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Inheritance of water use efficiency in diallel hybrids of spring barley under varied nutrition and soil moisture

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Abstract. Inheritance of water use efficiency (WUE) at the whole-plant level was investigated in a diallel set (Ps+F_2s) of spring barley. Plants were grown in 9 dm^3 pots under optimal conditions, low NPK nutrition and low soil moisture. GCA effects were found to be of major importance for the variance in vegetative and economic WUE measures. A significance of SCA effects was observed only under nutrient and soil moisture stresses. The stress conditions used did not considerably affect the sign and magnitude of combining ability effects. Consistency between GCA and parental means was found. The efficiency of water use under stress did not correlate with stress tolerance indices, but stress-induced changes in the harvest index and WUE were closely related to the tolerance. An analysis of genetic components of variation indicated that additive gene effects were of major importance for the vegetative and economic WUE measures. Moderately high narrow-sense heritabilities of WUE under optimal conditions (0.64-0.69) were found to decrease to 0.46-0.53 and 0.13-0.35 under limited fertilization and simulated drought, respectively. Partial dominance of genes was observed. The degree of dominance of genes was found to increase under stress. The results suggest that a low WUE is a recessive character. It is supposed that the preponderance of additive gene effects should facilitate selection efforts to improve WUE in spring barley.

Key words: drought, *Hordeum vulgare*, heritance, low nutrition, stress tolerance, water use efficiency.

Introduction

Soil and climatic conditions of Poland do not favour stable yielding of cereals. On the prevailing permeable and light-textured acid soils, nutrient imbalances and periodical rainfall deficits that occur after the sowing and during reproductive

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growth stages frequently contributed to considerable grain yield reductions. Especially in the central-west regions of the country, there is a negative balance between the evapotranspiration and precipitation (BYSZEWSKI 1977, LISTOWSKI 1979, RYSZKOWSKI et al. 1996). Therefore, breeding for a more efficient use of soil resources and a better adaptation to the less favourable environmental conditions appears to be a justified strategy in this region (CZEMBOR 1989).

There are various morpho-physiological characteristics which may be involved in the response to water and nutrient shortages (GÓRECKI, GRZESIUK 1978, BLUM 1987, BALIGAR, DUNCAN 1990, ARNAU, MONNEVEUX 1995, RICHARDS 1996, BELHASSEN 1997). Many of them appear to be typical constitutive traits affecting crop performance under stress (BLUM 1996). Among others, characters associated with the rooting ability, photosynthetic activity of leaves, stomatal function, allocation of plant assimilates through vegetative and generative plant organs and the efficiency of water and nutrient use, seem to be the most important for the complex plant performance under such conditions.

A high efficiency of water use, defined here at the whole-plant level as the dry matter produced per unit of water transpired, appears to be a crucial attribute for satisfactory plant productivity in such environments. According to the common equation (PASSIOURA 1977):

$$Y = T \times WUE \times HI \,,$$

the grain yield (Y) is the product of the amount of transpired water (T), water use efficiency at the plant or crop level (WUE) and harvest index (HI). As frequently emphasized in studies on the progress in cereal breeding (e.g. AUSTIN et al. 1980, WYCH, RASMUSSON 1983, LYNCH, FREY 1993), the considerable increase in grain yield of cultivars released during the past 70-80 years appears to be mainly attributed to an enhanced HI. Much less efforts were made by breeders to improve WUE.

Successful breeding for more efficient water use requires basic information on the genetics of WUE. A broad genotypic variation in WUE was frequently reported in cereals, including spring barley (e.g. FARQUHAR, RICHARDS 1984, BLUM 1987, RICHARDS et al. 1993, EHDAIE 1995, Van den BOOGAARD 1995, MENDEL, GÓRNY 1996, GÓRNY 1999). On the other hand, however, our knowledge on the genetic control of WUE in cereal plants appears to be very limited. As far as the whole-plant level is concerned, only EHDAIE and co-workers (1993) reported on relatively high broad-sense heritabilities (0.78-0.69) of transpiration efficiency in wheat plants grown under wet and dry conditions. No such data are available for barley. There are reasons to believe that methodological questions associated with laborious measurements of the water transpired in possibly numerous populations of pot- and/or field-grown plants cause the almost total lack of information on the genetic nature of this character.

The objective of this study was to make a preliminary assessment of the genetic control of WUE in spring barley as well as to evaluate the possible effects of reduced nutrition and low soil moisture on the manner in which WUE is inherited.

Materials and methods

Plant material

All the possible diallel cross combinations excluding reciprocals were made between five inbred lines of spring barley (*Hordeum vulgare* L.). The parents originated from the Dutch cvs. 'Aramir' and 'Menuette', German cv. 'Trumpf', Russian cv. 'Luch' and the Polish cv. 'Lubuski' that are known to exhibit differences in yield potential, yield stability, nutrients efficiency and rooting ability (GÓRNY 1992, 1993, 1994). After a greenhouse-reproduction, the parents and F_2 cross generations were investigated in the experiment.

Experimental procedure

The combined factorial experiment was arranged as a split-plot design with 15 genotypes (parents and F_2s), three soil nutrition/moisture treatments and five pot-replications. In each replication, all soil treatments were represented. Using a procedure described elsewhere (e.g. GÓRNY, SZOŁKOWSKA 1996), plants were grown in double-walled Kick-Brauckman's experimental pots in a partially conditioned greenhouse. Pots were uniformly filled with 9 dcm^3 of a sieved soil mixture (sandy loam soil : peat : quartz sand, 2 : 1 : 1 v/v, pH 6.2) previously moistened as required and mechanically mixed with fertilizers to achieve required macronutrient rates and standard concentrations of micronutrients. Nitrogen was added to the soil at two rates as NH_4NO_3 (before sowing and after the tillering stage). The following three soil treatments were used:

1. Control – optimal fertility and moisture of the soil, i.e. 17% water content (70% of field capacity); 100 mg N, 100 mg P and 150 mg K kg^{-1} soil;
2. Low NPK – reduced soil fertility and optimal soil moisture, i.e. 17% water content (70% of field capacity); 50 mg N, 60 mg P and 80 mg K kg^{-1} soil;
3. Drought – optimal soil fertility and reduced soil moisture, i.e. 7.5% water content (30% of field capacity); 100 mg N, 100 mg P and 150 mg K kg^{-1} soil.

In the 3rd treatment, the low soil moisture stress was applied during two periods of plant growth, i.e. at the tillering stage (10-32 days after the sowing of pregerminated seeds) and at the reproductive growth stage (between heading and dough maturity; 55-85 days after sowing).

Uniform, surface-sterilized and pre-germinated seeds (24 h, 22°C) were sown into pots. Ten plants were grown in each pot-replication. After sowing, the soil surface was covered with a 2.5 cm layer of perlite to minimize soil water evaporation (E). Check pots without plants were included to record possible E. Depending upon the growth stage and photoperiod cycling, the plants were grown under 12-16 h light, at least 300-700 μM PAR m^{-2} s^{-1} at plant level ensured by an enhanced density of sodium- and mercury-lamps (400 W), 55-85% relative air humidity and 20-26/8-14°C day/night temperatures. To minimize possible effects of light and temperature gradients, the pots were frequently displaced around the experimental area.

The amount of transpired water (WT) was recorded by frequent (at least 3-4 times/week) weighing of pots on a digital balance, and the initial soil moisture was maintained constant by addition of deionized water into pots. The soil moisture stress levels were attained by withholding of watering. For precise estimation of WT, the evaporative water (E) monitored in check pots (about 1.2 L water/pot/season) was subtracted from the finally recorded water use. All plants were harvested at full maturity. The harvested material was divided into straw, leaves and grains, and the dry matter of these plant parts was determined by oven-drying (48 h, 65°C). The vegetative (WUE_{VEG}) and economic (WUE_{ECO}) measures of water use efficiency (mgDM mol^{-1}) were estimated for the vegetative and economic plant parts by dividing the dry matter of both straw and leaves by moles of WT and the dry matter of grains by moles of WT, respectively. Similarly, the tolerance to limited nutrition (T_N) and drought resistance index (R) were calculated for the vegetative and economic plant parts using a modified standard equation (FISCHER, MAURER 1978):

$$R = (S_i / C_i)/D ,$$

where S_i and C_i are the dry matters of the *i*-th genotype at the low and high fertilization or soil moisture, respectively, and the D value $(= (\bar{x}S / \bar{x}C))$ is a measure of the mineral or water stress intensity. Additionally, relative values, i.e. stress/control ratios, were calculated for all characters.

Statistics

Standard procedures were used for statistic data computations (MSTAT-C package, Michigan Univ. 1990). Following the analysis of variance, comparisons among treatment means were made using the multiple Duncan's range test. The combining ability analysis (GRIFFING 1956, method 3) and estimation of genetic components of variation (HAYMAN 1954, MATHER, JINKS 1982) in the diallel set were performed using the SAS DGH 1.0 package (KALA et al. 1994).

Results

Variation of characters

Average genotypic and soil treatment effects on shoot performance and water use efficiency are summarized in Table 1. The parents and F_2-populations exhibited considerable differences in the vegetative plant biomass, grain yield and the vegetative (WUE_{VEG}) and economic (WUE_{ECO}) measures of water use efficiency. Among the parents, 'Trumpf' and 'Lubuski 73' combined both high WUE_{VEG} and high WUE_{ECO}, while 'Luch 73' was distinguished by the lowest WUE. Generally, no close association between WUE_{VEG} and WUE_{ECO} was found in the study. For instance the Dutch cv. 'Aramir' utilized water much more effectively in generative organs, whereas 'Menuette' showed an effective use of water only in vegeta-

Table 1. Genotype (hybrid) and soil treatment effects on the variation in the vegetative plant biomass (BIOM), grain yield (GY), harvest index (HI), amount of transpired water (WT) and the vegetative (WUE_{VEG}) and economic (WUE_{ECO}) water use efficiency.

Variation source	BIOM (dry) g	GY (dry) g	HI (dry) %	WT mol	WUE_{VEG} mg mol^{-1}	WUE_{ECO} mg mol^{-1}
Genotypes:						
Trumpf (Tr)	34.0	45.8	57.2	1065	32.3	43.3
Aramir (Ar)	33.3	46.9	58.5	1082	30.8	43.4
Menuette (Me)	35.2	43.4	55.3	1071	33.0	40.9
Lubuski 73 (Lb)	37.9	50.0	56.9	1136	33.5	44.2
Luch (Lu)	33.5	42.9	56.1	1146	29.6	37.7
F_2(Tr × Ar)	35.2	49.5	58.4	1116	31.6	44.4
F_2(Tr × Me)	34.7	47.1	57.7	1109	31.4	42.8
F_2(Tr × Lb)	36.5	49.0	57.1	1119	32.9	43.9
F_2(Tr × Lu)	33.6	45.2	57.4	1128	29.9	40.3
F_2(Ar × Me)	35.7	47.5	57.1	1106	32.2	43.0
F_2(Ar × Lb)	35.3	49.4	58.4	1087	32.6	45.7
F_2(Ar × Lu)	33.7	46.8	58.2	1117	30.4	42.3
F_2(Me × Lb)	36.8	49.6	57.5	1114	33.1	44.8
F_2(Me × Lu)	35.2	45.4	56.4	1094	32.4	41.9
F_2(Lb × Lu)	36.0	47.9	57.1	1122	32.2	43.1
$LSD_{0.05}$	1.6	2.7	1.1	46	1.3	1.8
Soil treatments:						
Control	42.9	56.7	56.8	1364	31.5	41.6
Low NPK	30.6	41.6	57.6	1031	29.7	40.4
Drought	31.8	43.0	57.5	928	34.3	46.4
$LSD_{0.05}$	0.7	1.2	0.5	21	0.6	0.8

tive plant tissues. Among the F_2-hybrids, the highest economic WUE was exhibited by the hybrids (Ar × Lb), (Me × Lb), (Tr × Ar) and (Tr × Lb), while the hybrid (Tr × Lu) utilized water with the lowest efficiency.

The applied shortages of nutrients and water reduced shoot production considerably. The vegetative plant biomass and grain yield decreased by 29-27% under low NPK nutrition and by 26-24% under drought, respectively. On average, the stress conditions contributed to a 0.7-0.8% increase in harvest index as compared with control conditions. The efficiency of water use decreased significantly under the limited nutrition, whereas the vegetative and economic WUE measures were about 9% and 11.5% higher under drought conditions than under optimal

Table 2. Pooled analysis of variance for the vegetative plant biomass (BIOM), grain yield (GY), harvest index (HI), amount of water transpired (WT) and the vegetative (WUE$_{VEG}$) and economic (WUE$_{ECO}$) water use efficiency

Variation source	d.f.	Means square					
		BIOM	GY	HI	WT	WUE$_{VEG}$)	WUE$_{ECO}$
Treatments (T)	2	3466.1**	5204.1**	11.6**	3896.6**	405.0**	770.7**
Genotypes (G)	14	26.7**	74.4**	12.2**	8.1*	22.0**	59.8**
T × G	28	7.9*	17.1	2.4	4.7	3.9	4.9
Error	176	4.7	13.5	2.3	4.0	3.1	6.1

*, ** – significant at the P = 0.05 and P = 0.01 levels, respectively

conditions, respectively. In the study, the lines and hybrids of barley tended to show a similar response to soil treatments used. Except for the vegetative biomass, the analysis of variance did not detect any significant effects of genotype-treatment interaction on the variation of other characters (Table 2).

Covariation of characters

Phenotypic correlations between the investigated characters of plants grown under stress conditions are presented in Table 3. There was a positive relationship

Table 3. Coefficients of correlations between the characters directly measured under stress conditions and their relative values (i.e. stress/control ratios) and the vegetative and economic tolerance and resistance indices

Trait under stress or their relative values	Low nutrition			Soil drought		
	grain yield	tolerance index		grain yield	resistance index	
		T$_{VEG}$	T$_{ECO}$		R$_{VEG}$	R$_{ECO}$
Vegetative biomass (BIOM)	0.70*	0.20	0.18	0.30	0.24	–0.10
Grain yield (GY)	1.00	0.12	0.27	1.00	–0.30	0.02
Harvest index (HI)	0.51*	–0.09	0.14	0.74**	–0.45^{+}	0.05
WUE$_{VEG}$	0.39	–0.11	–0.19	0.09	0.11	–0.04
WUE$_{ECO}$	0.80**	–0.18	–0.09	0.86**	–0.40	0.01
Relative BIOM	0.12	1.00	0.82**	–0.30	1.00	0.63*
Relative GY	0.27	0.82**	1.00	0.02	0.63*	1.00
Relative HI	0.26	0.11	0.66**	0.32	–0.55*	0.30
Relative WUE$_{VEG}$	–0.04	0.38	0.05	–0.53*	0.76**	0.25
Relative WUE$_{ECO}$	0.24	0.43	0.69**	–0.24	0.24	0.65**

+, *, ** – significant at the P = 0.10, P = 0.05 and P = 0.01 levels, respectively.

under low nutrition between grain yield and the economic measure of WUE, vegetative biomass and harvest index. Under reduced soil moisture, however, the vegetative biomass did not correlate with grain yield, while the correlation between grain yield and harvest index was found to be much closer under drought than under a low NPK supply.

As expected, the relative values for both the vegetative biomass and grain yield were positively correlated with stress tolerance indices, but these correlations were found to be much closer under limited nutrition than under soil drought.

The parents and hybrids of a higher harvest index (HI) under drought tended to form a more drought-sensitive vegetative biomass. The stress-induced relative alterations in HI were negatively correlated with the vegetative indices of drought resistance but did not exhibit any significant association with the economic measures of the resistance. Under limited nutrition, however, the relative HI showed a highly significant correlation with the economic index of stress tolerance indicating that the higher was the low NPK-induced increase in HI, the higher was the tolerance to nutritional stress.

Under both the stress conditions used, we did not find any association between both the WUE measures and the stress tolerance indices. Nevertheless, the higher was the drought-induced increase in the vegetative measure of WUE, i.e. the higher was the stress/control ratio for WUE_{VEG}, the lower was grain yield under drought. In opposition to low nutrition, the relative WUE_{VEG} indicated a significant correlation with the vegetative index of drought resistance (R_{VEG}), but did not correlate with R_{ECO}.

On the other hand, the relative WUE_{ECO} showed highly significant correlations with the economic indices of tolerance to low nutrition and drought resistance. This indicates that the higher was the relative value of WUE_{ECO}, i.e. the lower was the low NPK-induced reduction in WUE_{ECO} and the higher was the drought-induced increase in WUE_{ECO}, the higher was the tolerance to both stress fators used in the study.

Combining ability for WUE

General combining ability (GCA) effects were highly significant for the variation in water use efficiency under all the three soil treatments (Table 4). A slightly enhanced significance of specific combining ability (SCA) effects for both the economic and vegetative measures of the efficiency was noticed only under stress conditions. Under all the soil treatments, the relative proportion of mean squares due to GCA effects was found to be higher than that of SCA effects. In comparison with the control conditions and/or a low NPK supply, however, the preponderance of GCA effects markedly declined under drought stress, as indicated by the considerably lower GCA/SCA ratios under drought.

As shown in Table 5, the applied stress conditions did not show any strong influence on parental GCA effects. Generally, consistency was apparent more in the sign and less in the magnitude of GCA values over all the soil treatments.

Table 4. Analysis of variance for combining ability in the vegetative (WUE_{VEG}) and economic (WUE_{ECO}) water use efficiency under the control conditions (C), low NPK nutrition (L) and drought stress (D)

Variation source	d.f.	Mean square					
		WUE_{VEG}			WUE_{ECO}		
		C	L	D	C	L	D
Hybrids	14	9.43**	12.47**	7.95*	26.75**	20.58**	22.29**
GCA	4	27.48**	35.48**	11.15*	75.18**	59.23**	43.97**
SCA	10	2.22	3.26*	6.67	7.37	5.12*	13.61*
Error	56	2.16	1.61	4.06	5.38	2.39	5.96
GCA/SCA		12.38	10.88	1.67	10.20	11.57	3.23

*, ** – significant at the P = 0.05 and P = 0.01 levels, respectively

Table 5. General (GCA) and specific (SCA) combining ability effects for the vegetative (WUE_{VEG}) and economic (WUE_{ECO}) water use efficiencies under the control conditions (C), low NPK nutrition (L) and drought stress (D)

Effect	WUE_{VEG}			WUE_{ECO}		
	C	L	D	C	L	D
GCA:						
Trumpf (Tr)	–0.14	0.05	–0.23	0.09	–0.16	0.68^{+}
Aramir (Ar)	–0.03	–0.50*	–0.66*	1.37**	0.59*	0.41
Menuette (Me)	0.61**	0.60**	0.48^{+}	$–0.57^{+}$	–0.20	–0.27
Lubuski 73 (Lb)	0.93**	1.23**	0.69*	1.28**	1.66**	1.01**
Luch 73 (Lu)	–1.37**	–1.39**	–0.28	–2.18**	–1.90**	–1.82**
SCA:						
F_2(Tr × Ar)	0.86	–0.03	–0.27	1.32	0.20	0.47
F_2(Tr × Me)	–0.70	–0.52	–1.52*	–0.02	0.72	–0.22
F_2(Tr × Lb)	–0.59	0.75^{+}	0.48	0.12	–1.56**	0.31
F_2(Tr × Lu)	–0.51	–1.57**	–0.33	0.23	–1.25*	–1.05
F_2(Ar × Me)	0.49	0.77^{+}	–0.69	0.82	–0.23	–1.28
F_2(Ar × Lb)	–0.47	0.56	0.52	–0.08	1.09^{+}	1.41
F_2(Ar × Lu)	0.16	0.27	–0.64	–0.25	0.69	1.55^{+}
F_2(Me × Lb)	0.17	–0.38	–0.79	1.31	0.38	1.41
F_2(Me × Lu)	0.56	–0.17	2.69**	1.83*	0.24	2.14*
F_2(Lb × Lu)	0.94^{+}	0.48	–0.17	0.27	1.16*	1.37

+, *, ** – significant at the P = 0.10, P = 0.05 and P = 0.01 levels, respectively

The highest GCA effects for both the WUE measures were exhibited by the Polish cv. 'Lubuski', while the more extensive Russian cv. 'Luch' showed the lowest GCA effects. Under all conditions, the ranking of parents for GCA was also generally consistent with the parental means for WUE (not all the data are shown in Table 1). For instance, the high-combiner 'Lubuski' displayed the highest efficiency of water use, while the low-combiner 'Luch' did not use water effectively under the experimental conditions.

The two Dutch cultivars exhibited different GCA effects. Cv. 'Aramir' tended to show a negative GCA for the vegetative measure of WUE, but did show a positive GCA for the economic WUE measure. In contrast, cv. 'Menuette' showed a positive GCA for the vegetative measure and a low negative GCA for the economic measure of WUE.

Generally, the soil treatments appeared to have a slightly stronger influence on the variation in SCA effects than on that in GCA. In some hybrid populations, e.g. in (Tr × Lb), (Ar × Me), (Ar × Lb), (Ar × Lu) or (Me × Lu), stress-induced changes in the magnitude and sign of SCA were observed, suggesting that SCA of some hybrids did interact with the stressed conditions. It is noteworthy that significant SCA effects were more frequently noticed under stresses than under optimal conditions. When comparing SCA of hybrid generations with parental GCA, in some crosses gene interactions may be detected. For instance, some importance of non-additive gene interactions for the economic WUE was indicated by the high SCA of the hybrid (Me × Lu) that originates from a cross between parents of low GCA.

Genetic components and heritability of WUE

Estimates of genetic components of the variation in the diallel set corroborate that additive (D) gene action was of major importance for the variance in water use efficiency (Table 6). Additive genes did not express any significance only for the vegetative measure of WUE under drought, where dominance components (H) were slightly more important. With this exception being suggestive for overdominance of genes, partial dominance of genes for WUE was indicated by $[0.25(H_1/D)]^{1/2}$ lower than 1.

Dominance components were of low significance for both the WUE measures only under both stress conditions. The values of H_1 tended to be somewhat larger than H_2, indicating unequal gene frequencies in the parents under stress. The negative F values found for the vegetative WUE under both stress conditions and for the economic WUE measure under a low NPK supply, suggest some unequality of gene frequencies with an excess of recessive over dominant alleles in the parents. Under control conditions, however, dominant alleles tended to exceed the recessive ones.

Both the WUE measures exhibited moderately high heritabilities. Under optimal conditions, the narrow-sense heritability values ranged between 0.64 and 0.69 for the economic and vegetative measures of WUE, respectively. However,

Table 6. Estimates of genetic components of variance, average degree of dominance ($(0.25H_1/D)^{½}$) and narrow-sense heritabilities (h^2_{NS}) of the vegetative (WUE_{VEG}) and economic (WUE_{ECO}) water use efficiency under the control conditions (C), low NPK nutrition (L) and drought stress (D)

Component	WUE_{VEG}			WUE_{ECO}		
	C	L	D	C	L	D
D	2.753**	2.521**	0.451	7.026**	4.910**	4.953**
F	1.215	–0.890	–0.498	1.307	–0.135	5.164
H_1	0.231	5.260^{+}	7.080^{+}	0.342	7.717^{+}	15.731^{+}
H_2	0.262	3.238^{+}	6.928^{+}	1.736	5.846^{+}	12.855*
h^2	0.382	0.009	0.240	14.098^{+}	0.948	17.139*
E	0.450	0.308	1.135	1.140	0.586	1.938
$[0.25(H_1/D)]^{½}$	0.145	0.722	1.982	0.110	0.627	0.891
h^2_{NS}	0.688	0.457	0.127	0.638	0.531	0.352

+, *, ** – significant at the P = 0.10, P = 0.05 and P = 0.01 levels, respectively

the heritabilities decreased to 0.53 and 0.46 under nutrient shortage and to 0.35 and 0.13 under drought stress.

As shortly summarized in Table 7, there were negative relationships between the mean parental efficiencies and the sum of array variance and parent-offspring covariance (Wr + Vr). The associations were highly significant for both the WUE measures under control conditions and for the economic WUE under limited nutrition. This suggests that the genes responsible for WUE in the investigated barley collection tended to be dominant.

Comparison of the order of dominance of the parents with their WUE means under various soil treatments (see also Table 1) indicated that the most efficient

Table 7. Correlation coefficients between the parental WUE means (Yr) and (Wr+Vr) for the economic and vegetative WUE depending on soil treatments and the order of dominance of the parents

Character	Soil treatment	r between Yr and (Wr+Vr)	Order of dominance of parents[a]
WUE_{ECO}	Control	–0.955**	Lb - Ar - Tr - Me - Lu
	Low NPK	–0.918*	Lb - Me - Ar - Tr - Lu
	Drought	–0.393	Lb - Me - Ar - Tr - Lu
WUE_{VEG}	Control	–0.948**	Lb - Me - Ar - Tr - Lu
	Low NPK	–0.282	Lb - Me - Lu - Ar - Tr
	Drought	–0.615	Lb - Ar - Tr - Me - Lu

*, ** – significant at the P = 0.10, P = 0.05 and P = 0.01 levels, respectively

[a] – see Table 1 for the symbol of parents

cv. 'Lubuski' exhibited the highest dominance, while the inefficient cv. 'Luch' possessed the most recessive genes.

Discussion

In the study on spring barley of a local breeding collection, a considerable genetic variation in the efficiency of water use (WUE) by the vegetative and generative plant tissues was evident under all the soil treatments used. Generally, the limited NPK nutrition and low soil moisture indicated different effects on WUE. Nutrient shortage caused a 3-6 % reduction in WUE, whereas its 9-11.5% increase was observed in plants grown under soil drought. Such effects of the environmental factors on WUE are in consistency with data previously reported for wheat (HEITHOLT 1989, Van den BOOGAARD 1995, MENDEL, GÓRNY 1996).

The results confirmed that the variation in WUE was polygenic in nature. Both the vegetative and economic WUE measures in barley exhibited a relatively advantageous mode of inheritance in which additive gene effects accounted for a major portion of the genetic variation. Thus, selection for an improved WUE would be effective among materials presently utilized by local breeders. It should be noted, however, that only additive gene action was involved in the inheritance of WUE under optimal conditions. The additive genes expressed their prevailing importance also under NPK-limited nutrition. However, the consistent preponderance of additive gene action for WUE appeared to decrease under soil drought. This effect was accompanied by a higher degree of dominance of genes and considerably lower heritabilities of WUE measures. This suggests that an improvement in this character could be more easily achieved in barley through conventional selection procedures performed under conditions without water stress.

Depending on the increased importance of SCA, i.e. non-additive gene effects under water- and nutrition-stressed conditions, selection for a high WUE in spring barley under unfavourable conditions should be more effective when postponed to later generations and performed in less favourable environments. Such a conclusion seems to be in accordance with that reported for cowpea by MENÉNDEZ and HALL (1995). The authors demonstrated that due to the low realized heritability of carbon isotope discrimination (Δ), i.e. of the character that negatively correlated with WUE, selection for a high transpiration efficiency in early generations may not be as efficient as family selection in later generations.

Numerous studies on cereals indicated that stress-induced genotypically specific alterations in the partitioning and redistribution of dry matter and plant assimilates through vegetative and reproductive plant organs may have an adaptive value (PALTA et al. 1994, EHDAIE, WAINES 1996, FATHI et al. 1997). The significant correlations between the harvest index and/or its stress-induced relative changes, relative WUE_{VEG}, grain yield and the stress tolerance indices that were noticed in the study on barley (Table 3), are in accord with the above-mentioned findings. However, no correlations were identified in barley between water use efficiency under stress conditions and stress tolerance indices. As pointed by BLUM (1996), the water use efficiency, a basically constitutive plant characteristic associated with the potential yield or the potential dry matter production, is not related to drought adaptation and drought resistance. This appears to be corroborated by the findings of READ and co-workers (1993) who found in crested wheatgrass that selection for a low carbon isotope discrimination, i.e. for a high WUE, did not positively alter the drought resistance of the species. No correlation between WUE and drought resistance indices was also noticed in a collection of old and modern cultivars of winter wheat (MENDEL, GÓRNY 1996), and among selected lines and cultivars of oat (GÓRNY, SZOŁKOWSKA 1996).

Conclusions

Additive gene effects were mainly responsible for the variation in WUE in the studied diallel hybrids of spring barley. A lowly significant contribution of non-additive gene action was only observed under the reduced NPK-nutrition and simulated soil drought. Although the implications of the results for barley breeders can be fully assessed when also data concerning WUE under field conditions are complete, we conclude that the major contribution of gene additivity and the consistency between GCA and parental means should facilitate selection efforts to enhance WUE in barley. As far as the examined lines derived from local collections of spring barley are concerned, the prevailing importance of additive genes and the obtained narrow-sense heritabilities of WUE appear to be high enough to warrant selection responses already at conventional selection procedures performed under optimal environmental conditions or moderately limited soil fertility. However, because of the stress-induced decrease of the heritability and the enhanced importance of non-additive effects under drought such a selection method for WUE may be less effective in water-limited environments.

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