ARTICLE

Effects of drought on photosynthetic parameters and heat stability of PSII in wheat and in *Aegilops* species originating from dry habitats

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ABSTRACT　　　The effects of water deficit induced by withholding water in soil pots were examined on processes related to photosynthesis and heat stability of PSII in wheat cultivars and in *Aegilops* species. Decrease in relative water content (RWC) of leaves resulted in fast and considerable stomatal closure and decrease in net photosynthetic CO_2 fixation (A) in *Ae. bicornis* and in wheat cultivars, while in *Ae. tauschii* and *Ae. speltoides* stomatal conductance (g_s) and A remained relatively high between 90 and 70% RWC. Parallel with this, A was limited by the CO_2 diffusion to the intercellular spaces (stomatal limitation, L_s) even at a lower RWC in *Ae. taushii* and in *Ae. speltoides*, while a significant mesophyll limitation (L_m) was observed for *Ae. bicornis* and for wheat. On the other hand, drought stress resulted in a significant increase in the thermal stability of PSII in wheat and *Aegilops* genotypes. The results indicate that some genotypes of *Ae. taushii* and *Ae. speltoides* have better drought tolerance with satisfactory heat stability than wheat, making them appropriate for improving the heat tolerance of wheat to survive dry and hot periods in the field.　　　**Acta Biol Szeged 50(1-2):11-17 (2006)**

Aegilops species with good tolerance to some major abiotic stress factors are closely related to wheat (Van Slageren 1994) and widely used as genetic resources for *Triticum* species (Molnár et al. 2004). As reported, the tetraploid goat grass (*Aegilops biuncialis* L., 2n = 4x = 28, $U^bU^bM^bM^b$) has a good drought tolerance, which makes it suitable to improve the drought tolerance of wheat (Molnár et al. 2004). However, in the case of other *Aegilops* species there are hardly any data on the tolerance to abiotic stress factors like drought and heat stress (Rekika et al. 1977; Zahireva et al. 2001). In addition, diploide goat grasses, such as *Ae. tauschii* Coss. (DD), *Ae. bicornis* (S^bS^b) and *Ae. speltoides* Tausch. (SS) have some other advantages since the B and D genome of wheat are originated from *Ae. speltoides* and *Ae. tauschii* species (Jauhar and Chibbar 1999). Consequently, the chromosome mediated gene transfer from these species to hexaploide wheat is easier than from *Ae. biuncialis*. Moreover, several PCR based molecular markers specific to the B or D genome could facilitate the isolation of genes responsible for drought tolerance in these goat grasses (Röder et al. 1998). It follows that it is worth looking for accessions of various *Aegilops* species with good drought and heat tolerance that are more closely related to wheat than *Ae. biuncialis*.

Ae. speltoides and *Ae. tauschii* are wide-spread in the western Asiatic region and the latter in Central Asia, as well;

Ae. bicornis grows in North Africa characterised by hot summers with a low amount of seasonal or annual rainfall. Although the *Aegilops* plants mentioned above are able to effectively survive these unfavorable environmental factors, no information has been provided on their drought and heat tolerance.

Drought and heat are important biomass-limiting stress factors (Berry and Björkman 1980; Araus et al. 2002) in the field causing the suppression of cultivated plants in growth and in crop production (Blum et al. 1997). During drought the water potential (ψ), relative water content (RWC) and net photosynthetic CO_2 fixation (A) substantially decrease (Bajji et al. 2001; Molnár et al. 2004). The reduction of A partially results from the closure of stomata due to water deficit, since decrease of stomatal conductance (g_s) is the most efficient way to reduce water loss, and parallel with this the CO_2 diffusion into the leaves is restricted, resulting in a decrease in intercellular CO_2 concentration (C_i) (Cornic 2000). On the other hand, the limitation of CO_2 fixation during water deficit is also influenced by the diffusion of CO_2 from the intercellular spaces to chloroplasts (Delfine et al. 1999; Loreto et al. 2003; Molnár et al. 2005), and by other metabolic factors such as changes in the capacity of ribulose-1,5-bisphosphate-carbosilase-oxigenase (Rubisco) and perturbed regeneration of ribulose-1,5-bisphosphate, etc (Medrano et al. 1997; Maroco et al. 2002; Centritto et al. 2003; Chaves et al. 2003; Molnár et al. 2004).

The heat sensitivity of plants is closely connected to the thermal stability of PSII. It is more or less clear that the thermal tolerance of the photosynthetic apparatus in some higher plants is influenced by other stress factors like light (Havaux and Tardy 1996; Molnár et al. 1998), and by water deficit in a desiccation tolerant moss (Dulai et al. 2004). The study of these problems is further justified by the fact that under natural conditions high light intensity, heat stress, and water deficit occur in combination with each other: the effects of the three stress factors need to be tolerated at the same time.

In connection with the above-mentioned facts the examined *Aegilops* species are natives in the Mediterranean and in Asiatic arid or semi-arid continental regions, which are characterised by hot vegetation periods with a low amount of rainfall. On the other hand, physiological acclimation features in some measure depend on the climate of the original habitat of plants (Zahireva et al. 2001; Bultynck et al. 2003; Molnár et al. 2004). Since the vegetation period in native habitats of the examined *Aegilops* species is dry and hot, these plants had to develop various acclimation strategies to drought and to heat.

In this paper we compare some photosynthetic responses to drought and heat in three diploid *Aegilops* species originating from arid habitats with two wheat genotypes presumably characterised by a different drought tolerance to indicate that some of them have better drought tolerance with low temperature sensitivity than wheat, making them suitable for improving the drought and heat tolerance of wheat by intergeneric crossing, enabling it to survive the dry and hot periods in the field.

Materials and Methods

Plant materials

Aegilops species originating from areas with differing annual rainfalls (*Ae. speltoides* MvGB 1042 450-1450 mm, *Ae. tauschii* MvGB 605 100-350 mm and *Ae. bicornis* MvGB 585 75-275 mm) were provided by the gene bank of the Agricultural Research Institute of the Hungarian Academy of Sciences, Martonvásár, Hungary). The winter wheat (*Triticum aestivum* L.) Mv9kr1 has presumably moderate drought tolerance and Sakha is drought tolerant (Trivedi et al. 1991). The examined *Aegilops* lines were selected previously from thirteen accessions by germination ability in 15% (w/v) polyethylene-glycol solution. All experiments were performed on intact leaves or leaf segments of *Triticum aestivum* and of *Aegilops* sp. Seeds were germinated under laboratory conditions. After germination, these plants were grown in 1.5 kg soil pots in an unheated greenhouse for 5 weeks under natural sunlight. The water deficit was induced by withholding the water supply in the soil. The water status of plants was traced by determining the relative water content (RWC) according to the following equation: $RWC = (FW - DW) \times 100 / (SW - DW)$ where FW is the fresh weight, SW the water saturated weight and DW the dry weight after drying for 12 h at 105°C.

Chlorophyll a Fluorescence Measurements

The *in vivo* chlorophyll a fluorescence was measured in dark-adapted intact leaves with a pulse amplitude modulation fluorometer (PAM 101-103, Walz, Effeltrich, Germany) as described by Dulai et al. (1998), and recorded with a potentiometric chart recorder (NE-244, EMG, Budapest, Hungary) and a computer. The initial level (F_0) of fluorescence was excited by a weak 650-nm light beam modulated at 1.6 kHz (0.01 μmol m^{-2} s^{-1}). The fluorescence was detected by a PIN S1723 photodiode. The maximal fluorescence level (F_m) of the dark-adapted leaves was induced by a white saturating flash (4000 μmol m^{-2} s^{-1}) of 0.8 s duration, provided by a Schott KL-1500 light source (Schott, Essex, UK). Photosynthesis was induced for 15 min by continuous actinic light of 1000 μmol m^{-1} s^{-1}. The variables and equations for quenching analysis were determined according to van Kooten and Snel (1990). The quantum efficiency of photochemistry was calculated as $\Delta F/F_m$', as described by Genty et al. (1989).

Heat-induced Chlorophyll Fluorescence

For the determination of the breakpoints (T_c,) of initial (F_0) and steady-state (F_s) fluorescence vs. temperature (T) curves the method of heat induction of fluorescence was applied as described by Schreiber and Berry (1977). The leaves were dark-adapted for 30 min, and then placed on the thermoelectric module. During heating from 25°C to 60°C at a rate of 1°C min^{-1}, the temperature was monitored by a thermocouple thermometer. Heating for F_s vs. T curves was started when the photosynthesis was steady. T_c was determined from the F_s vs. T curves.

Gas exchange measurements

CO_2 assimilation of intact leaves was measured with an infrared gas analyser (LCA-2, Analytical Development Co. Ltd, Hoddesdon, UK) in a semi-closed gas-exchange system. The white light for excitation of photosynthesis was provided by a Schott KL-1500 light source through a fiberopticable. The rates of net CO_2 fixation (A), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) fixation were calculated in the light saturated state of photosynthesis by using the equations of von Caemmerer and Farquhar (1981). The light response curve of A was determined in the range of 100-1200 μmol m^{-2} s^{-1}. The responses of A to changing in ambient CO_2 concentration was measured between 3-1000 ppm CO_2 at 1000 μmol m^{-2} s^{-1} light intensity using a gas diluter (Analytical Development Co. Ltd, Hoddesdon, UK). Stomatal (L_s) and mesophyll (L_m) limitation were determined on the basis of the A *vs*. C_i curves as described Lawror (2002).
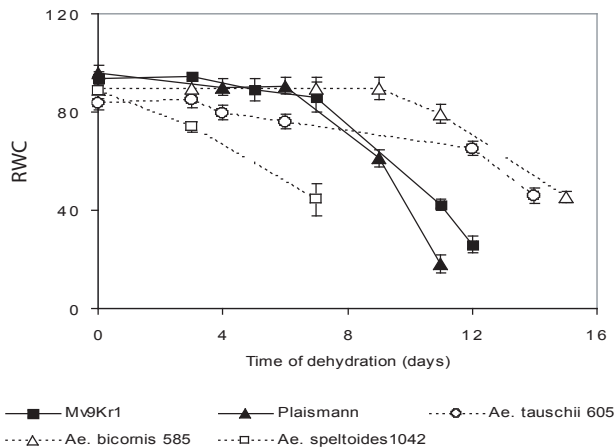
Figure 1. Effects of drought stress on relative water content (RWC) for wheat cultivars and for *Aegilops* species.

Figure 2. Effects of decrease in relative water content on stomatal conductance (g_s mmol H_2O m^{-2} s^{-1}) for wheat cultivars and for *Aegilops* species.

Statistical analysis

Student *t*-tests were performed using MS Excel (Microsoft Corporation, Seattle, USA). Differences between results are described as being significant where $P \leq 0.01$, and not significant where $P > 0.01$.

Results and Discussion

Effects of drought stress on the water content of the leaves

During drought stress, the water balance of plants is disrupted, as a result of which the RWC and water potential (ψ) of leaves decreases (Bajjii et al. 2001). In most cases stomatal closure can be observed, parallel with which stomatal conductance (g_s) decreases (Cornic 2000; Molnár et al. 2004) to reduce the water loss. If plants are able to hold the water effectively, that is, when the water potential is kept high in the dry period as well, they may have a good chance to survive the dry period, which however does not mean that the related physiological and photosynthetic processes are not susceptible to the low water content. After the withholding of water supply, the time dependence of RWC decrease was considerably different in *Ae. bicornis* MvGB 585 from that of wheat (Fig. 1). In this plant, water loss was substantially slower than in wheat cultivars, with a significant decrease of RWC only after the 9th-10th day, and its water content was significantly higher than that of wheat even at the end of the dry period. The originally high g_s decreased significantly at a slight water loss (Fig. 2), and stomatal closure, as is well-known, is the most efficient way of reducing transpirational water loss (Cornic 2000). It is interesting that *Ae. tauschii* MvGB 605, while efficiently keeping water, was not characterised by abrupt and significant stomatal closure; its RWC during drought did not decrease drastically, despite the higher g_s. As opposed to the ones mentioned above, it is a line
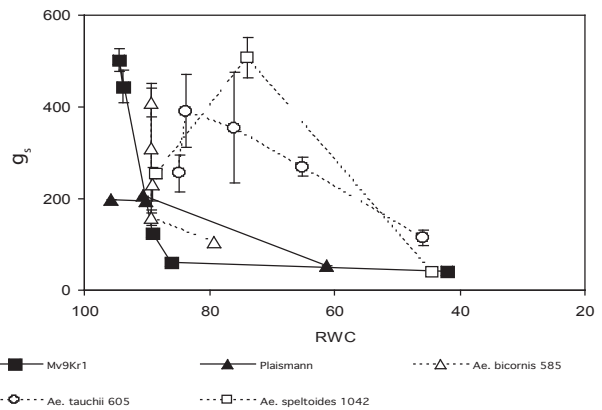
in which water loss was faster than in wheat (*Ae. speltoides* MvGB 1042,). In this plant, under normal water conditions g_s was lower than in *Ae. bicornis* and wheat, but decreased less with water loss and can even increase at the beginning of the desiccation period. However, despite this fast and considerable decrease in RWC *Ae. speltoides* was capable of maintaining a relatively high rate of A until 70% RWC compared with wheat and *Ae. bicornis* MvGB585.

Effects of drought stress on the gas exchange and fluorescence induction parameters

It is well known that during water deficit stomata play an important role not only in the regulation of transpiration water loss but, also, a primary physiological effect of drought is the inhibition of photosynthetic CO_2 fixation partly by stomatal closure (Sharkey 1990; Chaves 1991; Cornic 1994; Molnár et al. 2004) g_s, though not to the same degree and not with the same RWC values, decreased in all examined genotypes with the decrease in RWC (Fig. 2). The strongest stomatal closure was detected in wheat cultivars, especially in Mv9kr1 and in *Ae. bicornis*. Contrary to this, stomata in *Ae. tauschii* and *Ae. speltoides* remained open in a wider range of RWC than those in wheat. When other factors do not limit the carboxylation processes, this decrease of stomatal conductance (g_s), which may restrict the diffusion of CO_2 into the leaves, has been reported to lead to a modification in intercellular CO_2 level and, as a result, to a decrease in photosynthetic CO_2 fixation (Flexas and Medrano 2002). As can be clearly seen in Figure 3 A was strongly restricted as RWC fell in the case of wheat cultivars and *Ae. bicornis*. However, despite the water loss *Ae. speltoides* and *Ae. tauschii* were capable of maintaining a satisfactory rate of net photosynthesis even at lower RWC values. These results indicate that the latter two goat grasses, similarly to some *Aegilops biuncialis* accessions (Molnár et
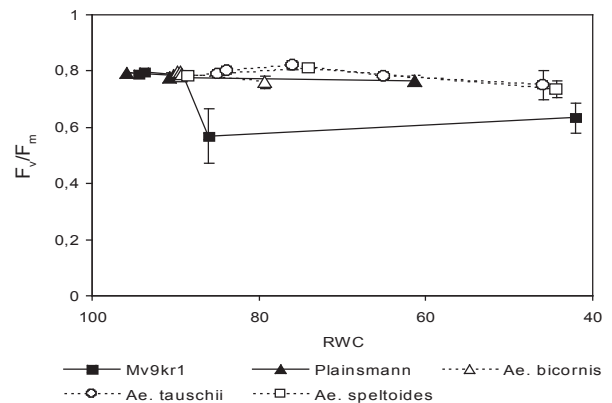
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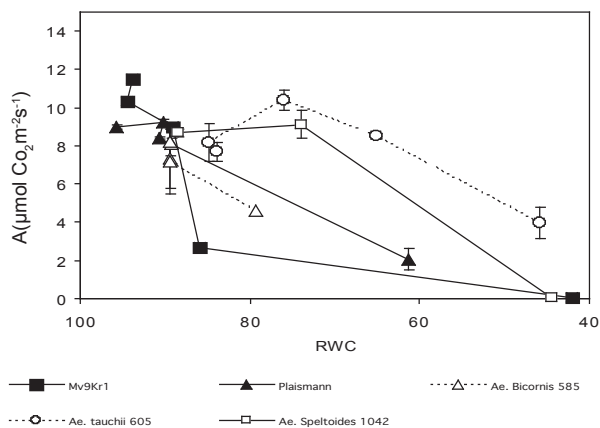
Figure 3. Effects of decrease in relative water content on net photosynthetic CO_2 fixation (A, $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) for wheat cultivars and for *Aegilops* species.

al. 2004), could retain their CO_2 fixation rate in spite of high water deficit.

In water-saturated C_3 plants, with environmental CO_2 concentration and corresponding C_i, at saturating light intensity, A does not reach the maximum level which is measurable at saturating CO_2 concentration (A_{max}). As suggested previously, stomatal closure is the main limitation to CO_2 fixation during drought since A_{max} can be recovered by a high CO_2 level (Cornic
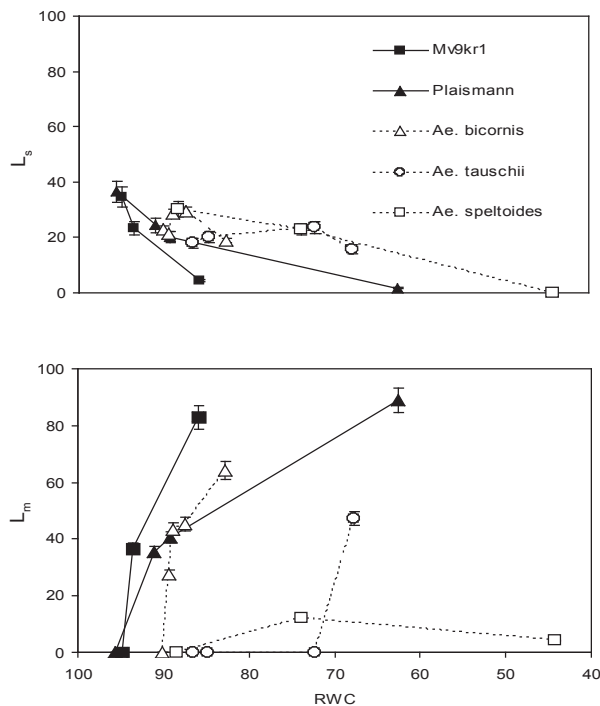

Figure 4. Stomatal (L_s) and mesophyll (L_m) limitations of net photosynthetic CO_2 fixation in relation to relative water content (RWC) for wheat cultivars and for *Aegilops* species.

Figure 5. Effects of decrease in relative water content on optimal quantum yield (F_v/F_m) of PSII for wheat cultivars and for *Aegilops* species.

2000; Cornic and Fresneau 2002); however, other studies have reported that the maximal rate of net photosynthesis is not fully recovered by the increased CO_2 concentration: decrease of A can also result from the reduced mesophyll conductance (Delfine et al. 1999; Flexas et al. 2002; Loreto et al. 2003) or important metabolic factors (Tezara et al. 1999; Delfine at al. 2001; Lawror and Cornic 2002; Centritto et el. 2003; Chaves et al. 2003). In accordance with the above mentioned facts the factors affecting photosynthetic CO_2 fixation during water deficit have been termed "stomatal" (L_s) and mesophyll (L_m) limitations (Lawror 2002). As can be seen in Figure 4 the extent of L_s decreased intensively as the RWC fell in wheat cultivars and in *Ae. bicornis*, while remained almost unchanged for *Ae. tauschii* and *Ae. speltoides* between 90 and 70% RWC. At lower RWC values (≤90%) L_m increased drastically in the case of wheat and *Ae, bicornis* indicating the primary role of the mesophyll limitation in the inhibition of A. Contrary to this, the relative importance
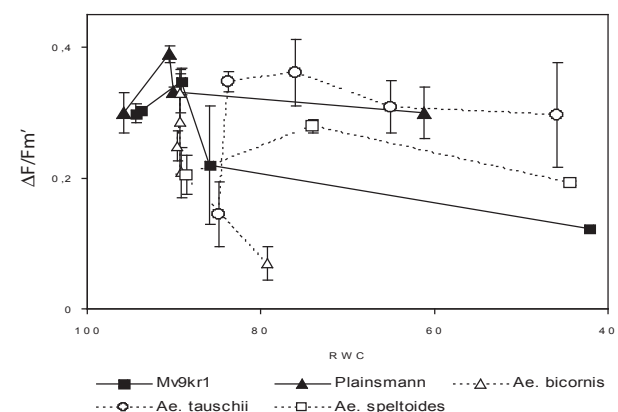
Figure 6. Effects of decrease in relative water content on effective quantum yield ($\Delta F/F_m'$) of PSII for wheat cultivars and for *Aegilops* species.

Table 1. Effect of water deficit on the breakpoints (T_c) of the F_0 vs. T (practically recorded in darkness) and F_s vs. T curves at 1000 μmol m^{-2} s^{-1} actinic light (AL) intensity. $T_{c\,dark}$, T_c values of F_0 vs. T curves in non-stressed plants; T_{c0}, T_c values of F_0 vs. T curves in non-stressed plants; T_{c1}, T_c values of F_0 vs. T curves measured at the end of the dry period.

Species, cultivars	$T_{c\,dark}$	T_{c0} (1000 μmol m^{-2} s^{-1})	T_{c1} (1000 μmol m^{-2} s^{-1})
Mv9Kr1	43,5±0,817	45,7± 0,173	49,0±0.000
Plaismann	42,7±0,251	46,2±0,251	47,5±0.500
Ae. tauschii 605	43,0±0,000	46,4±0,360	51,0±0.500
Ae. bicornis 585	43,4±0,655	46,8±0,404	48,0±0.000
Ae. speltoides 1042	43,0±0,642	46,5±0,286	49,0±0.000

of L_m was not significant in this range of RWC in *Ae. tauschii* and in *Ae. speltoides* (Fig. 4). These results indicate that L_m is the main limitation to photosynthesis in leaves of *Ae. bicornis* and wheat during water stress, attributed to the decrease of CO_2 diffusion from intercellular spaces to chloroplasts and the inhibition of some key metabolic processes. In spite of this, the processes in the background of mesophyll limitation are not significant in the case of *Ae. speltoides* and *Ae. tauschii* accessions. In the same way, a weak metabolic limitation has previously been reported based on oxygen sensitivity of photosynthesis in *Ae. biuncialis* accessions originating from arid habitats by Molnár et al. (2004).

Although, data have been published on the role of photochemical and electron transport processes (Keck and Boyer 1974; Giardi et al. 1996) in metabolic limitation, the optimal quantum yield (F_v/F_m) was not significantly affected by water deficit in the range 95-40% RWC (Fig. 5), as was also reported in other studies (Ben et al. 1987; Grieu et al. 1995). Therefore, our results suggest that drought has a marginal effect on the primary charge separation in the *Aegilops* species and in wheat cv. Plainsmann, whereas a slight decrease was observed in wheat cv. Mv9kr1 as the RWC fell. Nevertheless, already at medium water deficit the photosynthetic electron transport processes were significantly down regulated in Mv9kr1 as reflected in the decrease of effective quantum yield of PS II photochemistry ($\Delta F/F_m'$, Fig. 6). Contrary to this, $\Delta F/F_m'$ increased significantly in the case of *Ae. tauschii* and *Ae. speltoides* parallel with medium water deficit, probably indicating the increased proportion of open PS II centres, and it changed independently from the efficiency of primary charge separation (F_v/F_m). It is interesting that mesophyll limitation was also slight at this level of water stress in these plants while it became significant in wheat Mv9Kr1 and in *Ae. bicornis* parallel with the decrease of ($\Delta F/F_m'$).

On the basis of similar responses of g_s, A, L_s, L_m and photochemical efficiency it seems that besides some *Ae. biuncialis* accessions certain genotypes of *Ae. tauschii* and *Ae. speltoides* are also suitable to improve drought tolerance of wheat.

Heat tolerance changes of PSII during drought stress

The sensitivity of the photosynthetic apparatus to heat stress is closely connected to the thermal stability of PSII, which is well characterised by the critical values of the temperature dependence of the initial fluorescence level (F_0) of dark-adapted leaves (Schreiber and Berry 1977; Smillie and Nott 1979; Bilger et al. 1984). This method is also used to estimate heat tolerance of wheat and *Aegilops* species (Rekika et al. 1997). The heat tolerance of PSII in wheat and in *Aegilops* genotypes determined on the basis of the F_0 vs. T curves (practically in darkness) was not sufficient (42-43°C) for tolerating such high temperatures that are peculiar to their original habitats above the surface (Table 1) coupled with high irradiation and drought. Similarly to F_0, the breakpoints (T_c) of temperature dependence of steady state fluorescence (F_s) appropriately show the thermal stability of samples with a steady-state photosynthesis level (Molnár et al. 1998; Dulai et al. 2004). In connection with this, T_c values of F_s vs. T curves measured at moderately high AL intensity (1000 μmol m^{-2} s^{-1}) are shifted towards significantly higher temperatures (~46°C), indicating the higher thermal tolerance of PSII for wheat cultivars and for goat grasses (Table 1).

Although during drought the relative water content and the activity of some photosynthetic processes decrease, there are observations to the effect that in higher plants the slow dehydration of removed leaves resulted in an increase of the thermal stability of PSII (Havaux 1992). As a result of severe water deficit, in wheat cultivars and in examined goat grasses with steady-state photosynthesis at 1000 μmol m^{-2} s^{-1} AL intensity, the critical values of the F_s vs. T curves were shifted significantly higher, compared to the unstressed plants (Table 1). This enhanced thermal stability was more or less also manifested by the temperature dependence of the effective quantum yield of PSII (not shown by data). Although considerable differences were not detected between wheat and *Aegilops* accessions in these phenotypic responses (Table 1) to heat, these may be important in tolerating the high temperatures which occur during drought in their natural habitats.

On the basis of the results presented it seems that, although parallel with different degrees of water loss, *Ae. tauschii* MvGB 605, *Ae. speltoides* MvGB 1042 originated from dry habitats are able to maintain a sufficient CO_2 fixation and, at the same time, a high heat tolerance of the photosynthetic apparatus during drought. Besides, the slight mesophyll limitation of net photosynthesis in these plants may provide a good chance for the rapid recovery from a not too severe water stress. These properties make them a good candidate for improving the drought tolerance with low heat sensitivity of wheat by intergeneric crossing, to effectively survive the forecasted dry and hot periods in the fields of central Europe.

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Acknowledgements

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