

Water and Nutrient Use Efficiency in Diploid, Tetraploid and Hexaploid Wheats

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Abstract

Three diploid (*Triticum boeoticum*, AA; *Aegilops speltoides*, BB and *Ae. tauschii*, DD), two tetraploid (*T. dicoccoides*, AABB and *T. dicoccon*, AABB) and one hexaploid (*T. vulgare*, AABBDD) varieties of wheat, which are very important in the evolution of wheat were chosen in this study. A pot experiment was carried out on the wheat under different water and nutrient conditions (i) to understand the differences in biomass, yield, water use efficiency (WUE), and nutrient (N, P and K) use efficiency (uptake and utilization efficiency) among ploidies in the evolution of wheat; (ii) to clarify the effect of water and nutrient conditions on water and nutrient use efficiency; and (iii) to assess the relationship of water and nutrient use efficiency in the evolution of wheat. Our results showed that from diploid to tetraploid then to hexaploid during the evolution of wheat, both root biomass and above-ground biomass increased initially and then decreased. Water consumption for transpiration decreased remarkably, correlating with the decline of the growth period, while grain yield, harvest index, WUE, N, P and K uptake efficiency, and N, P and K utilization efficiency increased significantly. Grain yield, harvest index and WUE decreased in the same order: *T. vulgare* > *T. dicoccon* > *T. dicoccoides* > *Ae. tauschii* > *Ae. speltoides* > *T. boeoticum*. Water stress significantly decreased root biomass, above-ground biomass, yield, and water consumption for transpiration by 47–52%, but remarkably increased WUE. Increasing the nutrient supply increased wheat above-ground biomass, grain yield, harvest index, water consumption for transpiration and WUE under different water levels, but reduced root biomass under drought conditions. Generally, water stress and low nutrient supply resulted in the lower nutrient uptake efficiency of wheat. However, water and nutrient application had no significant effects on nutrient utilization efficiency, suggesting that wheat nutrient utilization efficiency is mainly controlled by genotypes. Compared to the other two diploid wheats, *Ae. squarrosa* (DD) had significant higher WUE and nutrient utilization efficiency, indicating that the D genome may carry genes controlling high efficient utilization of water and nutrient. Significant relationships were found between WUE and N, P and K utilization efficiency.

Key words: diploid; evolution; hexaploid; nutrient uptake efficiency; nutrient utilization efficiency; tetraploid; water use efficiency; wheat.

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Species of wheat are classified according to the number of chromosomes found in the vegetative cell. They are divided into three series: the diploid, or einkorn, containing 14 chromosomes; the tetraploid, or emmer, containing 28 chromosomes; and the hexaploid, containing 42 chromosomes (Gill et al. 1991). Wheat species crossbreed relatively frequently in nature (Harris 1990). The selection of the best varieties of wheat for domestication took place over many centuries in many regions. Today, only varieties of common, club and durum wheats are of commercial importance, but other species are still grown to suit local conditions and provide essential stock for formal breeding programs (Talbert et al. 1991). Remains of both emmer and einkorn wheat have been found by archaeologists working on sites in the Middle East dating from the 7th millennium BC. Emmer was grown in predynastic Egypt, and in prehistoric Europe it was grown in association with barley, einkorn, and club wheats. Bread wheat was identified at a 6th-millennium BC site in southern Turkestan, and hexaploid wheat was found at Knossos in Crete (Harlan 1987). According to the regions in which they are grown, certain types of wheat are chosen for their adaptability to altitude, climate and yield. The common wheats grown in China, the USA and Canada are spring and winter wheat, planted either in the spring for summer harvest or in the fall for spring harvest. The color of the grain varies from one type to another; white grains are mostly winter wheats, while red ones are spring wheats. Closely related to the common wheats are the club wheats, which have especially compact spikes, and spelta, in which the glumes (reduced, scale-like leaves) tightly enclose the grains. Durum wheat (Latin durum) is so called because of the hardness of the grain. It is grown in north to central regions of the USA. Compared with rice, all kinds of wheat seem to be distributed in water-limited areas (Deng et al. 2005).

Wheat, one of the most important crops in the world, is mainly cultivated in arid and semiarid areas, and is always suffering from water and nutrient deficiency. Soil water and nutrients are the two most important abiotic factors limiting wheat production and yield stability (Fischer and Turner 1978; Latiri-Souki et al. 1998; Shan 1998; Deng et al. 2003). Wheat water use efficiency (WUE) in dryland is lower than that in irrigated land (Deng et al. 2006). Carrying out breeding schemes increasing wheat water and nutrient use efficiency may be the best approach for improving wheat yield in arid areas (Shan 1985). In the evolution of wheat, there are lots of wheat genotypes that differ in their drought resistance and nutrient use (Zhang 2001), and these wheat evolution materials may be valuable and readily accessible sources of new genetic diversity for wheat improvement (Valkoun 2001). In the past decades, plant physiologists have carried out many studies on wheat evolution materials. With the increment of chromosome ploidy from diploid to hexaploid in the evolution of wheat, wheat yield and harvest index increased significantly (Evans and Dunstone 1970;

Bamakhramah et al. 1984; Batten 1986). However, rates of net photosynthesis of the flag leaves were in general highest for the diploid species, intermediate for the tetraploid species and lowest for *Triticum aestivum* (hexaploid) (Austin and Morgan 1982). Zhang and Shan (1997) found that water conditions affect the decreasing order of flag leaf WUE of different ploidy levels, which is hexaploid > tetraploid > diploid under irrigation, but tetraploid > hexaploid > diploid under water stress. Consistent reports exist on wheat nitrogen use efficiency that increased from diploid to tetraploid then to hexaploid (Liu et al. 2002; Li et al. 2003), but not for phosphorus efficiency (Batten 1986; Li et al. 2003).

Environmental factors, such as water and nutrient supply in the soil significantly affect plant water and nutrient use characteristics (Papakosta and Gagianas 1991; Latiri-Souki et al. 1998; Timsina et al. 2001; He et al. 2002; Deng et al. 2003). However most previous investigations into water and nutrient use efficiencies on wheat evolution materials are based on single water or single nutrient treatment, and relatively little information concerning the interactive effects of nutrient and water availability when imposed in combination is available. So, in this study, we selected six wheat evolution species, including three diploid (*T. boeoticum*, *Ae. speltoides* and *Ae. tauschii*), two tetraploid (*T. dicoccoides* and *T. dicoccon*) and one hexaploid (*T. vulgare*) wheat, to study water and nutrient use efficiency under different water and nutrient conditions with the following objectives: (i) to understand the differences in biomass, yield, water use efficiency, and nutrient use efficiency among ploidy levels in the evolution of wheat; (ii) to clarify the effect of soil water and nutrient conditions on them; and (iii) to assess the relationship of water and nutrient use efficiency in the evolution of wheat.

Results

Wheat biomass and grain yield

ANOVA showed that the effects of genotype (G) and water supply (W) on root and above-ground biomass were different significantly ($P < 0.01$). Effects due to nutrient application (Nt) were significant for above-ground biomass ($P < 0.01$) and root biomass ($P < 0.05$). G × W were significant for root biomass ($P < 0.01$) and above-ground biomass ($P < 0.05$), and W × Nt interaction were significant for both at the 0.01 level. However, G × Nt and G × W × Nt interaction were not significant for both. All of three main factors (G, W and Nt) and their interaction were significant for wheat grain yield and harvest index (HI) ($P < 0.01$).

Values of root biomass, aboveground biomass, grain yield and HI for every treatment are shown in Table 1. With the evolution of wheat from diploid to tetraploid then to hexaploid, root

and above-ground biomass were all increased initially and then decreased, but grain yield and HI increased significantly. For diploid, tetraploid and hexaploid wheats, root biomasses were 3.0, 4.5 and 3.0 g/pot, above-ground biomass 23.4, 33.9 and 31.1 g/pot, grain yield 1.9, 6.4 and 9.7 g/pot, and HI 8.7, 19.1 and 29.9%. Remarkable differences existed among different ploidies for above-ground biomass, grain yield and HI. Mean values of root biomass for six wheat genotypes decreased in this order: *T. dicoccon* > *T. dicoccoides* > *Ae. speltooides* > *T. vulgare* > *Ae. tauschii* > *T. boeoticum*. The decreasing order for above-ground biomass was *T. dicoccon* > *T. dicoccoides* > *T. vulgare* > *Ae. speltooides* > *Ae. tauschii* > *T. boeoticum*, and that for grain yield and HI was in the same: *T. vulgare* > *T. dicoccon* > *T. dicoccoides* > *Ae. tauschii* > *T. boeoticum* > *Ae. speltooides*.

It could be obtained from Table 1 that water stress significantly decreased root biomass, above-ground biomass and grain yield of different wheat genotypes by 30–64%, 27–45% and 36–59% (except the grain yield of *T. boeoticum*), respectively. And *T. vulgare* (6n) was the one whose above-ground biomass and grain yield were reduced most by water stress among six genotypes. Under wet conditions, high nutrient treatment of different wheat genotypes had more root biomass, above-ground biomass and grain yield than low nutrient treatment by 7–54%, 18–75% and 13–63% (except the grain yield of *T. boeoticum*). Under water stress, high nutrient supply reduced root biomass of different wheat species by

3–38%, but increased above-ground biomass and grain yield of them by 3–52% and 11–78%. It is necessary to note that under well-watered conditions, every replication of *T. boeoticum* with low nutrient supply had very low grain yields, which resulted in the lower grain yield (23%) of *T. boeoticum* with wet treatment than that with drought treatment. Analysis of the stability of grain yield showed that the coefficient of variance (CV) for *T. boeoticum* was 60%, the highest, indicating that environmental factors as water and nutrient supply have significant effects on the yield of *T. boeoticum*. CV for *T. vulgare*, *Ae. tauschii*, *Ae. speltooides* and *T. dicoccoides* was 50%, 39%, 38% and 35%, respectively, and that for *T. dicoccon* was the lowest, 29%. So, it can be concluded that the yield of tetraploid is more stable than that of hexaploid, and the yield stability of diploid is the worst that was related to the significant differences of the yield among three diploid wheats (AA, BB and DD).

As shown in Table 1, both water and nutrient application had no consistent effects on HI of different wheats. Water stress decreased HI of *Ae. speltooides*, *T. vulgare*, *T. dicoccon* and *T. dicoccoides* by 10–25%, but elevated that of *T. boeoticum* and *Ae. tauschii*. Under different water conditions, adding nutrient application reduced HI of *Ae. speltooides*, but increased that of the other five wheat genotypes.

Water consumption for transpiration

Analysis of variance showed that three major factors and their

Table 1. Biomass, grain yield (g/pot) and harvest index (%) of different wheat genotypes under different water and nutrient conditions

Plant	<i>Triticum boeoticum</i>	<i>Aegilops speltooides</i>	<i>Ae. tauschii</i>	<i>T. dicoccoides</i>	<i>T. dicoccon</i>	<i>T. vulgare</i>
Root biomass						
WH	3.0 ± 0.4	5.2 ± 0.02	4.9 ± 0.3	6.2 ± 0.3	7.8 ± 1.2	5.5 ± 1.2
WL	3.1 ± 0.4	3.5 ± 0.1	3.5 ± 0.7	4.6 ± 0.5	7.3 ± 0.3	3.6 ± 0.4
DH	1.2 ± 0.1	3.0 ± 0.2	1.3 ± 0.001	2.0 ± 0.2	2.6 ± 0.3	1.7 ± 0.2
DL	1.9 ± 0.2	3.1 ± 0.1	1.8 ± 0.1	2.7 ± 0.2	2.9 ± 0.9	2.2 ± 0.4
Above-ground biomass						
WH	33.1 ± 1.2	38.7 ± 0.6	32.8 ± 2.6	42.3 ± 1.5	46.6 ± 3.8	46.5 ± 0.1
WL	18.9 ± 2.0	27.3 ± 0.8	22.3 ± 2.8	30.6 ± 3.4	39.7 ± 1.4	37.1 ± 3.6
DH	20.9 ± 3.8	21.6 ± 2.0	17.0 ± 0.02	29.8 ± 3.2	32.5 ± 1.1	24.1 ± 1.4
DL	13.8 ± 0.3	15.2 ± 0.1	16.5 ± 0.3	23.7 ± 3.0	25.9 ± 3.6	21.9 ± 2.7
Grain yield						
WH	1.5 ± 1.1	1.3 ± 0.04	6.0 ± 1.5	9.2 ± 0.7	8.5 ± 1.4	17.5 ± 0.2
WL	0.1 ± 0.1	1.1 ± 0.1	3.7 ± 0.7	6.5 ± 0.6	8.1 ± 0.4	11.8 ± 1.8
DH	1.8 ± 0.3	0.7 ± 0.06	3.7 ± 0.01	4.1 ± 0.8	5.7 ± 0.9	6.5 ± 0.7
DL	1.0 ± 0.2	0.5 ± 0.02	2.5 ± 0.04	4.3 ± 0.9	4.9 ± 0.8	5.7 ± 1.5
Harvest index						
WH	4.4 ± 3.3	3.3 ± 0.08	18.1 ± 0.6	21.7 ± 1.7	18.1 ± 3.0	37.7 ± 0.5
WL	0.7 ± 0.7	4.1 ± 0.3	16.5 ± 1.3	21.1 ± 0.5	20.4 ± 0.6	31.8 ± 5.0
DH	8.4 ± 0.6	3.1 ± 0.04	21.9 ± 0.03	13.7 ± 1.4	17.4 ± 2.9	26.8 ± 2.5
DL	7.1 ± 1.9	3.3 ± 0.1	15.3 ± 0.3	17.8 ± 2.4	19.0 ± 0.6	25.7 ± 3.8

DH, drought with high nutrient; DL, drought with low nutrient; WH, wet with high nutrient; WL, wet with low nutrient.

interaction were significant for water consumption for transpiration ($P < 0.01$). During the evolution of wheat, water consumption for transpiration of diploid and tetraploid were significantly higher than that of hexaploid, but there was no significant difference between diploid and tetraploid wheat (11.2 and 11.3 kg/pot). Water consumption for the transpiration of different wheats decreased in this order: *Ae. speltoides* > *T. dicoccon* > *T. boeoticum* > *T. dicoccoides* > *T. vulgare* > *Ae. tauschii*, and significant differences of water consumption for transpiration existed among six wheat genotypes. The amounts of water consumption for transpiration were related closely with the length of the growing period, and a positive cubic relation between them can be seen in Figure 1 ($r^2 = 0.88$, $P < 0.05$). For six wheat genotypes, *Ae. speltoides* had the longest growing period, accordingly its water consumption for transpiration was the highest.

As Table 2 shows, water application had a greater affect on water consumption for transpiration than nutrient supply.

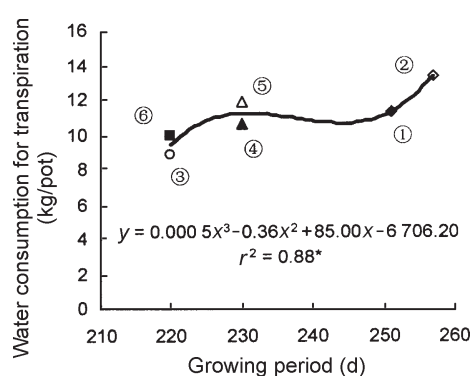


Figure 1. Correlation between water consumption for transpiration and growing period.

① *Triticum boeoticum*; ② *Aegilops Speltoides*; ③ *Ae. tauschii*; ④ *T. dicoccoides*; ⑤ *T. dicoccon*; ⑥ *T. aestivum*

Water stress reduced water consumption for transpiration of six wheat species by 47–52%. However, adding nutrient application increased it under different water conditions. High nutrient treatment had more water consumption for transpiration than low nutrient treatment by 8–32% under wet conditions, but only by 0.2–17% under water stress.

Water use efficiency

Genotype, nutrient application and $G \times W$ interaction were significant for WUE ($P < 0.01$), but there were no significant effects of water, $G \times Nt$, $W \times Nt$ and $G \times W \times Nt$ interaction on WUE. In the evolution of wheat, WUE increased significantly, and significant differences of WUE existed among three ploidy levels. WUE of tetraploid was 1.7 times higher than that of diploid, and WUE of hexaploid was higher than that of tetraploid by 67%. For six wheat genotypes, the decreasing order of WUE was *T. vulgare* > *T. dicoccon* > *T. dicoccoides* > *Ae. tauschii* > *T. boeoticum* > *Ae. speltoides*, and unremarkable differences of WUE were found between *T. dicoccon* and *T. dicoccoides*, and between *T. boeoticum* and *Ae. speltoides*.

Water treatment had different effects on WUE of different ploidy wheats (Table 3). Water stress elevated WUE of diploid and tetraploid by 1.4–180%, but decreased that of hexaploid (*T. vulgare*) by about 19%. So, in the case of WUE, wheat drought resistance decreased with the evolution of wheat. High nutrient treatment had higher WUE than low nutrient treatment under different water levels. Under well-watered conditions, high nutrient application almost had no effect on WUE of *Ae. speltoides*, but significantly increased WUE of *T. boeoticum* and WUE of the other four wheat genotypes by 5–38%. Under water-deficient conditions, the positive effect of nutrient application on diploid's WUE (AA, BB and DD) was the biggest (by 53%, 22% and 38%, respectively); that on hexaploid's (AABBDD) was in the middle (by 14%); and that on tetraploid's (AABB) was the smallest (by 0 and 5%).

Table 2. Mean values of water consumption for transpiration (kg/pot) and water use efficiency (g/kg) of different wheat genotypes

Species	<i>Triticum boeoticum</i>	<i>Aegilops speltoides</i>	<i>Ae. tauschii</i>	<i>T. dicoccoides</i>	<i>T. dicoccon</i>	<i>T. vulgare</i>
Water consumption for transpiration						
WH	17.4 ± 0.5	20.3 ± 0.6	13.2 ± 0.4	15.1 ± 0.9	16.3 ± 0.6	14.4 ± 0.5
WL	13.2 ± 0.3	16.1 ± 0.5	10.1 ± 0.3	13.0 ± 0.4	15.1 ± 0.3	12.7 ± 0.8
DH	7.9 ± 0.3	9.0 ± 0.3	6.5 ± 0.5	7.6 ± 0.4	8.2 ± 0.3	7.0 ± 0.3
DL	6.8 ± 0.1	8.4 ± 0.2	5.9 ± 0.4	7.0 ± 0.2	7.8 ± 0.2	6.9 ± 0.3
Water use efficiency						
WH	0.12 ± 0.03	0.06 ± 0.002	0.46 ± 0.10	0.60 ± 0.05	0.56 ± 0.07	1.22 ± 0.08
WL	0.01 ± 0.01	0.068 ± 0.01	0.37 ± 0.07	0.50 ± 0.03	0.54 ± 0.02	0.94 ± 0.22
DH	0.22 ± 0.03	0.07 ± 0.005	0.61 ± 0.06	0.61 ± 0.12	0.67 ± 0.12	0.93 ± 0.11
DL	0.15 ± 0.04	0.06 ± 0.002	0.44 ± 0.006	0.61 ± 0.12	0.64 ± 0.09	0.82 ± 0.19

DH, drought with high nutrient; DL, drought with low nutrient; WH, wet with high nutrient; WL, wet with low nutrient.

Table 3. Mean values of N, P and K uptake efficiency (%) of every treatment

Parameters		<i>Triticum boeoticum</i>	<i>Aegilops Speltoides</i>	<i>Ae. tauschii</i>	<i>T. dicoccoides</i>	<i>T. dicoccon</i>	<i>T. vulgare</i>
NUE	WH	5.41 ± 0.58	4.95 ± 0.41	4.74 ± 1.81	6.35 ± 0.75	6.71 ± 0.16	7.9 ± 0.30
	WL	2.99 ± 0.28	4.02 ± 0.23	3.79 ± 0.67	4.39 ± 0.49	5.60 ± 0.4	6.26 ± 0.49
	DH	2.84 ± 0.75	2.19 ± 0.42	2.15 ± 0.16	4.00 ± 0.39	4.22 ± 0.13	4.03 ± 0.11
	DL	1.80 ± 0.13	1.66 ± 0.15	2.10 ± 0.14	2.92 ± 0.43	3.38 ± 0.65	3.40 ± 0.45
PUE	WH	0.66 ± 0.06	0.46 ± 0.02	0.64 ± 0.29	0.86 ± 0.10	0.92 ± 0.04	0.86 ± 0.12
	WL	0.41 ± 0.04	0.42 ± 0.03	0.55 ± 0.08	0.63 ± 0.08	0.74 ± 0.04	0.83 ± 0.06
	DH	0.36 ± 0.08	0.26 ± 0.07	0.26 ± 0.05	0.48 ± 0.05	0.53 ± 0.03	0.51 ± 0.05
	DL	0.21 ± 0.03	0.17 ± 0.01	0.23 ± 0.03	0.34 ± 0.04	0.36 ± 0.05	0.45 ± 0.07
KUE	WH	0.25 ± 0.02	0.19 ± 0.09	0.16 ± 0.08	0.27 ± 0.03	0.32 ± 0.03	0.28 ± 0.02
	WL	0.13 ± 0.01	0.14 ± 0.01	0.11 ± 0.01	0.17 ± 0.02	0.25 ± 0.02	0.19 ± 0.01
	DH	0.15 ± 0.03	0.14 ± 0.03	0.09 ± 0.001	0.18 ± 0.02	0.21 ± 0.02	0.11 ± 0.01
	DL	0.09 ± 0.008	0.08 ± 0.003	0.08 ± 0.004	0.12 ± 0.01	0.15 ± 0.02	0.10 ± 0.004

DH, drought with high nutrient; DL, drought with low nutrient; NUE, nitrogen uptake efficiency; PUE, phosphorus uptake efficiency; KUE, potassium uptake efficiency; WH, wet with high nutrient; WL, wet with low nutrient.

Nutrient uptake efficiency

Nutrient use efficiency can be divided into nutrient uptake efficiency and nutrient use efficiency, analogous to similar terms defined for N use efficiency (Moll et al. 1982). ANOVA for N, P and K uptake efficiency (NUE, PUE and KUE) revealed that the main effects of genotype, water and nutrient levels were significant for all ($P < 0.01$). $G \times W$ interaction were significant for KUE ($P < 0.01$), and for NUE ($P < 0.05$). But $G \times Nt$ interaction were only significant for PUE ($P < 0.05$). $W \times Nt$ interaction were significant for all ($P < 0.01$) except for PUE. However, $G \times W \times Nt$ interaction were not significant for all.

N uptake efficiency, PUE and KUE all increased continuously with the evolution of wheat from diploid to tetraploid and then to hexaploid. NUE increased from 3.24% to 4.69% then to 5.17%, and the differences among ploidies were all significant; PUE increased from 0.39% to 0.61% then to 0.65%, and there was no significant difference of PUE between tetraploid (4n) and hexaploid (6n) wheats; KUE increased from 0.13% to 0.16% then to 0.21%, and the differences among them were all significant. Mean values of NUE, PUE and KUE (%) of six genotypes with four treatments (WH, WL, DH and DL) are shown in Table 3. For all treatments, *T. vulgare* (6n) had the highest NUE and PUE among six wheat genotypes, and *T. dicoccon* (4n) had the highest KUE. Six wheat genotypes responded similarly to water and nutrient application. Generally, water stress and low nutrient application resulted in the lower NUE, PUE and KUE. Furthermore, water supply had more influences on nutrient uptake efficiency than nutrient application. Water stress significantly reduced NUE, PUE and KUE of diploid, tetraploid and hexaploid by 36–57%, 43–59% and 32–54%, compared to well-watered treatment. Correspondingly, low nutrient supply also decreased NUE, PUE and KUE by 14–41%, 6–38% and 25–55%, compared to high nutrient treatment.

Nutrient utilization efficiency

Analysis of variance showed that only genotype had significant ($P < 0.01$) effect on nutrient utilization efficiency (UTE) of N (NUTE), P (PUTE), and K (KUTE), but water and nutrient supply had no significant effects on all of them. Both $G \times W$ and $G \times Nt$ interaction were significant for NUTE and PUTE ($P < 0.01$), and $W \times Nt$ interaction were only significant for PUTE. However, $G \times W \times Nt$ interactions were not significant for all.

With the increment of wheat ploidies, NUTE, PUTE and KUTE increased remarkably, and the differences among them were all significant. NUTE of tetraploid wheat (20.6 g/g) was 1.2 times higher than that of diploid wheat (9.5 g/g), and NUTE of hexaploid wheat was 29% greater than that of tetraploid wheat and reached 26.6 g/g. The changing trend of PUTE (71.0, 149.8 and 184.4 g/g) was similar to that of NUTE during wheat evolution. With the increase of wheat ploidies, KUTE increased by degrees, and KUTE of diploid, tetraploid and hexaploid were 8.6, 16.4 and 30.7 g/g, respectively. Mean values of NUTE, PUTE, and KUTE across four treatments (WH, WL, DH and DL) are presented in Table 4. Consistent decreasing order existed in NUTE and PUTE of wheat: *T. vulgare* > *T. dicoccon* > *T. dicoccoides* > *Ae. tauschii* > *T. boeoticum* > *Ae. speltooides*. But KUTE decreased in this order: *T. vulgare* > *Ae. tauschii* > *T. dicoccon* > *T. dicoccoides* > *T. boeoticum* > *Ae. speltooides*. For all of these three parameters, there were no significant differences between *T. boeoticum* (AA) and *Ae. speltooides* (BB), and among *T. dicoccon* (AABB) and *T. dicoccoides* (AABB).

Relationships between WUE and NUTE, PUTE and KUTE

Both water and nutrient use efficiency increased remarkably during the evolution of wheat, and correlations between WUE

Table 4. Mean values of N, P and K utilization efficiency of different wheat genotypes

Parameters	<i>Triticum boeoticum</i>	<i>Aegilops speltoides</i>	<i>Ae. Squarrosa</i>	<i>T. dicoccoides</i>	<i>T. dicoccum</i>	<i>T. vulgare</i>
NUTE (g/g)	5.83a	4.25a	18.43b	20.47c	20.74c	26.64d
PUTE (g/g)	44.27a	37.43a	137.32b	146.46b	153.04b	195.92c
KUTE (g/g)	4.07a	3.48a	18.19c	17.06bc	15.75b	30.73d

Mean values followed by the same letter within each row for every treatment are not significantly different at $P < 0.05$ (LSD). NUTE, N utilization efficiency; PUTE, P utilization efficiency; KUTE, K utilization efficiency.

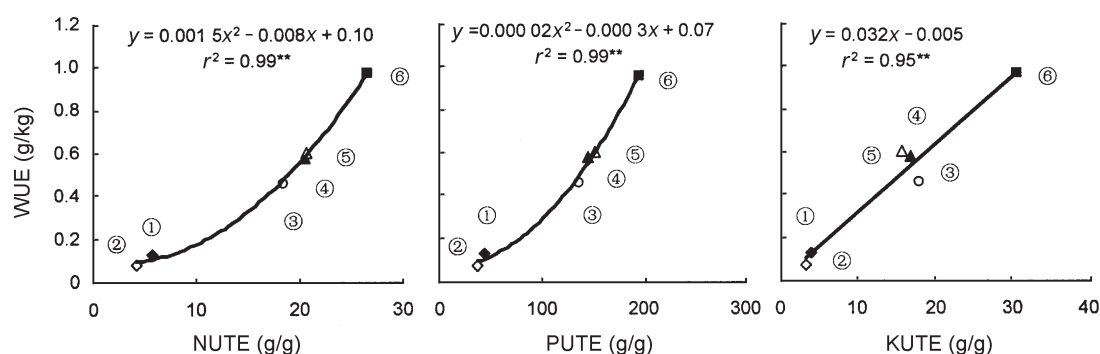


Figure 2. Correlation between water use efficiency (WUE) and N utilization efficiency (NUTE), P utilization efficiency (PUTE) and K utilization efficiency (KUTE).

① *Triticum boeoticum*; ② *Aegilops speltoides*; ③ *Ae. tauschii*; ④ *T. dicoccoides*; ⑤ *T. dicoccum*; ⑥ *T. aestivum*

and NUTE, WUE and PUTE, and WUE and KUTE are presented in Figure 2. On an average of four treatments, WUE was positively correlated with NUTE (quadratic relationship: $r^2 = 0.99$, $P < 0.01$) with the increasing chromosome ploidy during wheat evolution. WUE was also positively correlated with PUTE (quadratic relationship: $r^2 = 0.99$, $P < 0.01$) and KUTE (linear relationship: $r^2 = 0.95$, $P < 0.01$), respectively. It can be seen from Figure 2 that in terms of WUE and nutrient utilization efficiency, *Ae. tauschii* (DD, diploid) was more similar to tetraploid wheats (*T. dicoccoides* and *T. dicoccum*, AABB), and two diploid wheats *T. boeoticum* and *Ae. Speltoides* were similar to each other, but hexaploid wheat *T. vulgare* differed from all of them.

Discussion

As the main organ absorbing soil water and nutrients, the root affects directly the formation of the above-ground biomass. Our data show that significant relationships exist between root and above-ground biomass ($r = 0.74$, $P < 0.01$). A previous study (Zhu et al. 2001) showed that old wheat cultivars had less root biomass than modern wheat, but Zhang et al. (2002) found that root biomass decreased with the increment of ploidies during the evolution of wheat. It can be obtained from our study that both root and above-ground biomass increased initially

and then decreased, but grain yield and HI increased significantly with the increasing chromosome ploidy, which may indicate that the increment of yield in the evolution of wheat is more attributable to the increase of the ability of transporting matters to grain (HI) than to the increment of above-ground biomass. Comparing hexaploid wheat to primitive diploid wheats, previous researchers (Evans and Dunstone 1970; Austin and Morgan 1982) also pointed out that the major reason of the increment of modern wheat yield was the increment of HI. Yield of *Ae. speltoides* (BB) and *T. boeoticum* (AA) were 1.3 and 0.9 g/pot, but yield of their offspring (*T. dicoccoides* and *T. dicoccum*, AABB) (6.2 and 7.0 g/pot) was 5.2 times higher. Similarly, high-yield *T. vulgare* (AABBDD) (9.7 g/pot) were obtained from the natural crossing of *Ae. tauschii* (DD) with *T. dicoccum* (AABB). So, it can be concluded that wheat yield increased significantly with every mating of different chromosome sets. The yield of *Ae. tauschii* (DD) was markedly higher than that of the other two diploid wheats (AA and BB), indicating that there may be genes controlling high yield on the D chromosome.

A previous study revealed that wheat WUE increased markedly with the increment of chromosome ploidy during the evolution of wheat (Zhang et al. 2002), which was significantly correlated with the increase of HI ($r = 0.96$, $P < 0.01$). The declining order of WUE was *T. vulgare* > *T. dicoccum* > *T. dicoccoides* > *Ae. tauschii* > *T. boeoticum* > *Ae. speltoides*,

and remarkable differences were found among them. The significant increment of wheat WUE was correlated with shortening of the whole growing period, remarkable decline of water consumption for transpiration, and the increment of biomass and yield, which coincided with the idea of Siddique et al. (1990) who attributed the improved WUE in modern cultivars to faster development, earlier flowering, improved canopy structure and higher harvest index.

Our data showed that water stress reduced root and above-ground biomass, and eventually decreased wheat yield, which may be related to the reduction of photosynthesis and the worsening of water conditions due to water stress (Duan et al. 2006; Zgallai et al. 2006). But nutrient application compensated for the negative effect of water stress on them. High nutrient supply had a positive effect on root biomass under well-watered conditions, but had a negative effect on root biomass under water stress. The reason for this phenomenon can be explained by the effect of phosphorus enlarging the root to obtain more water and nutrient (Liang and Chen 1996; Zhang and Zhang 2001) may be restricted by the limiting pot cubage, and the negative effect of nitrogen on root growth (Brown 1971; Nielsen and Halvorsen 1991; Li and Shao 2000) may become dominant under water stress.

Heitholt (1989) considered that light water stress almost had no effect on WUE, while serious water stress always reduced WUE. In this experiment, water deficiency decreased WUE of *T. vulgare* (6n), but increased WUE of the other five, indicating that drought in the same degree was mild for diploid and tetraploid wheats while serious for hexaploid wheat. So, it could be presumed that drought resistance decreased with the evolution of wheat. Under different water levels, a high nutrient supply elevated wheat WUE, which may be correlated with its positive effects on the improvement of plant water conditions, the maintaining of high photosynthesis rate, the increment of the assimilation products, and the translocation of assimilation products into grain (Huang et al. 2003). Therefore, reasonable nutrient application was also favorable for the improvement of wheat WUE (Liang 1996; Du et al. 1999; Li and Shao 2000) during the evolution of wheat.

Despite the major effect of genotypes on nutrient use, environmental factors, such as soil water and nutrient significantly affect nutrient-use traits, such as nutrient uptake and utilization efficiency in wheat (Papakosta and Gagianas 1991; Timsina et al. 2001). Generally, decreasing water and nutrient supply decreased N, P and K uptake efficiency of different wheat species. Under water stress, root growth is restricted and nutrient is not effectively dissolved in the soil water, so nutrient availability was reduced and nutrient uptake was low (Boatwright et al. 1964; Latiri-Souki et al. 1998). Timsina et al. (2001) found that N uptake efficiency under irrigation was 47–63%, while under rainfed conditions it was 45–51%. Increases in soil moisture content also increased the total plant N and P

uptake of wheat (Clarke et al. 1990; He et al. 2002). This study shows that water supply has more influences on N, P and K uptake efficiency than nutrient application. Water stress significantly reduced NUE, PUE and KUE of diploid, tetraploid and hexaploid by 36–57%, 43–59% and 32–54%, and low nutrient supply decreased NUE, PUE and KUE by 14–41%, 6–38% and 25–55%. Correspondingly, previous studies also showed that nutrient uptake efficiency rose at increasing nutrient application rates (Whitfield and Smith 1992; Delogu et al. 1998; Rrez-Boem and Thomas 1998; Zhang et al. 1999; Timsina et al. 2001; He et al. 2002).

Li et al. (2003) reported that nitrogen use efficiency increased gradually during the long evolution process from diploid to hexaploid, and water use efficiency was positively correlated with nitrogen use efficiency across nine evolution materials. However, there was no consistent result of changes of phosphorus use efficiency during the evolution of wheat. Batten (1986) found phosphorus efficiency (PUTE) increased as the yield per culm and dry-matter partitioning increased, with hexaploid > tetraploid > diploid. But Liu et al. (2002) reported that phosphorus use efficiency gradually decreased during the wheat evolution from diploid to tetraploid then to hexaploid. On the average of different water and conditions, our experiment showed that all of the N, P and K uptake and utilization efficiencies increased significantly with the increment of wheat ploidy during the evolution of wheat, and WUE markedly correlated with N, P and K utilization efficiency (Figure 2). *T. vulgare* (6n) had the highest N and P uptake efficiency, but *T. dicoccon* (4n) had the greatest K uptake efficiency. Compared to the other two diploid wheats, *Ae. tauschii* (DD) had significantly higher NUTE, PUTE and KUTE, indicating that the D genome may carry genes controlling high use of nutrients (including N, P and K). Cakmak et al. (1998) also found that the D genome also carries genes affecting the expression of a high Zn efficiency of synthetic wheats when grown under Zn-deficient conditions. So, the D genome may be very valuable in the prospect of wheat breeding for high nutrient efficiency.

It was interesting to note that the effects of water and nutrient application on N, P and K use efficiency were not significant in our study, indicating that nutrient use efficiency may be mainly controlled by genotype, and there is little effect due to environmental factors. This deduction was consistent with the property of nutrient use efficiency which reflects the efficiency in using the nutrients actually absorbed and approximates the effects of plant factors (Timsina et al. 2001), and is similar to the results of Bassam (1998) that cultivar response to inputs is under genetic control. So, nutrient utilization efficiency may be mainly controlled by genotypes and a stable genetic property during the evolution of wheat.

In the evolution of wheat, water consumption for transpiration of wheat decreased remarkably (Table 2), but grain yield increased significantly (Table 1). So, it can be concluded that

the capability of wheat using water to produce substances forming yield (WUE) increased substantially. Nutrient uptake efficiency increased significantly in the evolution of wheat, but wheat above-ground biomass increased initially and then decreased, which indicated that the increasing of nutrient uptake efficiency was attributed more to the increment of the capacity of wheat absorbing nutrient than to that of above-ground biomass. NUTE, PUTE and KUTE were significantly ($P < 0.01$) positive correlated with HI ($r = 0.97, 0.93$ and 0.97), which was consistent with the findings of previous studies; that increased HI may improve P use efficiency (Batten 1986), indicating that the increase of biomass and grain yield had some effect on the increment of nutrient use. It is suggested that nutrient use efficiency is strongly linked with HI or remobilization of carbohydrates. However, more studies should be carried out to investigate nutrient use mechanisms.

Carrying out breeding schemes that combine efficient use of water and nutrients under stress conditions with high yield responsiveness under favorable conditions seems to be the perfect approach for dryland farming (Braun et al. 1992; Calhoun et al. 1994; Richards 1996; Rajaram 2001). In order to breed high nutrient efficiency, it is important to identify the genotypes with higher water and nutrient use efficiency and understand the mechanism of differences in response to water and nutrient application between genotypes (Zhang et al. 1999; Deng et al. 2003). Major environmental factors (water and nutrient) affecting wheat evolution in arid areas were considered in this experiment, so our analysis under different water and nutrient conditions may be closer to the truth in the evolution of wheat. Results obtained in this study showed that with the evolution of wheat from diploid to tetraploid then to hexaploid, water use efficiency, N, P and K uptake efficiency and N, P and K use efficiency all increased significantly. *Ae. tauschii* (DD) may be a valuable wheat genotype that can be used in breeding programs to improve WUE, and N, P and K use efficiency. The information encapsulated in our study of the nutrient use efficiency of diploid, tetraploid and hexaploid wheats under diverse water and nutrition supply can be used to breed high nutrient using wheat genotypes.

Materials and Methods

Wheat materials

Six wheat genotypes with different ploidy chromosome sets, which are very important in the evolution of wheat (Zhang 2001), were grown in pots under different soil, water and nutrient conditions. Certain relationships exist among these six wheat genotypes in the evolution of wheat (Zhao et al. 2005), which were proven by cytology (Zhang 2001). They included wide einkorn, *Triticum boeoticum* Bioss., an AA-genome diploid;

wide goat-grass, *Aegilops speltoides* Tausch., a diploid with genome BB; *Ae. tauschii* Cosson Syn., a diploid with genome DD; wide emmer, *T. dicoccoides* Koern., a tetraploid with genome AABB; cultivated emmer, *T. dicoccon* Schrank, a tetraploid with genome AABB; and modern domesticated bread-wheat, *T. vulgare* Vill, a hexaploid with genome AABBDD. Seeds were obtained from the Chinese Wheat Breeding Center at the Northwest Sci-Tech University of Agriculture and Forestry.

Experimental design

Experiments were conducted under a waterproof shed, which allowed the plants to grow under natural conditions except rainfall, on the experimental farm of the Institute of Soil and Water Conservation, the Chinese Academy of Sciences, China. Seeds from each genotype were germinated on moist filter paper at 20 °C in the dark. Twenty-four hours later, 20 germinated seeds were sown in plastic pots. Each pot contained 9.00 kg air-dry soil, containing 7.23 g/kg organic matter, 0.07% total N, 0.08% total P and 2.17% total K with a water-holding capacity of 25.20% by weight. Water was supplied from plastic pipes inserted vertically into the soil, as described by Deng et al. (2000). Each pot was brought to water-holding capacity prior to planting 20 seedlings, and then 10 seedlings were kept. Fifty grams of perlite was added to the top of each pot to restrain surface evaporation of soil.

Treatments of each wheat genotype were arranged in a split plot design with water management as main plots and nutrition application (including N, P and K) as subplots. All treatments were replicated five times. Main plots consisted of two irrigation treatments, namely wet (W) and drought (D) treatments. Wet treatments keep soil water content between 70% and 75% water-holding capacity all the time, and drought treatments maintain soil water content between 40% and 45% water-holding capacity from elongating stage to maturity. Subplots consisted of two levels of nutrient treatments, high (H) and low (L) nutrient treatments. Mineral fertilizers were applied at high levels, corresponding to 0.12 g N, 0.06 g P₂O₅ and 0.06 g K₂O/kg air-dry soil, and the applied amount of the low levels was one half of that of high nutrient treatments.

Analysis

Whole plants were harvested after full maturation, which was determined by the complete loss of green color from glumes (Hanft and Wych 1982). Wheat roots were carefully washed to remove the soil through a sieve. The plants were divided into grains, shoots (including leaves) and roots, dried for 48 h at 75 °C, weighed, and then the total N, P and K was analyzed. Each tissue sample was ground with an electric mill. Subsamples were wet-digested in a mixture of H₂SO₄ and H₂O₂. N concentration was measured by Kjeldahl digestion, distillation, and

titration (Bremner and Keeney 1966), P concentration was analyzed colorimetrically with the molybdate-vanadium method (Kitson and Melon 1944), and K concentration was measured by the ZL5100 atomic absorption spectrophotometer (PE Inc. Cincinnati, Ohio, USA).

Data on water consumption for transpiration were obtained by recording the added water during the whole life of the wheat. The following variables were calculated: harvest index (HI = grain dry matter/dry matter of above-ground biomass × 100%), water use efficiency (WUE = grain yield / water consumption for transpiration), nutrient uptake efficiency (nutrient uptake per nutrient supply and soil nutrient), nutrient use efficiency (grain yield per nutrient uptake by plant). Statistic analysis of data was carried out with the SPSS 10.0 (SPSS, Chicago, IL, USA) for Microsoft Windows.

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