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WATER USE EFFICIENCY AND RESPONSE TO NUTRIENT SHORTAGE IN MATURE PLANTS OF *Aegilops* AND *Triticum* SPECIES

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Introduction

Wild and primitive *Aegilops* and *Triticum* species are widely distributed over diverse habitats that considerably differ in soil and climatic factors. Since the most of morpho-physiological variation among them was probably induced by natural selection, these species are commonly believed to posses better adaptation to biotic and abiotic stresses. In fact, these wild progenitors and primitive taxa appear to be a potential and still not fully recognised source of novel genes for the resistance to fungal diseases and/or tolerance to Al, low temperatures and salinity [SEARS 1982; DVOŘÁK, KNOTT 1990; FORSTER 1992; DVOŘÁK et al. 1994; FRIEBE et al. 1996; ŁUKASZEWSKI 1997].

However, extremely little is known on their efficiency of soil resources use and adaptation to such abiotic stresses like water and nutrient shortages. As far as we know, only WAINES et al. [1993] comparing the carbon isotope discrimination (i.e. a trait that negatively correlates with the efficiency of water use) in diploid wheat species observed an enhanced water use efficiency in *Aegilops tauschii* (genome D) and *Ae. sharonensis* (genome S). AL HAKIMI et al. [1996] reported that the primitive tetraploid *T. polonicum* may be used to improve water use efficiency in durum wheat. Other available data concern nitrogen and phosphorus efficiency at the juvenile growth stages only, but the reported results may lead one to conflicting conclusions [BATTEN 1986; GÓRNY 1997; ČERNOHORSKA et al. 1999; NÁTR et al. 1999].

The aim of the study done till full plant maturity was (a) to evaluate interspecific differences in water use efficiency and response to reduced NPK nutrition among *Aegilops* and *Triticum* accessions, (b) to discriminate for genome and ploidy effects on the variation, and (c) to identify potential donors of efficiency and adaptation.

Materials and methods

Twenty inbred lines representative for the wild, primitive and cultivated *Aegilops* and *Triticum* species of different genomic constitution, ploidy level and worldwide origin (Table 1) were investigated in a factorial experiment. The most

Table 1; Tabela 1

Mean genotypic (species) and nutrition effects on the variation in plant yielding, water use efficiency and tolerance to nutrient shortage

Przeciętny wpływ genotypu (gatunku) i nawożenia na zmienność w plonowaniu roślin, efektywności wykorzystania wody i tolerancji obniżonego nawożenia

Variation source (ploidy, species, nutritions) Źródło zmienności (ploidalność, gatunek, nawożenie)		Short name* Skrót nazwy*	Genome Genom	Form* Forma*	Vegetative dry matter Sucha masa wegetatywna	Grain dry matter Sucha masa ziarna	Harvest index Indeks plonu	Water transpired Ilość wytranspirowanej wody	Water use efficiency Efektywność wykorzystania wody		Tolerance Tolerancja	
									WUEveg**	WUEgen**	Tveg**	Tgen**
					g	g	%	dm³	mg·mol⁻¹			
Genotypes (species); Genotypy (gatunki):												
2×	*Triticum beoticum*	beot	A^b	w	58.5	26.4	30.8	35.3	29.9	13.3	0.92	0.89
	T. monococcum cv. Einkorn	mono	A^b	c	51.7	29.1	36.0	35.1	27.1	14.8	1.11	0.87
	T. urartu	urar	A^u	w	50.3	15.2	22.9	29.6	30.5	9.1	0.73	0.69
	Aegilops speltoides	spel	S^s (B)	w	60.3	14.6	19.2	32.2	33.9	8.1	0.98	0.81
	Ae. sharonensis	shar	S^{sh} (B)	w	45.5	13.6	22.9	24.5	33.1	9.8	0.77	0.77
	Ae. tauschi 1	tau1	D	w	46.6	21.1	31.2	23.4	36.0	16.3	0.97	1.01
	Ae. tauschi 2	tau2	D	w	48.7	24.5	33.3	20.0	44.1	22.0	1.19	1.06
4×	*T. turgidum* cv. Alaska	turg	BA	c	64.5	45.6	41.8	33.5	34.5	24.8	0.79	0.94
	T. durum cv. Langdon	duru	BA	c	52.1	40.5	43.8	32.5	29.7	23.2	0.90	0.94
	T. carthlicum	cart	BA	p	69.4	48.0	40.8	39.7	31.8	21.9	1.09	1.08
	T. dicoccoides	dico	BA	w	80.9	45.6	36.1	41.8	35.0	19.7	1.04	1.11
	T. polonicum	polo	BA	p	54.4	35.4	39.1	28.5	34.8	22.5	1.07	1.04
	T. timopheevii	timo	GA	w/p	76.0	37.8	33.2	39.4	34.9	17.3	1.24	1.16
	T. araraticum	arar	GA	w	52.4	19.6	26.6	25.0	38.1	13.8	0.92	0.75

6×	*T. zhukovskyi*	zhuk	GAA	w/p	67.8	40.9	37.5	31.1	39.7	23.8	1.08	1.05
	T. sphaerococcum	spha	BAD	w/p	51.0	40.4	44.1	25.6	36.0	28.4	1.10	1.09
	T. vavilovii	vavi	BAD	w/p	73.5	36.5	32.9	30.5	44.1	21.5	1.12	1.00
	T. aestivum cv. Grana	aes1	BAD	c	47.9	44.2	48.0	29.9	28.9	26.6	1.08	1.11
	T. aestivum cv. Dańkowska Sel.	aes2	BAD	c	70.0	41.9	37.6	34.0	37.0	22.4	0.95	1.08
	T. aestivum cv. Graniatka	aes3	BAD	c	77.5	50.0	39.1	40.6	34.7	22.3	0.96	0.97
LSD$_{0.05}$; NIR$_{0,05}$					6,1	3.4	2.3	2.8	2.3	1.2	–	–
Nutritions; Poziomy nawożenia:												
High NPK; Wysokie NPK					69.1	39.6	35.8	37.6	33.5	19.0	–	–
Low NPK; Niskie NPK					50.8	27.5	33.9	25.6	35.9	19.1	–	–
LSD$_{0.05}$; NIR$_{0,05}$					1.9	1.1	0.7	0.9	0.7	*ns*	–	–

* – shortened names used in Fig. 1; wild (w), primitive (p) and cultivated (c) form of a species; name of species according to van Slageren's (*Aegilops*) and Dorofeev's (*Triticum*) classifications; skróty nazw stosowane na rys. 1; dzika (w), prymitywna (p) i uprawna (c) forma gatunku; nazwy gatunkowe zgodnie z klasyfikacją van Slageren'a (*Aegilops*) i Dorofeev'a (*Triticum*)

** – the vegetative (WUEveg, Tveg) and generative (WUEgen, Tgen) indices of water use efficiency and stress tolerance; wegetatywne (WUEveg, Tveg) i generatywne (WUEgen, Tgen) indeksy efektywności wykorzystania wody i tolerancji stresu of these accessions were kindly supplied for our study by Dr. Wilson, Kansas State University, Manhattan, USA, Dr. H. Bockelman, National Plant Germplasm Resources Lab., USDA-ARS, Beltsville, USA and Prof. G. Stefanowska, Agricultural University, Lublin, Poland. The three cultivars Graniatka, Dańkowska Selekcyjna and Grana of the hexaploid winter wheat were released by Polish breeding institutions in 1912, 1956 and 1970, respectively.

The experiment was arranged in a randomized design with twenty genotypes, two NPK-nutrition levels, three-pot replications and 12 plants per pot. Using the procedure described elsewhere [e.g. GÓRNY 1999], plants were grown during November-May/June in a partly regulated greenhouse, in double-walled Kick-Brauckman's pots (9 dm^3) filled with a mechanically prepared and sieved soil medium (pH 6.8) of optimal concentration of micro-elements and low macro-nutrient content (35 N : 54 P : 95 K, mg·dm^{-3}). The concentration of the plant-available N, P and K in the soil was monitored by a modified Spurway's method [NOWOSIELSKI 1972]. Soil probes were extracted with an acetic acid 0.03 mol·dm^{-3} solution in the ratio of soil to solution of 1 : 10 (w/v). After the sowing (end of November) and the 1st leaf emergence, the soil surface was covered with a thin layer (about 2.5 cm) of pure perlite to eliminate soil water evaporation, and the juvenile plants of all genotypes were vernalized in the pots at 1–5°C for eight winter weeks under natural lighting. During further growth phases, plants were grown under 10–28/6–15°C mean day/night temperatures, 55–85% relative humidity and natural lighting prolonged to 10–18 h using an artificial lighting system (an enhanced density of sodium- and mercury-lamps (both 400 W), at least 300–800 μmol·m^{-2}·s^{-1} PAR energy at the plant level), all varying in relation to the growth stage and photoperiod cycling.

Two NPK nutrition levels were used. Plants were fertilised with water-soluted nutrients at the high (165 N : 140 P : 200 K, mg·dm^{-3}) and low (95 N : 70 P : 105 K) rates. N was added in three (before sowing, tillering, late booting), while P and K – in two sub-portions (before sowing, tillering). During the whole plant vegetation, the initial soil moisture was kept constant (70% of field capacity). Total amount of water transpired (WT) was recorded by frequent (at least 3–7 times per week) weighing of pots and addition of deionized water into pots.

Plants were hand-harvested at the full maturity. Harvested materials (all plants in replication) were divided on straws, leaves and grains. Because of rachis shattering in the wild species, special care was taken to harvest all subsequently maturing spikelets. To estimate the real grain weight in the wild accessions, rachis and glumes of each spikelet were separated from grains by hand. Dry matter (DM) of the vegetative parts and grains was determined by oven-drying (72 h, 65°C). Vegetative (WUEveg) and generative (WUEgen) indices of water use efficiency were estimated as the dry matters of the vegetative parts and grains produced per mol of water transpired, respectively. Vegetative and generative indices of tolerance (Tveg, Tgen) to nutrient shortage were determined using the equation: (DM of a genotype at reduced NPK/DM of a genotype at high NPK)/(general mean DM at reduced NPK/general mean DM at high NPK). Standard statistic methods were used for data evaluation. After the analysis of variance, comparisons among means were made using the multiple Duncan's range test.

Results and discussion

There was a broad genotypic variation in the components efficiency and response to limited nutrition among the studied *Aegilops* and *Triticum* accessions. Means for major morpho-physiological components of water use efficiency and response indices are summarized in Table 1 to show general nutrition and genotype (species) effects on plant performance. On average, nutrient shortage caused 26.5–32 % depression in the vegetative and grain dry weights and the amount of water transpired. Efficiency of water use in vegetative mass formation (WUEveg) significantly enhanced by about 7% under NPK shortage, while no significant alterations were noticed in the generative WUE measure (WUEgen).

In the present study, the diploid *Triticum* and *Aegilops* species with A and S (B) genome were the least efficient in water use and did not tolerate nutrient shortage. However, accessions of the diploid wheat progenitor with D genome, *Ae. tauschii*, were found to be at least moderately tolerant, and to utilise water more efficiently than did the other diploids. These observations on WUE correspond well with data reported by WAINES et al. [1993] who noticed usually lower values of carbon isotope discrimination Δ (i.e. likely a higher WUE) in *Ae. tauschii* accessions than in other diploids. On the other hand, an enhanced WUE (i.e. a low Δ) of the B genome species previously reported by RAFI and WAINES [1998] could not be confirmed by the results of our study.

Except for *T. araraticum*, all the wild/primitive tetraploids *T. carthlicum, T. dicoccoides, T. polonicum* and *T. timopheevii* exhibited much higher tolerance to reduced NPK nutrition in comparison with the tetraploid cultivars of turgidum (cv. Alaska) and durum wheat (cv. Langdon). However, all these wild/primitive species did not utilise water more efficiently than did the both cultivated tetraploids. Among the hexaploid wheats, the Chinese accession of *T. sphaerococcum* and the relatively new Polish cv. Grana were the most efficient in water use and showed the highest stress tolerance.

Table 2; Tabela 2

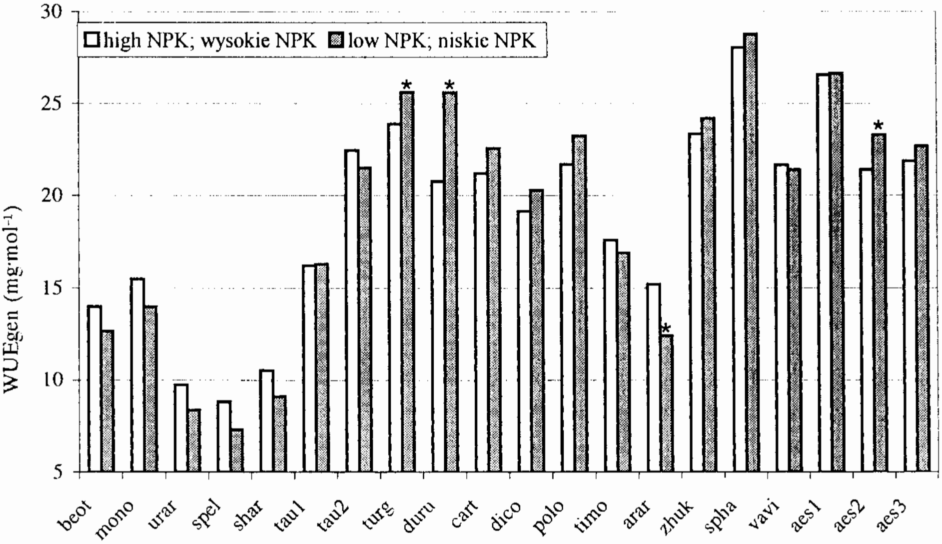
Analysis of variance (mean square values) and estimated broad-sense heritabilities for the major components of water use efficiency (WUE)

Analiza wariancji (wartości średnich kwadratów) i oszacowane wartości odziedziczalności w szerokim sensie dla głównych komponentów efektywności wykorzystania wody (WUE)

Features; Cechy	Mean squares; Średnie kwadraty				Heritability Odziedziczalność
	nutrition nawożenie (N)	genotypes genotypy (G)	N × G	error błąd	
Vegetative DM; Sucha masa wegetatywna *(g)*	10021.1**	793.5**	86.8**	28.1	0.728
Grain DM; Sucha masa ziarna (g)	4397.1**	862.5**	18.3**	8.5	0.924
Harvest index; Indeks plonu *(%)*	99.7**	351.2**	8.4*	4.2	0.912
Water transpired; Wytranspirowana woda (dm^3)	4325.4**	220.2**	20.8**	5.8	0.768
Vegetative WUE; Wegetatywne WUE ($mg \cdot mol^{-1}$)	181.9**	123.4**	11.4**	4.2	0.751
Generative WUE ($mg \cdot mol^{-1}$); Generatywne WUE	0.8	211.1**	4.5**	1.1	0.940

*,** – significant at the P = 0.05 and P = 0.01 levels, respectively; kolejno, istotne na poziomie P = 0,05 i P = 0,01

Results of the analysis of variance confirmed the considerable genotype (species)- and nutrition-dependent variation of most features (Table 2). No significant nutrition effects were found only for the generative WUE measure. For all features, however, the examined genotypes did significantly interact with nutrition levels, but the interspecific differentiation was relatively stable under conditions used, and distinct crossover N × G interactions were rarely noticed for the WUE measures (Fig. 1). There was a tendency that WUEgen in wild accessions usually decreased, while in cultivated and primitive species this efficiency measure enhanced under NPK shortage. These stress-induced alterations in WUEgen were significant only in the cultivated *T. turgidum, T. durum* and *T. aestivum* cv. Dańkowska Sel. (increase) and the wild *T. araraticum* (decrease).



* – significantly (P = 0.05) different from the mean value at high NPK; istotnie (P = 0,05) różne od wartości średniej przy wysokim NPK

Fig. 1. Efficiency of water use in grain mass formation (WUEgen) in *Aegilops* and *Triticum* species under high and low nutrition

Rys. 1. Efektywność wykorzystania wody w formowaniu masy ziarna (WUEgen) u gatunków *Aegilops* i *Triticum* przy wysokim i niskim nawożeniu

Considering the relative importance of variance components, experimental error for the vegetative features and amount of water transpired was much higher (12.4–16% of the total variance) than that for the dry matter, harvest index and generative WUE (3–6.6%). Similarly, N × G interaction effects for vegetative features contributed to 9.1–11.2%, while those for the generative ones – only to 2.1–3% of the total variance. In consequence, operative heritabilities of the former features were much lower (0.73–0.77) than those of the letter ones (0.91–0.94).

At the examined maturity stage, differences between species were markedly dependent upon the ploidy levels, identity of genomes present and on interactions between them. Averaged genome and ploidy effects on major WUE com-

Table 3; Tabela 3

Averaged genome and ploidy effects on the expression of major WUE components under reduced NPK nutrition and tolerance to nutrient shortage

Przeciętny wpływ genomu i poziomu ploidalności na ekspresję głównych komponentów WUE przy obniżonym nawożeniu i na poziom tolerancji obniżonego nawożenia

Genome/ploidy Genom/ploidalność	Vegetative dry matter Sucha masa wegetatywna	Grain dry matter Sucha masa ziarna	Harvest index; Indeks plonu	Water transpired; Ilość transpirowanej wody	Water use efficiency Efektywność wykorzystania wody		Tolerance; Tolerancja	
					WUEveg**	WUEgen**	Tveg**	Tgen**
	g	g	%	dm^3	$mg \cdot mol^{-1}$			
Genomes; Genomy:								
A	42.9	17.3	27.9	26.0	29.7	11.7	0.918	0.817
S (B)	41.8	10.1	19.9	22.4	33.3	8.2	0.877	0.791
D	42.0	19.1	31.2	18.3	41.6	18.9	1.076	1.036
BA	53.8	35.8	40.1	27.8	34.8	23.5	0.978	1.024
GA	57.3	23.6	28.0	27.7	37.7	14.7	1.077	0.956
GAA	60.1	34.6	36.5	25.7	42.1	24.2	1.083	1.053
BAD	55.3	35.8	39.7	26.5	37.6	24.6	1.044	1.049
Ploidy; Ploidalność:								
diploids; diploidy	42.3	15.7	26.5	22.8	34.1	12.7	0.951	0.872
tetraploids; tetraploidy	54.8	32.3	36.6	27.8	35.6	21.0	1.006	1.005
hexaploids; heksaploidy	56.1	35.6	39.2	26.4	38.4	24.5	1.051	1.050

** – see Table 1 for trait explanations; objaśnienia cech patrz tabela 1 ponents and stress tolerance are presented in Table 3. In general, both WUE components and stress tolerance tended to enhance with increased ploidy levels. The diploid species were markedly less efficient in water use and showed much lower tolerance to limited NPK supply than the hexaploid wheats. A similar pattern of variability in the efficiency of nitrogen and phosphorus utilisation was observed previously at the juvenile growth stage [GÓRNY 1997]. However, no close consistency with the juvenile parameters was evident for tolerance indices. At the juvenile growth stage, the Sitopsis group of diploid *Aegilops* (genome S) was found to be the most tolerant to N and P limitations, while juvenile plants of hexaploid wheats (including cv. Grana) showed the lowest tolerance. This is in some opposition to tolerance indices observed in these two groups of species at the maturity stage. Thus, genotype-growth stage interactions may affect the variation in tolerance to limited nutrition among the wild and cultivated wheat species, and great care is needed when extrapolating observations of vegetative growth stages for the whole plant vegetation.

Opportunities for further breeding progress in wheat adaptation to less favourable environmental conditions appear to be dependent upon the access to a possibly wide genetic variation of components of such adaptation. According to common opinions, the relatively limited gene pool present in locally collected cultivars and breeding lines, may be less attractive for wheat breeders who start to select for improved use efficiency and better adaptation. This germplasm was usually developed under more and more favourable conditions of well-managed breeding stations with conscious man-made selection forces for improved distribution of assimilates to generative organs, higher harvest index and yield potential [EVANS, DUSTONE 1970; AUSTIN et al. 1986]. This may be a reason to believe, therefore, that depending upon likely lower pressure of environmental stresses on materials selected in such locations, the wheat genotypes available in modern breeding collections may be less adapted to unfavourable cultivation conditions than the wild or primitive accessions.

The above-mentioned work hypothesis was generally corroborated by the present results, but not at the whole. As presented in Table 1, no diploids with A and S (B) genome were found to be tolerant to nutrient shortage, an only the *Ae. tauschii* accessions (donors of the wheat D genome) did tolerate such stress. Except for the non-tolerant *T. araraticum* (genome GA), all the wild or primitive tetraploids with BA genome exhibited much higher tolerance than the cvs. Alaska (*T. turgidum*) and Langdon (*T. durum*). In the study, the primitive *T. timopheevii* (genome GA) was distinguished by the highest tolerance. Almost all hexaploid wheats were tolerant to NPK shortage, and the lowest stress-induced depressions in the vegetative and grain mass were observed in the Chinese *T. sphaerococcum* and the Polish cv. Grana. This is noteworthy, however, that the cv. Grana, the first modern Polish cultivar of intensive type was released in 1971 and distinguished by a relatively high and stable yielding, predominated the local wheat production for many years. In some regions of the country, Grana was desired for cultivation by farmers even in 1990's.

Conclusions

As far as concerning the examined collection of species, we conclude that there is a broad interspecific variation in the water use efficiency and response to limited nutrition among *Aegilops* and *Triticum* accessions. At least partially this variation may be explained with pressions acting at nature selection or man-made selection and domestication history. This would give an alternate chance to local wheat breeders dealing with an improved adaptation to less favourable fertilisation. Obtained results suggest that a search for novel variation in water use efficiency (UE) and enhanced tolerance to nutrient shortage among wild or primitive wheats may be essential for local wheat breeders. The tetraploids *T. carthlicum, T. dicoccoides* and *T. timopheevii,* the hexaploid *T. sphaerococcum* and partially also the diploid *Aegilops tauschii* (donor of wheat D genome) seem to be the most promising sources of stress tolerance. Among all wild and primitive taxa, however, only the *T. sphaerococcum* appears to be a valuable donor of improved WUE. Heritability of this feature is high enough to facilitate such selection efforts. However, since genotype-stage and genotype-nutrition interactions may affect the interspecific variation, testing till full plant maturity over diverse levels of soil fertility would be necessary for a precise discrimination of the most water efficient genotypes.

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Key words: *Aegilops, Triticum,* genetic variation, water use efficiency, reduced nutrition, stress tolerance

Summary

A factorial experiment was performed to evaluate whether wild and primitive *Aegilops* and *Triticum* species may be used in wheat breeding as donors of an improved water use efficiency (WUE) and/or tolerance to nutrient shortage. Seventeen lines representative for *Aegilops* and *Triticum* species of different origin, ploidy level and genomic structure were compared with three local cultivars of hexaploid wheat *T. aestivum.* The genotypes were grown till maturity in experimental pots (9 dm^3) under high and reduced NPK nutrition. There was a broad genetic variation in the response to nutrient shortage and efficiency of water use in the vegetative and grain mass formation. The variation was dependent upon species, ploidy level and genome present. Results suggest that a search for enhanced tolerance and novel variation in WUE among wild or primitive wheats may be essential for wheat breeders. The tetraploids *T. carthlicum, T. dicoccoides* and *T. timopheevii* and the hexaploid *T. sphaerococcum* were found to be the most promising potential sources of stress tolerance.

However, only the primitive *T. sphaerococcum* appeared to be a valuable donor of improved WUE. Despite a high operative heritability of WUE, testing till plant maturity over diverse levels of soil nutrient status would rather be necessary for a precise discrimination of the most efficient genotypes as indicated by the genotype-stage and genotype-nutrition interactions.

EFEKTYWNOŚĆ WYKORZYSTANIA WODY I REAKCJA NA NIEDOBÓR SKŁADNIKÓW POKARMOWYCH U ROŚLIN GATUNKÓW *Aegilops* I *Triticum* W STADIUM DOJRZAŁOŚCI

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Słowa kluczowe: *Aegilops, Triticum,* efektywność wykorzystania wody, obniżone nawożenie, tolerancja stresu, zmienność genetyczna

Streszczenie

Przeprowadzono doświadczenie wazonowe w celu określenia czy dzikie i prymitywne gatunki *Aegilops* i *Triticum* mogą być wykorzystane w hodowli pszenicy jako donory efektywniejszego wykorzystania wody (WUE) i/lub tolerancji na niedobór składników pokarmowych. Siedemnaście linii reprezentujących gatunki *Aegilops* i *Triticum* o różnym pochodzeniu, ploidalności i strukturze genomowej porównano z trzema krajowymi odmianami pszenicy heksaploidalnej *T. aestivum*. Genotypy rosły do stadium dojrzałości w wazonach doświadczalnych (9 dm^3) przy wysokim i obniżonym nawożeniu NPK. Obserwowano szeroką zmienność genetyczną w reakcji na obniżone nawożenie i efektywności wykorzystania wody w tworzeniu masy wegetatywnej i plonu ziarna. Zmienność ta była zależna od gatunku, poziomu ploidalności i obecności danego genomu. Wyniki sugerują, że poszukiwanie zwiększonej tolerancji i nowej zmienności w WUE wśród dzikich i prymitywnych pszenic dla celów hodowlanych jest uzasadnione. Tetraploidalne *T. carthlicum, T. dicoccoides* i *T. timopheevii* oraz hexaploidna *T. sphaerococcum* były potencjalnie najlepszymi źródłami tolerancji stresu. Jednak tylko prymitywna *T. sphaerococcum* okazała się cennym źródłem zwiększonej WUE. Obserwowane interakcje typu genotyp-stadium i genotyp-nawożenie wskazują, że pomimo wysokiej odziedziczalności WUE, dla precyzyjnego doboru najefektywniejszych genotypów raczej niezbędne będzie testowanie roślin uprawianych aż do stadium dojrzałości przy odmiennych poziomach żyzności gleby.

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