*. 2000, Karim *et al*. 2003). The inhibition of PS 2 by heat stress leads to a decrease in the variable chlorophyll fluorescence. Thus, *in vivo* chlorophyll fluorescence has been shown to be a sensitive and reliable method for detection and quantification of temperature-induced changes in the photosynthetic apparatus (Jiang and Huang 1999, Liu and Huang 2000, Xu and Huang 2001, Camejo *et al*. 2005). Moreover, inactivation of Rubisco at high temperature could also limit leaf photosynthetic activity (Xu and Huang 2001, Karim *et al*. 2003, Salvucci and Crafts-Brandner 2004).

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Abbreviations: c_a - ambient CO_2 partial pressure in the leaf chamber; CE - carboxylation efficiency; Chl - chlorophyll; c_i - leaf internal CO_2 concentration; EL - electrolyte leakage; F_0 - initial chlorophyll fluorescence yield; F_v/F_m - maximum photochemical efficiency of photosystem 2 in dark adapted leaves; g_s - stomatal conductance; MDA - malondialdehyde; P_N - net photosynthetic rate; PPFD - photosynthetic photon flux density; ROS - reactive oxygen species; RSL - relative stomatal limitation; Φ - quantum efficiency.

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High temperature stress could induce oxidative stress, which subsequently provokes cell membrane injury, pigment bleaching, protein synthesis and stability degradation (Sairam *et al.* 2000, Sun *et al.* 2002, Wahid and Close 2007). The injury of the cell membrane is also related to the inactivation of photosynthesis by high temperatures, and it is a primary symptom of heat injury (Maheswari *et al.* 1999, Camejo *et al.* 2005). In this sense, the level of cell membrane lipid peroxidation of unsaturated fatty acids in phospholipids, and electrolyte leakage (EL) have been used as good indicators of free radical damage to cell membranes and membrane thermostability under heat stress (Liu and Huang 2000, Karim *et al.* 2003).

Tall fescue (*Festuca arundinacea*) is one of the most widely used cool-season species but declines in turf quality and growth in warm climatic regions during summer are common. For this reason, it is important to obtain new heat-tolerant cultivars. There is no consensus on how photosynthesis and cell membranes of tall fescue respond to high temperature. The aim of the present study was to compare the response of the two tall fescue cultivars, Jaguar 3 (heat tolerant) and TF 66 (heat sensitive), to a 20-d high temperature treatment to obtain more insight into the physiological backgrounds of the genotypic variability of high temperature sensitivity in the genus *Festuca arundinacea.*

Materials and methods

Seeds of *Festuca arundinacea* Schreb. cv. Jaguar 3 (heat tolerant), and cv. TF 66 (heat sensitive) were sown and grown in a mixture of sand, vermiculite and organic matter (3:1:1) in polyethylene pots (14 cm in height and 13 cm in diameter with 0.9 g seeds in each pot). Plants were kept in growth chambers at 20/15 °C (day/night), using a photosynthetic photon flux density (PPFD) of 200 µmol m^{-2} s^{-1}, and a 14-h photoperiod for 70 d (including 8 d for germination) before they were subjected to high temperature stress. Then two identical groups of plants were transferred to two growth chambers with a high temperature (35/30 °C) and a normal temperature (20/15 °C), respectively, for 20 d. Before and during the temperature treatments, grasses were clipped weekly to a height of 8 cm with electric hair clippers, watered daily and fertilized weekly with a full strength Hoagland's nutrient solution (Hoagland and Arnon 1950). In this paper, we deal with heat stress in the absence of radiation stress.

Twenty seedlings from each treatment were sampled randomly at days 0, 10 and 20. Leaf areas were measured using a *Li-3100* leaf area meter. For dry mass (DM) of leaves and roots determination samples were oven dried at 70 °C for 72 h. According to Lambers and Poorter (1992), relative growth rate (RGR), leaf area ratio (LAR), and component specific leaf area (SLA) were calculated.

Leaf net photosynthetic rate (P_N) and stomatal conductance (g_s) were measured at 20 and 35 °C using a *Licor 6400* photosynthetic system (*LI-6400*, *Li-Cor*, Lincoln, NE, USA). Artificial radiation was supplied to the leaf from a red-blue LED, and ambient CO_2 partial pressure was supplied by a CO_2 mixer. A photosynthetic irradiance response curve was monitored following these procedure: steady state P_N was reached at PPFD of 800 µmol m^{-2} s^{-1} and CO_2 concentration 400 µmol mol^{-1} and then P_N was monitored as a function of PPFD ranging from 1800 to 0 µmol m^{-2} s^{-1}. Asymptotic exponential equation of Prioul and Chartier (1977) was fitted by nonlinear least square regression to obtained data. Quantum efficiency ($\Phi = dP_N/dPPFD$) was calculated. Similarly, a response of P_N to leaf internal CO_2 concentration (c_i) was measured with the exception that once a steady state was attained, ambient CO_2 partial pressure in the leaf chamber (c_a) was lowered in steps from 400 down to 0 µmol(CO_2) mol^{-1}(air), and then increased upto 1400 µmol(CO_2) mol^{-1}(air), under a saturated PPFD of 1200 µmol m^{-2} s^{-1}. From these curves, relative stomatal limitation (RSL) was calculated using the equation of Hendrickson *et al.* (2004) and a carboxylation efficiency (CE) was calculated as $CE = dP_N/dc_i$.

Chlorophyll fluorescence parameters were measured on attached leaves using a plant photosynthesis efficiency analyzer (*Hansatech Instrument*, Kings Lynn, UK). Initial chlorophyll fluorescence, F_0, variable chlorophyll fluorescence, F_v, and maximum chlorophyll fluorescence, F_m, were read in dark adapted leaves either at 20 or 35 °C.

The content of chlorophyll (Chl) *a* and *b* was determined in 80 % acetone following Lichtenthaler's (1987) method using a UV-visible Spectrophotometer (*Hitachi U-3000*, Tokyo, Japan).

The lipid peroxidation in the leaf and root tissue was determined by estimating the malondialdehyde (MDA) content in according to Huang *et al.* (2001). MDA content was measured spectrophotometrically (*Hitachi U-3000*) at 532 nm, after subtraction of non-specific absorption at 600 nm, using a coefficient of absorbance of 155 mM^{-1} cm^{-1}. Electrolyte leakage (EL) was measured by a conductivity method (*EC215* conductivity meter, *Shanghai Electric Technology Co*., Shanghai, China) according to Maheswari *et al*. (1999). After measuring initial electrolyte leakage (C_1), leaf or root samples were heat-killed (autoclaved at 121 °C, 124 kPa for 15 min) and final electrolyte leakage (C_2) was measured at room temperature [$LE = (C_1/C_2) \times 100$].

One-way analysis of variance was performed using the *SPSS 10.0* computer package for all sets of data, and means were compared using Duncan's multiple range test at $P < 0.05$.

Results

During the experimental period, TF 66 had significantly lower RGR as compared to Jaguar 3 (Fig. 1*A*). On day 10, the RGR decreased in TF 66 by 16.4 % and it remained almost unchanged in Jaguar 3. While on day 20, the RGR remarkably decreased in TF 66 by 93.7 %, but slightly decreased in Jaguar 3 by 10 %. Shoot to root ratio in Jaguar 3, significantly increased by 75.4 and 66.4 % on days 10 and 20, respectively, as compared to the control. But there was no significant change for shoot to root ratio in TF 66 (Fig. 1*D*). LAR and SLA increased remarkably in both cultivars during high temperature treatment, this change was more pronounced with the exposure time (Fig. 1*B*,*C*). LAR and SLA increased on day 20 in Jaguar 3 by 86.5 and 96.3 %, and in TF 66 by 136.6 and 137.7 %, respectively.

Light saturated g_s (PPFD = 800 µmol m^{-2} s^{-1}) for the two cultivars was reduced under heat stress (Fig. 2*B*,*D*) and after 20-d stress it was 39.1 and 45.9 % lower in

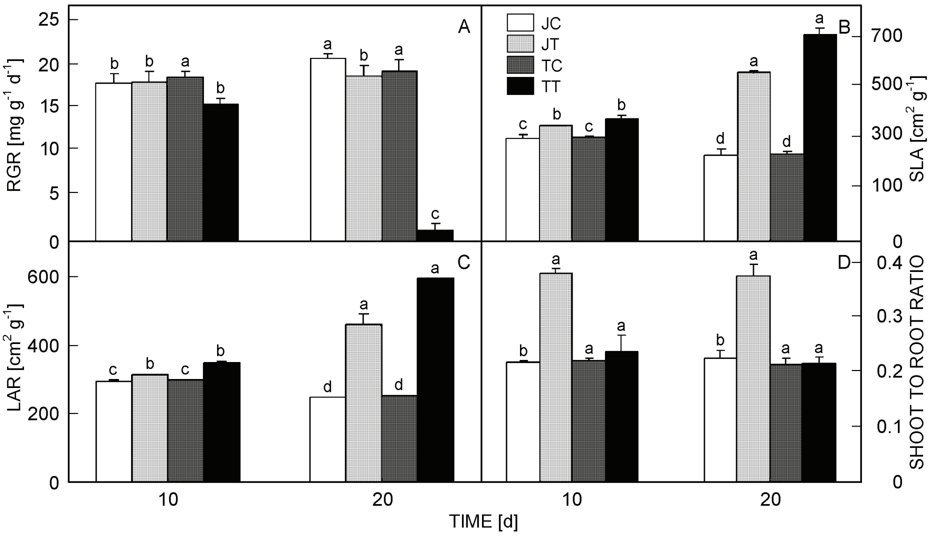

Fig. 1. Effects of high temperature stress on growth of two tall fescue cultivars, Jaguar 3 and TF 66. *A* - relative growth rate, RGR; *B* - specific leaf area, SLA; *C* - leaf area ratio, LAR; *D* - shoot to root ratio; JC - Jaguar 3 under normal condition; JT - Jaguar 3 after high temperature stress; TC - TF 66 under normal conditions; TT - TF 66 after high temperature stress. Means ± SE, $n = 20$. Means for each genotype that do not have a common letter are significantly different at $P < 0.05$ by Duncan's multiple range test.

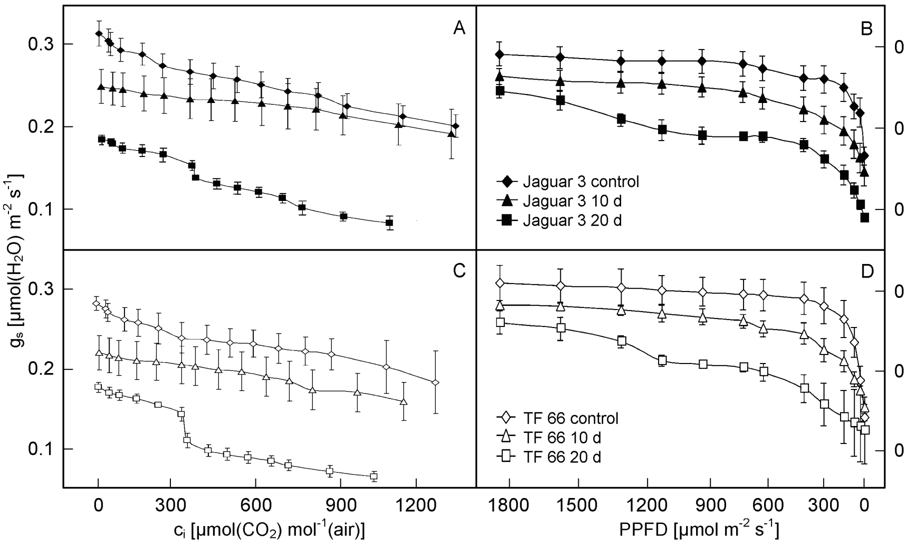

Fig. 2. Leaf internal CO_2 concentrations (c_i) and high temperature dependence of stomatal conductance (g_s) for leaves of Jaguar 3 (*A*) and TF 66 (*C*). Leaves were measured at 20 or 35 °C, with a saturated PPFD of 1200 µmol m^{-2} s^{-1}. Photosynthetic photon flux density (PPFD) and high temperature dependence of stomatal conductance (g_s) for leaves of Jaguar 3 (*B*) and TF 66 (*D*). Leaves were measured at 20 or 35 °C, with a CO_2 concentration around 400 µmol mol^{-1}. Each point is the mean ± SE of 4 replicates.

Table 1. Quantum efficiency (Φ), carboxylation efficiency (CE) and relative stomatal limitation (RSL) during high temperature treatment of two tall fescue cultivars (Jaguar 3 and TF 66). Means of four replicates ± SE. Means followed by the same letters are not significantly different at $P < 0.05$ within the two cultivars.

Parameters	Jaguar 3			TF 66		
	control	10 d stress	20 d stress	control	10 d stress	20 d stress
Φ [mol mol^{-1}]	0.080 ± 0.003^a	0.048 ± 0.009^c	0.063 ± 0.005^b	0.061± 0.003^a	0.044 ± 0.001^b	0.054 ± 0.006^a
CE [mol m^{-2} s^{-1}]	0.043 ± 0.001^b	0.047 ± 0.002^a	0.037 ± 0.003^c	0.042 ± 0.003^a	0.039± 0.008^a	0.032 ± 0.003^b
RSL	32.4 ± 4.1^a	30.0 ± 3.2^a	24.5 ± 2.8^b	34.2 ± 2.2^a	25.0 ±2.4^c	15.6 ± 3.1^c

Jaguar 3 and TF 66 than in controls. The g_s of TF 66 (Fig. 2*D*) was lower that of Jaguar 3 (Fig. 2*B*) at PPFD 800 µmol m^{-2} s^{-1}.

CO_2-saturated g_s (c_a = 400 µmol CO_2 mol^{-1} air) for the two grasses under high temperature stress were lower than those of the control plants (Fig. 2*A*,*C*) but g_s was higher Jaguar 3 (Fig. 2*A*) than in TF 66 (Fig. 2*C*). Compared to the control, CE of the two heat stressed plants was lower with except for a slight increase in CE for Jaguar 3 at 10 d heat stress (Table 1). Moreover, quantum efficiency (Φ) in the two heat-stressed plants was also decreased, but at day 10 it was lower than at day 20 (Table 1). Jaguar 3 had a higher Φ than TF 66.

Relative stomatal limitation (RSL) was significantly reduced at high temperatures, and this change was more pronounced with the exposure time (Table 1). RSL in TF 66 was not significantly different from that in Jaguar 3 at normal conditions, but was much lower than in Jaguar 3 at high temperatures.

F_0 in the two heat-stressed plants increased compared to the control (Fig. 3*A*). F_v/F_m ratio, and leaf Chl *a*+*b* content in the two cultivars was reduced at high temperatures at 10- and 20-d treatments (Fig. 3*B*,*C*). By 20 d, F_v/F_m ratio and Chl *a*+*b* of Jaguar 3 and TF 66 were 7.0 and 33.5 % and 19.6 and 40.9 %, respectively, lower than those of the control plants. Jaguar 3 retained significantly higher F_0 value, F_v/F_m ratio and Chl *a*+*b* content than did TF 66 during high temperature stress.

Malondialdehyde (MDA) content of leaves and roots increased significantly in both stressed cultivars (Fig. 4*C*,*D*). MDA contents in leaf and root of the stressed Jaguar 3 were 52.2 and 67.0 % higher than those of control plants after 20 d treatment, while in TF 66, they were 105.1 and 111.1 % higher. The increase of MDA content under high temperature stress was more pronounced in roots than in leaves for both cultivars, and TF 66 had a greater increase in both leaf and root MDA compared to Jaguar 3. During high temperature stress, TF 66 maintained a significantly higher content of MDA in both leaves and roots than did Jaguar 3.

EL of leaves and roots increased under high temperature stress (Fig. 4*A*,*B*). By 20 d, EL in leaves and roots of Jaguar 3 were 112.3 and 149.1 % higher than those in the control. The heat stressed TF 66 had a greater increase in leaf EL (172.2 %) and root EL (170.3 %). Compared to TF 66, Jaguar 3 had lower leaf and root EL ($P < 0.05$).

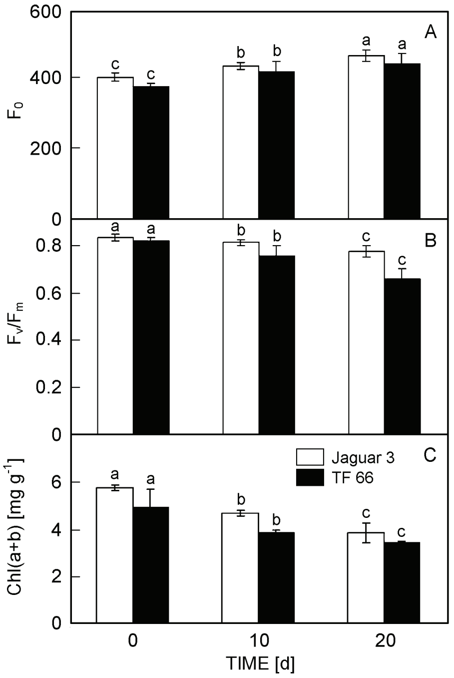

Fig. 3. Mean F_0 (*A*), F_v/F_m ratio (*B*) and Chl *a*+*b* content (*C*) of two tall fescue cultivars (Jaguar 3 and TF 66) during high temperature stress. Means ± SE, $n = 4$. Means for each genotype that do not have a common letter are significantly different at $P < 0.05$ by Duncan's multiple range test.

Discussion

High temperature stress inhibited the growth (RGR, SLA, LWR and shoot to root ratio) of two tall fescue cultivars, the changes were more pronounced in TF 66 than in Jaguar 3. This was mainly due to a depression of photosynthesis during stress (Cui *et al.* 2006). Photosynthesis is one of the most heat sensitive processes, and the

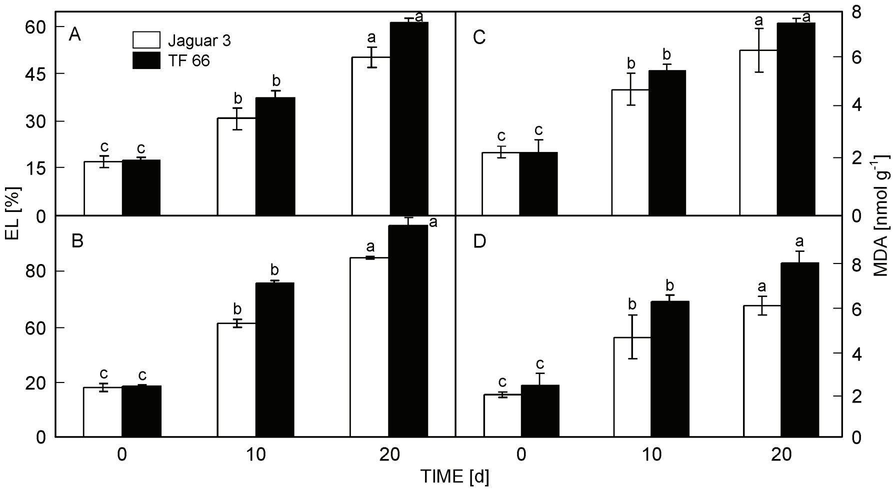

Fig. 4. Mean electrolyte leakage (EL) in leaves (*A*) and roots (*B*) and malondialdehyde (MDA) content in leaves (*C*) roots (*D*) of two tall fescue cultivars (Jaguar 3 and TF 66) during high temperature stress. Means ± SE, $n = 4$. Means for each genotype that do not have a common letter are significantly different at $P < 0.05$ by Duncan's multiple range test.

decrease in the two cultivars under stress conditions was mainly caused by two factors. One is g_s reduction leading to shortage of CO_2 supply. Lowering g_s is a main physiological response to high temperature and radiation stress (Su and Liu 2005). In our case, decreases of both light-saturated and CO_2-saturated g_s (Fig. 2) under high temperature stress indicated that reductions in CO_2 assimilation observed in the two plants were partly attributable to stomatal limitation. However, with the more reduced P_N in the two cultivars at 20-d heat treatment than at 10-d heat stress (Cui *et al.* 2006) lead to less RSL (Table 1). Thus P_N was decreased also by non-stomatal factors (*e.g.* reduced CE and Φ was observed). Our results were in agreement with an earlier report that photosynthesis under heat stress showed both stomatal and non-stomatal limitations in *Annona herimola* (Higuchia *et al.* 1999).

Under high temperature, reductions of CE in both cultivars confirmed previous observations (Xiong *et al.* 1999, Hamerlynck *et al.* 2000, Murakami *et al.* 2000, Karim *et al.* 2003). Φ in both Jaguar 3 and TF 66 was lower at 10-d heat stress than at 20-d treatment indicating that there was an acclimation of photochemical and biochemical processes to a long-term heat stress. The low P_N at high temperatures was caused, in part, by increased photorespiration and an imbalance in the carbon metabolism (Murakami *et al.* 2000).

Decrease in the F_v/F_m ratio of the two heat-stressed plants (Fig. 3*B*) indicated that structural and functional disorder of the photosynthetic apparatus occurred (Pereira *et al.* 2000, Murkowski 2001). It has been reported that increasing F_0 (Fig. 3*A*) and decreasing F_m (data not shown) in response to stresses can be attributed to separation of LHC 2 from the PS 2 complex, inactivation of the PS 2 reaction centre, and perturbation of electron flow to PQ (Lee *et al.* 2004).

The capacity of the antioxidant defence system was increased under heat stress but the imbalance between ROS production and antioxidant defences led to oxidative damage, and PS 2 was the primary target for oxidative damage (Cui *et al.* 2006). This oxidative stress could enhance Chl degradation or the inhibition of its biosynthesis and further explained the reduction of leaf Chl *a*+*b* content in high temperature stressed plants in our case (Fig. 3*C*). Total Chl content as an important factor in determining heat-tolerance had been reported in creeping bentgrass (Liu and Huang 2000, Huang *et al.* 2001, Xu and Huang 2001), tall fescue, kentucky bluegrass (Jiang and Huang 2001), and tomato (Camejo *et al.* 2005).

The higher MDA content and EL in roots than in leaves suggested that more prominent oxidative damage occurred in roots under high temperature stress. This result was consistent with earlier reports that roots were more sensitive to high temperature than shoots (Larkindale and Huang 2004), and that leaf cells had higher antioxidant defence ability than root cells (Becana *et al.* 1998).

Considering all the results obtained from this study, we demonstrated that Jaguar 3, a heat-tolerant cultivar of fescue is more able to resist high-temperature induced functional disorder of the photosynthetic apparatus and damage to cellular membranes.

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