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Differences in Zinc Efficiency among and within Diploid, Tetraploid and Hexaploid Wheats

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Greenhouse experiments were carried out with six diploid, nine tetraploid and seven hexaploid wheats, including wild and primitive genotypes, to study the influence of varied zinc (Zn) supply on the severity of Zn deficiency symptoms, shoot dry matter production and shoot Zn concentrations. In addition to wild and primitive genotypes, one modern tetraploid cultivar with high sensitivity to Zn deficiency and two modern hexaploid cultivars, one highly sensitive to and one resistant to Zn deficiency, were included for comparison. Plants were grown for 44 d in a severely Zn-deficient calcareous soil, with (+Zn; 5 mg Zn kg^{-1} soil) and without (−Zn) Zn fertilization. Visible Zn deficiency symptoms, including whitish-brown necrotic patches on leaf blades, appeared very rapidly and severely in all tetraploid wheat genotypes. Compared with tetraploid wheats, diploid and hexaploid wheats were less sensitive to Zn deficiency. With additional Zn, shoot dry matter production was higher in tetraploid than diploid and hexaploid wheats. However, under Zn-deficient conditions tetraploid wheats had the lowest shoot dry matter production, indicating the very high sensitivity of tetraploid wheats to Zn deficiency. Consequently, Zn efficiency expressed as the ratio of shoot dry matter produced under Zn deficiency to Zn fertilization, was much lower in tetraploid wheats than in diploid and hexaploid wheats. On average, Zn efficiency ratios were 36% for tetraploid, 60% for diploid and 64% for hexaploid wheats. Differences in Zn efficiency among and within diploid, tetraploid and hexaploid wheats were positively related to the amount of Zn per shoot of the genotypes, but not to the amount of Zn per unit dry weight of shoots or seeds used in the experiments. The seeds of the accessions of tetraploid wild wheats contained up to 120 mg Zn kg^{-1}, but the resulting plants showed very high sensitivity to Zn deficiency. By contrast, hexaploid wheats and primitive diploid wheats with much lower Zn concentrations in seeds had higher Zn efficiencies. It is suggested that not only enhanced Zn uptake capacity but also enhanced internal Zn utilization capacity of genotypes play important roles in differential expression of Zn efficiency. The results of this study also suggest the importance of the A and D genomes as the possible source of genes determining Zn efficiency in wheat. © 1999 Annals of Botany Company

Key words: Seeds, *Triticum aestivum*, *Triticum monococcum*, *Triticum turgidum*, zinc concentrations, zinc deficiency, zinc efficiency.

INTRODUCTION

Zinc (Zn) deficiency occurs worldwide in soils and plants, particularly in calcareous soils of arid and semi-arid regions. Sillanpää (1990) found that about 50% of the soil samples collected from 25 countries show Zn deficiency. For example, in Turkey Zn deficiency exists in 14 million hectares of cultivated land (Eyupoglu *et al.*, 1994) and results in severe decreases in wheat grain yield (Cakmak *et al.*, 1996*c*). According to Graham and Welch (1996), Zn deficiency is an important nutritional problem in cereal-growing areas throughout the world, and it not only reduces grain yield, but also weakens the resistance of cereals to diseases, and impairs the nutritional quality of the grain.

Cultivated cereal species, especially wheats, show a large variation in Zn efficiency, i.e. the ability of a genotype to grow and yield better under Zn-deficient conditions in comparison with other genotypes (Graham, Ascher and Hynes, 1992; Rengel and Graham, 1995*a*; Cakmak and Braun, 1999). Among the cereal species, Zn efficiency was found to decline in the order rye > triticale > barley > bread wheat > oat > durum wheat (Cakmak *et al.*, 1998; Ekiz *et al.*, 1998), but in the literature there do not appear to be studies of differences in Zn efficiency among wild and less-advanced wheats. These wheats are widely used as a source of useful genes for the improvement of cultivated modern wheats. For example, the A-genome in wild and primitive diploid wheats has been used for the improvement of disease resistance of cultivated wheats (Kerber and Dyck, 1973; Valkoun, Kucerova and Bartos, 1986; Hussien *et al.*, 1997). Among several wild *Triticum* species (tetraploid wheats), *T. turgidum* ssp. *dicoccoides* showed a high heat resistance, whereas the wild diploid wheats, *T. monococcum* ssp. *boeoticum* and *T. urartu* were less-resistant (Ehdai and Waines, 1992; Waines, 1994). Wild tetraploid wheats also possess a high variation in sensitivity to rust diseases (Silfhout *et al.*, 1989; McVey, 1991). Batten (1986) compared diploid, tetraploid and hexaploid wheats for uptake and utilization of phosphorus (P) and found that P efficiency, expressed as grain yield per unit P in the shoot, increased in the order hexaploid > tetraploid > diploid.

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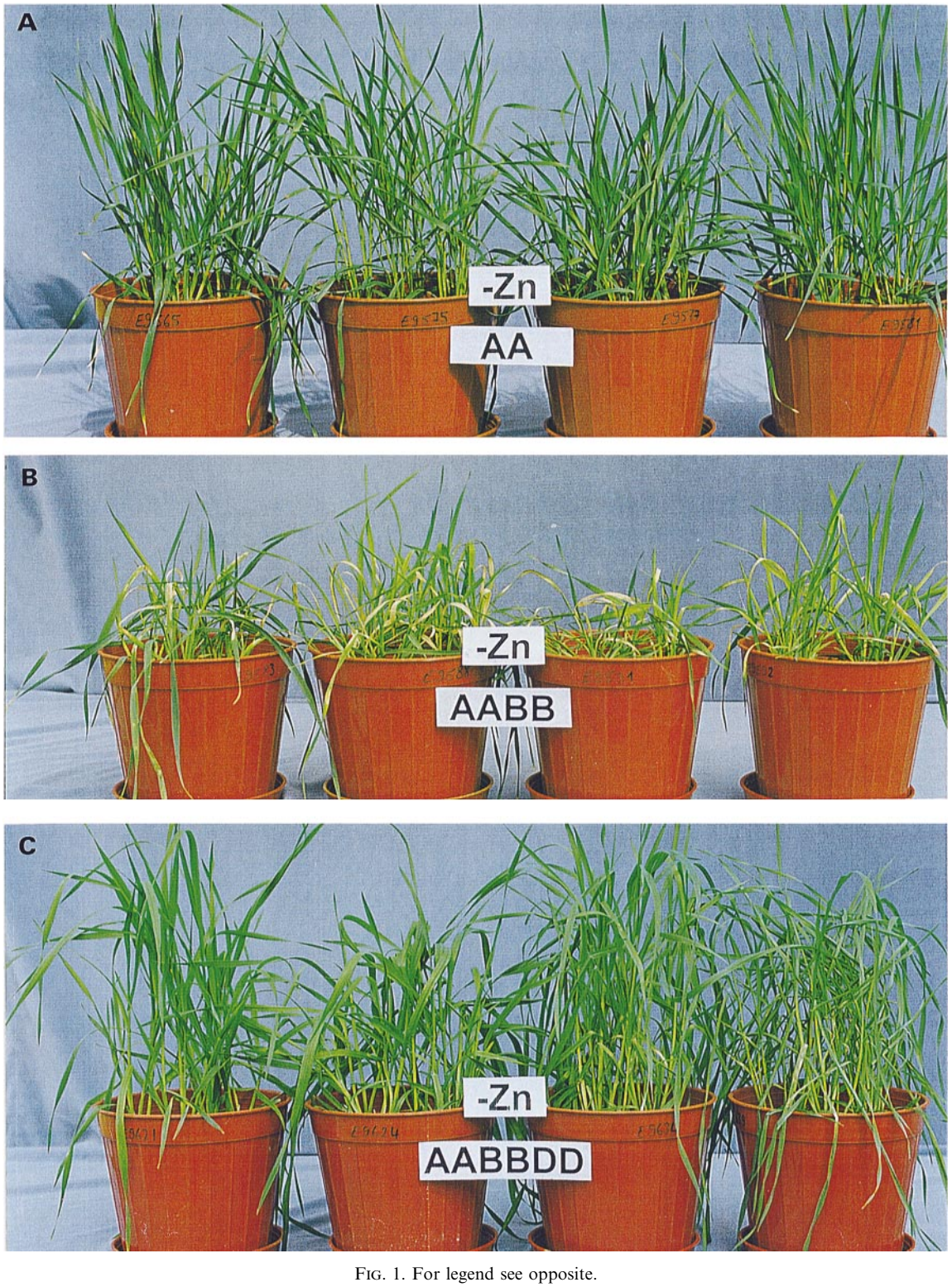


FIG. 1. For legend see opposite.

In the present study, six diploid (AA), ten tetraploid (BBAA) and nine hexaploid (BBAADD) wheats were compared in terms of the severity of Zn deficiency symptoms, shoot dry matter production, and Zn concentrations, when grown in a severely Zn-deficient calcareous soil, with and without Zn fertilization.

MATERIALS AND METHODS

Plant materials

Six genotypes of diploid, ten genotypes of tetraploid and nine genotypes of hexaploid wheats were used in the experiments (Table 1). Among the diploid wheats used, four

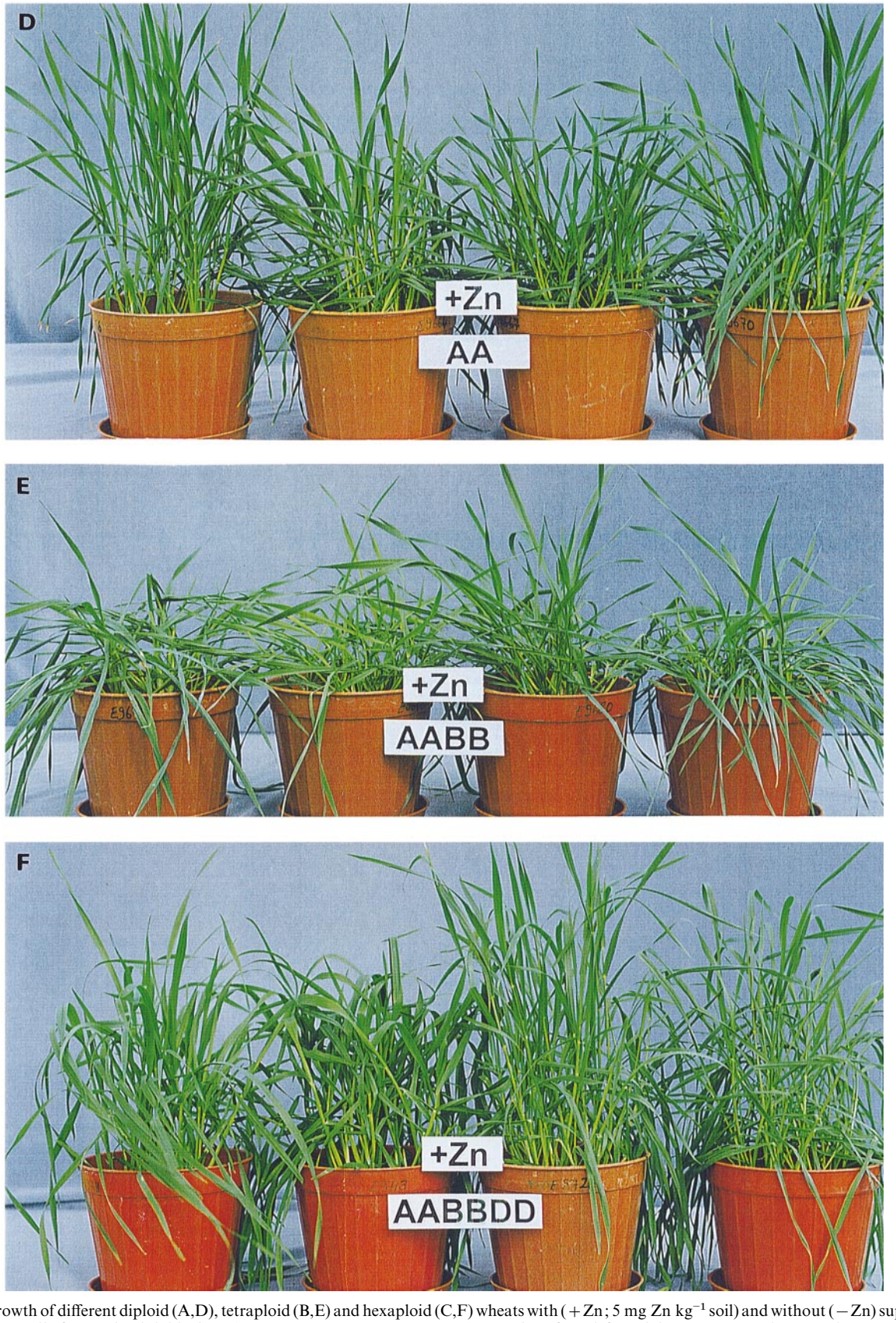


FIG. 1. Growth of different diploid (A,D), tetraploid (B,E) and hexaploid (C,F) wheats with (+Zn; 5 mg Zn kg^{-1} soil) and without (−Zn) supply in a Zn-deficient soil after 44 d. Diploid wheat (*T. monococcum* ssp. *monococcum*) accessions from left to right. TMM-03, FAL-29, FAL-31 and FAL-45; tetraploid wheat (*T. turgidum* ssp. *dicoccoides*) accessions from left to right: TTD-05, TTD-02, TTD-01 and TTD-04; hexaploid wheats (*T. aestivum*) from left to right: TAC-01 (ssp. *compactum*), Germany (ssp. *compactum*), TAS-01 (ssp. *spelta*) and TAS-06 (ssp. *spelta*).

accessions were from the primitive cultivated diploid wheat, ssp. *monococcum*, and two accessions from the wild diploid, ssp. *boeoticum*. Among the tetraploid wheats used, four accessions were wild tetraploid, ssp. *dicoccoides*, and five accessions were primitive cultivated tetraploids, two from ssp. *dicoccum* and three from ssp. *polonicum*. Seven accessions of primitive cultivated hexaploid wheats were used in the experiments, including two accessions each from ssp. *compactum* and spp. *sphaerococcum*, and three accessions from ssp. *spelta* (Table 1). Three modern cultivars grown in Central Anatolia were also used, including one tetraploid (ssp. *durum* 'Kunduru') and two hexaploids (ssp. *aestivum*, 'Bezostaja' and 'BDME-10'). These modern cultivars were included so as to compare their response to Zn deficiency with that of the wild and primitive accessions, as they differ greatly in their sensitivity to Zn deficiency: the cultivars 'Kunduru' and 'BDME-10' are very sensitive to Zn deficiency, whereas 'Bezostaja' is less sensitive (Cakmak *et al*., 1996*c*; 1998).

TABLE 1. *Diploid, tetraploid and hexaploid wheats used in the study, and their accessions and sources*

Species	Accession or cultivar	Seed source	Classification
Diploid, *T. monococcum* (AA)			
ssp. *monococcum*	TMM-03	Israel*	Primitive
ssp. *monococcum*	FAL-29	Germany†	Primitive
ssp. *monococcum*	FAL-31	Germany†	Primitive
ssp. *monococcum*	FAL-45	Germany†	Primitive
ssp. *boeoticum*	TMB-03	Iraq*	Wild
ssp. *boeoticum*	TMB-02	Turkey*	Wild
Tetraploid, *T. turgidum* (BBAA)			
ssp. *dicoccoides*	TTD-05	Israel*	Wild
ssp. *dicoccoides*	TTD-02	Israel*	Wild
ssp. *dicoccoides*	TTD-01	Israel*	Wild
ssp. *dicoccoides*	TTD-04	Israel*	Wild
ssp. *dicoccum*	FAL-02	Germany†	Primitive
ssp. *dicoccum*	FAL-03	Germany†	Primitive
ssp. *polonicum*	TTP-03	Israel*	Primitive
ssp. *polonicum*	FAL-11	Germany†	Primitive
ssp. *polonicum*	FAL-17	Germany†	Primitive
ssp. *durum*	Kunduru	Turkey	Modern cultivated
Hexaploid, *T. aestivum* (BBAADD)			
ssp. *compactum*	TAC-01	Israel*	Primitive
ssp. *compactum*	Germany	Germany†	Primitive
ssp. *sphaerococcum*	TAP-03	Israel*	Primitive
ssp. *sphaerococcum*	TAP-01	Israel*	Primitive
ssp. *spelta*	TAS-01	Israel*	Primitive
ssp. *spelta*	TAS-06	Israel*	Primitive
ssp. *spelta*	TAS-03	Israel*	Primitive
ssp. *aestivum*	Bezostaja	Turkey	Modern cultivated
ssp. *aestivum*	BMDE-10	Turkey	Modern cultivated

* Seeds obtained from Dr. M. Feldman, Weizmann Institute of Science.

† Seeds obtained from the State Plant Breeding Institute, University of Hohenheim-Stuttgart.

Plant growth

Plants were grown under greenhouse conditions in a Zn-deficient soil from the Central Anatolia region, where severe Zn deficiency occurs in wheats (Cakmak *et al*., 1996*c*, 1998). The soil had a clay loam texture, pH 7·6, $CaCO_3$ content of 16% o.d.s, and organic matter content of 2·6% o.d.s. The concentration of plant-available Zn was extremely low, at around 0·1 mg kg^{-1} DTPA-extractable Zn, measured by the method of Lindsay and Norvell (1978). Seven to ten seeds were sown in plastic pots containing 1·6 kg soil. Before potting, the soil was treated homogeneously with a basal application of 200 mg N kg^{-1} soil as $Ca(NO_3)_2$, and 100 mg P kg^{-1} soil as KH_2PO_4. Two levels of Zn (0 and 5 mg kg^{-1} soil; −Zn and +Zn, respectively) were established by adding Zn in the form of $ZnSO_4$. After emergence, the plants were thinned to five seedlings per pot and the pots were randomized every 4–5 d. For each treatment, three randomly-selected pots were used. Plants were watered daily with deionized water.

Measurements

After 44 d of growth in the greenhouse, the shoots were harvested and dried at 70 °C for determination of shoot dry matter production. At harvest, the plants were at the stem elongation stage. The dried shoot samples were then ground and ashed at 500 °C for 8 h, the ash was dissolved in 3·3% (v/v) HCl, and Zn was determined using an inductively coupled plasma (ICP) atomic emission spectrometer (Jobin Yvon-Paris). Zinc measurements were checked using the certified Zn values in reference leaf samples obtained from the National Institute of Standards and Technology (Gaithersburg, USA). The zinc efficiency of genotypes was calculated as the ratio of shoot dry matter produced under Zn deficiency (−Zn) to that under Zn fertilization (+Zn). Before harvest, plants were evaluated for the severity of visual symptoms of Zn deficiency on leaves (i.e. necrotic patches) using a scale of 1–5 (1: very severe symptoms; 5: symptoms very slight or absent). As the amount of Zn in seeds has an important role in growth and grain yield of wheat in Zn-deficient soils, and thus on the expression of Zn efficiency (Rengel and Graham, 1995*b*; Yilmaz *et al*., 1998), the Zn concentration of the seeds of all wheats used in the present study were analysed.

RESULTS

All the accessions of diploid wheats were similarly affected by Zn deficiency. The severity of visual Zn deficiency symptoms, such as the occurrence of whitish-brown necrotic patches on the middle parts of leaves, was generally slight in the diploid wheats (Fig. 1, Table 2). Shoot dry matter production of the diploid wheats increased with Zn application, by approx. 70%. Zinc efficiency ratios were similar for the different accessions of diploid wheats, and ranged from 56 to 66% with a mean value of 60% (Table 2). Irrespective of Zn supply, shoot dry matter production was clearly lower in wild diploid *T. monococcum* ssp. *boeoticum* than in cultivated diploid *T. monococcum* ssp. *monococcum* (Table 2).

TABLE 2. *Effect of variation in Zn supply (+Zn; 5 mg kg^{-1} soil) on leaf symptoms of Zn deficiency, shoot dry weight, and Zn efficiency of different diploid* (T. monococcum), *tetraploid* (T. turgidum) *and hexaploid* (T. aestivum) *wheats grown for 44 d in a Zn-deficient calcareous soil*

Species	Accession or cultivar	Deficiency symptoms*	Shoot dry weight (g per plant)		Zn efficiency** (%)
			−Zn	+Zn	
Diploid, *T. monococcum* (AA)					
ssp. *monococcum*	FAL-45	3·5	0·82 ± 0·09	1·45 ± 0·06	57
ssp. *monococcum*	TMM-03	3·3	0·68 ± 0·03	1·17 ± 0·06	58
ssp. *monococcum*	FAL-29	3·7	0·69 ± 0·06	1·15 ± 0·11	60
ssp. *monococcum*	FAL-31	4·0	0·72 ± 0·07	1·20 ± 0·07	60
ssp. *boeoticum*	TMB-02	4·0	0·39 ± 0·04	0·70 ± 0·05	56
ssp. *boeoticum*	TMB-03	3·7	0·55 ± 0·08	0·84 ± 0·04	66
MEAN		3·7	0·64	1·09	60
Tetraploid, *T. turgidum* (BBAA)					
ssp. *dicoccoides*	TTD-01	1·5	0·28 ± 0·07	1·61 ± 0·39	17
ssp. *dicoccoides*	TTD-02	1·0	0·43 ± 0·10	1·70 ± 0·73	25
ssp. *dicoccoides*	TTD-04	1·0	0·44 ± 0·13	1·29 ± 0·32	34
ssp. *dicoccoides*	TTD-05	2·0	0·69 ± 0·07	1·44 ± 0·15	47
ssp. *dicoccum*	FAL-03	1·3	0·72 ± 0·11	1·90 ± 0·13	38
ssp. *dicoccum*	FAL-02	2·0	0·96 ± 0·13	1·80 ± 0·09	53
ssp. *polonicum*	TTP-03	1·3	0·53 ± 0·03	1·91 ± 0·13	28
ssp. *polonicum*	FAL-17	1·0	0·66 ± 0·08	1·54 ± 0·12	43
ssp. *polonicum*	FAL-11	1·5	0·82 ± 0·16	1·83 ± 0·19	45
ssp. *durum*	Kunduru	1·5	0·53 ± 0·13	1·81 ± 0·16	29
MEAN		1·4	0·61	1·69	36
Hexaploid, *T. aestivum* (BBAADD)					
ssp. *compactum*	TAC-01	3·5	0·90 ± 0·04	1·39 ± 0·11	65
ssp. *compactum*	Germany	3·5	1·19 ± 0·14	1·59 ± 0·04	75
ssp. *sphaerococcum*	TAP-01	2·5	0·45 ± 0·03	0·92 ± 0·08	50
ssp. *sphaerococcum*	TAP-03	2·5	0·96 ± 0·08	1·43 ± 0·08	67
ssp. *spelta*	TAS-03	2·5	0·89 ± 0·15	1·59 ± 0·14	56
ssp. *spelta*	TAS-01	3·5	1·31 ± 0·16	1·84 ± 0·22	72
ssp. *spelta*	TAS-06	3·5	1·36 ± 0·09	1·76 ± 0·16	77
ssp. *aestivum*	BMDE-10	1·7	0·71 ± 0·11	1·53 ± 0·16	46
ssp. *aestivum*	Bezostaja	3·0	1·07 ± 0·15	1·38 ± 0·05	78
MEAN		3·0	0·98	1·49	65

* Severity of deficiency symptoms (necrotic patches on leaf blade); 1: very severe; 5: very slight or absent.
** Zn efficiency = (Dry weight at −Zn/Dry weight at +Zn) × 100.
Data represent means of three replications ± s.d.

Compared with diploid wheats, leaf symptoms of Zn deficiency occurred more rapidly and severely in tetraploid wheats (Fig. 1, Table 2). Consequently, decreases in shoot dry matter production due to Zn deficiency were greater in tetraploid than diploid wheats. On average, Zn deficiency resulted in a 2·8-fold decrease in shoot dry matter production of tetraploid wheats. Compared with diploid wheats, the shoot dry weight of tetraploid wheats was higher with additional Zn, but tended to be lower under Zn-deficient conditions (Table 2). Among and within the subspecies of tetraploid wheats there was little difference in severity of Zn deficiency symptoms; however there was a greater range of Zn efficiency (Table 2). The susceptibility of the cultivated durum wheat cultivar 'Kunduru-1149' to Zn deficiency was very similar to those of other tetraploid wheats (Table 2). Hexaploid wheats closely resembled diploid wheats in relation to the severity of Zn deficiency symptoms, and the Zn efficiency ratio (Table 2). Among the subspecies of hexaploid wheats, variation in Zn efficiency was small, with the exception of the modern hexaploid cultivars 'Bezostaja' and 'BDME-10'. As under field conditions, 'Bezostaja' and 'BDME-10' showed lower and higher sensitivity to Zn deficiency, respectively (Table 2).

Differences in Zn efficiency between the accessions were not related to either Zn concentration or content in seeds (Table 3). The wild tetraploid wheats (ssp. *dicoccoides*), with very low Zn efficiency (Table 2), had the second highest seed concentrations and contents of Zn among all subspecies (Table 3), and wild wheats in general had much more seed Zn than advanced and modern cultivated wheats. The cultivated hexaploid wheat 'Bezostaja', which is well adapted to Zn-deficient soils in Central Anatolia, contained the lowest Zn concentration (Table 3) but had the highest Zn efficiency of all the genotypes (Table 2).

Under Zn-deficient conditions, the concentrations of Zn in shoots were similar for diploid, tetraploid and hexaploid wheats, and averaged 5·9 mg kg^{-1} d. wt for diploids, 5·5 mg kg^{-1} d. wt for tetraploids and 6·1 mg kg^{-1} d. wt for hexaploids (Table 4). Zinc supply greatly increased the Zn concentrations of the plants. As found under Zn deficiency, the Zn concentrations of diploid, tetraploid and hexaploid wheats were similar when supplied with additional Zn

TABLE 3. *Concentration and content of Zn in seeds of diploid, tetraploid and hexaploid wheats used in the experiment*

Species	Accession or cultivar	Zn concentration (mg kg^{-1} d. wt)	Zn content (μg $seed^{-1}$)
Diploid, *T. monococcum* (AA)			
ssp. *monococcum*	TMM-03	48 ± 2	1·19 ± 0·12
ssp. *monococcum*	FAL-29	38 ± 4	0·91 ± 0·09
ssp. *monococcum*	FAL-31	29 ± 1	0·84 ± 0·02
ssp. *monococcum*	FAL-45	36 ± 0	1·15 ± 0·00
ssp. *boeoticum*	TMB-03	154 ± 6	2·15 ± 0·09
ssp. *boeoticum*	TMB-02	121 ± 5	1·00 ± 0·04
MEAN		71	1·21
Tetraploid, *T. turgidum* (BBAA)			
ssp. *dicoccoides*	TTD-05	117 ± 4	3·26 ± 0·12
ssp. *dicoccoides*	TTD-02	113 ± 6	2·92 ± 0·17
ssp. *dicoccoides*	TTD-01	122 ± 10	3·09 ± 0·02
ssp. *dicoccoides*	TTD-04	114 ± 11	3·71 ± 0·43
ssp. *dicoccum*	FAL-02	30 ± 4	1·73 ± 0·17
ssp. *dicoccum*	FAL-03	44 ± 1	2·13 ± 0·01
ssp. *polonicum*	TTP-03	39 ± 2	1·05 ± 0·07
ssp. *polonicum*	FAL-11	37 ± 3	1·81 ± 0·14
ssp. *polonicum*	FAL-17	36 ± 2	1·64 ± 0·08
ssp. *durum*	Kunduru	11 ± 1	0·45 ± 0·04
MEAN		66	2·18
Hexaploid, *T. aestivum* (BBAADD)			
ssp. *compactum*	TAC-01	26 ± 5	0·63 ± 0·03
ssp. *compactum*	Germany	30 ± 14	1·53 ± 0·32
ssp. *sphaerococcum*	TAP-03	31 ± 0	1·07 ± 0·00
ssp. *sphaerococcum*	TAP-01	73 ± 9	3·41 ± 0·43
ssp. *spelta*	TAS-01	33 ± 10	0·82 ± 0·18
ssp. *spelta*	TAS-06	31 ± 3	1·08 ± 0·11
ssp. *spelta*	TAS-03	34 ± 3	1·65 ± 0·14
ssp. *aestivum*	Bezostaja	13 ± 1	0·57 ± 0·04
ssp. *aestivum*	BDME-10	11 ± 1	0·38 ± 0·02
MEAN		31	1·24

Values are means of 3 determinants ± s.d.

(Table 4). In contrast to Zn concentrations, Zn content per shoot showed more variation among accessions or cultivars, according to shoot dry weight and Zn efficiency. The accessions with a high Zn efficiency ratio generally contained more Zn in the shoot than accessions with a low Zn efficiency (Table 4). However, in some Zn-efficient accessions with lower growth rates, high Zn efficiency was not associated with higher Zn content, for example, *T. monococcum* ssp. *boeoticum* (Table 2 and 4). Nevertheless, the Zn content of plants was better correlated with Zn efficiency than was Zn concentration (Fig. 2).

DISCUSSION

Diploid and hexaploid wheat accessions showed higher resistance to Zn deficiency, and had greater Zn efficiency ratios than the tetraploid wheat accessions (Table 2, Fig. 1). With additional Zn, tetraploid wheats produced, on average, the highest shoot dry weight per plant, whereas diploid wheats had the lowest shoot dry weight (Table 2). These results are similar to the findings of Bamakhramah, Halloran and Wilson (1984). However, under Zn-deficient conditions, tetraploid wheats showed the lowest shoot growth, indicating the very low Zn efficiency of tetraploid wheats.

Such low Zn efficiency has also been found in a number of cultivated durum wheat cultivars (Rengel and Graham, 1995*a*; Cakmak *et al*., 1996*b*, 1997*b*). Durum wheat cultivars also showed the lowest Zn efficiency in comparisons of different cultivars of rye, triticale, barley, oat and bread wheat (Cakmak *et al*., 1998, 1999*a*; Ekiz *et al*., 1998). The reason for the high sensitivity of tetraploid wheats to Zn deficiency is not well understood, but it is possibly related to slow release of Zn-mobilizing organic compounds (i.e. phytosiderophores) from roots (Cakmak *et al*., 1994, 1996*a*; Rengel, Marschner and Römheld, 1998) and the low Zn uptake capacity of the roots (Rengel and Graham, 1995*a*; Cakmak *et al*., 1998), when grown with a deficient supply of Zn. Phytosiderophores have a high capacity to complex and mobilize Zn in the rhizosphere and also within plants (Treeby, Marschner and Römheld, 1989; Welch, 1995). The role of phytosiderophores in the differential expression of Zn efficiency between and within diploid, tetraploid and hexaploid wheats should be studied in future experiments. Poor utilization of Zn within the plant tissues also seems to be an important factor in the very low Zn efficiency of tetraploid wheats (Rengel, 1995; Cakmak *et al*., 1997*a*). Although mycorrhizas play an important role in improvement of the Zn nutritional status of plants (Marschner, 1995), it has recently been shown that differences in Zn efficiency between durum and bread wheat genotypes are not related to differential rates of infection of roots with mycorrhizae (I. Cakmak, unpubl. res.).

It has been suggested that high Zn efficiency is a reflection of the high concentration or content of Zn in seeds (Rengel and Graham, 1995*b*; Khan, McDonald and Rengel, 1998). In field experiments with wheat, Yilmaz *et al*. (1998) showed that increases in Zn content from 0·35 to 1·47 μg per seed enhanced grain yield very significantly in Zn-deficient calcareous soils. However, as shown in this study, high Zn concentrations in seeds are not always associated with a high Zn efficiency or high dry matter production. On average, seeds of wild tetraploid wheats (ssp. *dicoccoides*) contained 3·25 μg Zn per seed (Table 3). Despite such a remarkably high Zn content in their seeds, the very low Zn efficiency of *dicoccoides* may indicate poor 'physiological availability' of Zn in seed tissue, and thus limited retranslocation of Zn to growing points during germination and early seedling growth. Studies of the internal mobility of Zn in *dicoccoides* are currently in progress.

From the data presented in Table 3, it appears that, with the domestication and modern cultivation of wheat, seed Zn concentration has decreased. One reason for this decrease might be the observed increase in harvest index with domestication of wheat (Guzy, Ehdai and Waines, 1989; Rafi, Ehdai and Waines, 1992). It is becoming clear that micronutrient deficiencies, including Zn deficiency, are a significant global problem, affecting more than 2 billion people in the world, with serious implications for human health (Graham and Welch, 1996; Welch, Combs and Duxbury, 1997; Cakmak *et al*., 1999*b*). High consumption of cereal-based foods, of low micronutrient content, has

TABLE 4. *Effect of varied Zn supply (+Zn; 5 mg kg^{-1} soil) on concentration and content (total amount) of Zn in shoots of different diploid* (T. monococcum), *tetraploid* (T. turgidum) *and hexaploid* (T. aestivum) *wheats grown for 44 d in a Zn-deficient calcareous soil*

Species	Accession or cultivar	Zn concentration (mg kg^{-1} d. wt)		Zn content (μg per shoot)	
		−Zn	+Zn	−Zn	+Zn
Diploid, *T. monococcum* (AA)					
ssp. *monococcum*	FAL-45	6·6±1·5	25±1	5·3±1·9	36±2
ssp. *monococcum*	TMM-03	6·1±1·7	26±2	4·2±1·0	30±4
ssp. *monococcum*	FAL-29	5·5±0·6	28±1	3·8±0·3	32±3
ssp. *monococcum*	FAL-31	7·1±0·5	27±1	5·1±0·9	32±2
ssp. *boeoticum*	TMB-02	5·4±1·5	31±7	2·1±0·8	21±4
ssp. *boeoticum*	TMB-03	4·6±0·9	29±5	2·7±0·9	24±3
MEAN		5·9	28	3·9	29
Tetraploid, *T. turgidum* (BBAA)					
ssp. *dicoccoides*	TTD-01	5·7±0·7	26±1	1·6±0·5	42±9
ssp. *dicoccoides*	TTD-02	5·8±0·2	25±2	2·3±0·6	41±13
ssp. *dicoccoides*	TTD-04	4·9±0·8	26±2	2·2±0·9	34±9
ssp. *dicoccoides*	TTD-05	6·0±0·1	25±4	4·2±0·5	36±3
ssp. *dicoccum*	FAL-03	6·3±0·2	26±2	4·5±0·6	49±6
ssp. *dicoccum*	FAL-02	5·5±0·3	27±4	5·3±1·0	48±9
ssp. *polonicum*	TTP-03	4·3±0·1	21±1	2·3±0·2	40±3
ssp. *polonicum*	FAL-17	6·4±0·2	26±2	4·2±0·3	40±6
ssp. *polonicum*	FAL-11	4·6±0·2	21±2	3·8±0·7	39±6
ssp. *durum*	Kunduru	5·6±0·6	30±4	3·0±0·9	43±7
MEAN		5·5	25	3·3	41
Hexaploid, *T. aestivum* (BBAADD)					
ssp. *compactum*	TAC-01	6·3±0·4	26±2	5·7±0·5	37±2
ssp. *compactum*	Germany	6·7±1·1	28±2	8·0±1·7	44±5
ssp. *sphaerococcum*	TAP-01	6·5±1·0	28±3	2·9±0·3	26±7
ssp. *sphaerococcum*	TAP-03	5·7±0·5	31±2	5·2±0·4	44±6
ssp. *spelta*	TAS-03	4·8±0·2	23±1	4·3±0·8	36±3
ssp. *spelta*	TAS-01	6·1±0·4	27±2	7·9±0·9	50±5
ssp. *spelta*	TAS-06	6·4±0·7	28±2	8·7±1·0	49±6
ssp. *aestivum*	BMDE-10	5·3±0·7	28±2	3·7±1·1	43±6
ssp. *aestivum*	Bezostaja	6·7±1·1	26±3	7·1±1·2	36±4
MEAN		6·1	27	5·9	41

Data represent means±s.d. of three replications.

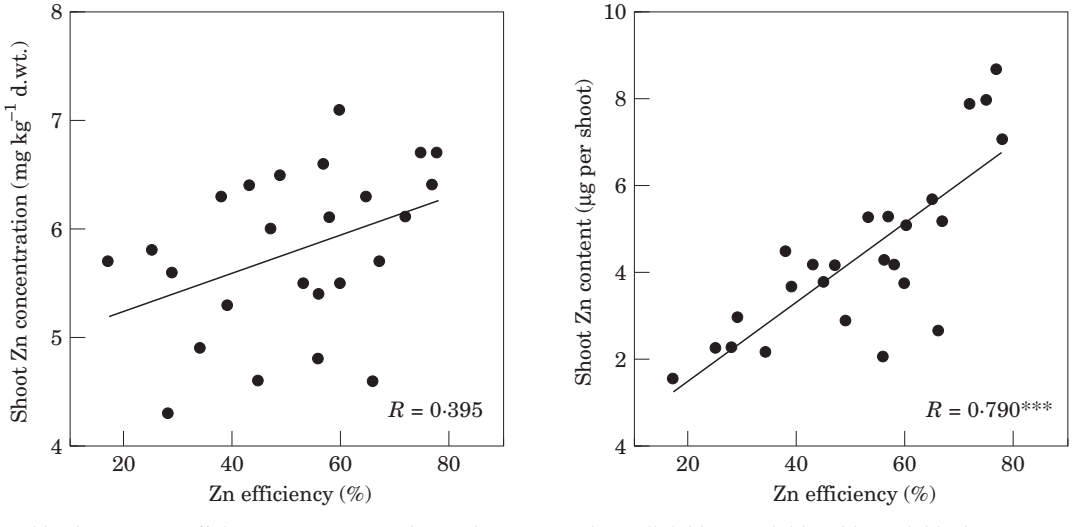


FIG. 2. Relationships between Zn efficiency, Zn concentration and Zn content in 25 diploid, tetraploid and hexaploid wheats. Data are compiled from Tables 2 and 4.

been suggested as a major reason for the widespread occurrence of micronutrient deficiency in humans, particularly in developing countries. Considering the results in Table 3, wild wheats such as *dicoccoides* and *boeoticum* may be considered to be valuable sources of genes for improved cultivated wheats with a higher Zn concentration.

The absence of the D genome in tetraploid wheat may be a reason for its low Zn efficiency. A recent study, using disomic *T. durum—T. aestivum* (Langdon-Chinese Spring) substitutions showed that none of the chromosomes of the D genome from hexaploid wheat could improve the Zn efficiency of tetraploid wheat (Schlegel and Cakmark, 1998). Thus, genes responsible for the expression of Zn efficiency appear to be located on several chromosomes of the D genome. Accordingly, transfer of the whole D genome from *Aegilops tauschii* (the source of the D genome of hexaploid wheat) to tetraploid wheat greatly improved root, and especially shoot, growth under Zn-deficient, but not under Zn-sufficient conditions (Cakmak *et al*., 1999*a*).

Interestingly, diploid wheats, which have only the A genome, showed higher Zn efficiency than tetraploid wheats which have the A and B genomes (Fig. 1, Table 2). Such different reactions of A genomes in diploid and tetraploid wheats are also known for salt tolerance. Gorham (1990) showed that tetraploid wheats possess higher salt sensitivity than diploid wheats, and suggested that the A genome of tetraploid wheat might be different from the A genome of diploid wheat, possibly due to modification of the A genome in tetraploid wheat during evolution.

Lack of expression of Zn efficiency genes in tetraploid wheat might also be related to the existence of suppressor genes for Zn efficiency in the B genome. This point needs to be clarified in future experiments. Recent results suggest the involvement of the A genome as a source of Zn efficiency genes: in studies with Chinese Spring and its nulli-tetrasomic aneuploids, it was shown that, among the A, B and D genomes, the chromosomes of the A genome contributed most to high Zn efficiency (Schlegel and Cakmak, 1998). The *T. monococcum*-derived expression of high Zn efficiency in synthetic hexaploid wheat (Cakmak *et al*., 1999*a*) was also demonstrated.

It appears that, like the D-genome donor, *A. tauschii*, A-genome donors, *T. boeoticum* and *T. monococcum*, represent an important source of Zn efficiency genes, that may be used to improve the performance of cultivated wheats under Zn-deficient conditions.

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