Cereal Research Communications 42(3), pp. 413–425 (2014)
DOI: 10.1556/CRC.42.2014.3.5

Heat Stress Response of Wheat Cultivars with Different Ecological Adaptation

J. BÁNYAI*, I. KARSAI, K. BALLA, T. KISS, Z. BEDŐ and L. LÁNG

Agricultural Institute, Centre for Agricultural Research, Hungarian Academy of Sciences,
Martonvásár, Hungary

(Received 16 July 2013; Accepted 22 October 2013;
Communicated by A. Goyal)

In the present study, heat treatment was carried out in five different phenological phases, from the first node detectable (DEV31) growth stage to 20 days after flowering, on four wheat genotypes with very different adaptation strategies. They were grown in a controlled environment in a phytotron chamber and exposed to a night temperature of 20ºC and a day temperature of either 30ºC, at DEV31, or 35ºC at all the later developmental phases, for an interval of 14 days. Plant height, leaf number, number of tillers, grain number and grain weight per main and side spikes, TKW per main and side spikes, length of the main and side spikes, and spikelet number per main and side spikes were recorded. High temperature enhanced the stem growth intensity, plant height and tiller number. In contrast, the length of side spikes, spikelet no./side spike, grain no./main and side spike, grain weight/main and side spike and TKW/main and side spike were significantly decreased. The stress response depended strongly on the developmental phase in which the heat stress was applied. Fleischmann 481 and Soissons showed definitely contrasting tendencies both in grain number and grain weight. In the case of the Plainsman V and Mv Magma pair, the higher heat stress tolerance of Magma compared to Plainsman V was evident also from the grain number and weight of the main spike at each developmental phase.

Keywords: winter wheat, heat stress, yield, yield components

Abbreviations: DEV – developmental stage, DAF10 – ten days after flowering, DAF20 – twenty days after flowering, TKW – thousand-kernel weight

Introduction

The warming of the global climate system is now undisputable, as is evident from the increases recorded in mean global air and ocean temperatures, the widespread melting of snow and ice and the rising mean global sea level. Global climate models predict an increase in mean ambient temperatures of between 1.1–6.4ºC from 2071 to 2100 (Barrow and Hulme 1996; IPCC 2007). The climate change is projected to high temperatures and

---

* Corresponding author; E-mail: banyai.judit@agrar.mta.hu; Phone: +36-22-569-500

drought, to climate variability, and to reduced water availability, hydropower potential, and crop productivity (Semenov 2007; Semenov and Halford 2009).

Heat stress due to increased temperature is now an agricultural problem in many areas of the world. Many studies have reported that high temperatures cause an array of morpho-anatomical, physiological, biochemical, molecular and cellular changes in plants (Wahid et al. 2007; Barnabás et al. 2008; Almeselmani et al. 2012). There is increasing evidence on the significant negative effects of heat stress on yield and yield components during the generative phases (Farooq et al. 2011; Semenov and Shewry 2011; Balla et al. 2012). Elevated temperature induces pollen sterility and seed abortion, resulting in lower seed weight, and also significantly affects flour yield and dough quality (Hays et al. 2007; Altenbach 2012). High temperature accelerates flowering and grain maturity, which is paralleled by reduced crop height, leaf growth and number of tillers per plant (Rahman et al. 2009; Zhang et al. 2010).

Heat stress may occur in different developmental stages (vegetative or reproductive phases) of the plant, and this is decisive for plant responses. However, responses also depend on the intensity and duration of heat stress and on the rate of temperature increase. Plants are still able to grow at temperatures above the optimal level, due to a phenomenon known as basal thermotolerance. If plants are pretreated with a mild non-lethal temperature (heat acclimation) or if the temperature increases gradually to a lethal level, they are capable of surviving even lethal high temperature stress; this is known as acquired thermotolerance (Qin et al. 2008; Mittler et al. 2012). Genotypes differ in their ability to cope with heat stress. Many have heat-coping strategies without actually being heat tolerant. Clearly, therefore, understanding how plants respond to heat stress and how heat tolerance can be improved is of the highest importance (Halford 2009).

Based on this, the aim of the present research was to evaluate the effects of heat stress in associations with various plant developmental phases on the phenological and yield related traits in wheat. For this purpose the reactions of four wheat cultivars, the parental lines of two mapping populations on heat stress were examined in details.

Materials and Methods

Four wheat genotypes, namely Fleischmann 481, Soissons, Plainsman V and Mv Magma were grown in the greenhouse at the Agricultural Institute (MTA-ATK-MGI) in 2012. One pair of parents consists of Fleischmann 481, which has high plant stature, is a non-intensive, day length-sensitive Hungarian landrace, bred before the Green Revolution and Soissons, which is an intensive, day-length insensitive French variety. The other pair of parents is the extensive, drought tolerant but relatively heat sensitive Plainsman V of USA origin and the intensive, drought sensitive but relatively heat stress tolerant Mv Magma bred in Martonvásár, Hungary. The basic allele types of these four cultivars in vernalization response and photoperiod sensitivity and in three Rht genes are listed in Table 1.

The effect of heat stress was studied in five plant developmental stages. The seeds were vernalised for 60 days at 4ºC in peat blocks. After vernalisation, twenty-four healthy seedlings of each variety were grown in individual pots, placed randomly in the greenhouse.

Table 1. Allele compositions of the cultivars in different plant developmental and dwarfing genes

	VRN-A1	*VRN-B1*	*VRN-D1*	*PPD-B1*	*PPD-D1*	*Rht1*	*Rht2*	*Rht8*
Fleischmann 481	winter	winter	winter	sensitive	sensitive	wild	wild	wild
Soissons	winter	winter	winter	sensitive	insensitive	dwarf	wild	wild
Plainsman V	winter	winter	winter	insensitive	insensitive	dwarf	wild	dwarf
Mv Magma	winter	spring	winter	sensitive	insensitive	dwarf	wild	dwarf

Plastic pots, 18.5 cm in height and 12 cm in diameter, were filled with 1.5 kg of a 3:2:1 mixture of garden soil, compost and sand. The plants were grown at controlled temperature and watered every day to ensure a uniform water supply in all the pots. All the plants were under continuous observation to note the exact dates of the following plant growth stages: first node detectable (DEV31), booting (DEV49), inflorescence emergence (DEV59), 10 days after flowering (DAF10) and 20 days after flowering (DAF20), based on the scale of Tottman and Makepeace (1979). Four plants of each variety, which reached the aforementioned stages of plant development, were moved into the phytotron heat stress chamber (Conviron PGV-36). In each case the heat stress treatment consisted of a night temperature of 20ºC and a day temperature of either 30ºC (for DEV31) or 35ºC, for all the later developmental phases, which was applied for 8 hours a day for an interval of 14 days. After the heat stress treatment, the plants were returned to the greenhouse and raised with the control plants until maturity.

During the course of the experiment the plant developmental patterns of the four genotypes were studied in details by measuring the following parameters regularly (twice a week): plant height, leaf number, number of tillers. After harvesting, the grain number and grain weight per main and side spikes, the TKW per main and side spikes, the length of the main and side spikes, and the spikelet number per main and side spikes were also recorded.

Results

Effect of heat stress on plant development and morphology

Of the morphological traits, the variance in final plant height and in the rate of intensive stem elongation was explained by the genotype main effect to the largest extent (the genotype SS% were 96.9 and 80.9%, respectively, both significant at $P = 0.0001$ level). The cultivar Fleischmann 481 with the wild alleles at all three Rht genes was significantly the tallest, and had the highest rate of intensive stem elongation, irrespective to the heat treatment (Table 2). In addition, it was Fleischmann 481 which showed the largest plant height changes due to heat stress at the various developmental phases. The other three cultivars were of the same height and possessed similar rate of stem elongation under control conditions, however, their response to heat stress measured in plant height characteristics varied across genotypes and developmental phases. In the case of Fleischmann 481, plants heat-treated in the DEV31, DEV49 and DEV59 stages of development were significantly taller than those in the control group. In response to heat stress at first node appearance

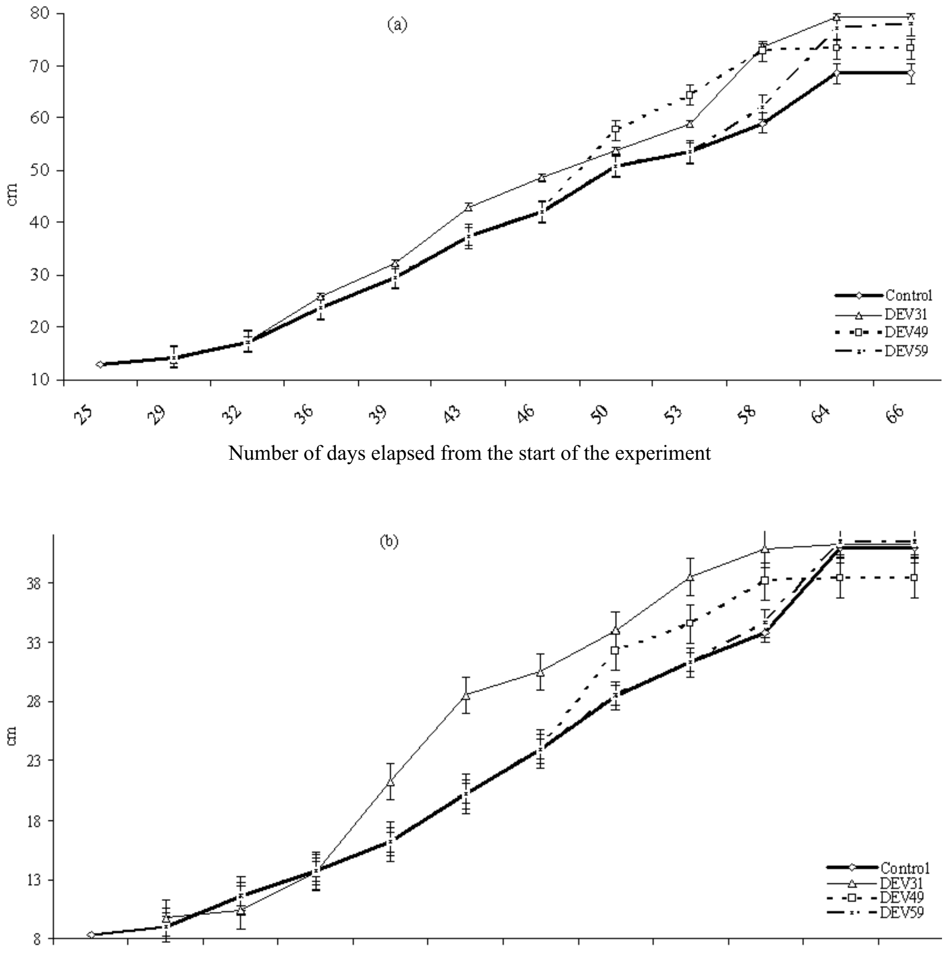
(DEV31), differences in plant height were already observed after five days compared with the control group (Fig. 1). Similar tendencies were characteristic to Plainsman V, though its extent was smaller. The final plant height and the other two plant height characteristics of Sossions were not significantly influenced by heat stress in any of the treatments, while the final plant height of Mv Magma was only influenced by heat stress at DEV31 stage resulting in significantly smaller plants. Though the rate of intensive stem elongation increased and was in most cases the highest with heat stress at DEV31; this increase reached the significance level only for Plainsman V. This cultivar was the only one which reacted for heat stress at each developmental phase between DEV31 and DEV59 with significant increase in the rate of intensive stem elongation and with significant decrease in the interval of intensive stem elongation. The interval of intensive stem elongation proved to be the less genotype and more heat treatment dependent among the plant height characteristics (the genotype and heat stress treatment SS% was 44.5% and 27.7%, respectively, both significant at $P = 0.05$ level). In addition to Plainsman V, Mv Magma showed a significant decrease in this interval but only at the DEV31 phase, while neither Fleischmann 481, nor Soissons showed significant variation across the various treatments in the interval of intensive stem elongation.

Table 2. Effect of heat stress applied at different developmental phases on the plant morphological traits of the four wheat cultivars

Cultivar	Treatment	Final plant height (cm)	Rate of intensive stem elongation	Interval of intensive stem elongation	Maximum tiller No.	Reproductive tiller No.
Fleisch481	Control	69	2.01	25	3.6	3.0
	DEV31	79***	2.30	25	5.8***	4.0**
	DEV49	73*	2.54**	22	3.5	3.3
	DEV59	78***	2.09	29	3.8	3.0
Soissons	Control	41	1.05	29	3.2	3.0
	DEV31	41	1.24	25	4.5**	4.0**
	DEV49	38	0.98	29	2.5	2.5
	DEV59	42	0.98	32	3.0	2.5
Plainsman	Control	37	0.95	30	3.6	3.5
	DEV31	41*	1.87***	18***	6.8***	4.3*
	DEV49	40	1.42**	21***	3.5	3.5
	DEV59	42*	1.62**	20***	3.8	3.8
Magma	Control	38	1.25	22	4.6	4.0
	DEV31	32*	1.49	15**	8.5***	6.3***
	DEV49	36	1.24	21	5.5*	3.5
	DEV59	39	1.14	25	5.5*	3.8

*, **, *** differences from the control treatment are significant at the $P < 0.05$, 0.01 and 0.001 levels, respectively

In the case of tillering, both genotype and the heat stress treatment played significant components in determining the variance in a similar ratio; the genotype SS% was 41.3 while the heat stress treatment SS% was 52.9, both significant at $P = 0.0001$ level. Of the cultivars, Mv Magma produced significantly the highest number of tillers, irrespective to the treatments. The tillering capacity of Fleischmann 481 and Plainsman V was similar in all but one treatment, which was heat stress at DEV31, while Soissons produced the lowest number of tillers in all treatments. When determining the effect of heat stress at the various plant developmental phases, the maximum number of tillers was significantly greatest in response to heat stress at first node appearance (DEV31) for all four varieties. Heat treatment at the four later stages of development caused neither an increase nor a decrease



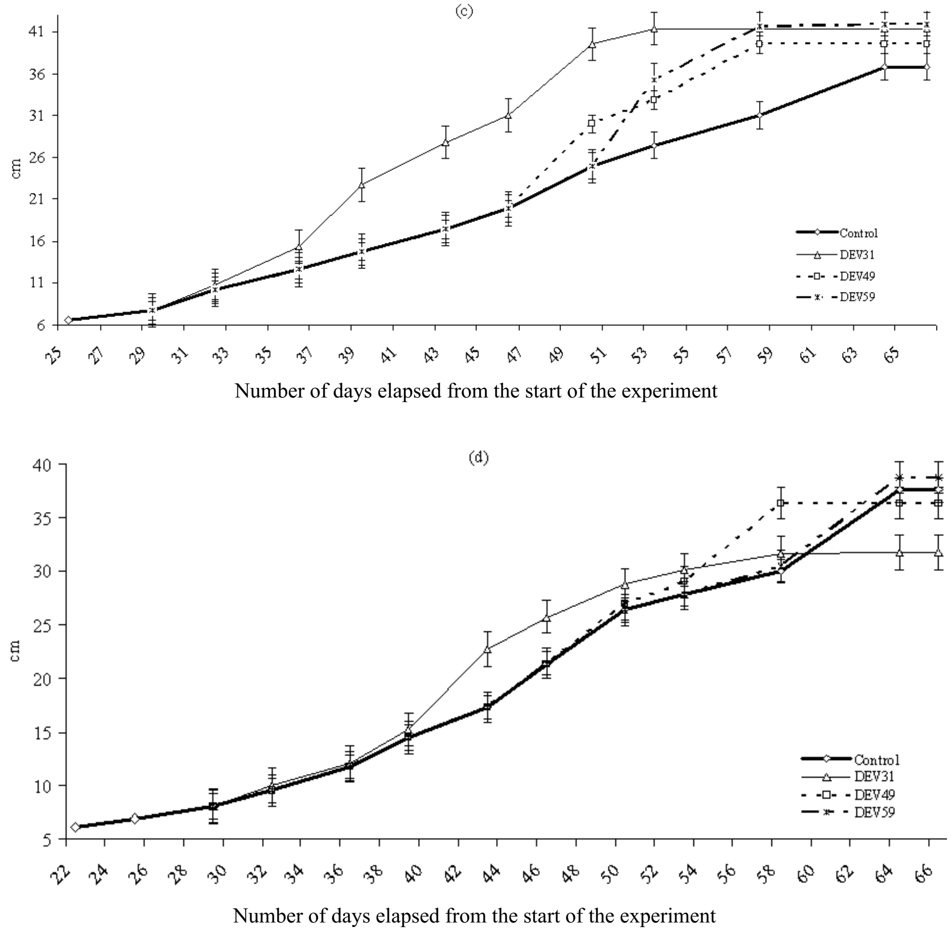


Figure 1. Changes in the plant height of (a) Fleischmann 481, (b) Soissons, (c) Plainsman V and (d) Mv Magma wheat cultivars in the course of time in response to heat stress applied at various developmental phases (Martonvásár, 2012). Differences significant at the $P = 0.05$ level

in tiller number, with the exception of Mv Magma. At DEV31, Mv Magma had the highest number of tillers (8.5) followed by Plainsman V (6.8), Fleischmann 481 (5.8) and Soissons (4.8) in a decreasing order, all significantly different from each other. The heat stress caused tendencies were similar for the number of reproductive tillers bearing fertile ears, however, the overall differences between the cultivars decreased. Again it was heat stress at DEV31 which resulted in significantly higher number of reproductive tillers in all the cultivars compared to the control treatment, but in this case Mv Magma produced only significantly higher reproductive tillers (6.3) than the other three cultivars, which had the same number of reproductive tillers (between 4.0 and 4.3).

Heat stress applied at DAF10 and DAF20 had no significant effect on either the plant height characteristics or on tillering.

Changes in yield components in response to heat stress

In the variance analysis of yield related traits, the genotype as variance component had larger contribution to the trait variances for the main spike than the side spikes. In the case of the main spike, the frequencies explained by the genotype decreased in the following order: number of spikelets (genotype SS% 91.6***), number of grains (71.0%***), grain weight (47.4%***) and thousand-kernel weight (40.3%***). As the contribution of the genotype decreased, increased the contribution of the timing of heat stress treatment, with the respective SS% values of 1.4, 9.6, 36.9** and 40.3***. In the case of the side spikes, the contribution of genotype to the trait variance was only larger than the effect of heat stress treatment for the number of spikelets per spike (SS% 56.3*** versus 28.1%**). For all the other traits the timing of heat stress were more pronounced, especially this was the case for the thousand kernel weight, where the contribution of cultivar vs heat stress were 27.1%*** and 61.2%***, respectively.

Heat stress at the different developmental phases had no significant effect on the number of spikelets in the main spike for none of the cultivars (Table 3). The difference between the four cultivars were significant irrespective to the timing of heat stress. Mv Magma had the highest spikelet number in the main spike, followed by Fleischmann 481, Soissons and Plainsman V. Under control conditions there was only a small reduction in the spikelet number of the side spikes compared to the main spike for three cultivars; the only exception was Mv Magma with a reduction of 13% in the spikelet number per side spike. Of the heat stress treatments, the heat stress applied at DEV31 had the strongest reducing effect on the spikelet number in the side spikes for all the cultivars. This reduction was already significant for Fleischmann 481 and Soissons. In addition, this treatment resulted in the largest differences between the spikelet numbers of the main and the side spikes, irrespective to the genotype.

Heat stress treatment in the various developmental phases had a substantial influence on the grain number, grain weight and thousand-kernel weight (Table 3), which was more pronounced in the case of the side spike than for the main spike. In the main spike the grain number was highest for Soissons and Mv Magma on average, while Fleischmann and Plainsman had significantly less seed number. This value showed decrease mostly in heat stresses applied in the middle plant developmental phases. Only one cultivar (Soissons), had significantly decreased grain number when heat stress was applied at DEV31, three cultivars (Fleischmann, Plainsman and Magma) showed significant decrease at DEV49 phase, two cultivars (Soissons, Plainsman) at DEV59, and one cultivar (Magma) at DAF10. From the aspect of grain number of the side spikes, Soissons proved to be the most sensitive to heat stress, with the exception of DEV59, this cultivar showed significant seed number decrease in all the other plant developmental phases. The opposing cultivar was Plainsman which had decreased seed number of the side spike only when heat stress was applied at DEV49. Fleischmann 481 and Mv Magma were mostly sensitive at the earlier developmental phases (DEV31 and DEV49).

Table 3. Effect of heat stress applied at different developmental phases on the yield components of the four wheat cultivars

Cultivar	Treatment	Main spike				Side spike			
		Spikelet No.	Grain No.	Grain weight	TKW	Spikelet No.	Grain No.	Grain weight	TKW
Fleisch481	Control	37.0	36.5	1.61	44.2	35.3	33.3	1.44	41.1
	DEV31	36.0	31.5	1.54	49.2	30.6***	19.6***	0.88**	45.2
	DEV49	36.0	25.3*	1.06**	42.6	39.3**	23.7*	0.84**	41.7
	DEV59	38.0	32.5	1.14**	34.9**	36.0	30.5	1.23	40.4
	DAF10	38.0	39.0	1.51	38.9*	36.1	31.0	0.98**	32.0**
	DAF20	38.0	38.8	1.63	41.9	37.2	36.5	1.37	37.5
Soissons	Control	35.0	48.8	2.31	48.0	34	47	2.17	44.1
	DEV31	34.0	35.3***	1.53***	44.0	27.8*	27.1***	1.13***	41.5
	DEV49	33.0	47.8	1.63***	34.1***	35.7	34.9**	1.28***	36.4*
	DEV59	33.0	42.0**	1.32***	31.3***	34.2	43.0	1.43***	33.4**
	DAF10	33.0	46.8	1.67***	35.6***	33.2	39.0*	1.12***	28.7***
	DAF20	33.0	45.0	1.73***	38.3***	32.2	35.1**	1.12***	28.2***
Plainsman	Control	32.0	37.0	1.46	40.1	30.9	30.1	1.17	38.9
	DEV31	35.0	36.3	1.33	34.8	28.8	25.2	0.9	35.8
	DEV49	32.0	30.0*	1.00***	33.6*	29.8	15.1*	0.54***	31.8*
	DEV59	32.0	32.5*	0.95***	29.1***	29.8	24.4	0.79**	32.6
	DAF10	31.0	33.5	1.01**	28.2***	30.8	29.8	0.69**	23.8***
	DAF20	31.0	33.8	1.24*	29.9***	28.6	29.2	0.79**	27.9**
Magma	Control	40.0	48.3	1.82	37.8	34.8	37.8	1.28	33.9
	DEV31	40.0	48.8	1.84	37.8	32.7	23.4***	0.94**	38.0
	DEV49	40.0	43.0*	1.52**	35.3	34.6	19.6***	0.81***	36.3
	DEV59	40.0	47.5	1.54**	30.2*	34.5	30.3*	1.04	35.4
	DAF10	39.0	43.3*	1.50**	32.7*	35.4	35.2	0.79***	24.9**
	DAF20	40.0	49.0	1.66	34.3	32.9	37.8	1.30	32.2

*, **, *** differences from the control treatment are significant at the $P < 0.05$, 0.01 and 0.001 levels, respectively

The grain weight both in the main and side spike showed a much stronger reduction compared to the grain number as a consequence of heat stress. The most sensitive cultivar from this aspect was again Soissons which reacted with significant decrease in grain weight with a similar fashion in both the main and the side spikes at all the developmental phases. Soissons was followed by Plainsman in sensitivity; the grain weight of this cultivar was significantly reduced by the heat stress at most of the developmental phases, the only exception was DEV31. The grain weight of Fleischmann 481 was the less affected by the heat stress; its grain weight in the mains spike was significantly reduced at DEV49 and DEV59, while in the side spike it was reduced at DEV31, DEV49 and DAF10.

The thousand-kernel weight, which is a summation of grain number and grain weight, showed again the strongest reduction for Soissons. With the exception of DEV31, heat stress at all the other stages significantly decreased the thousand-kernel weight both in the main and side spikes of this cultivar. The thousand-grain weight of the main spike was more sensitive to heat stresses in earlier developmental phases (DEV49 and DEV59), while the thousand-kernel weight of the side spike was more sensitive in the later developmental phases (DAF10 and DAF20). Plainsman was the second most sensitive based on the thousand-kernel weight, but the reduction in the main and side spike did not follow as clear a pattern as it was characteristic to Soissons. In Plainsman the thousand kernel weight of both the main and side spike showed the largest reduction at DAF10 phase. The reaction type of Fleischmann 481 and Mv Magma was similar to each other from the aspect of thousand-kernel weight. The thousand-kernel weight of the main spike showed significant but moderate decrease at two developmental phases (DEV59 and DAF10), while that of the side spike only at DAF10 for both cultivars.

As these cultivars are the parental lines of two wheat mapping populations, the pair wise comparisons of the parents of each population was also carried out based on the percentages of changes caused by the heat stress compared to the control values of each individual cultivar (Fig. 2). One parental pair is Fleischmann 481 and Soissons, the other is Plainsman V and Mv Magma. Fleischmann 481 and Soissons show definitely contrasting tendencies both in grain number and grain weight. Fleischmann 481 is significantly more heat tolerant than Soissons based on the grain number and grain weight in all the later plant developmental phases following after the heading. In the case of the Plainsman V and Mv Magma pair, the higher heat stress tolerance of Magma compared to Plainsman V is evident from the grain number and weight of the main spike at each developmental phase, while these values of the two cultivars are rather similar for the side spikes.

Discussion

Many excellent reports are available on the effects of heat stress on grain development, but only a few of these studies provide a detailed phenological characterisation combined with measurements of changes in yield due to heat stress (Shpiler and Blum 1990; Reynolds et al. 1994; Hossain et al. 2012). In the present study, heat treatment was carried out at five different phenological phases, from the first node detectable (DEV31) growth stage to 20 days after flowering, on four wheat genotypes with very different adaptation strategies, representing the pair wise parental lines of two wheat mapping populations (Balla et al. 2012).

One pair consists of Fleischmann 481 and Soissons. The old Hungarian landrace Fleischmann 481, which is well adapted to Hungarian climatic conditions, is considered to possess good heat and drought stress tolerance, while Soissons, of French origin, bred in an Oceanic climate, is considered to be sensitive to both types of stresses. The present results underlined the basic differences in the responses of these two cultivars, but also emphasised the probable impact of climate change. The habit, height, tillering ability and intensive stem elongation phase of the plant are all decisive for grain formation due to their influence on the quantity of assimilates available and their translocation to various plant organs (Borras et al. 2009; Reynolds et al. 2009). Differences were found for the two genotypes in terms of the intensive stem elongation phase and the final plant height. In the three development stages preceding flowering, heat-stressed plants of Fleischmann 481

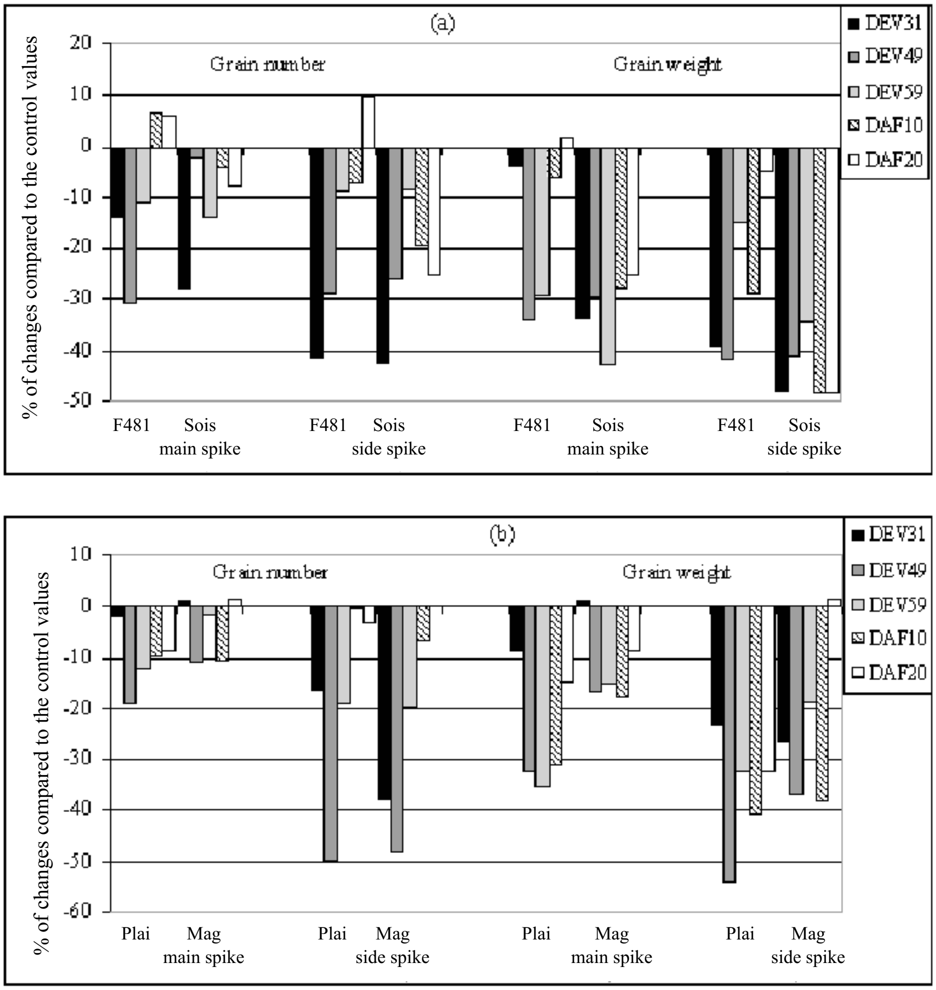


Figure 2. Pair wise comparisons of the heat stress responses of the two parents of a mapping population measured as changes in yield related traits. (a) Fleischmann 481 (F481) and Soissons (Sois) and (b) Plainsman V (Plai) and Mv Magma (Mag)

exhibited more intensive stem elongation than in the control over a similar period of time, resulting in taller plants. This in turn led to greater storage of stem reserves, which are extremely important for grain filling (Blum 1998; Foulkes et al. 2011). An acceleration in stem elongation was also observed for Soissons, but this was associated with the earlier cessation of stem growth, so there was no difference in the final plant height of the two groups. With respect to the grain yield per plant, the earlier phenophases (from first node appearance to heading) proved to be more sensitive to heat stress. This was particularly true for Soissons, with the exception of the boot stage. The difference between the two cultivars became more pronounced in the later stages, following flowering. The heat stress tolerance of Fleischmann 481, which is better adapted to Hungarian climatic conditions, gradually increased after heading, and by the 10th day after flowering it no longer exhibited sensitivity to heat stress. By contrast, the heat sensitivity of the variety Soissons, which originates from an oceanic climate, could still be detected 20 days after flowering.

The two members of the other pair are Plainsman V and Mv Magma, represented different levels and mechanisms of heat stress tolerance. Plainsman V is known as a drought tolerant, extensive genotype (Farshadfar et al. 2001), while Mv Magma is a modern Hungarian cultivar state registered in 1993 and thus is well adapted to the Hungarian conditions. In conducting experiments for studying the drought and heat stress tolerance in itself and in combinations on various wheat cultivars, Balla et al. (2009) also found that Plainsman V possessed a good level of drought tolerance, however, it proved to be quite sensitive to heat stress. Mv Magma on the other hand was one of the better heat tolerant genotypes in that wheat cultivar sample. Here it was again proven that the heat stress tolerance of Magma is better than that of Plainsman V, though the difference in stress tolerance is not as large between them compared to that of Fleischmann 481 and Soissons. Mv Magma possessed the ability of a good recovery after stress, which was manifested in the significantly increased tiller numbers. It was demonstrated by Kamal et al. (2010) that number, length and breadth of the leaves and the leaf area per main tiller were significantly affected by high temperature stress. In the present study no differences were found in the final leaf number between the control and treated groups, which could be attributed to the fact that the maximum possible number of leaves had already been determined by the time of the first heat stress period (from the DEV31 stage). A further biomass component involved in grain formation is the number of tillers (Reynolds et al. 2009). Reproductive tillers make up a considerable proportion of the total grain yield per plant. In the present experiments the side spikes were in various earlier stages of development compared with the main spikes when heat stress was applied, so in most cases they responded differently to the main spike in terms of spikelet number, grain number and grain weight. The extra tillering ability after heat stress was the largest for Magma among these four cultivars. In this case thus not the stem reservoirs could be utilised but the extra tillers behaved as extra sources of assimilate production helping in conserving the seed number and seed weight in the main spike to the largest extent among these cultivars and also contributing better to the seed weight of the side spikes.

In conclusion, considerable variation was detected among the four cultivars in their response to heat stress measured via phenology and yield component traits. The stress response also depended strongly on the developmental phase in which the heat stress was applied. Among these cultivars Fleischmann 481 proved to be the most heat tolerant, followed by Mv Magma, while Soissons was the most sensitive followed by Plainsman V. The fact that even Fleischmann 481, the heat tolerance of which was confirmed in the present work, was nevertheless sensitive to heat stress during the developmental phases preceding heading draws attention to the phenophase-dependent mechanism of heat stress tolerance, while also underlining the possible negative effects of global climate change. As a consequence of climate change, unusually high temperatures in late spring may occur increasingly earlier and more frequently, affecting the plants in earlier phenophases than usual and thus inducing heat stress even in genotypes known to be heat tolerant. In order to study this phenomenon in greater depth, the two doubled haploid populations developed from these cultivars will be used to evaluate the responses of the individual lines to heat stress in various stages of development and to determine the genetic components of heat stress tolerance.

Acknowledgement

Funding from the TÁMOP-4.2.2.A-11/1/KONV-2012-0064, EU FP7-244374 DROPS and EU BONUS 12-1-2012-0017 projects is gratefully acknowledged.

References

Almeselmani, M., Deshmukh, P.S., Chinnusamy, V. 2012. Effects of prolonged high temperature stress on respiration, photosynthesis and gene expression in wheat (*Triticum aestivum* L.) varieties differing in their thermotolerance. Plant Stress **6**:25–32.

Altenbach, S.B. 2012. New insights into the effects of high temperature, drought and post-anthesis fertilizer on wheat grain development. J. Cereal Sci. **56**:39–50.

Balla, K., Bencze, S., Janda, T., Veisz, O. 2009. Analysis of heat stress tolerance in winter wheat. Acta Agron. Hung. **57:**437–444.

Balla, K., Karsai, I., Kiss, T., Bencze, S., Bedő, Z., Veisz, O. 2012. Productivity of a doubled haploid winter wheat population under heat stress. Cent. Eur. J. Biol. **7**:1084–1091.

Barnabás, B., Jäger, K., Fehér, A. 2008. The effect of drought and heat stress on reproductive processes in cereal. Plant Cell Environ. **31**:11–38.

Barrow, E.M., Hulme, M. 1996. Changing probabilities of daily temperature extremes in the UK related to future global warming and changes in climate variability. Clim. Res. **6**:21–31.

Blum, A. 1998. Improving wheat grain filling under stress by stem reserve mobilisation. Euphytica **100**:77–83.

Borras, G., Romagosa, I., van Eeuwijk, F., Slafer, G.A. 2009. Genetic variability in duration of pre-heading phases and relationships with leaf appearance and tillering dynamics in a barley population. Field Crops Res. **113**:95–104

Farooq, M., Bramley, H., Palta, J.A., Siddique, K.H.M. 2011. Heat stress in wheat during reproductive and grain-filling phases. Plant Sci. **30**:1–17.

Farshadfar, E., Farshadfar, M., Sutka, J. 2001. Combining ability analysis of drought tolerance in wheat over different water regimes. Acta Agron. Hung. **48**:353–361.

Foulkes, M.J., Slafer, G.A., Davies, W.J., Berry, P.M., Sylvester-Bradley, R., Martre, P., Calderini, D.F., Griffiths, S., Reynolds, M.P. 2011. Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. J. Exp. Bot. **62**:469–486.

Halford, N.G. 2009. New insights on the effects of heat stress on crops. J. Exp. Bot. **60**:4215–4216.

Hays, D.B., Do, J.H., Mason, R.E., Morgan, G., Finlayson, S.A. 2007. Heat stress induced ethylene production in developing wheat grains induces kernel abortion and increased maturation in a susceptible cultivar. Plant Sci. **172**:1113–1123.

Hossain, A., da Silva, J.A.T., Lozovskaya, M.V., Zvolinsky, V.P. 2012. High temperature combined with drought affect rainfed spring wheat and barley in Shout-Eastern Russia: I. Phenology and growth. Saudi J. Biol. Sci. **19**:473–487.

IPCC Intergovernmental Panel on Climate Change Fourth Assessment Report: Climate Change 2007. Synthesis Report. World Meteorological Organization, Geneva, Switzerland.

Kamal, U.A., Kamrun, N., Masayuki, F. 2010. Sowing date mediated heat stress affects the leaf growth and dry matter partitioning in some spring wheat (*Triticum aestivum* L.) cultivars. The IIOAB Journal **3**:8–16.

Mittler, R., Finka, A., Goloubinoff, P. 2012. How do plants feel the heat? Trends Biochem. Sci. **37**:118–125.

Qin, D., Wu, H., Peng, H., Yao, Y., Ni, Z., Li, Z., Zhou, C., Sun, Q. 2008. Heat stress-responsive transcriptome analysis in heat susceptible and tolerant wheat (*Triticum aestivum* L.) by using wheat genome array. BMC Genomics **9**:432.

Rahman, M.A., Chikushi, J., Yoshida, S., Karim, A.J.M.S. 2009. Growth and yield components of wheat genotypes exposed to high temperature stress under control environment. Bangl. J. Agril. Res. **34**:361–372.

Reynolds, M., Foulkes, M.J., Slafer, G.A., Berry, P., Parry, M.A.J., Snape, J.W., Angus, W.J. 2009. Raising yield potential in wheat. J. of Exp. Bot. **60**:1899–1918.

Reynolds, M.P., Balota, M., Delgado M.I.B., Amani, I., Fischer, R.A. 1994. Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. Aust. J. Plant Physiol. **21**:717–730.

Semenov, M.A. 2007. Development of high resolution UKCIP02-based climate change scenarios in the UK. Agr. Forest Meteorol. **144**:127–138.

Semenov, M.A., Halford, N.G. 2009. Identifying target traits and molecular mechanisms for wheat breeding under a changing climate. J. Exp. Bot. **60**:2791–2804.

Semenov, M.A., Shewry, P.R. 2011. Modelling predicts that heat stress, not drought, will increase vulnerability of wheat in Europe. Scientific Reports **1**: 66.

Shpiler, L., Blum, A. 1990. Heat tolerance of yield and its components in different wheat cultivars. Euphytica **51**:257–263.

Tottman, D.R., Makepeace, R.J. 1979. An explanation of decimal code for the growth stages of cereals, with illustrations. Ann. Appl. Biol. **93**:221–234.

Wahid, A., Gelani, S., Ashraf, M., Foolad, M.R. 2007. Heat tolerance in plants: An overview. Environ. Exp. Bot. **61**:199–223.

Zhang, B., Liu, W., Chang, S.X., Anyia, A.O. 2010. Water-deficit and high temperature affected water use efficiency and arabinoxylan concentration in spring wheat. J. Cer. Sci. **52**:263–269.