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ORIGINAL ARTICLE

Genotypic variation in phosphorus efficiency between wheat cultivars grown under greenhouse and field conditions

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Abstract

Phosphorus (P) efficiency (relative growth), which is described as the ratio of shoot dry matter or grain yield at deficient P supply to that obtained under adequate P supply, was compared in 25 winter wheat cultivars grown under greenhouse and field conditions with low and adequate P levels in a P-deficient calcareous soil. Adequate P supply resulted in significant increases in shoot dry weight and grain yield under both experimental conditions. In the greenhouse experiment, the increases in shoot dry weight under adequate P supply (80 mg kg^{-1}) were from 0% (cv: C-1252) to 34% (cv: Dagdas). Under field conditions, the cultivars showed much greater variation in their response to adequate P supply (60 kg ha^{-1}): the increases in shoot dry weight and grain yield with adequate P supply were between –2% (cv: Sivas-111/33) and 25% (cv: Kirac-66) for shoot dry matter production at the heading stage and between 0% (cv: Kirkpinar-79) and 76% (cv: Kate A-1) for grain yield at maturity. Almost all cultivars behaved totally different in their response to P deficiency under greenhouse and field conditions. Phosphorus efficiency ratios (relative growth) under greenhouse conditions did not correlate with the P efficiency ratios under field conditions. In general, durum wheat cultivars were found to be more P efficient compared with bread wheat cultivars. The results of this study indicated that there is wide variation in tolerance to P deficiency among wheat cultivars that can be exploited in breeding new wheat cultivars for high P deficiency tolerance. The results also demonstrated that P efficiency was expressed differently among the wheat cultivars when grown under greenhouse and field conditions and, therefore, special attention should be paid to growth conditions in screening wheat for P efficiency.

Key words: genotypic variation, P deficiency, P efficiency, wheat cultivars.

INTRODUCTION

Phosphorus (P) availability in most acid and calcareous soils is very low, limiting crop production, because of the formation of sparingly soluble phosphate compounds with either Al or Fe in acidic, or with Ca in alkaline, soils (Marschner 1995). It is estimated that more than 30% of soils cultivated globally suffer from P deficiency stress, and that the world reserves of P might be depleted by 2050 (Batjes 1997; Vance *et al.* 2003). Phosphorus deficiency is also a critical nutritional problem in Turkey. In one survey, 60% of 1511 soil samples collected from different parts of Turkey showed very low levels of plant available P (Eyupoglu 1999; Gokmen and Sancar 1999). High pH and $CaCO_3$ and low levels of organic matter together with low rainfall are the main factors responsible for the low availability of P to plants in Turkish soils.

It is widely accepted that the most realistic solution to the problem of P deficiency in cultivated soils is to develop new plant cultivars that can adapt to P-deficient soils. Thus, the development of P-efficient genotypes with a greater ability to grow and yield under P-deficient soil conditions is an important goal in plant breeding (Ozturk *et al.* 2005; Rengel 1999). The adaptation of plants to P-deficient soils is related to the development of mechanisms in the rhizosphere and/or at the cellular level, including changes in rhizosphere pH, release of organic compounds, increases in root surface area and the efficient use of P at the cellular level (Gahoonia and Nielsen 2004; Lynch and Brown 2001; Raghothama and Karthikeyan 2005; Rengel and

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Marschner 2005) and increased production and secretion of phosphatases to the rhizosphere (Gaume *et al.* 2001; Wasaki *et al.* 2003; Yun and Kaeppler 2001). Plant species, and also cultivars of a given plant species, differ greatly in their response to P deficiency in soils. In the case of wheat, genotypic variation in P efficiency is well documented in the literature (Gahoonia *et al.* 1999; Manske *et al.* 2000; Mittal and Sethi 2005; Osborne and Rengel 2002; Ozturk *et al.* 2005). In the present study, P efficiency is defined as the ability of cultivars to yield better under P deficient conditions, and was calculated as the ratio of shoot dry matter or grain yield at the deficient P supply to that obtained
4 under adequate P supply (Graham 1984; Ozturk *et al.* 2005)

According to Gerloff (1977) plant genotypes can be classified into four groups with respect to their response to nutrient deficiency: (1) efficient responders: plants producing high yields at low levels of nutrition and showing high response to nutrient additions, (2) inefficient responders: plants producing low yields at low levels of nutrition and showing high response to added nutrients, (3) efficient non-responders: plants producing high yields at low levels of nutrition but not responding to nutrient addition, (4) inefficient non-responders: plants producing low yields at low levels of nutrition and also showing low response to nutrient additions.

Despite the existence of large genotypic variation in P efficiency, the mechanisms affecting the high expression of P efficiency in wheat and other crop species are not well understood. One major reason for the poor clarification of the P efficiency mechanism is related to the number of cultivars used in P efficiency studies. In most cases, only a few wheat cultivars are used for screening P efficiency and for the characterization of P efficiency mechanisms (Fageria and Baligar 1999; Gahoonia *et al.* 1999; Horst *et al.* 1996; Yao *et al.* 2001). According to Ozturk *et al.* (2005), P efficiency mechanisms can differ from one genotype to other within a given plant species. Therefore, to better understand and characterize P efficiency mechanisms, a large number of cultivars are needed for screening. Another concern in studies dealing with P efficiency is the environment used for screening. Very little information is available on the effect of the growth medium (soil or nutrient solution culture) and the environment (field and greenhouse) on genotypic variation for P efficiency between cultivars. According to Caradus (1994), genotypic variation for P efficiency between white clover cultivars under greenhouse conditions is not identical and is poorly correlated with the variation found under field conditions. Recently, by using only two wheat cultivars, Hayes *et al.* (2004) showed that screening in nutrient solution culture is not reliable for P efficiency differences found in soil culture. These studies using only a few genotypes indicate that the P efficiency results obtained under controlled greenhouse or growth chamber conditions cannot be used for field conditions. It is, therefore, important to use large numbers of genotypes growing in both greenhouse and field conditions. In the present study, 25 wheat cultivars were used to test their response to P deficiency under both greenhouse and field conditions. The wheat cultivars were evaluated based on shoot dry matter production, grain yield, the concentration and content (total amount) of P in the shoots and P efficiency (relative growth).

MATERIALS AND METHODS

Wheat cultivars

A total of 25 wheat cultivars (20 bread, *Triticum aestivum*, and 5 durum wheat, *Triticum durum*) were used in the greenhouse and field experiments. These cultivars were developed for the Central Anatolia region, where soils are calcareous and precipitation is very low (long-term average: 320 mm).

Greenhouse experiment

A pot experiment was carried out using plastic pots (11.5 cm diameter and 17.5 cm depth) holding 1600 g air-dried soil taken from the field experiment site. The physical and chemical characteristics of the soil used in the pot experiment were as follows: texture, clay loam (31% clay, 42% silt and 27% sand); $CaCO_3$, 21%; pH (1:2.5 water), 8.0; electrical conductivity (EC), 0.20 mS cm^{-1}; organic matter, 1.8%; total N, 0.18%. The plant available ($NaHCO_3$ extractable) P was 6.50 mg kg^{-1}. The experimental design was a two factor completely randomized design with four replications. Plants were supplied with 20 mg kg^{-1} P (low P) and 80 mg kg^{-1} P (adequate P) in the form of KH_2PO_4. Potassium in all treatments was adjusted to 100 mg kg^{-1} K with K_2SO_4. A basal treatment of 200 mg N kg^{-1} as $Ca(NO_3)_2 \cdot 4H_2O$ was applied to all pots. All nutrients were mixed thoroughly with the soil before seed sowing. Fifteen seeds from each wheat cultivar were sown in each pot and thinned to twelve after emergence. The water content of the soil was maintained at 75% of field capacity gravimetrically by adding water daily. After 49 days of growth in the greenhouse, the shoots were harvested and dried at 80°C. After the determination of dry weight (expressed as mg $plant^{-1}$), the plants were ground and digested for P analysis.

Field experiment

Using the same wheat cultivars as those used in the pot experiment, a field experiment was conducted in the 1999–2000 cropping season under rainfed conditions

at the Research and Experiment Station of the Faculty of Agriculture, Ankara University. The total precipitation during the vegetation period was approximately 290 mm. Seeds were sown at the start of October 1999 in 6 m^2 (1.2 m × 5 m) plots using an experimental drill
5 (HEGE 75–90). The seeding rate was 120 g seed per plot. The experimental design was a two factor, randomized complete block design in strip plots with four replications. Phosphorus was applied at 30 kg ha^{-1} (low P) and 60 kg ha^{-1} P (adequate P) rates in the form of triple super phosphate. The basal fertilizer application at sowing was 40 kg N ha^{-1} as ammonium sulfate and then 6 kg N ha^{-1} was top-dressed as ammonium nitrate at the tillering stage in early spring.

At the beginning of the heading stage, 20 aboveground wheat plants from each plot were randomly selected and shoot samples were taken to measure shoot dry weight and to determine the concentration of P in
6 the shoot tissues. Plant shoot dry weight in the field experiment was expressed as g $plant^{-1}$. Plants were
7 harvested in July 2000 using an experimental machine harvester (HEGE 140) to determine grain yield.

Measurement of phosphorus

Plant shoot samples from greenhouse and field plants were washed thoroughly in deionised water, dried at 65°C until they reached a constant weight and ground for the determination of P concentration. Samples were
8 ashed at 500 ± 50°C in a muffle furnace (Heraeus) and the ash was dissolved in 3.3% HCl. Phosphorus was measured spectrophotometrically (Shimadzu UV-VIS
9 1201) following the method of Kitson and Mellon (1944). Phosphorus uptake (total amount of P) in the greenhouse study was calculated by multiplying dry weights with P concentrations.

Calculation of phosphorus efficiency

Phosphorus efficiency (PE) (relative growth or yield) of the cultivars was calculated as the ratio of yield (shoot dry weight or grain yield) at deficient P supply to the yield at adequate P supply ([shoot dry weight at low P/shoot dry weight at high P] × 100) as described by Ozturk *et al.* (2005). The cultivars were ranked as efficient if the PE values were over the mean and as inefficient when the PE values were below the mean.

Statistical analysis

The experimental data were analyzed using ANOVA and the differences were compared using the Least Significant Difference Test (LSD) with a significance level of $P < 0.05$. Regression and curve fittings were carried out with MS Excel software using the Statistical Analysis
10 ToolPak.

RESULTS

Dry matter yield and P efficiency of the cultivars in the greenhouse

Shoot dry weight of the 25 wheat cultivars grown in the greenhouse under the low P treatment ranged from 189 mg $plant^{-1}$ for cv. Yilmaz-98 to 315 mg $plant^{-1}$ for cv. Kutluk, with an average of 254 mg $plant^{-1}$ for all cultivars (Table 1). In the case of the adequate P

Table 1 Effect of P fertilization on the shoot dry weight and P efficiency of 20 bread and 5 durum wheat cultivars grown for 49 days in the greenhouse

Cultivars	Shoot dry weight (mg $plant^{-1}$) P20	Shoot dry weight (mg $plant^{-1}$) P80	P efficiency (%)
Bread wheat			
1. Gun 91	270 ± 10.7	329 ± 9.20	82
2. Ikizce 96	231 ± 3.59	280 ± 9.28	83
3. Yakar 99	226 ± 26.0	281 ± 4.73	80
4. Mizrak 98	246 ± 9.96	281 ± 7.84	88
5. Turkmen 98	282 ± 6.99	317 ± 4.85	89
6. Uzunyayla 98	279 ± 2.53	305 ± 11.3	92
7. Bezostaja	275 ± 17.1	319 ± 5.75	86
8. Gerek 79	267 ± 8.56	327 ± 15.0	82
9. Hatay 98	230 ± 8.39	258 ± 8.08	89
10. Kirac 66	277 ± 5.37	331 ± 1.93	84
11. Bolal 2973	274 ± 3.37	278 ± 26.1	99
12. Kate A-1	255 ± 18.2	286 ± 10.6	89
13. Pehlivan	260 ± 5.86	291 ± 16.2	89
14. Dagdas	216 ± 9.94	290 ± 5.02	75
15. Kirkpinar 79	246 ± 9.68	263 ± 7.20	94
16. Kirgiz	274 ± 5.41	311 ± 14.3	88
17. Kutluk	315 ± 3.07	344 ± 7.73	92
18. Sultan	269 ± 4.13	289 ± 2.74	93
19. Sivas 111/33	271 ± 7.36	293 ± 3.77	93
20. Yektay 406	274 ± 11.1	291 ± 8.82	94
Average	262	298	88
Durum wheat			
21. C-1252	225 ± 3.24	225 ± 4.52	100
22. Kiziltan 40/98	214 ± 12.6	219 ± 14.6	98
23. Altin 40/98	234 ± 3.07	245 ± 7.13	96
24. Ankara 98	248 ± 1.44	261 ± 9.41	95
25. Yilmaz 98	189 ± 16.5	208 ± 5.69	91
Average	222	232	96
General average	254 ± 3.30	285 ± 4.05	90
F-test:			
Cultivars (C): 18.02***			
P treatments (P): 103.30***			
C × P interaction: 2.22***			
Least significant difference test for interaction: 28.80			

***$P < 0.01$. Phosphorus efficiency was calculated as ([shoot dry yield at P20/shoot dry yield at P80] × 100). The data represent mean ± standard error of four independent replications with 12 plants for each replication. P20, 20 mg P kg^{-1}; P80, 80 mg P kg^{-1}.

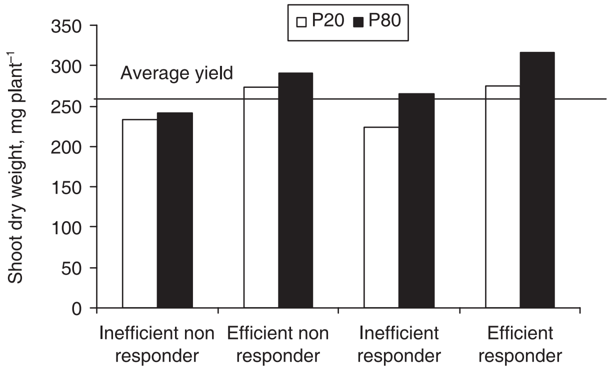

Figure 1 Nutrient efficiency response groups of 25 wheat cultivars grown in greenhouse conditions according to Gerloff (1977). Efficient means are cultivars with a shoot dry yield higher than average (254 mg plant^{-1}) and responder means are cultivars with a shoot dry yield increase higher than 10% as a result of P application. Inefficient non-responder cultivars, Kirkpinar-79, C-1252, Kiziltan-40/98, Altin-40/98 and Ankara-98; efficient non-responder cultivars, Uzunyayla, Bolal-2973, Sultan, Sivas-111/33 and Yektay-406; inefficient responder cultivars, İkizce-96, Yakar-99, Mizrak-98, Hatay-98, Dagdas and Yilmaz-98; efficient responder cultivars, Gün-91, Türkmen-98, Bezostaja, Gerek-79, Kirac, Kate A-1, Pehlivan, Kirgiz and Kutluk.

treatment shoot dry weight of the cultivars varied between 208 mg plant^{-1} for cv. Yilmaz-98 to 344 mg plant^{-1} for cv. Kutluk, with an average of 285 mg plant^{-1}. With the exception of cv. C-1252, almost all of the cultivars responded positively to P application. In general, the response of durum wheat cultivars to adequate P supply was lower than that of bread wheat cultivars (Table 1). There was significant variation in P efficiency among the wheat cultivars, ranging from 75% to 100%. When compared to bread wheat cultivars, durum wheat cultivars had a higher P efficiency ratio. Among the wheat cultivars, the lowest P efficiency ratio was found in cv. Dagdas while cv. C-1252 showed the highest P efficiency ratio (Table 1).

When the response of the cultivars to P supply and the shoot dry weight potential of the wheat cultivars at low P supply (Table 1) are taken into consideration as described by Gerloff (1977), the cultivars can be classified as follows: inefficient non-responder cultivars, Kirkpinar-79, C-1252, Kiziltan-40/98, Altin-40/98 and Ankara-98; efficient non-responder cultivars, Uzunyayla, Bolal-2973, Sultan, Sivas-111/33 and Yektay-406; inefficient responder cultivars, Ikizce-96, Yakar-99, Mizrak-98, Hatay-98, Dagdas and Yilmaz; efficient responder cultivars, Gün-91, Türkmen-98, Bezostaja, Gerek-79, Kirac, Kate A-1, Pehlivan, Kirgiz and Kutluk (Fig. 1).

Phosphorus concentration and P content of wheat cultivars in the greenhouse

The phosphorus concentration and P content (the total amount per shoot) of wheat cultivars in the shoots are presented in Table 2. All wheat cultivars grown in the low P treatment were P deficient and had lower concentrations than the widely accepted critical deficiency concentration of 2,000 mg kg^{-1} (Jones *et al.* 1991). On average, the shoot concentration and content of P in all cultivars increased by 78% and 99% with P supply, respectively. The increases in P concentration and content with P supply differed greatly between the cultivars. For example, in the case of P content, P supply enhanced the P content by 67% in cv. Sivas 111/33 and by 153% in cv. Bezostaja. The difference in the increase in P content with P supply between these cultivars is almost twofold (Table 2).

Grain yield and P efficiency of the cultivars grown under field conditions

Grain yield of wheat cultivars at low P ranged from 3,512 kg ha^{-1} for cv. Hatay-98 to 6,065 kg ha^{-1} for cv. C-1252, resulting in an average yield of 4,664 kg ha^{-1} (Table 3). With adequate P application, the range for grain yield was between 4,078 kg ha^{-1} for cv. Sivas-111/33 and 6,183 kg ha^{-1} for cv. C-1252 with an average yield of 5,568 kg ha^{-1}. Increases in grain yield with P fertilization ranged from –2% for cv. Sivas-111/33 to 76% for cv. Kate A-1 (Table 3). Genotypic variation for P efficiency was greater in the bread (57–102%) than the durum wheat (91–98%) cultivars. The most P efficient bread wheat cultivars under field conditions were cvs Kirkpinar, Sivas-111/33, Kirgiz, Dagdas and Ikizce-96, while the most inefficient bread wheat cultivars were cvs Kate A-1, Uzunyayla-98, Hatay-98, Gun-91 and Mizrak-98. As reported by Gerloff (1977), when the response of cultivars to P supply and their yield potential at low P supply (Table 3) are taken into consideration, cultivars can be classified as follows: inefficient non-responder cultivar, Sivas-111/33; efficient non-responder cultivars, Kirkpinar-79, Kirgiz, Ikizce-96, Dagdas, C-1252, Altin-40/98, Ankara-98 and Yilmaz-98; inefficient responder cultivars, Gun-91, Yakar-99, Mizrak-98, Turkmen-98, Uzunyayla-98, Gerek-79, Hatay-98, Kirac-66, Bolal-2973, Kate A-1, Kutluk, Sultan and Kiziltan-40/98; efficient responder cultivars, Bezostaja, Pehlivan and Yektay-406 (Fig. 2).

Shoot dry weight and P efficiency of wheat cultivars grown under field conditions

Shoot dry weight and P efficiency based on the shoot dry weight of 25 wheat cultivars grown in field conditions are given in Table 4. There were differences

Table 2 Effect of P fertilization on P concentration and content (total amount per shoot) of shoots of 20 bread and 5 durum wheat cultivars grown for 49 days in the greenhouse

	P concentration (mg kg^{-1} dry weight)			P content (μg shoot^{-1})		
Cultivars	P20	P80	% increase by P80	P20	P80	% increase by P80
Bread wheat						
1. Gun 91	1760 ± 12.2	3129 ± 93.3	78	474 ± 15.6	1031±41.7	118
2. Ikizce 96	1843 ± 83.4	3097 ± 55.9	68	426 ± 19.4	868 ± 32.6	104
3. Yakar 99	1689 ± 79.3	2885 ± 84.2	71	382 ± 52.5	811 ± 19.3	112
4. Mizrak 98	1625 ± 30.5	2898 ± 74.2	78	401 ± 21.8	812 ± 20.4	102
5. Turkmen 98	1580 ± 73.8	3116 ± 59.9	97	444 ± 17.2	988 ± 32.2	123
6. Uzunyayla 98	1567 ± 64.3	2538 ± 279	62	437 ± 13.7	784 ± 115	79
7. Bezostaja	1721 ± 136	3758 ± 26.6	118	473 ± 47.3	1196 ± 26.1	153
8. Gerek 79	1953 ± 48.4	3451 ± 54.2	77	520 ± 3.57	1127 ± 50.2	117
9. Hatay 98	2011 ± 59.9	3399 ± 112	69	464 ± 28.0	879 ± 54.2	89
10. Kirac 66	1915 ± 84.6	2789 ± 106	46	529 ± 19.8	922 ± 38.3	74
11. Bolal 2973	1593 ± 42.5	2776 ± 192	74	436 ± 7.12	763 ± 76.1	75
12. Kate A-1	1888 ± 96.6	3226 ± 250	71	486 ± 54.1	927 ± 95.0	91
13. Pehlivan	1548 ± 37.1	3149 ± 80.2	103	403 ± 17.2	913 ± 42.5	127
14. Dagdas	1927 ± 113	3477 ± 39.9	80	418 ± 40.3	1008 ± 23.3	141
15. Kirkpinar 79	1831 ± 84.4	3573 ± 43.8	95	450 ± 24.2	939 ± 32.8	109
16. Kirgiz	1876 ± 28.5	3335 ± 236	78	514 ± 5.41	1042 ± 97.6	103
17. Kutluk	1798 ± 43.9	3303 ± 119	84	567 ± 16.5	1136 ± 38.0	100
18. Sultan	1798 ± 55.9	3026 ± 120	68	483 ± 18.6	875 ± 41.7	81
19. Sivas 111/33	1715 ± 37.9	2641 ± 208	54	465 ± 18.0	775 ± 63.8	67
20. Yektay 406	1843 ± 21.0	3104 ± 54.7	68	505 ± 23.8	903 ± 37.9	79
Average	1774	3133	77	464	935	102
Drum wheat						
21. C-1252	1991 ± 61.6	3496 ± 171	76	448 ± 19.5	789 ± 47.7	76
22. Kiziltan 40/98	1882 ± 107	3367 ± 34.0	79	406 ± 45.5	737 ± 50.3	82
23. Altin 40/98	1824 ± 70.6	3586 ± 176	97	426 ± 11.0	882 ± 66.6	107
24. Ankara 98	1747 ± 55.8	3329 ± 97.5	91	434 ± 11.9	867 ± 10.2	100
25. Yilmaz 98	1657 ± 51.8	2570 ± 172	55	311 ± 20.5	537 ± 49.7	73
Average	1820	3270	80	405	762	88
General average	1783 ± 18.1	3161 ± 40.5	78	452 ± 7.05	896 ± 17.4	99
F-test:						
Cultivars (C)	7.51***	9.82***				
P Treatments (P)	1992.22***	1346.27***				
C × P interaction	3.32***	3.69***				
Least significant difference test for concentration: 304.81						
Least significant difference test for content: 119.63						

***$P < 0.01$. The data represent mean ± standard error of four independent replications with 12 plants for each replication. P20, 20 mg P kg^{-1}; P80, 80 mg P kg^{-1}.

among the shoot dry weight of cultivars in both the low and adequate P treatments. On average, the application of P increased shoot dry weights of all durum wheat cultivars by 7%, while this increase was 13% in bread wheat cultivars. When compared with the remaining cultivars, the response of a number of the bread wheat cultivars (Kirac-66, Ikizce-96, Kate A-1, Kutluk and Sultan) was found to be higher (Table 4). Phosphorus efficiency of durum wheat cultivars showed very little variation and ranged from 89% to 96%, while the variation in bread wheat cultivars was greater (e.g. 80–101%). The most P efficient cultivars based on shoot dry matter production in the field were Mizrak-98, Dagdas and Sivas-111/33, while the most inefficient bread wheat cultivars were Kirac-66, Ikizce-96, Kutluk and Kate A-1 (Table 4).

Phosphorus concentration and P content of wheat cultivars grown under field conditions

The phosphorus concentrations of wheat cultivars at the beginning of the heading stage in the field are presented in Table 4. At low P treatment, P concentrations

Table 3 Effect of P fertilization on grain yield and P efficiency of 25 wheat cultivars

Cultivars	Grain yield (kg ha^{-1}) P30	Grain yield (kg ha^{-1}) P60	P efficiency (%)
Bread wheat			
1. Gun 91	4071 ± 272	5633 ± 257	72
2. Ikizce 96	5520 ± 216	5979 ± 422	92
3. Yakar 99	4512 ± 391	5984 ± 487	75
4. Mizrak 98	4329 ± 102	5892 ± 190	74
5. Turkmen 98	4350 ± 497	5654 ± 240	77
6. Uzunyayla 98	3687 ± 332	5646 ± 205	65
7. Bezostaja	5188 ± 208	6179 ± 359	84
8. Gerek 79	3933 ± 213	4762 ± 293	83
9. Hatay 98	3512 ± 333	5000 ± 325	70
10. Kirac 66	4150 ± 348	4816 ± 256	86
11. Bolal 2973	4571 ± 486	5700 ± 430	80
12. Kate A-1	4167 ± 237	7316 ± 241	57
13. Pehlivan	4960 ± 264	6116 ± 223	81
14. Dagdas	5060 ± 276	5358 ± 108	94
15. Kirkpinar 79	5413 ± 459	5400 ± 520	100
16. Kirgiz	5375 ± 194	5613 ± 265	96
17. Kutluk	4570 ± 360	5960 ± 322	77
18. Sultan	4627 ± 333	5138 ± 364	90
19. Sivas 111/33	4154 ± 29.5	4078 ± 64.2	102
20. Yektay 406	4733 ± 322	5354 ± 157	88
Average	4544	5579	82
Durum wheat			
21. C-1252	6065 ± 391	6183 ± 262	98
22. Kiziltan 40/98	5081 ± 439	5596 ± 382	91
23. Altin 40/98	4588 ± 398	4977 ± 473	92
24. Ankara 98	4877 ± 327	5342 ± 104	91
25. Yilmaz 98	5119 ± 345	5544 ± 157	92
Average	5146	5528	93
General average	4664 ± 83.1	5568 ± 81.3	84
F-test			
Cultivar (C)	4.78***		
P Treatment (P)	100.04***		
C × P interaction	2.60***		
Least significant difference test for interaction: 894			

***$P < 0.01$. Phosphorus efficiency was expressed as ([grain yield at P30/grain yield at P60] × 100). The data represent mean ± standard error of four independent replications. P30, 30 kg P_2O_5 ha^{-1}; P60, 60 kg P_2O_5 ha^{-1}.

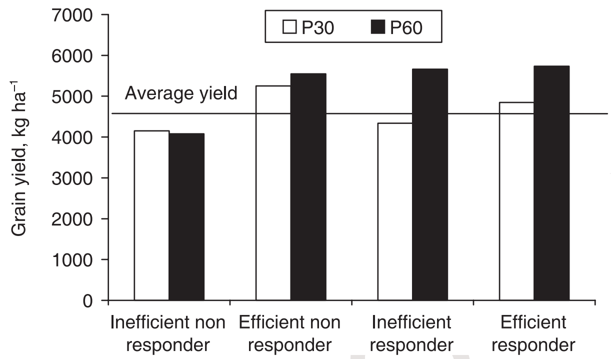

Figure 2 Nutrient efficiency response groups of 25 wheat cultivars grown under field conditions according to Gerloff (1977). Efficient means are cultivars with a grain yield higher than average (4,664 kg ha^{-1}) and responder means are cultivars with a grain yield increase higher than 10% as a result of P application. Inefficient non-responder cultivars, Sivas; efficient non-responder cultivars, Kirkpinar-79, Kirgiz, Ikizce-96, Dagdaş, C-1252, Altin-40/98, Ankara-98 and Yilmaz-98; inefficient responder cultivars, Gun-91, Yakar-99, Mizrak-98, Turkmen-98, Uzunyayla-98, Gerek-79, Hatay-98, Kirac-66, Bolal-2973, Kate A-1, Kutluk, Sultan and Kiziltan-40/98; efficient responder cultivars, Bezostaja, Pehlivan and Yektay-406.

in the shoots ranged from 1,606 mg kg^{-1} to 2,051 mg kg^{-1} with a mean of 1,837 mg kg^{-1}. The phosphorus concentration of the wheat cultivars increased slightly with adequate P supply (60 kg ha^{-1}).

DISCUSSION

Most of the P fertilizers applied to soils are converted to unavailable forms that cannot be readily absorbed by plant roots. Development of plant genotypes with a high genetic ability to use both native soil P and added fertilizer P is, therefore, very important (Cakmak 2002; Holford 1977; Rengel and Marschner 2005). To develop such genotypes in breeding programs, the existence of sufficient genotypic variation for adaptation to P-deficient soils is essential. In the present study, the wheat cultivars tested under both greenhouse and field conditions showed a wide range of variation in response to P deficiency and, thus, in P efficiency ratio (relative growth). On average, the P efficiency ratios calculated based on grain yield ranged from 57% to 92% under field conditions (Table 3), and in the case of shoot dry weight the P efficiency ratios ranged from 83% to 101% in the field and 83% to 100% under greenhouse conditions. Great variation in P efficiency between wheat cultivars was also recorded by Manske *et al.* (2000), Osborne and Rengel (2002), Wang *et al.* (2005) and Ozturk *et al.* (2005). Based on the results using 5 durum and 20 bread wheat cultivars, P deficiency tolerance was higher in durum and bread wheat cultivars (Tables 1,3). A similar result was also found by Ozturk *et al.* (2005) in greenhouse studies using 39 bread and 34 durum wheat genotypes. The reason for such differential expression of P deficiency tolerance between bread and durum wheat genotypes is unknown, but might be related to the higher seed P content of durum wheat compared with bread wheat genotypes (Ozturk *et al.* 2005). This point needs further investigation.

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When the combination of high P efficiency and high grain yield is considered for plants grown in the field, the cultivars Kirkpinar-79, C-1252, Kirgiz, Dagdas and

Table 4 Effect of P fertilization on shoot dry weight and P concentration at the beginning of the heading stage and P efficiency in the field based on the shoot dry weight of 25 wheat cultivars

	Shoot dry weight (g plant^{-1})			P concentration (mg kg^{-1})	
Cultivars	P30	P60	P efficiency (%)	P30	P60
Bread wheat					
1. Gun 91	2.11 ± 0.04	2.42 ± 0.06	87	1805 ± 29.4	1829 ± 53.9
2. Ikizce 96	1.90 ± 0.07	2.29 ± 0.05	83	1884 ± 77.6	1931 ± 119
3. Yakar 99	1.84 ± 0.08	2.06 ± 0.15	89	1991 ± 103	1952 ± 66.6
4. Mizrak 98	1.89 ± 0.04	1.87 ± 0.08	101	1666 ± 172	1858 ± 90.9
5. Turkmen 98	2.11 ± 0.08	2.31 ± 0.04	91	1858 ± 34.9	1984 ± 60.3
6. Uzunyayla 98	1.78 ± 0.07	1.93 ± 0.03	92	1665 ± 127	1878 ± 72.7
7. Bezostaja	2.41 ± 0.14	2.60 ± 0.07	93	1970 ± 34.1	2044 ± 56.8
8. Gerek 79	1.44 ± 0.11	1.69 ± 0.17	85	1606 ± 98.3	1858 ± 41.1
9. Hatay 98	2.11 ± 0.16	2.53 ± 0.11	83	1931 ± 84.6	2009 ± 112
10. Kirac 66	1.68 ± 0.07	2.10 ± 0.14	80	1965 ± 117	2014 ± 52.4
11. Bolal 2973	1.66 ± 0.04	1.81 ± 0.12	92	1679 ± 104	2083 ± 64.4
12. Kate A-1	1.99 ± 0.05	2.39 ± 0.06	83	1895 ± 33.5	1954 ± 149
13. Pehlivan	2.13 ± 0.18	2.44 ± 0.06	87	1881 ± 43.0	1739 ± 50.0
14. Dagdas	2.39 ± 0.08	2.42 ± 0.17	99	2007 ± 117	2053 ± 128
15. Kirkpinar 79	1.78 ± 0.08	2.10 ± 0.25	85	1752 ± 138	1812 ± 72.2
16. Kirgiz	1.74 ± 0.12	1.99 ± 0.17	87	1774 ± 96.1	1788 ± 62.5
17. Kutluk	1.92 ± 0.17	2.30 ± 0.07	83	1741 ± 83.0	1991 ± 50.1
18. Sultan	1.92 ± 0.04	2.29 ± 0.05	84	2051 ± 256	2146 ± 134
19. Sivas 111/33	1.51 ± 0.07	1.54 ± 0.04	98	1664 ± 203	1705 ± 126
20. Yektay 406	1.31 ± 0.06	1.38 ± 0.05	95	1934 ± 72.0	1977 ± 55.7
Average	1.88	2.12	89	1836	1930
Durum wheat					
21. C-1252	2.05 ± 0.27	2.31 ± 0.21	89	1896 ± 120	2083 ± 114
22. Kiziltan 40/98	2.00 ± 0.06	2.07 ± 0.11	97	1928 ± 126	1948 ± 25.2
23. Altin 40/98	1.95 ± 0.24	2.18 ± 0.14	89	1861 ± 70.5	2236 ± 87.7
24. Ankara 98	2.56 ± 0.03	2.67 ± 0.13	96	1679 ± 97.8	2263 ± 72.3
25. Yilmaz 98	2.19 ± 0.14	2.27 ± 0.07	96	1839 ± 138	2130 ± 63.6
Average	2.15	2.30	93	1841	2132
General average	1.93 ± 0.04	2.16 ± 0.04	90	1837 ± 23	1971 ± 20
F-test:					
Cultivars (C)	12.91***			2.32***	
P treatments (P)	44.60***			21.56***	
C × P interaction	0.63ns			1.21ns	
Least significant difference test for shoot dry weight: 0.23					
Least significant difference test for P concentration: 201.12					

ns, non significant; ***$P < 0.01$. Phosphorus efficiency was expressed as ([shoot dry weight at P30/shoot dry weight at P60] × 100). The data represent mean ± standard error of four independent replications with 20 plants for each replication. P30, 30 kg P_2O_5 ha^{-1}; P60, 60 kg P_2O_5 ha^{-1}.

Ikizce-96 were the best cultivars (Table 3) and can be recommended for P-deficient calcareous soils. Despite great variation in tolerance to P deficiency between genotypes in the greenhouse and the field, there was very little variation in shoot P concentrations (Tables 2,4), revealing a poor relationship between P efficiency and shoot P concentration in both the field and greenhouse experiments. A similar result was also reported by Fageria and Baligar (1999) and Ozturk *et al.* (2005) for different wheat cultivars. The relationship between P content (total uptake of P per shoot) and P efficiency ratios (Tables 1,2) is also very poor. For example, under P-deficient conditions, many bread wheat cultivars with a high P efficiency ratio had lower P content in the shoots than the average P efficiency value of all genotypes. These results indicate that utilization of P at the cellular level (internal P utilization efficiency) differed greatly between P-deficiency tolerant and sensitive genotypes. This is an important aspect contributing to the understanding of P efficiency mechanisms between plant genotypes (Gourley *et al.* 1994; Marschner 1995; Rengel 1999). Based on several reports there is, however, no general mechanism responsible for the expression of high P efficiency. To date, a large number of mechanisms

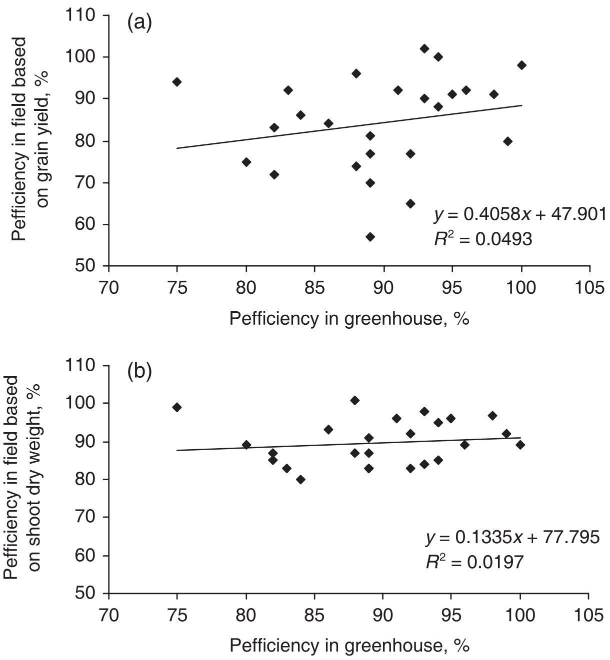

Figure 3 Relationship between the P efficiency ratios calculated based on shoot dry matter production in the greenhouse and the P efficiency ratios based on (a) grain yield and (b) shoot dry weight in the field.

for P efficiency have been reported, operating both at a cellular level and at the soil–root interface (Gourley *et al.*
13 1994; Vance *et al.* 2003; Raghothama and Karthikeyan 2005; Rengel and Marschner 2005). According to the results obtained in a wheat germplasm with 73 genotypes, P efficiency mechanisms can be totally different from one genotype to other (Ozturk *et al.* 2005). Therefore, it has been suggested that the P efficiency mechanism(s) identified in one genotype cannot be applied to other genotypes of the same or different species.

The main aim of the present work was to compare 25 wheat cultivars for their P efficiency when grown under field and greenhouse conditions in pots by using the same soil from the field. This comparison is very important because most studies dealing with P efficiency in wheat, and also in other crops, have been conducted under greenhouse or growth chamber conditions. It is quite possible that genotypical variation in P deficiency tolerance could be very different in greenhouse pot experiments compared with field conditions because of the factors discussed below. As shown in Fig. 3, there was no relationship between the P efficiency ratios (relative growth) in greenhouse and field cultivars for the same genotypes, indicating a differential response of cultivars to P deficiency under greenhouse and field conditions. The 25 wheat genotypes behaved totally different in their ability to tolerate P deficiency in the field and in the greenhouse, indicating that greenhouse pot experiments are not be useful in screening genotypes for P deficiency tolerance. Consequently, the results obtained under greenhouse conditions by growing genotypes for only a few weeks with and without adequate P supply are not useful for field conditions. A large number of studies have examined P deficiency tolerance under greenhouse conditions using plants that are only a few weeks old (Fageria and Baligar 1999; Gaume *et al.* 2001; Osborne and Rengel 2002; Ozturk *et al.* 2005; Wang *et al.* 2005). The results obtained under greenhouse conditions cannot be used in breeding programs aimed at improving P deficiency tolerance. There is a great need for verification and validation of the greenhouse results through field trials. In most greenhouse experiments only a few kilograms of soil is used in pots measuring 20–40 cm in length, resulting in extensive root binding within the pots. Such conditions are unrealistic for ranking genotypes for P deficiency tolerance. Root growth and root morphological parameters play a critical role in P acquisition (Lynch 1995; Ho *et al.* 2004; Gahoonia and Nielsen 2004) and this effect can be very different in the field compared with pots with very limited soil depth and volume. Extensive root binding and curling at the bottom of the pots can also affect microbial activity and consequently the mobilization and uptake of P in pot experiments. Obviously, these effects contributed to the differential expression of P deficiency tolerance of the same genotypes under greenhouse and field conditions. A similar observation has been made for different white clover cultivars. The response of clover cultivars to P deficiency in the field and the greenhouse was not identical (Caradus 1994). Interestingly, differences in P deficiency tolerance between two wheat cultivars growing in nutrient solution and soil cultures in pots were not the same (Hayes *et al.* 2004). All these results indicate that growth conditions greatly affect the expression of P efficiency mechanisms, and support the idea that P efficiency is a very complex phenomenon. These points need to be considered when screening genotypes for P efficiency and in the identification of P efficiency mechanisms at both physiological and molecular levels.

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