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ARTICLE

Chlorophyll *a* fluorescence induction parameters of flag leaves characterize genotypes and not the drought tolerance of wheat during grain filling under water deficit

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ABSTRACT Chlorophyll *a* fluorescence induction parameters of two drought tolerant (MV Emese and Plainsman V) and two sensitive (GK Élet and Cappelle Desprez) wheat cultivars were compared on the day 16 post anthesis (DPA) under control and water stressed conditions. It was found that under drought stress the chlorophyll *a* (Chl) content declined earlier in the sensitive genotypes, but the rate of Chl loss was much higher in the tolerant cultivars and also in the controls of cv. Plainsman after 12 DPA. The *trans*-zeatin content, a transport form of cytokinins also significantly declined to 16 DPA in the sensitive GK Élet. Because cytokinins prevent Chl loss, it may be a cause of the decreased Chl level in this cv. under drought. Neither net CO_2 assimilation rate (P_N) nor other Chl *a* fluorescence induction parameters such as Fv/Fm or Φ_{PSII}, qP and NPQ as a function of increasing photon flux densities (PFD) exhibited a special change which could characterize only tolerant or sensitive cultivars. Instead, these changes characterized the genotypes. In cvs MV Emese and Plainsman the flag leaf senescence could result in faster and better remobilization of the pre-stored carbon from vegetative tissues, and ultimately better yield than in GK Élet and Cappelle Desprez under drought. **Acta Biol Szeged 53(1): 1-7 (2009)**

KEY WORDS

Chlorophyll *a* fluorescence
drought tolerance
grain filling
wheat genotypes

Under the temperate zone early-summer droughts are increasingly frequent. This may severely limit grain yield since the water shortage coincides with the grain filling period of most cereals, including wheat, one of the main crops consumed by humans.

In grain filling period water deficit induces fast senescence in wheat, especially in older leaves. The primary expression of leaf senescence is the breakdown of chlorophyll and the decline of photosynthetic activity. It is generally accepted, that the genotypes which are able to sustain photosynthesis in flag leaf for longer time, tend to yield more (Richards 2000).

Since photosynthesis is one of the main metabolic processes determining crop production, chlorophyll fluorescence was used as an effective tool for monitoring the function of the photosynthetic apparatus in response to water stress (Flexas et al. 2002; Fracheboud and Leipner 2003; Zlatev and Yordanov 2004). The effect of drought on photosynthesis has long been controversial and it is still not clear whether chlorophyll *a* (Chl-*a*) fluorescence parameters are good indicators for drought sensitivity. Photosystem II (PSII) is sensitive to environmental limiting factors, but drought stress, as indicated by a number of studies with different plant species resulted in conflicting results.

Water-limiting conditions probably have no significant effect on the primary photochemistry of PSII in wheat or durum wheat (Subrahmanyam et al. 2006; Hura et al. 2007) because the maximal quantum yield (variable/maximal fluorescence, Fv/Fm), the rapid fluorescence induction kinetics and polyphasic fluorescence transients were not significantly affected in dark-adapted leaves of six-week-old plants (Lu and Zhang, 1999). In contrast, the actual quantum yield of PSII electron transport (Φ_{PSII}) decreased, non photochemical quenching (NPQ) increased, but photochemical quenching coefficient (qP) did not change under water deficit in light adapted leaves in wheat (Lu and Zhang 1999; Hassan 2006; Subrahmanyam et al. 2006). It was found in other experiments that Fv/Fm decreased under drought stress conditions in young leaves (Hassan 2006) or was also reduced in flag leaves of wheat plants (Paknejad et al. 2007). Increase in the ground state fluorescence (Fo) or decrease in Fv/Fo and Fv/Fm can be considered to be reliable indicators for screening drought tolerance of barley genotypes (Li et al. 2006). Paknejad et al. (2007) also found that Fv, Fv/Fm and Fo had high correlation coefficients with drought sensitivity and with grain yield.

Yield is the most important economic trait, and grain production is the main selection criteria for drought resistance of wheat. Many environmental factors, such as high air or soil

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temperature (Ugarte et al. 2007), time and application of fertilizers (Erdei et al. 1986), water or ozone stress (Fangmeier et al. 1994) may influence the productivity, and ultimately the grain yield.

It was found that yield components were infuenced by hormonal status of wheat plants under drought. Bernier (1988) suggested that the stress hormone, abscisic acid (ABA), which accumulates during water deficit, inhibited flowering, and ABA has also been shown to reduce leaf growth (Dodd et al. 1996). Another stimulus from the root system that may hasten flowering, may increase the number of kernels per ear and the cell number in the endosperm during early phase of the grain filling and ultimately may increase the grain yield, is cytokinin, which is transported from the root system to the shoot in the xylem. However, the synthesis in the root tip and transport to the shoot of cytokinin-like compounds has been shown to decrease due to drought (Davies et al. 1986). Furthermore, cytokinins may also delay the senescence of flag leaves.

Our aim was to compare the chlorophyll-*a* fluorescence induction parameters in drought tolerant and sensitive cultivars in well-watered and drought-stressed conditions during early phase of grain filling before the visible sign of leaf senescence and we were also interested whether these water stress-induced changes characterize the sensitive or tolerant cultivars or they characterize genotypes themselves.

Materials and Methods

Plant material and water stress treatment

Two Hungarian wheat cultivars, *Triticum aestivum* L. cv. MV Emese, a drought tolerant and cv. GK Élet, a drought sensitive genotype and two well-known standards, the drought tolerant Plainsman and the drought sensitive Cappelle Desprez have been investigated under well watered and drought stress conditions.

The experiments were carried out in the grain filling period. The plants were grown in plastic plots (3 plants per pot) containing a mixture of soil (type Terra, Hungary) and sand (1:1, v/v) at 300 μmol m^{-2} s^{-1}light intensity, 12/12 hour day/night illumination, at 26/20°C day/night temperature and 55-60% air humidity (Tari et al. 2008). From 4 days before the booting stage two watering schedules were applied. The first group of the plants, the control plants, received sufficient irrigation, while the other group was subjected to water stress (WS) treatment by withholding irrigation. Irrigation occurred every 2nd day to reach 60% of the total soil water capacity for control plants, and 25% for stressed plants. Samples were prepared and *in vivo* measurements were made on the 16th days post anthesis (DPA). At maturity, ears were harvested from five pots per variety and per treatment to determine the grain mass per ear, the number of grains per ear and the thousand grain mass. The experiments were repeated three times.

Pigment analyses

For pigment analysis a two step extraction was applied. The fully expanded flag leaves were homogenized in ice-cold 100% (v/v %) acetone (1,5 ml for 250 mg sample), and extracted for 24 hours. Samples were centrifuged at 5000 g for 15 minutes at 4°C. The pellet was extracted again with 80% (v/v %) acetone (1,5 ml for 250 mg sample) for 24 hours. After centrifuging (5000 g, 15 minutes, 4°C), the supernatants were collected. The pigment composition was measured by spectrophotometer according to Lichtenthaler and Wellburn (1983).

Measurement of chlorophyll fluorescence parameters

Chlorophyll-*a* (Chl *a*) fluorescence was measured on flag leaves with a portable photosynthesis system (LI-6400, LI-COR, Inc.; Lincoln, NE). After 20 minutes of dark adaptation the ground state fluorescence level (F_0) with all PSII reaction centres open was determined by a modulated measuring light, which was sufficiently low not to induce any significant variable fluorescence. The maximal fluorescence level (F_m) with all PSII centres closed was measured after 20 min of dark adaptation by 0,2 s saturating pulse at 8000 μmol m^{-2} s^{-1}. Then the leaf was continuously illuminated with white actinic light at an intensity of 500 μmol m^{-2} s^{-1}. After 20 minutes the steady-state value of fluorescence (Fs) was recorded and a second saturating pulse (8000 μmol m^{-2} s^{-1}) was imposed to determine the maximum fluorescence level (Fm') in light-adapted state. The actinic light was removed and the minimum fluorescence level in the light-adapted state (F_0') was determined by illuminating the leaf with 3 s far-red light (5 μmol m^{-2} s^{-1}). Light response curves were generated by varying light intensities (50, 150, 300, 400, 500, 700, 1200, 1500 μmol/m^2s) after 10 minutes of dark adaptation. The light curves measured on the 16th days after anthesis.

By using fluorescence parameters determined in both light- and dark-adapted leaves, the following calculation were made (1) the maximal quantum yield of PSII photochemistry, Fv/Fm, (2) the photochemical quenching coefficient, qP = (Fm'-Fs)/(Fm'-Fo') (Bilger and Schreiber 1986), (3) non-photochemical quenching NPQ=(Fm-Fm')/Fm' (Bilger and Björkman, 1990), (4) the actual quantum yield of PSII electron transport in the light adapted-state, Φ_{PSII} = (Fm'-Fs)/Fm' (Genty et al. 1989). The net photosynthetic rate (P_N) of the flag leaves as a function of photon flux density (PFD) was also determined.

Determination of trans-zeatine content of flag leaves

Samples of 1000 mg leaf tissues were ground and extracted for 4 hours at 0°C in 2,5 ml of 80% (v/v) methanol containing 1 mg butylated hydroxytoluene as an antioxidant. After

Table 1. The effects of soil drought on the chlorophyll-*a* and *b* contents in μg DW^{-1} (g)$^{-1}$ in flag leaves of wheat plants during grain filling period. (DPA: days post anthesis.)

Triticum aestivum L. cultivar	Treatment	Number of grains per ear	Mass of grains per ear (g)	1000-grain dry mass (g)
cv MV Emese	Control	27.05 ± 7,4	1.32 ± 0.54	52.57 ± 4.8
	Drought	19.63 ± 4.4** (-27.40%)	0.80 ± 0.1*** (-39.53%)	41.74 ± 12.2** (-21.22%)
cv. GK Élet	Control	31.6 ± 4.9	1.59 ± 0.3	50.32 ± 6.9
	Drought	17.76 ± 6.5*** (-43.78%)	0.38 ± 0.2 *** (-75.71%)	18.76 ± 1.9** (-62.71%)
cv. Plainsman	Control	17.72 ± 8.1	0.64 ± 0.4	40.83 ± 3.0
	Drought	15.80 ± 4.2 (-10.77%)	0.58 ± 0.1 (-9.41%)	39.58 ± 1.6 (-4.01%)
cv. Cappelle D.	Control	27.71 ± 8.2	1.80 ± 0.7	65.73 ± 16.7
	Drought	15.85 ± 4.5*** (-42.78%)	0.63 ± 0.4** (-64.57%)	34.83 ± 13.5*** (-47.00%)

centrifugation at 3000 rpm for 10 min, the pellet was extracted further in 7.5 ml of the same medium for 12 hours. After a second centrifugation, the supernatants were combined and the samples were purified by Discovery C18 Cartridge (Supelco, USA), pre-washed with 10 ml of 100% and 5 ml of 80% methanol. The hormone fractions were then eluted from the columns with 7.5 ml of 100% methanol and 7.5 ml of diethyl ether. The leaf extracts were evaporated to dryness and before quantification they were dissolved in Tris-buffered saline (TBS) (800 ml of dH2O, 3.03 g Tris, 5.84 g NaCl, 0,2 g $MgCl_2$ hexahydrate and 0.2 g Na azide, (pH 7.5; 2500 μl/1000 mg sample). *Trans*-zeatin riboside (ZR) was analysed by ELISA employing Phytodetek Assay Kit (Agdia) supplied by Sigma Ltd. Colour absorbancy following reaction with the substrate was read at 405 nm using a plate auto reader (Dynatech MR 4000). Percentage binding was calculated using established procedures (Weiler et al. 1981). The recovery was determined as described by Yang et al. (2003).

Statistical analysis

Data presented in the figures are means of three to five replications ± SD. Data from each sampling date were analyzed separately by Student's t-test using a SigmaStat 3.1 software. Means denoted by *, ** or *** were significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$ levels, respectively.

Results

Plant water status

Witholding irrigation resulted in reduction of leaf water potential both in sensitive and tolerant genotypes and the reduction was more pronounced in GK Élet and Cappelle Desprez, the more sensitive cultivars. Under drought stress water potential (ψ_w) values were lower between 4 and 12 DPA in GK Élet and Cappelle Desprez than in MV Emese. In the sensitive cultivars ψ_w decreased and remained near -1,5, while in the more tolerant MV Emese ψ_w reached -1,3 just at 12 DPA. In Plainsman there was a slight decrease in ψ_w at 12 DPA under water deficit, but ψ_w of stressed and control plants also decreased dramatically until 24 DPA (Guóth et al. 2009).

Water stress (WS) reduced also the relative water content (RWC) in the sensitive genotypes and in MV Emese. In GK Élet and in Cappelle Desprez, the differences were significant between the well-irrigated and stressed plants from the booting stage to the end of the experiment, while in MV Emese no differences were observed until the 4 DPA. The RWC values in the stressed plants were much higher in MV Emese compared to GK Élet and Cappelle Desprez. In Plainsman, RWC values under WS decreased in parallel with the control (Gallé et al. 2009).

Chlorophyll and trans-zeatin riboside contents

Chlorophyll *a* and *b* (Chl-*a* and *b*) contents did not decrease markedly in response to water stress until 12 DPA and no significant changes were found between the controls and water stressed plants in Chl-*a* contents in case of tolerant cultivars cvs Emese and Plainsman. Chl-a contents decreased significantly in flag leaves exposed to WS in sensitive cultivars Élet and Cappelle and in Chl-*b* contents in case of Cappelle Desprez at 12 DPA (Table 1). In cv. Plainsman the senescence process of flag leaves began also earlier in control plants than in MV Emese and GK Élet. Between 12 and 24 DPA, however, the rate of Chl loss was much higher in the tolerant cultivars cvs Emese and Plainsman.

Trans-zeatin riboside, a transport form of citokinins, also accumulated in flag leaves. ZR concentration was 40-43% greater than that of zeatin and its concentration changed parallel with that of zeatin in wheat flag leaves during grain filling (Yang et al. 2003). In our experiments there were no significant differences in ZR content of flag leaves in control and droughted plants with the exception of cv. GK Élet, a

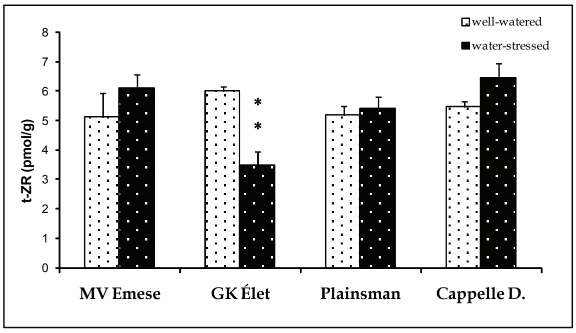

Figure 1. *Trans*-zeatin riboside contents in well-watered (o) and water-stressed (●) flag leaves at 16 DPA during grain filling in MV Emese, GK Élet, Plainsman and Cappelle Desprez wheat cultivars. Data are means ± SD of 3-5 independent samples. *, **, *** are for significant differences comparing to the control at 0.05, 0.01, 0.001 levels, respectively.

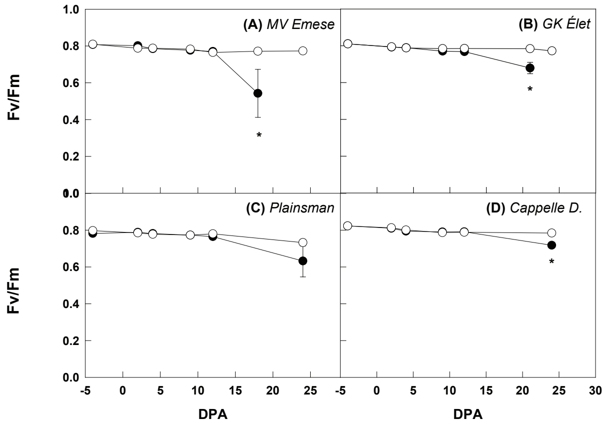

Figure 2. Changes of the maximal quantum yield of PSII photochemistry (Fv/Fm) in well-watered (o) and water-stressed (●) flag leaves during grain filling in MV Emese (A), GK Élet (B), Plainsman (C) and Cappelle Desprez (D) wheat cultivars. Data are means ± SD of 3-5 independent samples. SD bars are not shown where smaller than symbols. *, **, *** are for significant differences comparing to the control at 0.05, 0.01, 0.001 levels, respectively.

sensitive cultivar (Fig. 1). In this genotype, a significant reduction in ZR content occurred in parallel with a significant decrease of Chl-*a* contents (Table 1).

Chlorophyll *a* fluorescence and photosynthetic rate

Fv/Fm was measured on the flag leaves during whole grain filling period. The changes of Φ_{PSII}, qP, NPQ and P_N were determined on 16 DPA as a function of increasing PFD.

The values of maximal efficiency of PS II photochemistry (F_v/F_m) remained around 0.77-0.8 until the 12th day after anthesis in all varieties. Values decreased significantly under water deficit faster in the tolerant cv. MV Emese and in the sensitive GK Élet. In the two other cultivars Fv/Fm values decreased only on the last measuring days. In Plainsman, on the 24 DPA, Fv/Fm values decreased also in control plants (Fig. 2).

The $\Phi_{PSII,}$ qP, NPQ and P_N did not change considerably until 12 DPA under drought stress compared to the controls at 500 µmol m^{-2} s^{-1} light intensity in the investigated cultivars, and with the exception of Plainsman, the decreases in Φ_{PSII}, qP and P_N became significant on the last measuring days in the stressed plants. (Guóth et al. 2009). In case of cv Plainsman, these parameters changed parallel in control and water-stressed plants.

The responses of the actual $P_{N,}$ Φ_{PSII}, qP and NPQ to different photon flux densities (PFDs) at 16 DPA are summarized in Figure 3.

In control plants the photosynthetic rate at light saturation (A_{max}) was highest in case of cv Élet, the other cultivars exhibited lower saturation values and severe photoinhibition at 1500 µmol m^{-2} s^{-1}. The net CO_2 fixation rate was limited under drought stress in three cultivars, among them cv. MV Emese was seriously affected, and interestingly, there were no significant changes between the P_N/PFD curves of control and water-stressed plants in case of the sensitive genotype, Cappelle Desprez, at 16 DPA.

In MV Emese the Φ_{PSII}, qP and at higher light intensities NPQ values differed significantly between control and stressed plants at all PFDs, this contrasts with the data found in cv. Cappelle Desprez where no differences were found at any PFDs. In cv. MV Emese Φ_{PSII} and qP markedly decreased under WS, and NPQ stopped increasing in the stressed plants above 700 µmol m^{-2} s^{-1} PFD. In GK Élet only slight differences can be observed in Φ_{PSII}, qP and NPQ from 700 µmol m^{-2} s^{-1}. In Plainsman qP decreased and NPQ increased significantly only at 1200 and 1500 µmol m^{-2} s^{-1} compared to the control (Figure 3).

Yield parameters

The number of grains per ear, the mass of grains per ear and the grain weight decreased during water deficit in MV Emese, GK Élet and Cappelle Desprez. The difference between the tolerant MV Emese and the sensitive varieties was significant, and the yield parameters of GK Élet and Cappelle-Desprez declined at higher rate than in MV Emese. In cv. Plainsman the crop yield did not decrease significantly under drought stress (Table 2).

Discussion

There are several physiological traits related to water stress, and scientists make considerable effort to find direct correlations between these parameters and grain yield to facilitate the screening and selection of cultivars for drought tolerance. A strong relationship between biomass at anthesis and yield has been demonstrated in bread wheat (van den Boogard et

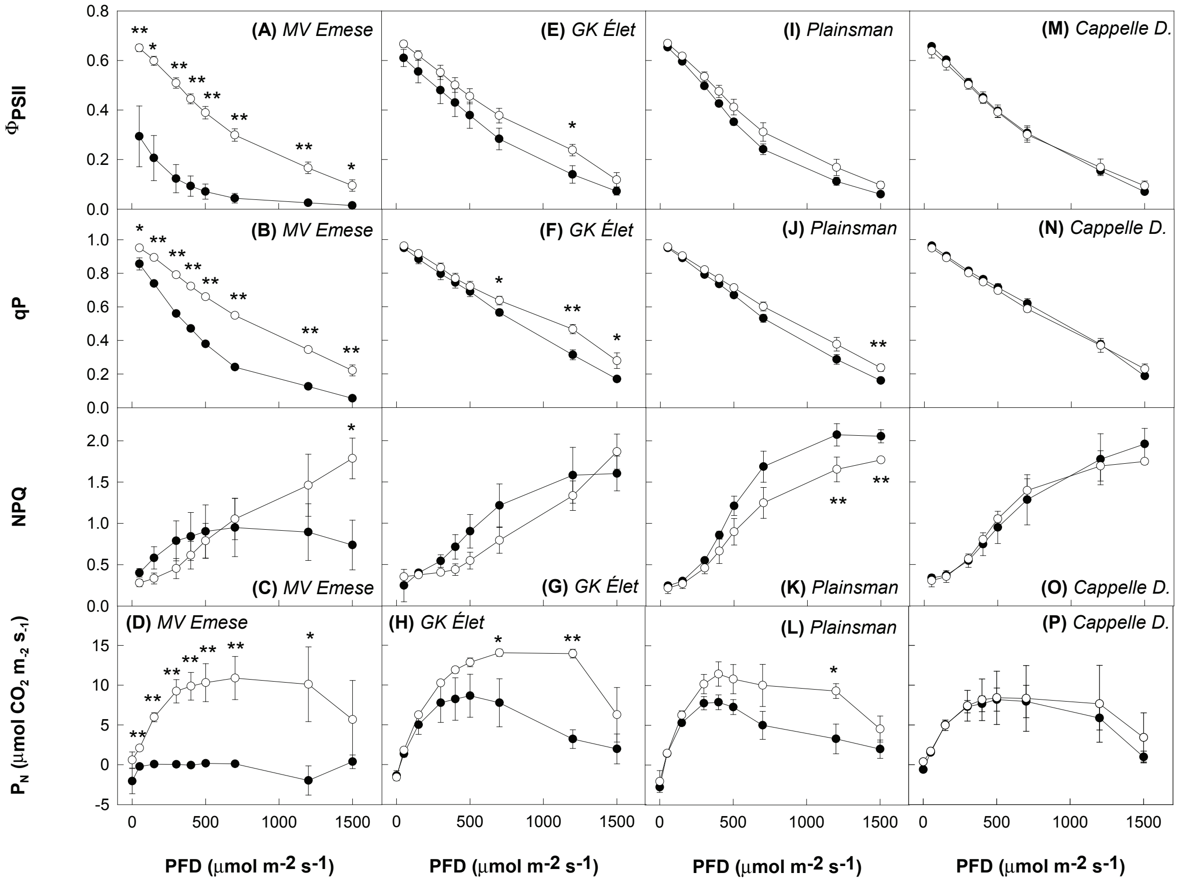

Figure 3. Responses of the actual quantum yield of PSII photochemistry (Φ_{PSII}), photochemical quenching parameter (qP) and non-photochemical quenching (NPQ) to increasing photon flux densities (PFD) in well-watered (o) and water-stressed (●) flag leaves during grain filling in MV Emese (A, B, C), GK Élet (D, E, F), Plainsman (G, H, I) and Cappelle Desprez (J, K, L) wheat cultivars. Data are means ± SD of 3-5 independent samples. SD bars are not shown where smaller than symbols. *, **, *** are for significant differences comparing to the control at 0.05, 0.01, 0.001 levels, respectively.

al. 1996), the variation in leaf area and duration of flag leaf photosynthesis proved also to be important factors under stress conditions (Richards 2000). However, selection for higher rates of leaf photosynthesis has not generally resulted in improved yield under temperate conditions (Evans 1993). Selection for higher photosynthetic rate of flag leaves in early generations improved the grain weight but decreased the total yield (t ha^{-1}) of $F_{5:7}$ imbred lines of wheat (Gutiérrez-Rodríguez et al. 2000).

The yield parameters of the sensitive GK Élet and Cappelle-Desprez declined much more than those of the tolerant MV Emese and Plainsman genotypes. For instance, both the numbers of grains per ear and the thousand-grain dry mass of GK Élet and Cappelle-Desprez decreased to about half of its control and resulted in shrivelled caryopses, while cvs MV Emese and Plainsman showed a mere 21% and 4% decrease, respectively, with apparently filled grains.

The water potential of one tolerant and two sensitive genotypes changed significantly under water deficit, but GK Élet and Cappelle Desprez reached lower Ψ_w, indicating that these plants were physiologically more sensitive. In Plainsman, however, drought affected the plant water status less significantly because water potential was also reduced from 15 DPA in the controls (Guóth et al. 2009). Because rates of aging of leaves accounted for the major differences in carbon fixation per leaf among wheat cultivars (Rawson et al. 1983), the decrease of chlorophyll content shows the rate of flag leaf senescence in control plants and under soil drought. Loss of chlorophyll may be even beneficial in the later stages of grain filling because earlier senescence may indicate an effective mobilization of stored assimilates to the grain (Blum 1998).

The decline in Chl content as a visible symptom of flag leaf senescence could be detected only in sensitive cultivars, Élet and Cappelle upto 12 DPA, and the leaf ZR content decreased significantly only in cv. Élet. Because citokinins maintain the chlorophyll content of tissues and act as antisenescence agents, the decline in ZR in flag leaf of cv. Élet may be in close correlation with an earlier loss of Chls.

Table 2. Effect of soil drought on the final number of grains per ear, mass of grains per ear and thousand-grain dry mass of MV Emese, GK Élet, Plainsman and Cappelle Desprez wheat cultivars. Data are means of the yield parameters in 2007 and 2008 years. Numbers in brackets indicate the percentage of decrease compared to control. *, **, *** are for significant differences comparing to the control at 0.05, 0.01, 0.001 levels, respectively.

		Chlorophyll *a*		Chlorophyll *b*	
	DPA	well-watered	drought stress	well-watered	drought stress
	0	15.18 ± 1.6	15.60 ± 1.4	5.88 ± 0.8	6.78 ± 0.7
MV Emese	4	16.06 ± 0.6	15.74 ± 0.6	6.09 ± 0.5	6.21 ± 0.1
	9	15.30 ± 3.4	12.44 ± 2.7	5.84 ± 1.3	5.11 ± 1.2
	12	13.74 ± 1.1	13.41 ± 1.4	3.62 ± 0.9	3.62 ± 0.5
	24	15.11 ± 0.9	5.96 ± 2.2 ***	3.09 ± 1.7	1.46 ± 0.5 **
	0	14.18 ± 0.6	12.94 ± 0.4	4.90 ± 0.3	5.02 ± 0.3
GK Élet	4	11.76 ± 1.2	11.49 ± 2.8	4.26 ± 0.5	4.81 ± 1.1
	9	12.75 ± 1.4	9.62 ± 0.5 *	5.04 ± 0.3	4.76 ± 1.1
	12	13.78 ± 1.7	11.98 ± 0.6	5.13 ± 0.5	4.80 ± 0.3
	24	13.91 ± 0.7	4.19 ± 1.5 ***	6.12 ± 0.7	4.61 ± 2.0 ***
	0	15.50 ± 0.3	13.98 ± 1.9	5.75 ± 0.1	5.43 ± 1.0
Plainsman	4	16.31 ± 1.2	15.08 ± 0.4	6.01 ± 1.0	6.18 ± 0.5
	9	14.40 ± 0.7	12.49 ± 2.4	5.27 ± 0.2	4.92 ± 0.8
	12	16.45 ± 0.9	13.32 ± 1.9	6.38 ± 0.5	6.16 ± 1.0
	24	11.78 ± 1.8	1.37 ± 0.2 ***	4.64 ± 0.6	0.76 ± 0.2 ***
	0	14.64 ± 1.1	12.12 ± 0.8 *	5.27 ± 0.3	4.78 ± 0.4
	4	11.90 ± 0.4	11.42 ± 0.9	4.13 ± 0.0	4.50 ± 0.50
Capelle Desprez	9	12.60 ± 0.8	11.74 ± 0.5	4.63 ± 0.3	4.85 ± 0.4
	12	13.70 ± 0.3	10.08 ± 0.9 *	5.11 ± 0.2	4.01 ± 0.3 **
	24	8.64 ± 0.5	3.02 ± 0.4 ***	4.82 ± 0.5	1.54 ± 0.4 ***

We have assessed chlorophyll *a* fluorescence induction parameters on 16 DPA during the grain filling period in order to reveal those components which are affected by drought and thus are useful physiological traits to screen the drought sensitivity of genotypes before the visible symptoms of fast senescence in flag leaves.

Compared with control plants, there were no significant differences in the maximal quantum yield of PSII photochemistry, F_v/F_m until the 12 DPA, but later a significant decline could be observed in MV Emese, GK Élet and in Cappelle Desprez under water stress demonstrating an earlier disorganisation of PSII reaction centers in water-stressed plants. In cv. Plainsman Fv/Fm tended to decrease in control plants to 24 DPA indicating that the changes were not exclusively induced by drought stress. With the exception of Cappelle Desprez, the A_{max} of light response curves decreased severely in all genotypes under drought that is the biomass production was limited by the stress. The effective quantum yield, Φ_{PSII} and photochemical quenching parameter, qP decreased significantly as a function of PFD in the drought tolerant Emese and in the sensitive GK Élet. Increases in NPQ due to soil drought could only be observed at low PFDs in cv. Emese. The significant decreases in P_N, Φ_{PSII} and qP under drought stress in cv Emese can be explained by the fast response of this cultivar to insufficient irrigation, and the sensitivity of this genotype to high light intensities. Although chlorophyll contents of sensitive genotypes, cvs Élet and Cappelle, were lower and declined from 0-9 DPA under water stress, the rate of chlorophyll loss was much higher in cv. Emese after 12 DPA under drought (Guóth et al. 2009). In the tolerant Plainsman the control plants also showed the symptoms of faster senescence, but Φ_{PSII}, qP and NPQ were slightly affected by WS. In spite the small but significant changes in Chl contents, there were no significant differences in Chl *a* fluorescence induction parameters in the sensitive cv. Cappelle Desprez at 16 DPA. Summarizing the results, neither changes of CO_2 fixation rate nor those of chlorophyll *a* fluorescence parameters in this experiment did not reveal common tendencies which could characterize either tolerant or sensitive genotypes.

Plant senescence induced by water deficit during post-anthesis can promote the remobilization of the pre-stored assimilates to the grains (Kobata et al. 1992; Palta et al. 1994; Zhang et al. 1998; Yang and Zhang 2006). In MV Emese and Plainsman the senescence could result in faster and better remobilization of the pre-stored carbon from vegetative issues, and an ultimately better yield than in GK Élet and Cappelle Desprez under drought. In spite of the sustained CO_2 fixation activity of the flag leaves, the limited utilization of stem reserves in the sensitive cultivars GK Élet and Cappelle Desprez led to severe shrivelling of the grains, and thus to a loss in 1000-grain mass under water stress. Lower citokinin transport from roots to leaves and possibly to developing grains in cv.

GK Élet may contribute to reduced grain number per ear in case of this cultivar.

Although chlorophyll fluorescence is considered a useful tool for screening wheat cultivars under dry conditions (Flagella et al. 1995), its combination with other methods may provide a more accurate assessment of drought tolerance.

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