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DROUGHT STRESS

Effect of Simulating Drought in Various Phenophases on the Water Use Efficiency of Winter Wheat

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Abstract

In Central Europe, drought is the most important limiting factor for autumn-sown cereals. Due to the decline in groundwater, it is a priority to use less water-demanding forms of crop production. Water use efficiency (WUE) can only be increased if cultivars with satisfactory water management traits are grown, so that they can exploit the water reserves of the soil even if drought occurs during the vegetation. Water consumption and water use efficiency of winter wheat genotypes were investigated in a model experiment carried out in a climate-controlled glasshouse. The plants were grown either with optimum water supplies or with simulated drought in three phenophases, and measurements were made on the yield parameters, phenological traits and water use parameters of the plants. Substantial differences were observed between the water demands of the cultivars, and it was found that the later the phenophase in which drought was simulated, the greater the decline in water uptake. The analysis of WUE led to the conclusion that the WUE values of cultivars with short vegetation periods dropped to the greatest extent when water deficit was suffered at first node appearance, while cultivars with longer vegetation periods were more sensitive to drought during the heading and grain-filling stages.

Introduction

One of the greatest challenges that will face earth's population over the next few decades will be the need to satisfy the food requirements of an ever growing population, while the available water reserves are declining steadily (Pask and Reynolds 2013). According to the predicted trends, warmer and drier summers are expected in Europe, particularly in the southern and central parts of the continent (IPCC 2007) and droughts are likely to occur with increasing frequency (Lehner et al. 2006). Climate scenarios suggest that irrigation will become necessary on a wider scale and that the present capacity will need to be increased. Winter cereals are not generally irrigated in Central Europe, and this situation is unlikely to change in the future, despite the fact that the need to improve irrigation facilities is greatest in this region (Fallon and Betts 2010). The fact that limited water supplies are available to farmers makes it especially important for the plants to utilise the available soil water reserves as efficiently as possible, which does not always mean that they will achieve the highest possible yields. Significant changes can also be observed in the variability of the climate and in the frequency of extreme weather events, further aggravating the risk of drought (IPCC 2007). Positive changes in climatic conditions and developments in cultivation technologies are expected to increase wheat yields by 37–101 % by 2050 (Ewert et al. 2005), but this will be associated with greater water demands. Droughts combined with heat waves and the greater yield variability resulting from extreme weather events may result in a considerable decrease in the potential yield level (Jones et al. 2003, Trnka et al. 2004). Water deficit is one of the main limiting factors in cereal production in many parts of the world, especially in arid and semi-arid regions (Shahbaz et al. 2009). The origin of wheat cultivars is closely related to the level of the abiotic stress tolerance (Shanmugam et al. 2013), and significant correlations were found between the non-optimal level of abiotic environmental factors and the yield parameters of spring wheat (Weldearegay et al. 2012) and spring barley (Rajala et al. 2011). Earlier predictions suggested that in the Mediterranean regions of Europe, climate change would lead to declining productivity in agriculture (Olsen and Bindi 2002). Although both the rising temperature and increasing radiation intensity have a positive influence on evapotranspiration, there may be a reduction in yield due to the increasingly frequent and intensive appearance of water deficit-induced stress (Trnka et al. 2004). Higher temperatures are expected to shorten the vegetation period, which will not only result in a drop in yields but will also influence the utilisation of water reserves (Olsen and Bindi 2002).

Water use efficiency (WUE) is a physiological parameter of key importance, expressing the ability of the crop to preserve the water reserves of the soil, thus combining drought tolerance and high yield potential (Fang et al. 2010). Numerous authors from various parts of the world have demonstrated substantial differences between the WUE values of individual winter wheat cultivars (Miranzadeh et al. 2011, Zhang et al. 2012), but have also emphasised the fact that WUE values change if the water supplies to the crop are limited (Varga et al. 2013).

Under both rain-fed and irrigated farming conditions, there is an increasing demand for an improvement in WUE (Condon et al. 2004). For farmers, WUE can best be interpreted as the correlation between the harvested yield and the water supplies (rainfall + irrigation water) available to the crop (Condon et al. 2004). However, the yield depends on both the water reserves stored in the soil and on the temporal distribution of rainfall and irrigation (Francia et al. 2011). Zhang et al. (1999) found wheat to be the most sensitive to water deficit during the shooting to heading and heading to milky ripeness stages, so balanced water supplies are most critical during these periods.

The aim of this model experiments was to determine (i) how drought applied during the winter wheat phenophases most critical for water uptake and yield development influenced the yield and various biomass components and (ii) how water deficit influenced the dynamics of plant water uptake and the utilisation of the water quantity consumed during the vegetation period. An answer was also sought to (iii) which plant morphological and yield factors and which environmental factors related to water uptake had the greatest influence on plant WUE values when drought was experienced in different phenophases.

Materials and methods

Plant materials and experimental layout

Five winter wheat (*Triticum aestivum* L.) genotypes (Mv Toborzó/TOB/, Mv Mambó/MAM/, Bánkúti 1201/BKT/, Plainsman/PLA/and Cappelle Desprez/CAP/) were examined in a greenhouse experiments at the Agricultural Institute, Centre for Agricultural Research, Hungarian Academy of Sciences in Martonvásár. The experimental greenhouse was constructed in 2010, and the regulation system was optimised for cereal research. Plainsman (drought-tolerant) and Cappelle Desprez (drought-sensitive) were included as control cultivars. Bánkúti 1201 is an old Hungarian wheat cultivar, with tall plants liable to lodge but with good yield quality. Mv Toborzó has moderate plant height and a short growing period, making it the earliest cultivar in the Martonvásár collection. Mv Mambó is a hard-grained winter wheat with high yield potential, which has proved to have excellent abiotic stress resistance in numerous experiments (Varga and Bencze 2009, Varga et al. 2012). Phenological development of winter wheat cultivars examined is presented in Fig. 1.

After 42 days of vernalisation, eight seedlings were planted in each pot containing 10 000 cm³ of a 3 : 1 : 1 (v/v) mixture of soil, sand and humus. The plants were watered three times a week, and nutrient solution was added once a week until the start of the drought treatment. The nutrient supplies were the same in all the treatments, regardless of water consumption. Water deficit was simulated by completely withholding water for 7–10 days in three phenophases, first node appearance (Zadoks growth stage, GS 21) (FNA), heading (GS 60) (H) and the

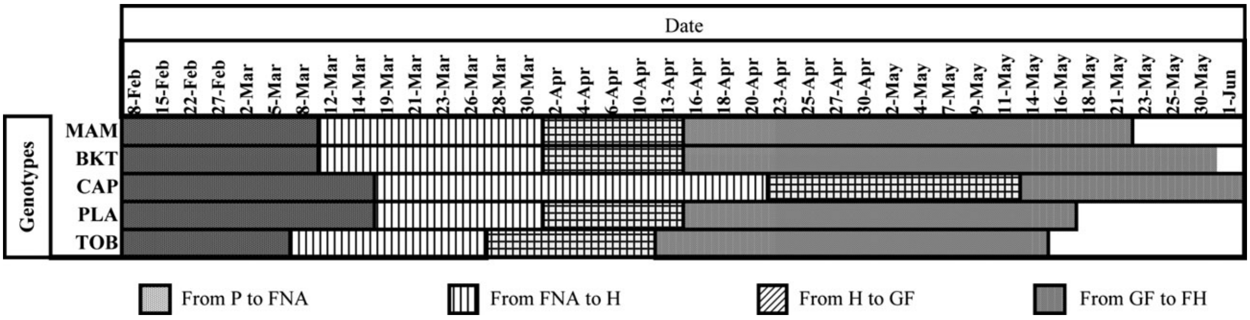

Fig. 1 Phenological development of winter wheat cultivars grown with control water supply. FH, Final harvest; FNA, first node appearance; GF, Grain filling; H, heading; P, planting.

milky ripe stage of grain filling (GS 75) (GF), and resulted in clearly visible symptoms. The treated plants were stressed on a single occesion; the manipulation of the water supplies was started when 50 % of the plants of each genotype had reached the required developmental stage. The experimental design involved five genotypes, four stress treatments (Control, FNA, H, GF) and three replicates. For plants given optimum water supplies, the soil water content was maintained at 60 % of the soil water-holding capacity, equivalent to a volumetric water content (v/v %) of 20–25 %. The soil water content was measured using a 5 TE soil water meter, and the data were recorded with an EM50 data logger (Decagon Devices Ltd., DC, USA). The soil water content dropped from the control level to 3–5 v/v % by the end of the stress treatment. After the simulated stress, watering was recommenced and the plants were given optimum supplies until full maturity. The water consumption was determined by weighing the pots on a digital balance (Mettler-Toledo Ltd., OH, USA). To minimise evaporation, the soil surface was covered with polythene. The air temperature and additional light intensity of the greenhouse chamber were regulated automatically. The 'Spring2-Summer2' climatic programme was based on the analysis of a 50-year time series for Hungary and is routinely used in fitotron studies (Tischner et al. 1997). Air temperature was increased from the initial 10–12 to 24–26 °C over a period of 16 weeks. Air humidity was kept between 60 % and 80 % and was regulated by ventilating the greenhouse chambers. Whenever necessary, the natural light intensity was enhanced by artificial illumination to a value of 500 μmol m^{-2} S^{-1} s at the beginning of the vegetation period while was gradually increased to 700 μmol m^{-2} S^{-1} s.

Analysis

Complete plant analysis involving the determination of the tiller and spikelet number and the plant height was made after the final harvest. The effect of water deficiency was studied by measuring changes in the grain weight (GW), thousand-kernel weight (TKW) and harvest index (HI), which was calculated by dividing the grain yield (kg) by the total aboveground biomass (kg). The total quantity of water taken up and utilised by the plants was measured throughout the vegetation period. The water use efficiency (WUE; kg m^{-3}) was calculated by dividing the grain yield (kg) by the water used during the vegetation period (WU; m^3) (Doorenbos and Pruitt 1977). The dynamics of water uptake for the individual plant species and cultivars was determined by calculating the water quantity utilised during each developmental phase. Water consumption was measured by weighting the pots and replacing the water on a weight basis.

Statistical analysis

The experimental design involved five genotypes, four stress treatments and three replicates. One-way analysis of variance was used to determine significant differences between the various genotypes and water treatments, as described by Kuti et al. (2012). Two-way ANOVA was applied to determine the interactions between the factors of the study with the MSTAT-C 1.42 program package (Michigan State University, MI, USA). Pearson correlation analysis was used to study correlations between WU, WUE and various phenological and yield parameters, with the SPSS 16.0 program package (IBM Inc, NY State, USA).

Results

Analysis of phenological and yield components

The most important phenological parameters of the cultivars included in the experiment are presented in Table 1. The cultivars MAM, PLA and TOB were of the moderate growth type; CAP was somewhat taller, while the greatest plant height was recorded for BKT.

Table 1 Phenological properties of winter wheat cultivars in various treatments

		Tiller number per plant		Spike number per plant		Plant height (cm)	
Genotype	Treatment	Mean	S.D.	Mean	S.D.	Mean	S.D.
MAM	C	4.79	0.33	4.50	0.31	67.08	3.45
	FNA	4.58	0.14	4.42	0.14	63.92	4.73
	H	4.61	0.41	3.67	0.13	63.55	0.64
	GF	4.21	0.63	3.63	0.62	64.83	3.31
BKT	C	6.67	0.76	5.79	0.85	116.42	2.96
	FNA	7.25	0.13	6.38	0.24	106.17	3.83
	H	7.00	0.40	5.83	0.38	92.42	1.50
	GF	5.50	0.38	4.17	0.45	104.33	1.46
CAP	C	6.54	0.22	5.25	0.47	77.75	2.25
	FNA	6.38	0.45	5.50	0.76	76.83	2.94
	H	7.50	0.19	4.83	1.54	73.08	3.77
	GF	6.04	0.13	4.75	0.47	79.58	3.86
PLA	C	8.00	0.97	5.54	3.61	65.50	0.70
	FNA	5.54	0.29	5.46	0.38	63.75	1.94
	H	4.92	0.26	4.54	0.47	55.04	4.43
	GF	5.38	0.73	5.17	0.75	57.54	2.89
TOB	C	5.54	0.26	4.79	0.89	63.17	4.96
	FNA	7.00	0.51	4.71	0.25	57.71	0.56
	H	4.58	0.59	3.96	0.83	56.58	1.16
	GF	4.63	0.13	4.00	0.45	64.29	3.25

BKT, Bánkúti 1201; C, Control; CAP, Cappelle Desprez; FNA, first node appearance; GF, Grain filling; H, heading; MAM, Mv Mambó; PLA, Plainsman; TOB, Mv Toborzó.

Among the genotypes examined, Mv Mambó gave the highest yields when given optimum water supplies, while the lowest yield was recorded for the drought-sensitive control (CAP). With the exception of the old Hungarian landrace (BKT), water withholding at first node appearance led to a significant yield reduction in all the cultivars, with the greatest decrease for the short-season cultivar TOB (44.7 %). When water deficit was simulated in the heading phenophase, there was a significant reduction in yields even compared with the FNA treatment, with the exception of TOB, where better yields were obtained when drought occurred in the early phase of development. For cultivars with longer vegetation periods, the greatest yield loss was caused by water deficiency during grain filling (70.0–80.3 %) compared to the control (Table 2), but in the modern cultivars, drought stress during ripening did not reduce the yield compared with water withholding at heading. For both the model cultivars and the old landrace, the later drought occurred, the greater the yield reduction.

The analysis of straw biomass revealed that the cultivars responded differently to water withholding. In the case of MAM, even water withholding at first node appearance resulted in a significant reduction in biomass, but this value then remained stable, exhibiting no further change when water was withheld in later stages of development (Table 3.). Stress in the FNA phenophase had no detectable effect in BKT, but treatment in the H and GF stages caused a significant reduction in biomass compared to the control (C). The biomass of PLA decreased in the FNA treatment compared to C and declined further compared to FNA in the H treatment. For the TOB cultivar, only water withholding in the H phenophase resulted in a significant drop in biomass compared to the control, while no difference could be detected between the water supply treatments for CAP. The greatest differences between the cultivars were observed for the control plants, while MAM, PLA and TOB responded to water withholding with a similar loss of biomass. The biomass of BKT was greater than that of the modern cultivars, but the highest value was recorded for CAP.

Table 3 Trends in the straw biomass (g per pot) of winter wheat cultivars in various treatments

Grain yield	Factor A					SD$_{5\ \%}$
	MAM	BKT	CAP	PLA	TOB	
Factor B						
C	53.17^{aA}	77.92^{aB}	96.41^{aC}	44.09^{aAD}	35.06^{aD}	10.763
FNA	38.38^{bA}	78.71^{aB}	86.42^{aC}	37.41^{bA}	32.67^{aA}	14.401
H	35.83^{bA}	68.90^{bB}	92.24^{aC}	30.20^{cA}	27.4^{bA}	12.307
GF	35.26^{bA}	66.31^{bB}	83.54^{aC}	34.82b^{cA}	32.67^{aA}	4.516
LSD$_{5\ \%}$	8.636	8.651	14.887	4.635	3.732	

LSD$_{5\ \%;\text{Two-way ANOVA}}$: Factor A × Factor B: Not significant.
One-way ANOVA: Different lower-case letters indicate significant differences in the given column and upper-case letters significant differences in the given row.

With the exception of CAP, there was no significant difference in TKW between the control plants and those stressed at first node appearance, so the yield losses recorded in this treatment were primarily due to reductions in the number of productive tillers and the grain number rather than in the size of the kernels (Table 4). Water deficit at heading caused a significant decrease in TKW compared with the C and FNA treatments in all the cultivars except CAP, where the drop in TKW was not significant compared with the FNA treatment. Water withholding during the grain filling resulted a force ripening by the control cultivars and by the old Hungarian cultivar. In the modern cultivars (MAM, TOB), water deficiency in the late stage of development had no effect on grain filling, and no further significant decline in TKW was observed (Table 4).

Table 2 Trends in the grain mass (g per pot) of winter wheat cultivars in various treatments

Grain yield	Factor A					SD$_{5\ \%}$
	MAM	BKT	CAP	PLA	TOB	
Factor B						
C	48.87^{aA}	39.37^{aB}	25.43^{aC}	37.65^{aB}	30.16^{aC}	8.448
FNA	37.23^{bA}	38.69^{aA}	19.12^{bB}	24.61^{bC}	16.66^{bB}	4.965
H	17.30^{cA}	8.57^{bB}	8.69^{cB}	16.03^{cA}	22.49^{bC}	3.925
GF	22.70^{cA}	5.00^{bB}	4.89^{cB}	11.30^{cB}	23.03^{bA}	7.084
LSD$_{5\ \%}$	8.00	7.66	5.00	7.21	6.49	

LSD$_{5\ \%;\text{Two-way ANOVA}}$: Factor A × Factor B: 8.809.
One-way ANOVA: Different lower-case letters indicate significant differences in the given column and upper-case letters significant differences in the given row.

Table 4 Trends in the thousand-kernel weight (g) of winter wheat cultivars in various treatments

Grain yield	Factor A					SD$_{5\ \%}$
	MAM	BKT	CAP	PLA	TOB	
Factor B						
C	47.1^{aA}	38.7^{aB}	25.5^{aC}	29.1^{aC}	42.6^{aB}	4.06
FNA	44.0^{aA}	38.1^{aB}	21.1^{bC}	29.7^{aD}	37.9^{abB}	4.12
H	33.2^{bA}	28.7^{bB}	19.5^{bC}	24.3^{bD}	32.5^{bA}	2.79
GF	29.7^{bA}	19.3^{cB}	13.9^{cC}	20.3^{cB}	32.1^{bA}	5.15
LSD$_{5\ \%}$	3.94	3.84	2.40	3.57	6.51	

LSD$_{5\ \%;\text{Two-way ANOVA}}$: Factor A × Factor B: 5.296.
One-way ANOVA: Different lower-case letters indicate significant differences in the given column and upper-case letters significant differences in the given row.

With the exception of Mv Toborzó, water withholding resulted in a significant reduction in HI when the treatment was carried out at heading or in the ripening stage (Table 5). The lowest HI values were recorded for BKT and CAP even in the control, and it was these cultivars that responded to water deficit with the greatest yield losses as a ratio of the total biomass. In cultivars with a shorter vegetation period, drought in the early stage of development caused a reduction in HI, parallel to the drop in WUE values, while for later maturing cultivars, water withholding in the later phenophases had a greater negative effect (Table 5).

Trends in water uptake and water use efficiency

Considerable differences were found between the cultivars examined in the quantity of water used over the whole growing period for vegetative and generative development even in the case of optimum water supplies (24.16–36.38 dm³ per pot). The highest water consumption was recorded for late maturing cultivars, while a shorter vegetation period was associated with lower water consumption. Stress at first node appearance did not result in a significant modification in the water uptake of late cultivars. In fact, greater water uptake was observed for the control plants in the later stages of development, due to the enhanced tiller formation. In the case of short-season cultivars, however, there was a significant drop (16.3 and 21.0 %) in the water consumption of plants stressed in the early phenophase compared to that of plants developing under optimum conditions. After heading, the water requirements of the plants declined to a very similar extent regardless of when water was withheld. The greatest decrease in water consumption was detected for BKT. Plants stressed in the grain-filling stage stopped taking up water within a few days, and this change proved to be irreversible. The water consumption over the whole growing season declined to the same level for all the cultivars except CAP when the plants were stressed at ripening (Table 6).

When investigating the utilisation of the water taken up by the plants, significant differences were again observed between the cultivars even with optimum water supplies. In the control plants, the water use efficiency ranged from 0.7 to 1.6 kg m^{-3}, declining in the order MAM-PLA-TOB-BKT-CAP (Table 7). Simulated drought at first node appearance reduced the WUE values to 0.53–1.39 kg m^{-3}, decreasing in the order MAM-PLA-BKT-TOB-CAP. Drought at heading resulted in a significant reduction in WUE values except for the cultivar TOB, where the value was similar to that in the control. This could be attributed to the fact that, although the water uptake declined compared with the C and FNA treatments, the grain weight did not exhibit a parallel reduction. The cultivar order at heading was TOB-MAM-PLA-BKT-CAP, with values ranging from 0.28 to 1.28 kg m^{-3}. When water deficit was simulated at ripening, a further significant drop in WUE compared to the H treatment was only observed for Plainsman. The WUE values of BKT and CAP reached the

Table 5 Trends in the harvest index (%) of winter wheat cultivars in various treatments

Grain yield	Factor A					
	MAM	BKT	CAP	PLA	TOB	SD$_{5\ \%}$
Factor B						
C	38.18^{aA}	26.03^{aB}	17.53^{aC}	38.26^{aA}	38.02^{aA}	3.178
FNA	38.68^{aA}	26.93^{aB}	15.06^{aC}	30.45^{abD}	27.5^{bB}	1.898
H	23.91^{bA}	8.60^{bB}	7.41^{bB}	20.02^{bcA}	35.99^{abC}	6.632
GF	26.28^{bA}	5.13^{bB}	4.14^{bB}	16.25^{cC}	30.77^{abA}	6.738
LSD$_{5\ \%}$	4.908	4.277	3.301	10.45	8.544	

LSD$_{5\ \%;\text{Two-way ANOVA}}$: Factor A × Factor B: 7.938.
One-way ANOVA: Different lower-case letters indicate significant differences in the given column and upper-case letters significant differences in the given row.

Table 6 Water use (dm³) of winter wheat cultivars over the whole growing season in various treatments

Grain yield	Factor A					
	MAM	BKT	CAP	PLA	TOB	SD$_{5\ \%}$
Factor B						
C	30.39^{aA}	36.23^{aB}	36.38^{aB}	25.48^{aC}	24.16^{aC}	3.405
FNA	27.39^{aA}	35.08^{aB}	35.57^{aB}	21.34^{aC}	19.09^{bC}	5.16
H	17.39^{bA}	25.71^{bB}	31.02^{bC}	16.22^{bA}	17.63^{bA}	2.83
GF	19.84^{bAB}	21.02^{cA}	30.95^{bC}	17.38^{bB}	19.18^{bAB}	2.53
LSD$_{5\ \%}$	4.3	4.002	4.483	4.48	2.732	

LSD$_{5\ \%;\text{Two-way ANOVA}}$: Factor A × Factor B: 4.459.
One-way ANOVA: Different lower-case letters indicate significant differences in the given column and upper-case letters significant differences in the given row.

Table 7 Water use efficiency (kg m^{-3}) of winter wheat cultivars in various treatments

Grain yield	Factor A					
	MAM	BKT	CAP	PLA	TOB	SD$_{5\ \%}$
Factor B						
C	1.6^{aA}	1.08^{aB}	0.7^{aC}	1.47^{aA}	1.25^{aD}	0.154
FNA	1.39^{bA}	1.1^{aB}	0.53^{bC}	1.15^{bB}	0.87^{bD}	0.078
H	1.0^{cA}	0.34^{bB}	0.28^{cB}	0.97^{bA}	1.28^{aC}	0.153
GF	1.12^{cA}	0.24^{bB}	0.16^{cB}	0.64^{cC}	1.18^{abA}	0.29
LSD$_{5\ \%}$	0.181	0.192	0.124	0.231	0.331	

LSD$_{5\ \%;\text{Two-way ANOVA}}$: Factor A × Factor B: 0.281.
One-way ANOVA: Different lower-case letters indicate significant differences in the given column and upper-case letters significant differences in the given row.

minimum level when water was withheld at heading, while for the modern cultivars, water deficit during the grain-filling period did not result in a further decrease in WUE, as also observed for the yield quantity (Table 7).

Correlation analysis

The object of the analysis was to determine which phenological and yield parameters influenced the water consumption during the vegetation period, and how the water use efficiency changed over the whole experiment and when drought was simulated by water withholding in various phenophases (Table 8). In the case of the whole experiment, it was found that traits determining growth habit, such as the number of tillers and spikes and the plant height, were directly proportional with the water demand. The straw biomass exhibited the closest correlation with water consumption. Although a significant positive correlation was also detected for the grain weight, this was considerably smaller than for the straw biomass. The spike number had no influence on WUE, but if the total number of tillers was considered, not just those bearing spikes, a significant correlation was observed. The values of WUE were closely correlated with TKW and HI. In all the

Table 8 Results of correlation analysis in the different treatments

	Correlations									
	All treatments		Control		FNA		H		GF	
	WU	WUE	WU	WUE	WU	WUE	WU	WUE	WU	WUE
WU										
Pearson correlation	1.000	−0.125	1.000	−0.514[1]	1.000	−0.292	1.000	−0.832[2]	1.000	−0.474[1]
Sig. (1-tailed)		0.171		0.025		0.145		0.000		0.037
N	60.000	60	15.000	15	15.000	15	15.000	15	15.000	15
Spike No.										
Pearson correlation	0.588[2]	−0.090	0.406	−0.222	0.571[1]	−0.186	0.580[1]	−0.745[2]	0.273	−0.293
Sig. (1-tailed)	0.000	0.247	0.067	0.213	0.013	0.254	0.012	0.001	0.162	0.145
N	60	60	15	15	15	15	15	15	15	15
Tiller No.										
Pearson correlation	0.430[2]	−0.231[1]	−0.038	−0.070	0.245	−0.496[1]	0.856[2]	−0.882[2]	0.549[1]	−0.546[1]
Sig. (1-tailed)	0.000	0.038	0.447	0.402	0.190	0.030	0.000	0.000	0.017	0.018
N	60	60	15	15	15	15	15	15	15	15
Plant height										
Pearson correlation	0.609[2]	−0.316[2]	0.696[2]	−0.371	0.755[2]	−0.060	0.708[2]	−0.770[2]	0.372	−0.574[1]
Sig. (1-tailed)	0.000	0.007	0.002	0.087	0.001	0.416	0.002	0.000	0.086	0.013
N	60	60	15	15	15	15	15	15	15	15
Steam and leaf weight										
Pearson correlation	0.842[2]	−0.548[2]	0.927[2]	−0.730[2]	0.884[2]	−0.502[1]	0.964[2]	−0.919[2]	0.863[2]	−0.762[2]
Sig. (1-tailed)	0.000	0.000	0.000	0.001	0.000	0.028	0.000	0.000	0.000	0.000
N	60	60	15	15	15	15	15	15	15	15
Grain weight										
Pearson correlation	0.389[2]	0.846[2]	0.111	0.791[2]	0.458[1]	0.696[2]	−0.645[2]	0.950[2]	−0.334	0.981[2]
Sig. (1-tailed)	0.001	0.000	0.347	0.000	0.043	0.002	0.005	0.000	0.112	0.000
N	60	60	15	15	15	15	15	15	15	15
Thousand-kernel weight										
Pearson correlation	0.120	0.734[2]	−0.193	0.595[2]	−0.214	0.743[2]	0.054	0.330	−0.497[1]	0.937[2]
Sig. (1-tailed)	0.181	0.000	0.245	0.010	0.222	0.001	0.425	0.115	0.030	0.000
N	60	60	15	15	15	15	15	15	15	15
Harvest index										
Pearson correlation	−0.114	0.959[2]	−0.741[2]	0.926[2]	−0.361	0.923[2]	−0.661[2]	0.930[2]	−0.477[1]	0.995[2]
Sig. (1-tailed)	0.193	0.000	0.001	0.000	0.093	0.000	0.004	0.000	0.036	0.000
N	60	60	15	15	15	15	15	15	15	15
WUE										
Pearson correlation	−0.125	1.000	−0.514[1]	1.000	−0.292	1.000	−0.832[2]	1.000	−0.474[1]	1.000
Sig. (1-tailed)	0.171		0.025		0.145		0.000		0.037	
N	60	60.000	15	15.000	15	15.000	15	15.000	15	15.000

[1] Correlation significant at the 0.05 level.

[2] Correlation significant at the 0.01 level.

treatments, the plant height and straw biomass were in positive correlation with WU and in negative correlation with WUE. In control plants, the grain weight had no influence on water uptake, but in plants treated at first node appearance, a positive correlation was detected, suggesting that plants which suffered less damage from simulated drought in the early phenophase produced a higher yield, resulting in greater water consumption. For plants treated in the heading and ripening stages, higher grain weight was associated with lower water uptake, because the water consumption of plants with greater grain weight was more drastically affected by water withholding. A negative correlation was observed between the HI and WU values in all the treatments, and a very close correlation between HI and WUE, irrespective of the period in which water was withheld. The closest correlation between WUE and WU was observed during the heading period, indicating that this phenophase was the most critical from the point of view of the water management.

Discussion

Drought appears likely to become the most important environmental limiting factor for the production of autumn-sown cereals not only in the Mediterranean but increasingly in the Central Europe, too (Blum 2009). The results of modelling using climate scenarios show that water deficit may occur in any stage of plant development, making it essential to know what effect drought has on the water use efficiency in various phenophases.

Satisfactory vegetative development is an essential criterion for the success of reproductive development. Adequate water supplies are especially important in the phenophases critical for plant development (first node appearance, grain filling) if the plants are to utilise water efficiently during the generative phase of development (Kato et al. 2008). Irrigation during the critical phases of development results in a substantial improvement in WUE values (Zhang et al. 2004, Fang et al. 2010). Water deficit before heading influences phenological traits rather than the grain yield, but drought after flowering results in earlier ageing and ripening, and the assimilates accumulated before flowering are more rapidly mobilised into the grain (Yang et al. 2003).

The present results indicated a considerable difference in the sensitivity of winter wheat cultivars to water withholding as a function of the length of the life cycle. While cultivars with short vegetation periods were most sensitive to drought at first node appearance, water deficit in the early phenophase only caused slight modifications in the yield components and water use efficiency in later maturing cultivars. In response to severe water deficit after heading, however, the plant water management was not regenerated even when water supplies were renewed.

In arable farming, the genetic characteristics of the cultivars are of outstanding importance. Zhang et al. (2012) demonstrated a close correlation between the genetic changes that have taken place in plant reproductive stocks over the last 30 years and both the yield and WUE. The present results showed that there are considerable differences in the water use traits of the cultivars currently grown. One of the relevant findings of this experiment is that the WUE values of the old landrace investigated were primarily competitive with those of modern cultivars under optimum environmental conditions, while its water use properties and water use efficiency were less favourable under stress conditions.

Based on the data of Passioura (1996), it was established by Reynolds and Tuberosa (2008) that WU, WUE and HI had a fundamental influence on the yield. In the light of this statement, extremely contradictory results have been published on the correlation between WUE and HI. While Kang et al. (2002) found that WUE increased linearly with HI, Zhang et al. (2008) reported that in winter wheat, HI decreased parallel with an increase in water supplies. Varga et al. (2013) found that changes in the HI values of winter wheat cultivars were paralleled by changes in WUE and that simulated drought resulted in various extents of reduction in HI. In the present experiment, a close correlation was detected between WUE and HI irrespective of the phenophase in which the plants suffered water withholding. The parallel analysis of WUE and HI indicated that the later the phenophase in which water deficit occurred, the more unfavourable its effect.

Earlier research suggested that WUE values increased as drought became more severe and water consumption dropped, that is, water deficit resulted in higher WUE values (Meyers et al. 1984, Peuke et al. 2006). It was reported by Varga et al. (2013) that water supplies well below the optimum level led to a reduction in WUE as a consequence of stress effects. Above-optimum water supplies could be expected to result in the opposite tendency. In the present work, WUE decreased in some cultivars even in response to water withholding at first node appearance, while this parameter dropped significantly when water was withheld at heading or grain filling except in the case of early maturing cultivars.

In the numerous investigations carried out on WUE in various experimental systems in many parts of the world, substantial differences were detected, determined primarily by the genetic background of the cultivars. On the basis of yield quantities, Qiu et al. (2008) reported WUE values of 1.1–2.1 kg m^{-3} for winter wheat and stated that the seed-setting and milky ripe stages were the most critical for the development of WUE.

The WUE values found for winter wheat cultivars in the present work were in agreement with those reported earlier.

In the case of optimum water supplies, considerable differences were observed between the cultivars, primarily as a function of the length of the vegetation period and the water demands of the plants. The WUE values ranged from 0.7 to 1.6 kg m^{-3}. The results confirmed that the water use efficiency varied to a substantial extent even for the same cultivar, mainly due to environmental effects (Xue et al. 2006, Qiu et al. 2008). Water deficit at different stages of development had different effects on the various cultivars in the present work. While for high-yielding cultivars with a long vegetation period, WUE exhibited no response to water deficit in the earliest phenophase tested, drought after heading had no influence on water use efficiency in the case of early maturing cultivars. In irrigated experiments, Dong et al. (2011) came to the conclusion that WUE tended to decrease as the intensity of irrigation increased, with values ranging from 0.584 to 1.894 kg m^{-3}. Many authors have proved that in regions where winter wheat can only be grown with supplementary irrigation, a reduction in the quantity of irrigation water led to an improvement in WUE values (Zhang et al. 2008, Zhang et al. 2013). In the present experiments, the highest values of WUE were obtained for plants developing with optimum water supplies, while with few exceptions, water deficit led to a reduction in the efficiency with which the plants utilised water.

In wheat selection programmes, the best results are obtained by means of joint selection for HI and transpiration efficiency under drought stress conditions (Siahpoosh and Dehghanianb 2011). Yang et al. (2003) found that plants exposed to drought stress flowered earlier, which thus brought the grain-filling period forward, helping the plants to avoid the negative effects of the very hot weather often experienced in early summer. This author reported that high WUE was correlated with low evapotranspiration (ET). A close positive correlation between WUE and HI was also observed in the present work, irrespective of the cultivar and the phenophase in which water was withheld. ET was negatively correlated with the WUE values, and the closest correlation was detected for plants exposed to drought at heading. Under optimum conditions, high water consumption was not necessarily associated with poor WUE, but in the case of limited water supplies, there was a steep decline in the WUE values of genotypes with high water requirements.

This experiment was carried out in a greenhouse under regulated environmental conditions; therefore, all these results should be considered as preliminary findings that could be a base for a widely performed validation.

Conclusions

If cereal production is based on natural rainfall supplies, the water deficit caused by drought in any period of winter wheat development may result in a substantial decline in the efficiency with which soil water reserves are utilised. Drought stress at heading or in later phenophases caused the greatest reduction in WUE values, but considerable differences were observed between the cultivars, due primarily to differences in the water demand over the vegetation period and the length of the vegetation period. The results demonstrated a very close correlation between HI and WUE not only in the case of optimum water supplies but also in the stress treatments.

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