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Full Length Research Paper

Effect of water deficit on growth and photosynthetic characteristics of 13 winter wheat

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Wheat is one of the major crops in the world and is rather sensitive to water deficit and differences between genotypes for water tolerance have been previously testified. Experiment was conducted in a greenhouse with 13 cultivars grown in control and water deficit conditions. Gas exchange, chlorophyll fluorescence parameters, above ground biomass and total leaf area were measured to determine water tolerance. Drought susceptibility indexes were used to estimate the relative tolerance of wheat cultivars to water deficit. Water deficit decreased total leaf area, above-ground biomass, net photosynthesis, stomatal conductance, internal CO_2 concentration and the actual quantum yield of PS II electron transport relative to cultivars that were grown under control condition. Measurement of stomatal conductance provided useful information to assess genetic differences in wheat for absolute performance when subjected to water deficit. Besides, CY20 and XN979 showed more drought tolerance than other wheat cultivars in terms of drought susceptibility indexes.

Key words: Wheat cultivars, growth, chlorophyll fluorescence, gas exchange, water deficit.

INTRODUCTION

Limited water availability is one of the main factors influencing crop growths globally. Survival strategies in response to water deficit in many plants have been extensively studied (Heschel and Hausmann, 2001; Nayyar and Walia, 2003; Pospíšilová and Baťková, 2004; Akhter et al., 2005; Wang et al., 2007). Some of the adaptive responses to drought are due to physiological and morphological changes, such as changes in plant structure, dry matter accumulation, tissue osmotic potential and stomatal conductance (Blum, 1997). Wheat is one of the widespread crops in the world, and is also affected by water deficit, water deficit commenced at anthesis stage and had the most depressing effects on photosynthesis and chlorophyll fluorescence parameters, and thereby affect grain yield (Harsharm, 2010). Photosynthesis often reduces in crop growing under water deficit (Athar and Ashraf, 2005). One of the earliest plant responses to water deficit is stomatal closure. Even a small drop in water potential impairs the photosynthesis in plants, resulting in the closing of stomata, which limits CO_2 diffusion to the chloroplasts (Muller and Whitsitt, 1996), and it has been widely reported that water deficit affects stomatal conductance, resulting in a decline in the availability of internal CO_2 and hence in photosynthesis (Athar and Ashraf, 2005), stomatal (closure of stomata) and non-stomatal (including damage to photosynthetic apparatus) factors may be involved in the reduction of CO_2 assimilation (Bethke and Drew, 1992). Furthermore, stomatal limitations typically are evaluated using gas exchange. Measurement of chlorophyll fluorescence has been used as a mean to evaluate the integrity of photosystem II (PSII) upon exposure to deficit (Shabala, 2002).

Chlorophyll (Chl) fluorescence provides useful information about leaf photosynthetic performance of many plants under water deficit (Baker and Rosenqvist,

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Abbreviations: A, Photosynthetic rate; **E,** transpiration rate; **Ci,** intercellular CO_2 concentration; **gs,** stomatal conductance; **IWUE,** instantaneous water-use efficiency; **PPFD,** Photosynthetic photon flux density; **Fo,** initial fluorescence; **Fm,** maximal fluorescence; **Fv/Fm,** maximal PSII photochemical efficiency; **ΦPSII,** effective quantum yield of PSII; **ETR,** electron transport rate; **NPQ,** non-photochemical; **TLA,** total leaf area; **AGB,** above ground biomass; **DSI,** drought susceptibility index.

Table 1. Cultivars names and their associated details

Genotype	Abbreviation	Annual rainfall (mm)	Climate region
Chuanyu19	CY19	918.2	wet
Chuanyu20	CY20	918.2	wet
Chuanmai41	CM41	918.2	wet
CD08-185C	185C	918.2	wet
CD08-184C	184C	918.2	wet
Shumai375	SM375	911.7	wet
Mianmaixin19	MM19	859.9	wet
Mianmai185	MM185	859.9	wet
Neimai9	NM9	<800	dry
Neimai11	NM11	<800	dry
Henanayl3	HN	607.0	dry
Xinong979	XN979	573.0	dry
Xinong889	XN889	573.0	dry

2004). In recent years, the use of Chl fluorescence has become commonplace in plant eco-physiology, to the extent that no investigation of the photosynthetic performance of plants growing in field conditions seems complete without some fluorescence data (Maxwell and Johnson, 2000). The *in vivo* effects of water deficit on chlorophyll fluorescence have been described for several crop species (Razavi et al., 2008). Interspecific differences for chlorophyll fluorescence para-meters have been documented. For example, in ground-nut (Danièle et al., 2006) and Paspalum soybean.

The objectives of this study were: (i) to compare differences in gas exchange, chlorophyll fluorescence parameters and growth parameters among 13 wheat cultivars in response to water deficit; (ii) to elucidate some of the possible reasons for differential physiological responses of these genotypes to a water deficit; (iii) to determine if any of these parameters may be useful as a selection criterion in breeding wheat for tolerance to water deficit.

MATERIALS AND METHODS

Plant materials

The experiment consisted of 13 winter wheat cultivars, which were released between 1999 and 2008. Seeds of most cultivars were widely distributed from the dry to wet climate regions and exhibits large genetic variation. All cultivar names and associated details are listed in Table 1.

Growth conditions

The experiments were carried out at the Xindu County Sichuan Province, China (104°12´E, 30°85´N; 500 m above sea level). Mean annual temperature and rainfall evaporation are 16℃ and 911.7 mm, respectively. The soil is clay loam, pH is 6.98, organic matter is 26.54 g/kg, total N, P and K are 1.59, 0.97, 17.43 g /kg, respectively, for the top tillage soil layer. The soil collections were mixed thoroughly; 4.0 kg soil was placed in each plastic pot, to a bulk density of 1.44 g/cm^3. 4.0 g slow release fertilizer (7% N, 5% P and 26% K) was added to each pot, in order to ensure that all plants could obtain sufficient nutrients. Six weeks later 10 pots were watered and allowed to drain freely until the weight was constant. The difference between this weight and soil dry weight was used to calculate water field capacity (FC). At the level of full water FC, mean water content of soil was 36.8%.

Winter wheat seeds were pre-soaked at 4℃ for vernalization and ten seeds per pot were sown at a depth of 3 cm into small plastic pots (25 cm diameters × 20 cm height) on November 6, 2008. All pots initially were well-watered (soil moisture was about 85%FC) in order to ensure seed germination. Shortly after emergence, seedlings were thinned to one plant per pot. The plants were grown to full maturity in a naturally light greenhouse under the semi-controlled environment with a day temperature range of 12 to 35℃ and a night temperature ranged of 9 to 20℃, and the relative humidity range of 30 to 81%.

Experimental design and management

The experiment consisted of two watering treatments and 13 wheat cultivars arranged in a completely randomized design. Two watering regimes were as follows:

1. Control condition (85% of FC, ranged from 80 to 85% of FC);
2. Water deficit (30% of FC, ranged from 25 to 30%).

15 pots of each cultivar were used in each watering regime. Transpiration water loss was measured gravimetrically by weighing all pots and calculating the weight loss between watering. The amount of water to add to each pot was the amount lost to transpiration. The watering treatment was initiated on March 6, 2009. During the experimental period, pots were watered every other day at 16:00, soil water content was always maintained at 0.29~31.33%, 7.37~9.21% under 85 and 30% FC water supply regimes, respectively.

Evaporation from the soil surface was minimized by covering with a 3 cm layer of quartz gravel (Liu et al., 2004). The experimental layout was surrounded with a single row of border plants to protect the experimental seedlings from external influences. All pots were put on bricks and randomized weekly.

Table 2. Effects of water deficit treatment, wheat cultivars, and their interaction for TLA, AGB, A, Ci, gs, IWUE and three chlorophyll fluorescence parameters (Fv/Fm, Φ_{PSII}, NPQ).

Parameter	Water deficit	Wheat cultivar	Interaction
TLA	<0.0001	<0.0500	0.3668
AGB	<0.0001	<0.0001	0.3774
A	<0.0001	<0.0001	<0.0001
gs	<0.0001	<0.0001	<0.0001
Ci	<0.0001	<0.0001	<0.0001
IWUE	<0.0001	0.1258	0.5124
Fv/Fm	0.3613	0.1915	0.0809
Φ_{PSII}	<0.0001	0.1220	0.4829
NPQ	<0.0001	0.2367	0.5201

TLA, total leaf area; AGB, above ground biomass; A, Photosynthetic rate; Ci, intercellular CO_2 concentration; gs, stomatal conductance; IWUE, instantaneous water-use efficiency; Fv/Fm, maximal PSII photochemical efficiency; ΦPSII, effective quantum yield of PSII; NPQ, non-photochemical quenching.,

Gas exchange

For each cultivar, the date at which 50% of plants reached the stage of anthesis was recorded. The photosynthetic parameters were taken between 10:00 and 16:00 h. The measurements with flag leaf were made at least five times per plant; five plants per cultivar were used, but the representative results were presented in this study. Net photosynthetic rate (A), transpiration rate (E), intercellular CO_2 concentration (Ci) and stomatal conductance (gs) were assessed using an open gas exchange system with a 6 cm^2 clamp-on leaf cuvette (LI-6400, LICOR Inc., Lincoln, NE, USA). Instantaneous water-use efficiency (IWUE) was calculated as the ratio between net photosynthesis (A) and transpiration (E) (Condon et al., 2002). Photosynthetic photon flux density (PPFD) was fixed at 1200 µmol $m^{-2}s^{-1}$, using a red-blue LED light source built into the leaf cuvette, though other environmental factors, such as air humidity and temperature, were not controlled, that is natural variation was permitted. The vapor pressure deficit in the cuvette was maintained below 2.5 kPa to prevent stomatal closure due to the low air humidity effect. The air collected outside the greenhouse was passed through a buffering gallon and then pumped into the system, with mean CO_2 concentration of 380 µmol·mol^{-1}.

Chlorophyll fluorescence

Chlorophyll fluorescence and leaf gas exchange measurements were taken simultaneously. Chlorophyll fluorescence was measured using a PAM-2100 fluorometer (Heinz Walz, Effeltrich, Germany). Initial fluorescence (Fo) and maximal fluorescence (Fm) were measured after a 30 min dark adaptation. The intensity of saturation pulses to determine the maximal fluorescence emission in the presence (Fm') and absence (Fm) of quenching was 4000 µmol (photon) $m^{-2}s^{-1}$, 0.8 s, whereas the "actinic light" was 1200 µmol (photon) $m^{-2}s^{-1}$. Maximal PSII photochemical efficiency (Fv/Fm), effective quantum yield of PSII (Φ_{PSII}), apparent electron transport rate (ETR) and non-photochemical (NPQ) fluorescence quenching coefficients were also recorded.

Growth parameters

Plants were harvested the day after gas exchange and chlorophyll fluorescence measurements were completed to assess total leaf area (TLA) and above ground biomass (AGB). Each plant was divided into root, stem and leaf, and leaves were recorded with a scanner (Model F6580, Founder Electronics Co., Ltd, Beijing), and images were digitized by the Arcview 3.2a [Environmental Systems Research Institute (ESRI), Inc., New York] software in order to determine total leaf area. Then each stem and leaf was dried in an oven for 48 h at 70°C for above ground biomass determination.

Statistical analysis

After Nogues et al. (1994), drought susceptibility index (DSI) for each of the several parameters was calculated for each wheat cultivar in experiment as:

$$DSI\ (\%) = (X_d/X_c) \times 100\%$$

Where, X_d is the mean value of the parameter measured under water deficit condition and X_c is the mean value of the parameter measured under control condition.

The effects of water deficit and differences wheat cultivars in TLA, AGB, A, Ci, gs, IWUE, Fv/Fm, Φ_{PSII} and NPQ were assessed using an analysis of variance of a two-way factorial. Each parameter was analyzed individually. Water deficit and wheat cultivars were fixed-effects factors. Differences among wheat cultivars or water deficit in TLA, AGB, A, Ci, gs, IWUE, Fv/Fm, Φ_{PSII} and NPQ were assessed using an analysis of variance of a one-way factorial. Each parameter was analyzed individually. Winter wheat or water deficit were defined as fixed factors. Duncan's multiple range tests was used to separate significant differences in mean values at the 0.05 level. Relationships among variables were determined using the Pearson's correlations coefficient test at the 0.05 level. All of the statistical analyses were performed using Statistical Analysis System (SAS, version8.0 for Windows, SAS Inc., IL, USA) software package.

RESULTS

Water deficit effects and differences among wheat cultivars were obvious to most parameters (Table 2). Effects due to water deficit were detected for all para-

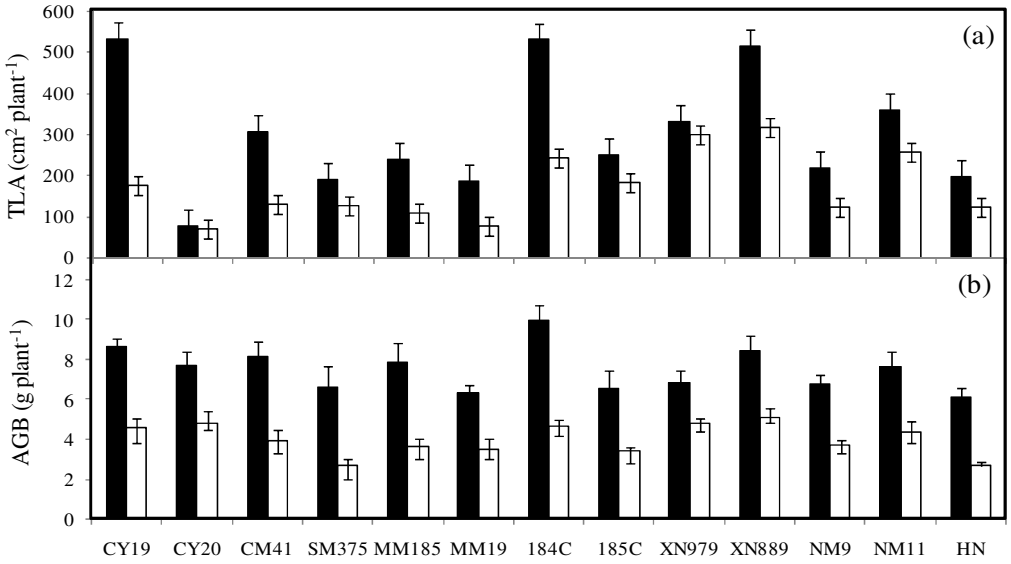

Figure 1. Mean for TLA (a) and AGB (b) for 13 wheat cultivars in control (solid bars) (80% FC) and water deficit (empty bars) (30% FC) conditions. Vertical bars represent standard errors based on variability among 5 plants.

meters except Fv/Fm. Differences among wheat cultivars were found for all parameters except IWUE, Fv/Fm, Φ_{PSII} and NPQ. We found evidence of interaction between water deficit treatments and wheat cultivars for A, gs, and Ci (Table 2).

Growth parameters

Genotypes and water deficit affected TLA, though no interaction was found between these effects (Table 2). Water deficit reduced TLA, regardless of wheat cultivars (Figure 1a). Under water deficit condition, XN889 and XN979 exhibited the highest value while CY20 and MM19 had the lowest ones (Table 3). CY20 and XN979 were least affected by water deficit as indicated by DSI for TLA (Table 4).

Under water deficit condition, AGB values were lower (Figure 1b) and relatively similar among wheat cultivars. AGB values differed significantly between XN979, XN889 and SM375, HN under water deficit condition (Table 3). Relative effects of water deficit, as measured by DSI for AGB, differed among wheat cultivars (Table 4). AGB for XN979 was less reduced than other cultivars (Table 4).

Gas exchange parameters

Water deficit reduced all wheat cultivars in A (Figure 2a). Under water deficit condition, XN889 and XN979 exhibited the highest A values while NM11 had the lowest one (Table 3). Five wheat cultivars (CY19, CM41, XN979, XN889 and HN) were the least affected by water deficit (Table 4). Water deficit negatively affected gs of all wheat cultivars (Figure 2c). Under control and water deficit conditions, XN889 and CY20 had the highest and lowest values for gs, respectively (Figure 2c, Table 3). CY20, MM19 and XN979 were relatively less affected by water deficit (Table 4). A differential response to water deficit by different cultivars for gs was reflected by the high number of significance between groups of wheat genotypes (Table 3) and the interaction found for this parameter in the general analysis of variance (Table 2).

Genotypes, water deficit and interaction affected Ci, as was found in Table 2 and Figure 2b. XN889 had the highest Ci values while CY20, MM19 and HN had the lowest ones under water deficit condition (Table 3). Relative effects of water deficit differed among wheat cultivars. CY20 and XN979 were relatively less affected by water deficit (Table 4). Furthermore, the correlation between DSI for gs and DSI for Ci was positive (Figure 3), indicating that wheat cultivars were most affected by water deficit for gs which tended to be most affected for Ci (r^2=0.448, P<0.001) (Figure 3). Across all wheat cultivars, we found increases of IWUE values in water deficit (Figure 2d). No differences were observed among wheat cultivars (Tables 2 and 3), in spite that genotypes differed significantly in their respective A and transpiration rates. Regarding DSI values for IWUE, CY20, CM41 and NM11 exhibited a significantly higher relative increase than that of others (Table 4).

Chlorophyll fluorescence parameters

Effects of Fv/Fm between water deficit and wheat cultivars are shown in Table 2 and Figure 4a. We found that all wheat cultivars did not differ in Fv/Fm and their

Table 3. Observed significance levels (p-values) for overall tests of wheat cultivar differences, and effects of 13 wheat cultivars in water deficit condition for TLA, AGB, A, Ci, gs, IWUE and three chlorophyll fluorescence parameters (Fv/Fm, ΦPSII, NPQ).

Genotype	TLA (cm^2)	AGB ($g \cdot plant^{-1}$)	A ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	gs ($mol \cdot m^{-2} \cdot s^{-1}$)	Ci ($\mu mol \cdot mol^{-1}$)	IWUE ($mmol \cdot mol^{-1}$)	Fv/Fm	ΦPSII	NPQ
p	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.3520	0.1527	<0.0001	<0.0001
CY19	176.02bcd	4.59abc	18.20ab	0.26abcdef	208abcd	4.60a	0.78a	0.64abc	0.17abc
CY20	70.10d	5.08ab	8.41ef	0.04g	121d	4.34a	0.77a	0.70ab	0.16abc
CM41	128.78cd	3.90abcd	16.60abcd	0.28abcde	234abcd	5.08a	0.82a	0.73ab	0.14bc
SM375	125.92cd	2.66d	9.85def	0.06fg	156cd	4.30a	0.71a	0.60abc	0.11c
MM185	110.40cd	3.61bcd	16.20abcd	0.20abcdefg	181bcd	4.85a	0.76a	0.66abc	0.16abc
MM19	77.06d	3.66bcd	7.90ef	0.45ab	118d	4.67a	0.73a	0.59abc	0.25ab
185C	203.64bcd	3.41cd	9.44def	0.14defg	252abc	4.90a	0.80a	0.70ab	0.17abc
184C	291.75abc	4.67abc	15.60bcd	0.16cdefg	180bcd	5.03a	0.80a	0.72ab	0.14bc
XN979	300.04ab	5.47a	19.00a	0.40abc	267ab	5.16a	0.78a	0.73ab	0.30a
XN889	318.58a	5.57a	19.20a	0.52a	287a	5.15a	0.79a	0.77a	0.18abc
NM9	122.63cd	3.69bcd	13.40cde	0.18bcdefg	211abcd	4.27a	0.71a	0.50bc	0.14bc
NM11	257.6abcd	3.36cd	7.05f	0.31abcd	251abc	4.71a	0.75a	0.45c	0.25ab
HN	122.55cd	2.61d	17.80abc	0.11efg	120d	5.17a	0.812a	0.67abc	0.25ab

respective DSI (Table 4). The Φ_{PSII} was affected only by water deficit (Table 2, Figure 4b). Under water deficit condition, XN889 exhibited the highest value (Table 3) differing significantly with NM11. NM11 had lower DSI value for Φ_{PSII} than others (Table 4). NPQ increased in all genotypes under water deficit condition (Figure 4c), we found that XN979 exhibited the highest absolute values for NPQ under water deficit condition while SM375 had the lowest (Table 3), CY20 and XN979 had higher DSI values than other wheat cultivars (Table 4).

DISCUSSION

Water deficit may occur on wheat cultivars in different developmental stages (Wang et al., 2007; Zlatev et al., 2009). This study emphasis on growth of wheat cultivars up to the anthesis stage because wheat was sensitive to water and nutrient at this stage (Harsharm, 2010). Under water deficit condition, XN889 showed the best overall performance with measured parameters (TLA, AGB, A, gs, Ci, Φ_{PSII}) for which we found significantly different groupings of genotypes (Table 3). Furthermore, XN889 also had the highest Ci, gs and Φ_{PSII} values under control conditions (Figures 2 and 4). In addition, relative values of growth and photosynthetic parameters, as assessed here by DSIs (Table 4), CY20 and XN979 seemed to be the most tolerant to water deficit as indicated by their respective DSI values, regarding parameters for which we found significantly different groupings of wheat cultivars (Table 4).

Monitoring gas exchange in plants is a common approach, with gs reported as one of the most sensitive indicators of deficit under drought for C_3 species (Medrano et al., 2002), or salinity for wheat and sorghum (James et al., 2002; Netondo et al., 2004). Stomatal and non-stomatal limitation of photosynthesis has been reported under water deficit (Tezara et al., 1999; Chaves et al., 2002). Generally, low A caused by water deficit are primarily the result of stomatal closure (Chaves et al., 2002). However, Tang et al. (2002) argued that A was limited by biochemical reactions. In addition, Tezara et al. (1999) concluded that low ATP content, caused by a reduction in ATP synthase, was responsible for decreases in A under severe drought condition.

In our study, a decrease in Ci occurred parallel to decreases in gs in response to water deficit (Figure 3), indicating that reduction of A was mainly due to stomatal closure (Table 3). The technique of chlorophyll fluorescence, as it is rapid, sensitive and non-destructive, could therefore become a useful method for determining variations in tolerance of the photosynthetic apparatus in breeding for resistance to drought. We found that most of Fv/Fm ratio values were above 0.75 under water deficit condition, indicating that water deficit at 30% FC did not

Table 4. Effects of 13 winter wheat for drought susceptibility index relative to for TLA, AGB, A, Ci, gs, IWUE and three chlorophyll fluorescence parameters (Fv/Fm, Φ_{PSII}, NPQ).

Genotype	Drought susceptibility index (DSI)								
	TLA	AGB	A	gs	Ci	IWUE	Fv/Fm	Φ_{PSII}	NPQ
CY19	33b	60ab	93a	55ab	67ab	166b	105a	92ab	252abc
CY20	90a	66ab	84ab	59a	75a	217a	95a	91ab	356a
CM41	42ab	48b	94a	43ab	56ab	212a	98a	99a	288ab
SM375	66ab	40b	53bc	49ab	52ab	132b	85a	89ab	204c
MM185	46ab	46b	79ab	33b	52ab	157b	96a	90ab	216bc
MM19	41ab	58ab	47c	57a	54bab	198b	93a	89ab	275ab
185C	81ab	52ab	51bc	47ab	64ab	176b	100a	92ab	215bc
184C	55ab	47b	80ab	31b	52ab	154b	98a	93ab	219bc
XN979	91a	80a	92a	59a	77a	183b	95a	93ab	355a
XN889	62ab	66ab	96a	44ab	63ab	158b	98a	98a	213bc
NM9	56ab	42b	85ab	36b	49b	165b	93a	92ab	210bc
NM11	72ab	73ab	38c	49ab	69ab	216a	99a	84b	215bc
HN	62ab	61ab	89a	47ab	55ab	120b	103a	93ab	222bc

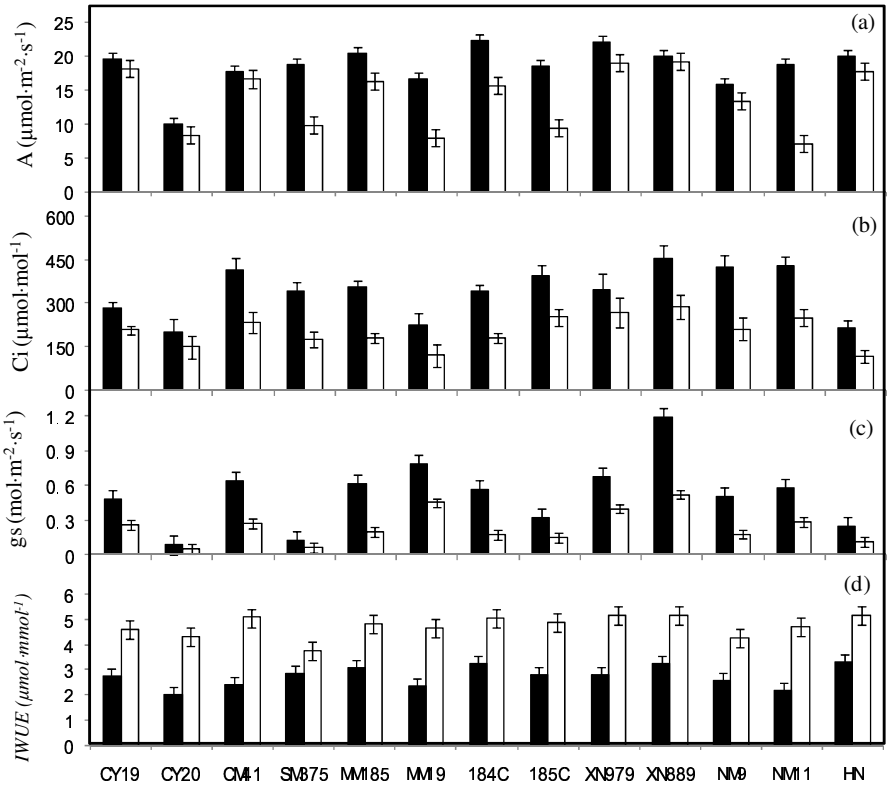

Figure 2. Mean for A (a), Ci (b), gs (c) and IWUE (d) of flag leaf for 13 wheat cultivars in control (solid bars) (80% FC) and water deficit (empty bars) (30% FC) conditions. Vertical bars represent standard errors based on variability among 5 plants.

damage PSII. Water deficit induced the reduction in gs and A (Table 3) but no changes in Fv/Fm (Table 2, Figure 4a). Therefore, the photosynthetically generated energy equivalents ATP and NADPH would be in excess of what was required for the decreased A. Water deficit could potentially lead to increased susceptibility to photoinhibition even at low drought, if excess excitation energy could not be dissipated safely (Björkman and

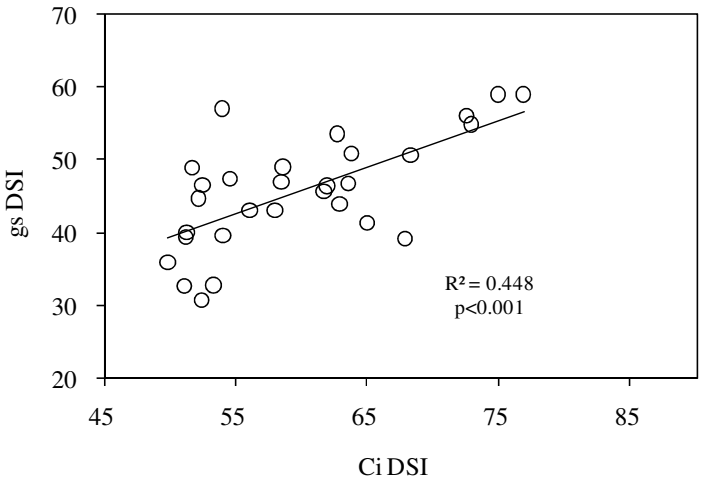

Figure 3. Relationship between gs and Ci of flag leaf for 13 wheat cultivars. Data are the average of 5 plants. Values of drought susceptibility index (DSI) for gs and Ci (both in %) are used for axis

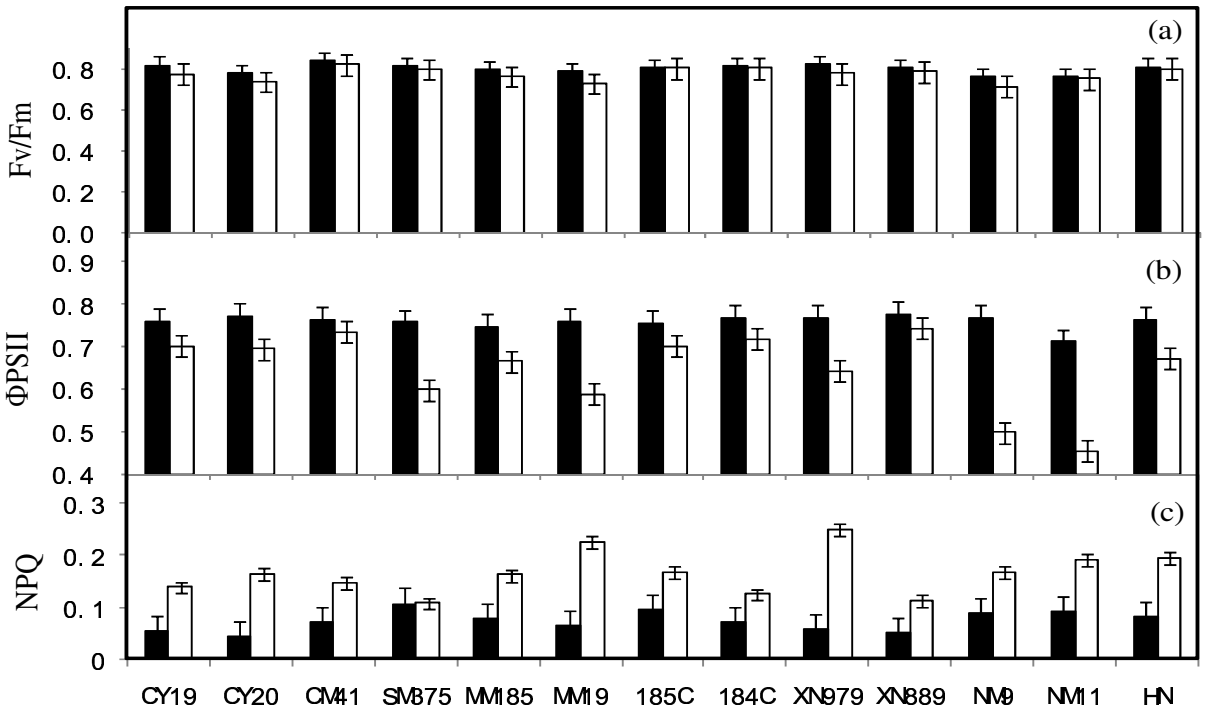

Figure 4. Means for Fv/Fm (a), ΦPSII (b) and NPQ (c) of flag leaf for 13 wheat cultivars in control (solid bars) (80% FC) and water deficit (empty bars) (30% FC) conditions. Vertical bars represent standard errors based on variability among 5 plants.

Powle, 1984).

However, plants may prevent this through the "down-regulation" of the quantum yield of PS II electron transport (Horton et al., 1996; Lu and Zhang, 1998; Shangguan et al., 2000; Zlatev et al., 2009). For NPQ, our study clearly showed that a significant increase was observed under water deficit condition (Figure 4c). We found that NPQ increased the susceptibility to photoinhibition under water deficit. Increasing NPQ (Figure 4c) may be an important adaptation to deal with excessive light energy when plants have low A (Figure 3a). This was agreed with Lu and Zhang (1998). Several

Table 5. Relationship between gs, Ci and parameters of flag leaf for 13 wheat cultivars.

Parameter	LA DSI	AB DSI	A DSI	Fv/Fm DSI	IWUE DSI	NPQ DSI	Φ_{PSII} DSI
gs DSI	0.3803*	0.4950**	0.2139ns	0.1041ns	0.016ns	0.3721*	0.1059ns
Ci DSI	0.3705*	0.4102*	0.2566ns	0.0036ns	0.1711ns	0.6721**	0.3071ns

*, ** Significance at 0.05, 0.01 levels, respectively. ns: no significance.

processes, for example photoinhibition, state transition and high energy state, can contribute to this increased NPQ, although, the relative contribution of state transition and high energy state is unknown during water deficit; it has been shown that high energy state is a major component of NPQ (Krause and Weis, 1991). An increased NPQ in water-deficit plants can therefore be seen as a regulatory response to water deficit for dissipating excess excitation, reducing the probability of photodamage to PSII, and maintaining a high proportion of PSII reaction centers in the open state (Dall'Osto et al., 2005). The increased NPQ also indicates the build up of protons in the thylakoids lumen as a result of a decreased turnover of ATP, probably due to a lower Calvin-Benson cycle activity. Increasing NPQ may also contribute to high energy state which was built up during water deficit and can be associated with an increase in zeaxanthin content in water deficit plants (Brestic et al., 1995).

Whether drought mainly limits photosynthesis through stomatal or non-stomatal impairment and has been debated for magnitude of evidences (Cornic, 2000; Flexas and Medrano, 2002a, b). During the last decade, stomatal closure was generally accepted to be the main determinant for decreased photosynthesis under mild to moderate drought (Cornic and Massacci, 1996). We found a relationship between the sensitivity of wheat cultivars to water deficit for stomatal conductance and TLA, AB and NPQ (Table 5). It is difficult to differentiate between an NPQ by stomatal closure or a co-regulation of these parameters by an undetermined factor. There is a renewed interest in the study of independence or link between stomatal conductance and parameters of photochemical and biochemical efficiencies (Medrano et al., 2002; Flexas et al., 2004). Furthermore, two genotypes could be recommended for water deficit conditions (XN979 and CY20) coped well with water deficit, as indicated by their relatively high DSI for A, with two simultaneous attributes, a relatively low impairment of gs and no impairment of Φ_{PSII} and NPQ (Table 4).

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