RESEARCH ARTICLE

III. Heat stress in *Triticum*: kinetics of Na, K and P accumulation

Ana S. Dias[1,2*], Ana L. Fernando[1,3] and Fernando C. Lidon[1,3]

[1] Grupo de Disciplinas de Ecologia da Hidrosfera, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Quinta da Torre, 2829-516 Caparica, Portugal

[2] Instituto Nacional de Investigação Agrária, Instituto Nacional dos Recursos Biológicos, I.P., Estrada de Gil Vaz, Elvas, Portugal.

[3] Unidade de Biotecnologia Ambiental / FCT-UNL, 2829-516 Monte de Caparica, Portugal.

* Corresponding author: Phone/Fax: 00351212948543; anasofia.almeida@mail.com.
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ABSTRACT

Genotypes of bread and durum wheat were submitted to heat stress after anthesis and the accumulation of Na, K and P, at booting, grain filling and maturity, were investigated. It was found that, after anthesis, the levels of Na in shoots were considerably higher in durum relatively to bread wheat, being this trend also observed in the total plant accumulation. In these genotypes, heat stress affected significantly Na concentration in shoots. In general, heat stressed plants had significant higher levels of K in the shoots and the proportion of this nutrient translocation from the roots also increased with heat stress. In general, the levels of P didn't show significant differences with heat stress. The effects of heat stress among the wheat genotypes life cycle are characterized and discussed.

Key words: *Triticum aestivum* L.; *Triticum turgidum subsp. Durum*; heat stress; nutrients uptake, nutrients translocation.

INTRODUCTION

The optimal mean temperature for the crops growth cycle might vary between 15-18ºC (Chowdhury and Wardlaw 1978), being 20ºC the optimal value for grain filling (Dupont and Altenbach 2003; Russell and Wilson 1994). Moreover, the yield performance of wheat genotypes is strongly affected by heat stress (Spiertz 1977; Wardlaw et al. 2002), being pointed (Wardlaw et al. 1989) that a global reduction of about 3-4% occurs in crops production when the temperature increases by 1ºC (i.e., mean temperatures above optimum). Ciaffi et al. (1996) further indicated that, even short periods of high temperature (35-40ºC) during grain filling can have a negative effect on yield and quality.

Within plant tissues, the accumulation of K^+ is required for pH stabilization of the cytoplasm, to increase the osmotic potential in the vacuoles (Marschner 1995), and to promote cellular growth which determines higher yields (Lindhauer 1983). The inorganic P can also stimulate plant growth, as it regulates carbon flux between starch and sucrose biosynthesis (Terry and Rao 1991; Usuda and Shimogawara 1991) and phosphate distribution of photosynthates among tissues (Qiu and Israel 1994; Rao and Terry 1989). Although Na is not essential for plant species (Subbarao et al. 1999; 2000) also stimulates plant

growth (Subbarao et al. 2003; Takahashi and Maejima 1998) since it has a high capacity to exchange K^+ (Subbarao et al., 2003). Nevertheless, as most plants have an high selectivity K^+ uptake (in the interface soil/roots), and translocation to the shoots (Subbarao and Johansen, 2002), the levels of Na are relatively low in grains (Subbarao et al. 2000; Subbarao and Johansen 2002).

Working with two genotypes of *Triticum aestivum* (Sever from Portugal and Golia from Italy) and *Triticum turgidum subsp. turgidum* (TE 9306 from Portugal and Acalou from France), having different tolerance to high temperature after anthesis (Dias et al., 2008, 2009; Dias and Lidon 2009, Maçãs et al. 1999; 2000), an insight in the magnitude of the implications of heat stress on Na, K and P uptake (by the roots) and translocation to the shoots, is presented. The implications on K, P and Na accumulation in the roots, shoots and spikes are characterized, since these nutrients are linked to cellular growth, being therefore hypothesized that the yield of crops reduction associated to heat stress implicates significant changes of these nutrients roots uptake and shoots translocation kinetics.

MATERIALS AND METHODS

***Plant material and growth conditions*:** Bread wheat (*Triticum aestivum* L., genotypes Sever and Golia) and durum wheat (*Triticum turgidum subsp. durum*, genotypes TE 9306 and Acalou) grains were washed in distilled water and sterilized by immersion in mercury dichloride solution (1:1000) for 2 minutes. The grains were next washed five times in deionizer water and placed in an oven at 28ºC for 24 hours. Immediately thereafter the seeds were grown in a greenhouse (under natural light, between March and May in Lisbon/Portugal – 38° 42' N; 9° 05' W; photoperiod varying between 12 and 14 hours) in 25 x 21 cm pots containing a 1:1 perlite and vermiculite mixture. The experiment was conducted using 136 pots. Half of these pots were putted under heat stress after anthesis. For each genotype 17 replicates were used (with and without heat stress). Ten seeds were grown per pot and two weeks later five were selected, being the others removed. Accordingly, 680 plants were used. In each plant all tillers were removed, keeping only the main culm. During all the experiment the position of the pots was changed weekly, to minimize the effects due to irradiance variations. Plants were irrigated weakly but alternatively with distillated water or with a standard nutrient solution, alternately (in ml/100L, starter/pre-anthesis/post-anthesis, Ca $(NO_3)_2$ 100/100/50; KNO_3 50/200/100; KH_2PO_4 100/100/100; $MgSO_4$ 200/200/100; K_2SiO_3 100/100/0; $Fe(NO_3)_3$ 20/5/5; EDTA 25/5/5; $MnCl_2$ 5/10/5; $ZnSO_4$ 20/10/10; H_3BO_3 10/5/2; $CuSO_4$ 5/5/3; Na_2MoO_4 15/5/5). During the vegetative and reproductive growth, plants were kept under similar environment conditions. At anthesis, the plants were divided in two groups and submitted to two different temperature conditions (controlled and heat stress). Under heat stress the plants were submitted to temperatures that rose until 40ºC. During the grain filling period, control plants grew under regimes with mean temperatures (day/night) of 25/14ºC and 31/20ºC (control and heat stress conditions, respectively). The average of day/night temperatures was calculated as the mean readings of each two hours, during each 24 hours period.

***Nutrients analysis*:** The concentrations of Na, K and P were determined in roots, shoots and spikes (at booting-69/70 days after anthesis; grain filling-108/109 and 109/112 days after anthesis, for the genotypes submitted to control and heat stress conditions, respectively). Five randomized plants of each genotype, from each heat treatment, were used for nutrients analysis. Plant samples were washed, the fresh weight was determined in each fraction and, therefore, dry weight was measured after dryness in an oven for 100ºC during 72h. For Na and K, one gram of dry material, from each sample, was mineralized through incineration at about 550ºC, and followed by nitric acid digestion (Vandecasteele and Block 1993). A Unicam model 939 absorption unit, equipped with a hollow cathode lamp was used for these metals determinations. For P concentrations determination, a hot digestion with HNO_3 and H_2SO_4 (Watts and Halliwell 1996) was carried out. Phosphates were determined by molecular absorption spectrophotometry (Cecil 9000 series), through formation of a chromophore with a solution of ammonium molibdato, in the presence of ascorbic acid and potassium tartarato and antimony (Watanabe and Olsen 1965). The mean concentration values of the nutrients and biomass yields of the roots, shoots and spikes (and grain weight) were

used to determine the total related mean content in *Triticum* plants. The net uptake was determined adding these values. The mean of the translocation rates were obtained by calculating, on a percentage basis, the ratio between the means of these metal contents in the shoot and their net absorption.

***Statistical analysis*:** Statistic analyses were performed with a two-way ANOVA ($p \leq 0.05$), using *STATISTICA*, version 6 (2001), by *StatSoft, Inc*.

RESULTS AND DISCUSSION

From previous studies (Dias and Lidon 2009; Dias et al, 2008, 2009< Maçãs et al. 1999, 2000) it was found that *Triticum aestivum* L. genotype Sever is more tolerant to heat stress after anthesis than the genotype Golia and that *Triticum turgidum subsp. durum* genotype TE 9306 tolerance prevails relatively to the genotype Acalou (Dias and Lidon 2009; Dias et al, 2008, 2009). In this experiment, when these genotypes were submitted to heat stress after anthesis faced a consistent period of moderate high temperatures. Under these growth conditions, along the growth cycle, the levels of Na in the roots of the control plants remained similar in both plant species, but expressing different genome characteristics (Schachtman et al., 1991), in the shoots and spikes, were considerably higher in the durum wheat genotypes (Table 1). Although the ability to limit the accumulation of Na in leaves may be an important mechanism of salt tolerance because the excessive accumulation of Na causes the premature senescence of leaves (Schachtman and Munns, 1992), in the heat stressed species, during grain filling and at maturity, the levels of Na were higher in durum wheat. During grain filling, the levels of Na in the shoots of the durum wheat genotypes were 5 and 9 fold higher (relatively to bread wheat), in the control and heat stress treatments, respectively (Table 1). In Golia, during this growth phase, the concentrations of Na in the shoots decreased significantly (between control and heat stress conditions), but an opposite trend was found at maturity. In Sever significant differences could not be found (Table 1). During grain filling, in the *Triticum durum* genotypes, the contents of Na in the shoots also increased significantly, and in TE 9306 this trend persisted at maturity (Table 1). In both temperature treatments, the levels of Na in the spike of the durum wheat genotypes were 2 fold (in average) higher than those found for bread wheat genotypes (Table 1), being these patterns similar to those reported by Hussain et al. (2002). Nevertheless, in the spike, at maturity, the levels of Na decreased significantly in Sever, whereas an opposite trend occurred in Acalou (Table 1). As a general pattern, it was found that, during grain filling and at maturity, the higher levels of Na in the shoot of all the genotypes, comparatively to the spike (Table 1), agree with Watt and Merrill (1975), about the low mobilization of Na for the reproductive structures in wheat grain, additionally expressing a lower rate of Na accumulation independent of the growth of individual leaves and probably regulated by some root process, and a compartmentation within leaves, which enhances the ability to tolerate high concentrations of Na in leaves (Schachtman and Munns, 1992). During grain filling, the total accumulation of Na in the durum wheat genotypes was considerably higher relatively to the bread wheat genotypes, being this pattern mainly due to the shoot accumulation (Fig. 1). These data point an higher root Na absorption of durum wheat, coupled to an higher efficiency of its translocation to the shoots (Fig. 1), being the accumulation rates of Na in durum wheat superior (Table 2). During grain growth, the difference of Na accumulation between the *Triticum* species became more evident in Golia, since the proportion of Na translocated to the shoots was almost half of that found in the durum wheat genotypes (Fig. 1). Under heat stress, during grain filling, the total and shoot accumulation of Na in Acalou increased 29% and 34%, respectively, but in the end of this growth phase only an increase of 17% and 23% was found. During grain filling, this trend did not persist in TE 9306 (Fig. 1). However, in this genotype, this effect did not affect the levels of Na in the shoots, although might have decreased (non-significantly) the levels of Na in the spike (Table 1). At maturity, the accumulation trend found for both durum wheat genotypes was quite similar (Fig. 1).

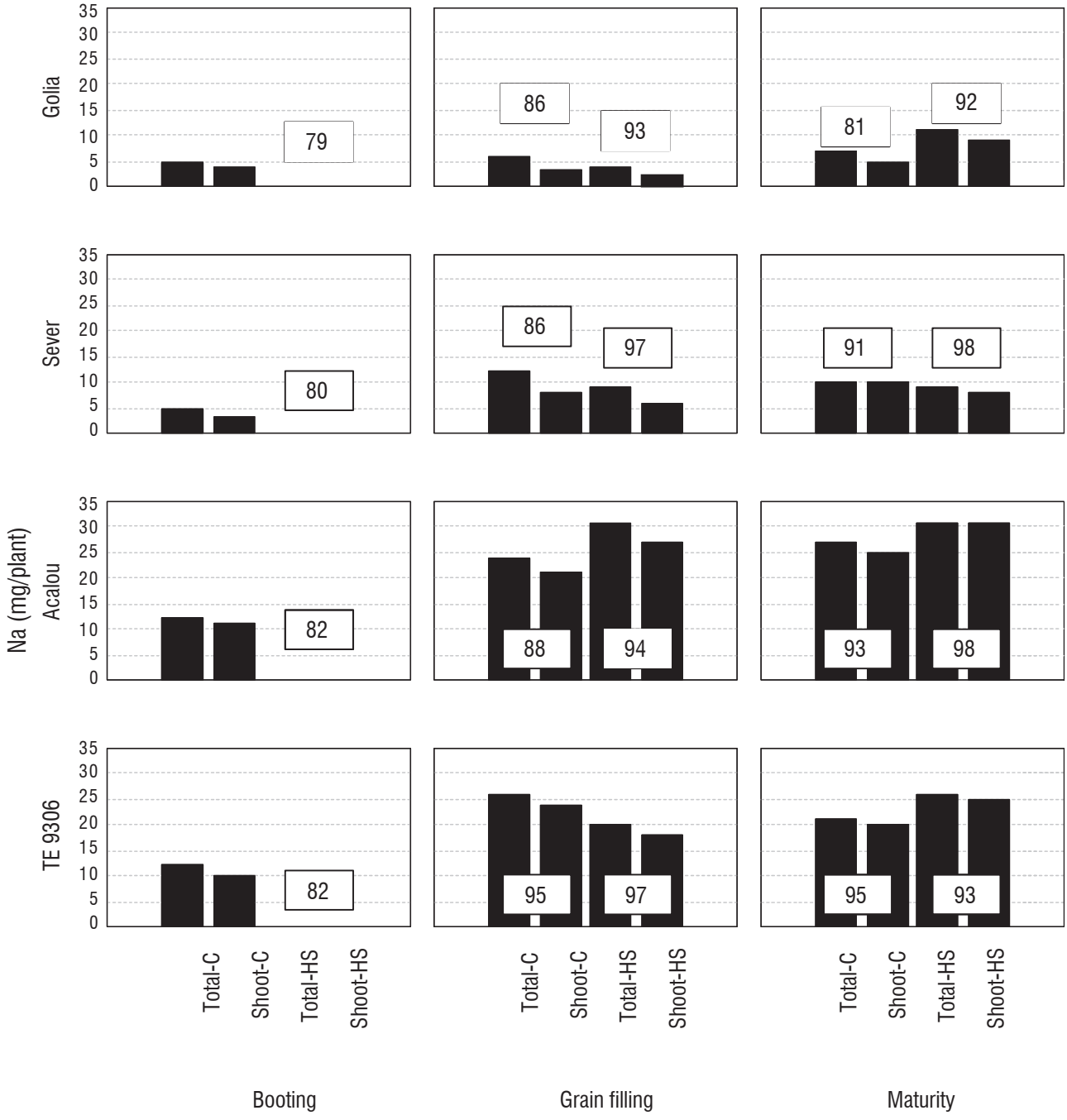

Figure 1. Total plant and shoot accumulation of Na in bread and durum wheat genotypes until the respective stage of growth cycle (booting, grain filling, maturity), in control and heat stress treatments. Values inside boxes refer to Na translocation (%) from roots to shoots. C and HS refer to control and heat stress treatments, respectively.

Table 1. Sodium concentration (mg/g_{dw}) in different plant parts, on three stages of plant growth (booting, grain filling and maturity), of control and heat stress bread and durum wheat genotypes. Each value is the mean ± S.E. of three replicates. Different letters in the same column refer to significant differences between genotypes. Between treatments, ns, *, **and *** refer to: non significant, $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

	Booting	Grain filling		Maturity	
		Control	Heat stress	Control	Heat stress
			Root		
Golia	3.56±0.23a	1.64±0.41a	2.55±0.23a ns	2.09±0.21a	1.71±0.03a ns
Sever	3.93±0.58a	2.64±0.54a	3.21±0.28a ns	0.77±0.03b	1.32±0.00b **
Bread wheat	3.74±0.26	2.14±0.40	2.88±0.24 ns	1.43±0.39	1.52±0.11 ns
Acalou	3.01±0.43a	2.62±0.38a	4.24±0.22a *	1.70±0.03a	1.85±0.30a ns
TE 9306	3.28±0.46b	2.45±0.06a	3.46±0.00a **	1.31±0.11a	3.33±0.11b **
Durum wheat	3.14±0.27	2.35±0.17	3.85±0.24 **	1.50±0.12	2.59±0.45 **
			Shoot		
Golia	2.61±1.12a	0.73±0.02a	0.38±0.08a *	1.13±0.13a	2.87±0.31a *
Sever	2.00±0.30a	1.57±0.06b	1.36±0.03b ns	1.84±0.06b	2.15±0.08a ns
Bread wheat	2.30±0.51	1.15±0.24	0.87±0.28 **	1.49±0.21	2.51±0.25 **
Acalou	5.03±0.00a	5.19±0.04a	8.25±0.38a *	8.49±0.08a	9.32±0.89a ns
TE 9306	4.41±0.05b	6.42±0.10b	7.58±0.11a *	6.84±0.38a	9.36±0.41a *
Durum wheat	4.72±0.18	5.81±0.36	7.91±0.25 ***	7.67±0.50	9.34±0.40 *
			Spike		
Golia		0.22±0.02a	0.32±0.14a ns	0.59±0.02a	0.77±0.09a ns
Sever		0.48±0.17a	0.49±0.08a ns	0.67±0.00a	0.46±0.01a **
Bread wheat		0.35±0.10	0.41±0.08 ns	0.63±0.03	0.61±0.09 ns
Acalou		0.58±0.11a	1.03±0.01a ns	1.23±0.03a	1.96±0.12a *
TE 9306		2.20±0.37a	0.58±0.21a ns	0.70±0.01b	1.03±0.08b ns
Durum wheat		1.39±0.49	0.80±0.15 ns	0.97±0.16	1.50±0.28 **

Table 2. Rate of total accumulation of K, P and Na ($mg.plant^{-1}.day^{-1}$), in three different periods of growth cycle, for control and heat stressed plants.

	Emergence-Booting	Booting-Grain filling		Grain filling-Maturity	
Genotypes	Control	Control	Heat stress	Control	Heat stress
			K ($mg.plant^{-1}.day^{-1}$)		
Golia	1.17	1.07	0.70	-2.36	-1.22
Sever	1.41	1.51	1.26	-1.80	-3.08
Acalou	1.48	0.34	0.79	-1.69	-1.50
TE 9306	0.99	0.95	1.05	0.05	-0.81
			P ($mg.plant^{-1}.day^{-1}$)		
Golia	-	-	-	-0.02	-0.28
Sever	-	-	-	0.09	-0.02
Acalou	-	-	-	0.14	0.18
TE 9306	-	-	-	0.15	0.14
			Na ($mg.plant^{-1}.day^{-1}$)		
Golia	0.07	0.03	-0.01	0.05	0.57
Sever	0.08	0.17	0.10	-0.08	0.00
Acalou	0.17	0.30	0.47	0.14	0.03
TE 9306	0.17	0.36	0.21	-0.22	0.49

In our study, as reported by Bergmann (1992), at booting, the contents of K in the shoots varied between 26-53 mg/g (Table 3), eventually displaying a close interaction with Na (Shirazi et al., 2005). It was also found that, as a general pattern, the concentrations of K in the control genotypes, decreased during the growth cycle in all tissues. This effect was similar to that reported by Lásztity (1987), with the additional K probably being involved in the regulation of cellular osmotic potential (Hsiao and Läuchli 1986). Under heat stress, it was found that the levels of K increased significantly: in the roots of Golia and TE 9306, during grain filling and at maturity, respectively; in the shoots of all genotypes (excepting Golia), during grain filling and at maturity, in Sever and TE 9306; in the spike of Acalou at maturity (Table 3). In the end of the growth cycle, total and shoot accumulation of K (thus, total uptake and the translocation rate) in the heat stressed Golia increased 14% and 20%, respectively (Fig. 2). In Acalou, during grain filling, total and shoot accumulation of K was also higher under heat stress conditions (Fig. 2), contributing to the significant effect of the high temperatures in the concentrations of K in the shoots, during grain filling and in the spike, at maturity (Table 3). Moreover, the decrease of the total amount of K accumulated in heat stressed plants of the genotype TE 9306 (Fig. 2), did not affect its shoot concentration.

Table 3. Potassium concentration (mg/g_{dw}) in different plant parts, on three stages of plant growth (booting, grain filling and maturity), of control and heat stress bread and durum wheat genotypes. Each value is the mean ± S.E. of three replicates. Different letters in the same column refer to significant differences between genotypes. Between treatments, ns, *, **and *** refer to: non significant, $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

	Booting	Grain filling		Maturity	
		Control	Heat stress	Control	Heat stress
			Root		
Golia	22.51±1.52a	8.79±0.42a	13.71±0.61a *	4.87±0.13a	3.29±0.63a ns
Sever	20.70±1.54a	14.45±0.24b	12.34±0.52a ns	3.88±0.14b	4.67±0.49a ns
Bread wheat	21.60±1.03	11.62±1.65	13.02±0.51 *	4.38±0.30	3.98±0.51 ns
Acalou	17.27±0.64a	10.34±0.94a	12.13±0.63a ns	7.00±0.13a	5.47±0.94a ns
TE 9306	16.09±0.03b	12.02±0.36a	15.79±0.94a ns	3.80±0.34a	7.23±0.03a **
Durum wheat	16.68±0.43	11.18±0.63	13.96±1.15 *	5.40±1.33	6.35±0.64 ns
			Shoot		
Golia	52.58±7.27a	26.22±1.20a	30.34±0.22a ns	25.30±0.87a	26.72±0.17a ns
Sever	50.83±2.07a	23.73±0.51a	32.33±0.18b **	22.66±0.07a	27.27±0.07a ***
Bread wheat	51.70±3.13	24.97±0.89	31.34±0.59 ***	23.98±0.84	27.00±0.18 **
Acalou	45.14±1.59a	20.21±0.71a	28.91±0.09a **	13.27±0.77a	21.27±1.84a ns
TE 9306	26.29±4.44a	25.50±0.30b	29.22±0.17a **	23.42±0.32b	27.70±0.57a *
Durum wheat	35.72±5.77	22.85±1.56	29.06±0.12 ***	18.34±2.95	24.49±2.02 **
			Spike		
Golia		8.50±0.30a	8.89±0.39a ns	6.56±0.71a	8.53±0.51a ns
Sever		10.36±0.20b	8.79±0.85a ns	8.06±0.32a	6.95±1.14a ns
Bread wheat		9.43±0.56	8.84±0.38 ns	7.31±0.54	7.74±0.68 ns
Acalou		7.83±0.38a	9.49±0.15a ns	8.72±0.22a	12.03±0.05a **
TE 9306		9.04±0.05a	9.35±0.42a ns	8.93±0.01a	7.91±0.19b ns
Durum wheat		8.43±0.38	9.42±0.19 *	8.83±0.14	9.97±1.19 **

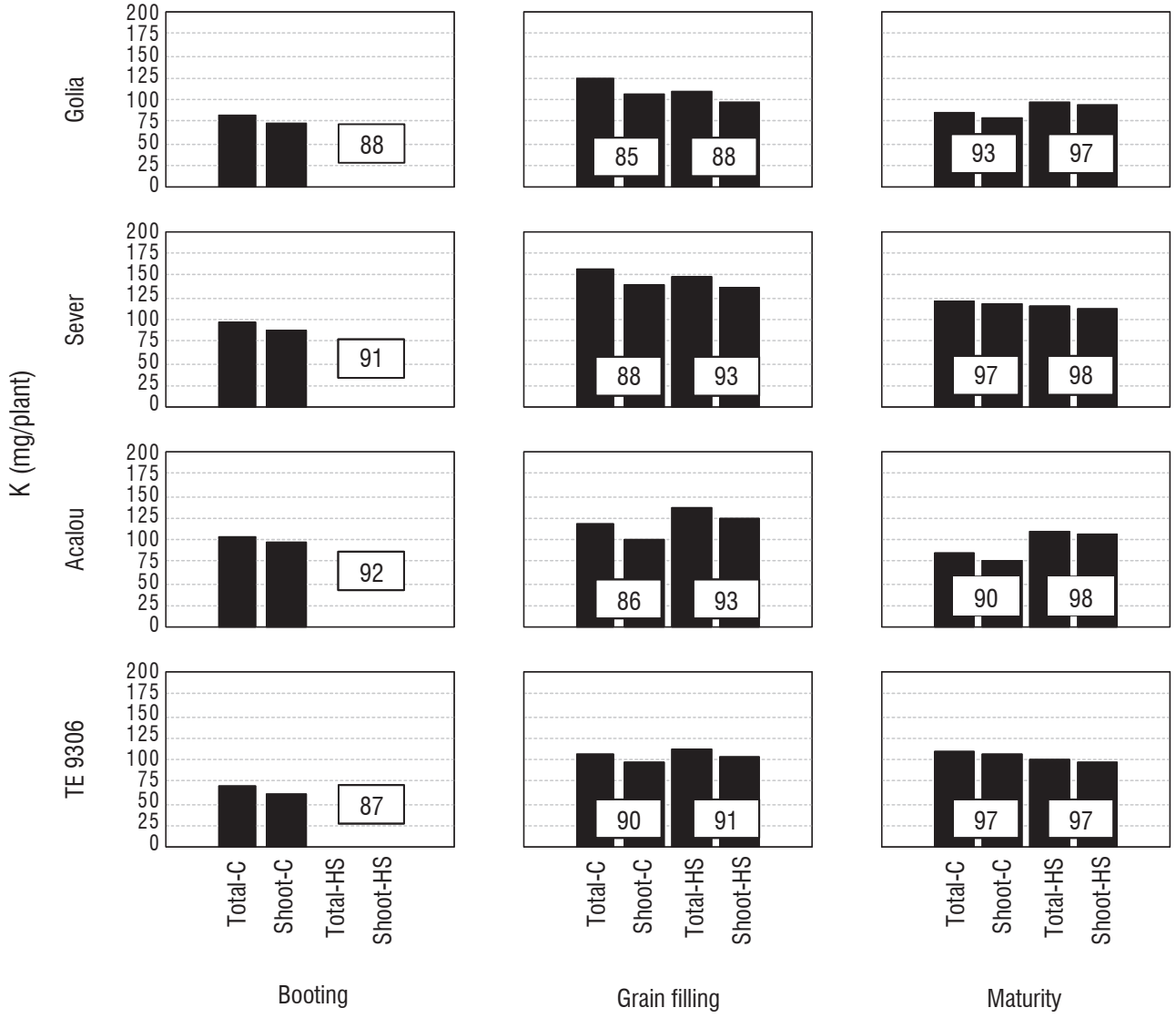

Figure 2. Total plant and shoot accumulation of K in bread and durum wheat genotypes until the respective stage of growth cycle (booting, grain filling, maturity), in control and heat stress treatments. Values inside boxes refer to K translocation (%) from roots to shoots. C and HS refer to control and heat stress treatments, respectively.

At booting, the shoot contents of P varied between 2.6 - 3.1 mg/g (Table 4), values that are similar to those reported for *Triticum* in this growth phase (Bergmann 1992; Marschner 1995). As previously reported (Lásztity 1987) in the *Triticum* genotypes, the concentrations of P under controlled conditions decreased during all the growth cycle, following a close interaction with Na (Perveen et al., 2003), which eventually favored starch synthesis (Rijven and Gifford 1983; Walker 1980). Nevertheless, the levels of P in the spike remained higher comparatively to shoot levels (Table 4). As a general pattern, the levels of P in the shoot increased with high temperatures. This trend was also found for maize by Ashraf and Hafeez (2004). During grain filling, the contents of P increased significantly in the spike of Golia and in the roots of TE 9306 (Table 4). At maturity, a significant increase of P contents was found in the shoot of Golia and in the root

of TE 9306 (Table 4). At maturity Sever, revealed a significant decrease of P contents, but the other genotypes showed an opposite trend (Table 4). In Acalou the levels of P didn't varied significantly during all the growth cycle (Table 4). The accumulation of P in the durum wheat genotypes showed only minor variations, but during grain growth, total and shoot accumulation of P was higher in heat stressed plants of Golia (Fig. 3). In this genotype, in the beginning of grain filling, the pronounced increase (46%) that occurred in the shoot accumulation of P (resulting of an high translocation from the roots) justified the significant increase of this nutrient concentration in the spike (Table 4). At the end of the growth cycle, the rate of total accumulation of P in the heat stressed plants of Sever was smaller comparatively to the control plants (Table 2). At maturity, this effect became evident in the decreased total and shoot accumulation of P (Fig. 3), which in conjunction with the absence of a significant variation (between temperature treatments) in its translocation to the shoot (Fig. 3) inhibited the contents (on a dry weight basis) in the shoots at the end of grain growth (Table 4).

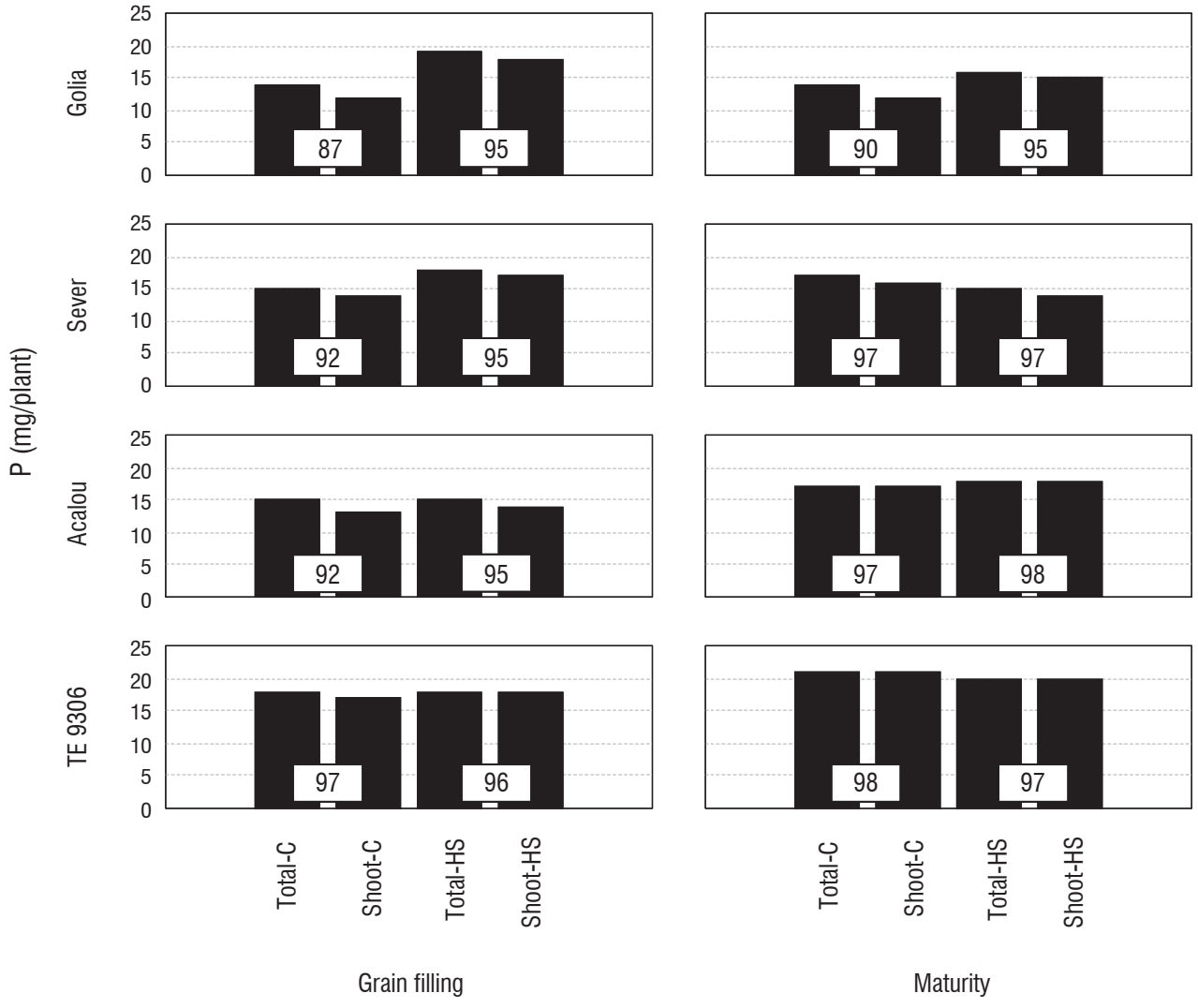

Figure 3. Total plant and shoot accumulation of P in bread and durum wheat genotypes until the respective stage of growth cycle (booting, grain filling, maturity), in control and heat stress treatments. Values inside boxes refer to P translocation (%) from roots to shoots. C and HS refer to control and heat stress treatments, respectively.

Table 4. Phosphorus concentration (mg/g_{dw}) in different plant parts, on three stages of plant growth (booting, grain filling and maturity), of control and heat stress bread and durum wheat genotypes. Each value is the mean ± S.E. of three replicates. Different letters in the same column refer to significant differences between genotypes. Between treatments, ns, *, **and *** refer to: non significant, $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

	Booting	Grain filling		Maturity	
		Control	Heat stress	Control	Heat stress
			Root		
Golia		0.85±0.04a	0.94±0.05a ns	1.05±0.04a	1.00±0.06a ns
Sever		0.85±0.05a	0.99±0.08a ns	0.63±0.03b	0.71±0.03b ns
Bread wheat		0.85±0.02	0.97±0.04 ns	0.84±0.12	0.86±0.09 ns
Acalou		0.76±0.01a	0.91±0.42a ns	0.53±0.03a	0.72±0.06a ns
TE 9306		0.50±0.03b	1.23±0.09a *	0.66±0.04a	1.64±0.08b **
Durum wheat		0.63±0.08	1.07±0.20 ns	0.60±0.04	1.18±0.27 ***
			Shoot		
Golia	3.10±0.06a	0.74±0.01a	0.55±0.06a ns	0.26±0.00a	0.31±0.01a *
Sever	3.59±0.05b	0.49±0.01b	0.44±0.01a ns	0.48±0.02b	0.32±0.02a *
Bread wheat	3.34±0.14	0.62±0.07	0.50±0.04 *	0.37±0.06	0.32±0.01 *
Acalou	2.59±0.05a	0.52±0.03a	0.48±0.08a ns	0.21±0.01a	0.34±0.04a ns
TE 9306	2.56±0.03a	0.55±0.02a	0.62±0.04a ns	0.47±0.02b	0.75±0.20a ns
Durum wheat	2.57±0.03	0.54±0.01	0.55±0.05 ns	0.34±0.08	0.54±0.14 ns
			Spike		
Golia		3.23±0.06a	4.63±0.20a *	2.95±0.09a	3.24±0.22a ns
Sever		2.99±0.05a	3.50±0.17a ns	2.88±0.11a	2.55±0.02a ns
Bread wheat		3.11±0.08	4.07±0.34 **	2.92±0.06	2.89±0.22 ns
Acalou		3.00±0.05a	2.61±0.17a ns	3.02±0.16a	3.41±0.01a ns
TE 9306		3.72±0.13a	3.65±0.02a ns	3.57±0.13a	3.74±0.10b ns
Durum wheat		3.36±0.21	3.13±0.31 *	3.30±0.18	3.58±0.10 ns

In general it is concluded that although heat stress affected the root uptake and shoot translocation kinetics of Na, P and K, tolerance to this stress is not linked to a selective accumulation of Na, K and P in durum and bread wheat.

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