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EXPLOITATION OF GENETIC VARIABILITY AMONG WHEAT GENOTYPES FOR TOLERANCE TO PHOSPHORUS DEFICIENCY STRESS

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□ *Forty six wheat genotypes from different origins were tested at stress (25 μM P) and adequate (250 μM P) levels of phosphorus (P) developed in a modified Johnson's nutrient solution. Response of wheat genotypes for tolerance to P deficiency stress was measured at two growth stages in terms of growth, P uptake, and P utilization efficiency. Substantial differences in shoot and root growth were observed among genotypes at both stress and adequate P levels in the growth medium. Reduction in shoot biomass due to P deficiency varied from >50% to 27%. Similarly P concentration in shoot and root, P uptake, specific absorption rate of P, and P utilization efficiency varied significantly at both levels of applied P. A significant negative correlation between P stress factor and root dry weight ($r = -0.396^{**}$), shoot P uptake ($r = -0.451^{**}$), and specific absorption rate of P ($r = -0.281^{**}$, $P < 0.01$) suggested that the genotypes with greater root biomass, higher P uptake potentials in shoots, and absorption rate of P were generally more tolerant to P deficiency in the growth medium. Wheat genotypes were grouped according to the ranking order of investigated plant characteristics and shoot dry matter yield per unit of P absorbed. Genotypes Inqlab-91, SARC-II, SARC-IV, Chakwal-86, 90627, 89626, and Parvaz-94 were P efficient, while genotypes Pak-81, Pato, 88042, 88163, 89295, 4072, 89313, and 91109 were P inefficient. All other genotypes were intermediate in P use efficiency.*

Keywords: genetic variation, P absorption rate, P deficiency, P use efficiency, wheat genotype

INTRODUCTION

Plant genotypes differ widely in ultimate yield when grown at the same nutrient levels (Jones et al., 1989, 1992; Liu et al., 1997; El-Bassam, 1998;

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Wang et al., 2000; Gunes et al., 2006). These differences are the outcome of an integrated effect of many root and shoot related mechanisms (Vose, 1990; Marschner, 1995; Gahoonia and Nielsen, 1996; Wang et al., 2000). However, it is difficult to define definite plant mechanisms responsible for differential yield (Batten, 1986, 1992; Jones et al., 1989; Vose, 1990; Ozturk et al., 2005), because these mechanisms vary with kind of nutrient and plant, and many of them are still poorly understood (Clark, 1983; Vose, 1990; Gunes et al., 2006).

Due to the possibility of exploiting genotype differences for improving nutrient use efficiency, crop plants have received increased attention in recent years (Gerloff, 1987; Gill et al., 1994a, 1994b; Gahoonia and Nielsen, 1996; El-Bassam, 1998). Phosphorus (P) efficient genotypes can be useful for maintaining high productivity on low P soils (Yaseen et al., 1998; Wang et al., 2000) and in low input agriculture (CGIAR, 1988; El-Bassam, 1998). From a mineral nutrition point of view, a genotype is more efficient than others if it mobilizes and absorbs more P from soil (P acquisition efficiency), and/or makes better use of the absorbed P to produce biomass (P use efficiency) (Gahoonia and Nielsen, 1996). Improvement of P efficiency of crop plants by selection seems possible (Caradus, 1994). Additional breeding of new crop genotypes with improved P efficiency may be a supplementary alternative for reducing the traditional amendments of soils by the application of fertilizers (Batten, 1992). For successful exploitation of such alternative approaches, the knowledge on the extent of genetic variation among the existing genotypes appears to be a primary step.

The extent of variability among crop plants to acquire P is influenced by both genetic and environmental factors (Nielsen, 1983). This makes it difficult to assess genetic superiority of germplasms (Mahon, 1983). Selection under controlled conditions in solution cultures has been suggested (Wild et al., 1987) to reduce environmental effects. The present study is mainly related to the identification/selection of wheat genotypes which are tolerant to P deficiency stress in nutrient solution, and partly to identify the plant characteristics (morphological and/or physiological) by which plants of a genotype are able to grow and produce more biomass, and uptake, accumulate or concentrate relatively higher amounts of P under P stress conditions.

MATERIALS AND METHODS

A glass-house experiment was conducted at the Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad, Pakistan, in which 46 wheat cultivars and/or inbred lines (Table 1) were grown at two P levels. Healthy seeds of each wheat genotype were sown in washed gravels in iron trays. Distilled water was used to keep the seeds moist. Two week old seedlings were transplanted in holes of thermopal sheets floating on

TABLE 1 Overview of parental germplasm of wheat genotypes used to test performance at stress P level and at adequate P level with ammonium phosphate in Johnson's modified solution culture experiment

Genotype	Parentage
Chakwal-86	FORLANI/ACCICO10//ANA-75
Kohinoor-83	OREF1 158/FDL//MEXIFEN/2 × TIBA63/3/COC75
Pak-81	KVZ/BUHO//KAL/BB
Pasban-90	INIA 66/A.DISTT//INIA66/3/2* GEN81
Pato	TZPP/SON64A//NAR59
Pitic-62	YT54/NIOB 126-IC
SARC-I	LU26S, SINGLE PLANT SELECTION
SARC-II	LU26S SINGLE PLANT SELECTION
SARC-III	LYL-73(BB/NOR), SINGLE PLANT SELECTION
SARC-IV	LYL-73(BB/NOR), SINGLE PLANT SELECTION
Blue Silver	11.5-388/AN/3/YT54/NIOB//LR64
FSD-83	FURY//KAL/BB
Inqlab-91	WL711/CROW 'S'
PB-85	KVZ/TRM//PTM/ANA
Lu-26s	KHUSHAL × BLUE SILVER
Lu-31	MEXI PAK 65 × AU49
PB-96	SA42/3/CC/INIA//BB/INIA/4/CND/HD832
Parvaz-94	(V-5648)CNO 'S'/LR64//SON64/3/SON/4/PRL 'S'
SHK-95	WL 711//$F_{3.71}$/TRM
TC-4881	TISSUE CULTURED MATERIAL
TC-4884	TISSUE CULTURED MATERIAL
TC-4926	TISSUE CULTURED MATERIAL
4943	LU26S × LYALLPUR 73
6500	(LRG-2 × LU26S) (LU26S × LU26S)
88042	BOW 'S L/PRL 'S'* CM.9019-B-4B-15Y-2B-OY
88163	BUL//$F_{3.71}$/TRM
89044	$F_{3.71}$/TRM//PB.81
89053	GHK 'S'//BLS/KLT
89295	$F_{3.71}$/TRM//VRE/VEE 'S'
5039	V79143 × LU26S × LU26S
6529-11	PAK.81 × MEMB
6544-6	LU31 × PARC 1/86
4072	LU26 × V 7950/K343 × LU26S
4770	LRG-2 × LU26S
89251	BOW S' * 2/PRL 'S'
89313	BLS//$F_{3.71}$/TRM.73
91109	2814 (Y88.89)A.ACUTUM
91116	3491(Y88-89)/A.SCIRPEUM
91141	WL711/BOW 'S'
91169	GEN#3/WHEATON
91173	F134-71/CROW 'S'
88678	YAV 79
89626	DACK 'S'/RABI 'S' /4/185-1 FATESEL//61-130/LDS/3/LECOSUM21)
90627	MARRCENT
90640	YAV79/ALO 'S'//ALTAR84
91773	CHAHBA-88

aerated 1/2 strength modified Johnson's solution (Johnson et al., 1957) minus P, contained in 200 L capacity polyethylene sheet lined tubs. Phosphorus treatments were imposed by supplying 25 μM P (stress level) and 250 μM P (adequate level) in the respective tubs. Monoammonium phosphate

($NH_4H_2PO_4$) was used to establish the required P levels. Two seedlings of each genotype per hole were repeated six times. Solution pH was maintained at 6 ± 0.5. First harvest of three repeats was taken four weeks after transplanting and again the P levels were maintained in the respective tubs. Second harvest was taken one week after the first harvest. The harvested plants were washed, dried, and separated into roots and shoots. Weights of roots and shoots were recorded after drying at 70°C for 48 hours. Plant material was ground and 0.25 g was digested in tri-acid mixture of nitric acid (HNO_3), perchloric acid ($HClO_4$), and sulfuric acid (H_2SO_4) in 2:1:1 ratio for P estimation. Phosphorus was determined by molybdate-venadate yellow method (Chapman and Pratt, 1961). Plant growth and P related parameters were statistically analyzed by standard procedures described by Steel and Torrie (1980). The following parameters were calculated to explain P relations in wheat genotypes.

Phosphorus Stress Factors (PSF)

$$PSF = \frac{SDM_{adequate\text{-}P} - SDM_{stress\text{-}P}}{SDM_{adequate\text{-}P}} \times 100$$

where SDM is shoot dry matter of genotypes in gram at second harvest.

Relative Growth Rate

Relative growth rate of shoot and root (mg g^{-1} day^{-1}) was calculated as described by Hunt (1978)

$$RGR = \frac{1nH_2 - 1nH_1}{T_2 - T_1}$$

where H_1 and H_2 are shoot or root dry weights (g) at harvest time interval (days) T_1 and T_2 (day), respectively.

Phosphorus Use Efficiency (PUE)

$$\text{PUE (g DM mg} - 1 \text{ P absorbed)} = \frac{1}{\text{Total P uptake}}$$

Total P uptake is the sum of P taken up by root and shoot.

Specific Absorption Rate of P (SAR)

Specific absorption rate (μmol P g^{-1} RDM day^{-1}) was calculated as described by Hunt (1978)

$$SAR = \frac{(P_2 - P_1)}{H_2 - H_1} \times (RGR_{root})$$

where P_1 and P_2 are total P uptake (shoot + root), and H_1 and H_2 are root dry weights (g) at first and second harvest, respectively, at a given P level. RGR_{root} is the relative growth rate of root (mg g^{-1} day^{-1}).

Phosphorus Transport Rate (PTR)

Phosphorus transport rate (μmol P g^{-1} SDM day^{-1}) in wheat genotypes was calculated as described by Pitman (1972)

$$PTR = \frac{P_2S - P_1S}{H_2S - H_1S} \times (RGR_{shoot})$$

where P_1S and P_2S are shoot P uptakes, and H_1S and H_2S are shoot dry weights (g) of wheat genotypes at first and second harvest in the respective P treatments. The RGR_{shoot} is relative growth rate of shoot (mg g^{-1} day^{-1}).

Phosphorus Accumulation Rate (PAR)

Phosphorus accumulation rate (μmol P g^{-1} SDM day^{-1}) of wheat genotypes was calculated as described by Elliot and Läuchli (1985)

$$PAR = \frac{1nP_2S - 1nP_1S}{T_2 - T_1}$$

where P_1S and P_2S are shoot P uptakes at time interval (days) T_1 and T_2, respectively, at a given P level.

Specific Utilization Rate of P (SUR)

Phosphorus utilization rate (mg DM mg^{-1} P day^{-1}) of wheat genotypes was calculated as Hunt (1978)

$$SUR = \frac{W_2 - W_1}{T_2 - T_1} \times \frac{1nP_2 - 1nP_1}{P_2 - P_1}$$

where W_1 and W_2 are total dry weights (shoot + root), and P_1 and P_2 are total P uptake (shoot + root) at harvest time (days) T_1 and T_2, respectively, at a given P level.

RESULTS

Plant Biomass

Biomass production is the final output of what is metabolized from the root absorbed material from the growth medium and interaction of many other plant functions. This potential of a plant to produce biomass is markedly variable due to marked differences in the plant nutritional requirement, plant genetic makeup, and environmental conditions. Biomass was differentiated into shoot and root dry matter, total plant dry matter, and partitioning of total plant dry matter between shoot and root, i.e., root:shoot ratio. Extent of relative reduction in biomass production due to P deficiency stress can be read out through P stress factor.

Shoot Dry Matter

Shoot growth was influenced by genotype and P level, and two way interaction of genotype and P level was also significant (Table 2). Genotypes showed a wide range of differences as judged by changes in dry matter production among all genotypes (Table 3). Shoot dry matter (SDM) of all genotypes increased with increasing P level (Figure 1a), confirming the definite role of P in dry matter production. Shoot dry matter in adequate P treatment increased almost more than the double of that produced at stress P level, when P supply level was increased from 25 μM P to 250 μM P (Table 3). Plants of all genotypes were well and normal in growth as one would expect from well-managed trials without nutrient stress. Plant analysis also confirmed that plants in adequate P treatment suffered from no evident P deficiency (P > 6 mg g^{-1}, Table 3). However, plants in stress P level clearly showed P deficiency symptoms on leaves, particularly at lower leaves and leaf tips (visual observation). Plants of genotypes with higher relative reduction in SDM due to P stress indicated the responsive behavior of these genotypes to P supply (Table 3) which resulted in significant interaction of genotype × P level ($P < 0.01$). Thirty one genotypes out of 46 showed > 50% reduction in SDM, 10 genotypes showed 50–40% and only five genotypes had < 40% relative reduction in SDM due to P stress (Figure 1c). Genotypes Parvaz-94 and 91773 exhibited least (< 30%) reduction in SDM due to P stress among all the wheat genotypes. Considerable variation in SDM among all the wheat genotypes was observed at both P levels. On the basis of genotypic response to P, these genotypes were grouped into responsive efficient, responsive inefficient, and non-responsive efficient with respect to SDM production.

TABLE 2 Analysis of variance for 46 wheat genotypes grown at stress P level and at adequate P level with ammonium phosphate in Johnson's modified solution culture experiment

		Mean square												
		Plant growth parameters						P concentration			P uptake			
Source of variation	df	SDM	RDM	TDM	Root:shoot ratio	RGR_{shoot}	RGR_{root}	Shoot	Root	Shoot/root	Shoot	Root	Total	Shoot/root
Genotype	45	0.136**	0.010**	0.184**	0.015**	2219.746**	1772.505**	6.742**	0.826**	11.076**	14.696**	0.196**	16.623**	23.488**
Phosphorus level	1	51.931**	1.652**	34.203**	12.595**	101583.424**	4.696^{NS}	2347.275**	2904.535**	413.193**	10342.189**	118.581**	12701.656**	261.282**
Genotype *X* phosphorus level	45	0.097**	0.008**	0.132**	0.016**	1957.854**	1738.836**	4.054**	1.618**	10.653**	9.920**	0.155**	11.432**	18.640**
Error	184	0.025	0.004	0.038	0.009	1028.728	953.815	0.740	0.301	1.049	2.143	0.040	2.184	3.996
Total	275													

		Mean square					
Source of variation	df	PUE	SAR	PTR	PAR	SUR	PSF
Genotype	45	0.015**	11.441**	0.343**	5455.531**	186.249^{NS}	759.104**
Phosphorus level	1	5.613**	2805.759**	23.164**	136904.380**	25578.438**	—
Genotype *X* phosphorus level	45	0.013**	11.760**	0.235**	3425.892**	172.09^{NS}	—
Error	184	0.03	2.084	0.46	1226.587	167.167	114.696
Total	275						

* = $P < .05$; ** = $P < 0.01$; NS = Non-significant; SDM = Shoot dry matter; RDM = Root dry matter; TDM = Total dry matter (shoot + root); RGR_{shoot} = Relative growth rate of shoot; RGR_{root} = Relative growth rate of root; PUE = Phosphorus use efficiency; SAR = Specific absorption rate of phosphorus; PTR = Transport rate of phosphorus; PAR = Accumulation rate of phosphorus; SUR = Specific utilization rate of phosphorus; PSF = Phosphorus stress factor.

TABLE 3 Highest and lowest dry matter (DM) weights, root:shoot ratio, relative growth rate, and P uptake for 46 wheat genotypes grown at stress P level and at adequate P level with ammonium phosphate in Johnson's modified solution culture experiment

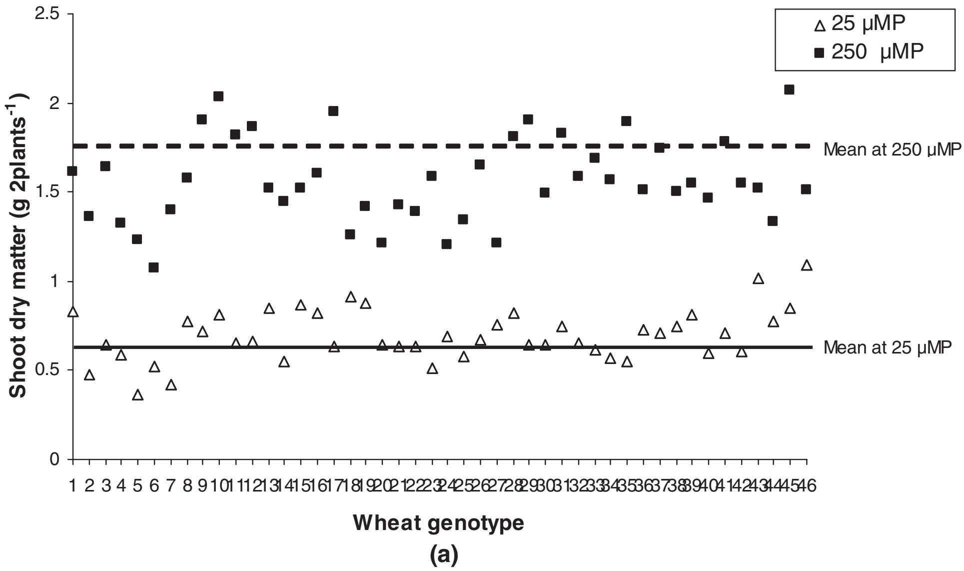
	Average (range) for DM and P related parameters in P treatments[z]	
Plant part/parameter	250 μM P	25 μM P
Dry matter	(g 2 plant^{-1})	
Shoot	1.56 (1.07–2.07)	0.70 (0.36–1.09)
Root	0.24 (0.18–0.32)	0.39 (0.24–0.55)
Total (shoot + root)	1.80 (1.25–2.38)	1.09 (0.60–1.52)
Root:shoot ratio	0.15 (0.11–0.20)	0.58 (0.40–0.87)
Phosphorus stress factor	—	54.2 (27.1–70.7)
Relative growth rate	(mg g^{-1} day^{-1})	
Shoot	99.8 (56.0–176.7)	61.4 (24.7–130.3)
Root	58.8 (16.7–132.0)	59.1 (4.3–110.7)
P concentration	(mg g^{-1})	
Shoot	9.67 (6.51–13.19)	3.84 (2.35–5.26)
Root	7.85 (6.26–8.96)	1.38 (0.43–2.60)
Shoot:root ratio	1.2 (0.8–1.6)	3.42 (1.50–9.80)
P uptake	(g 2 plant^{-1})	
Shoot	14.88 (10.12–21.21)	2.64 (1.42–4.56)
Root	1.84 (1.28–2.45)	0.53 (0.14–0.90)
Total (shoot + root)	16.73 (11.71–23.35)	3.17 (1.73–5.31)
Shoot:root ratio	8.26 (5.52–10.96)	6.31 (2.58–19.49)

[z]Values outside the parenthesis are mean while values within parenthesis are minimum and maximum attained by genotypes.

Differential response in respect of SDM to P supply impact depicted genetic variability among the genotypes. However, for purposes of revealing possible adaptation to P deficiency stress, the critical and meaningful source of variation in the ANOVA was the interaction of genotype × P level (Table 2). This interaction was found to be highly significant ($P < 0.01$). Shoot dry matter ranged from 0.36 to 1.09 g 2 plants^{-1} and 1.07 to 2.07 g 2 plants^{-1} at stress and adequate P levels, respectively (Table 3). Genotypes with the greatest SDM were 91773, 89626, and Parvaz-94 at stress P level, while Lu-26s, SARC-IV, PB-96, 89295, FSD-83, and 89251 were at adequate P level.

Root Dry Matter

Root dry matter (RDM) was markedly influenced by P supply, and treatment effects on RDM were significant for genotype, P level, and genotype × P level interaction (Table 2). In contrast to SDM, the RDM was greater in P stress conditions than in adequate P supply (Table 3). All the genotypes reduced their RDM with increase in P supply, but this reduction was to a varying extent. Averaged over 46 wheat genotypes, there was about 63% reduction in RDM.



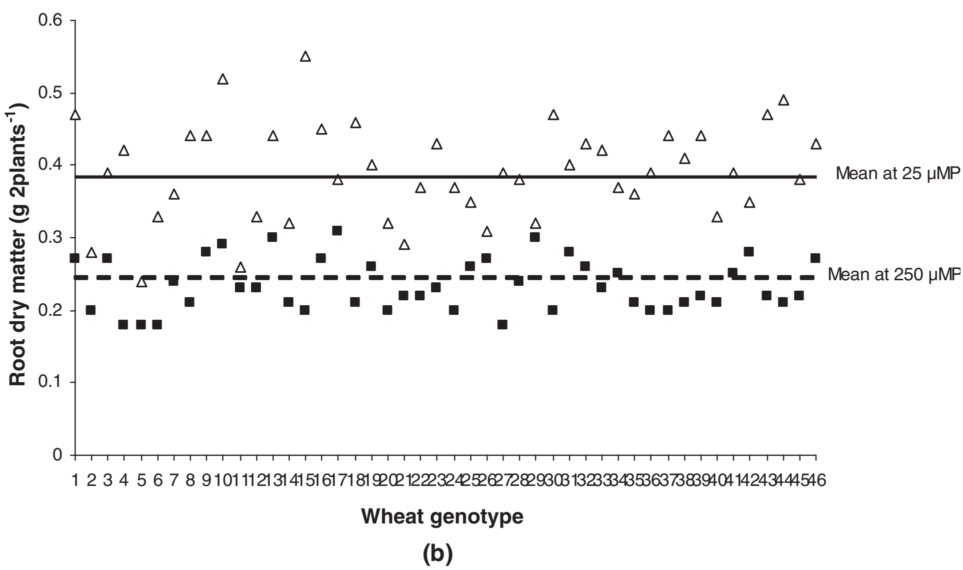


FIGURE 1 Variation in response of whet genotypes for (a) shoot dry matter, (b) root dry matter, (c) relative reduction in growth, (d) total plant dry matter, (e) root:shoot ratio, (f) relative growth rate of shoot, (g) relative growth rate of root, (h) phosphorus concentration in shoot, (i) phosphorus concentration in root, (j) phosphorus concentration in shoot:phosphorus concentration in root ratio, (k) phosphorus uptake in shoot, (l) phosphorus uptake in root, (m) total phosphorus uptake, (n) phosphorus uptake in shoot:phosphorus uptake in root ratio, (o) phosphorus use efficiency, (p) specific absorption rate of phosphorus, (q) phosphorus transport rate, (r) phosphorus accumulation rate, and (s) specific utilization rate of phosphorus, with mean values at stress P level (25 μM P) and at adequate P level (250 μM P) in a Johnson's modified solution culture experiment. The 46 genotypes are: 1) Chakwal 86, 2) Kohinoor-83, 3) Pak-81, 4) Pasban-90, 5) Pato, 6) Pitic-62, 7) SARC-I, 8) SARC-II, 9) SARC-III, 10) SARC-IV, 11) Blue Silver, 12) FSD-83, 13) Inqlab-91, 14) PB-85, 15) Lu-26s, 16) Lu-31, 17) PB-96, 18) Parvaz-94, 19) SHK-95, 20) TC-4881, 21) TC-4884, 22) TC-4926, 23) 4943, 24) 6500, 25) 88042, 26) 88163, 27) 89044, 28) 89053, 29) 89295, 30) 5039, 31) 6529-11, 32) 6544-6, 33) 4072, 34) 4770, 35) 89251, 36) 89313, 37) 91109, 38) 91116, 39) 91141, 40) 91169, 41) 91173, 42) 88678, 43) 89626, 44) 90627, 45) 90640, and 46) 91773. *(Continued)*

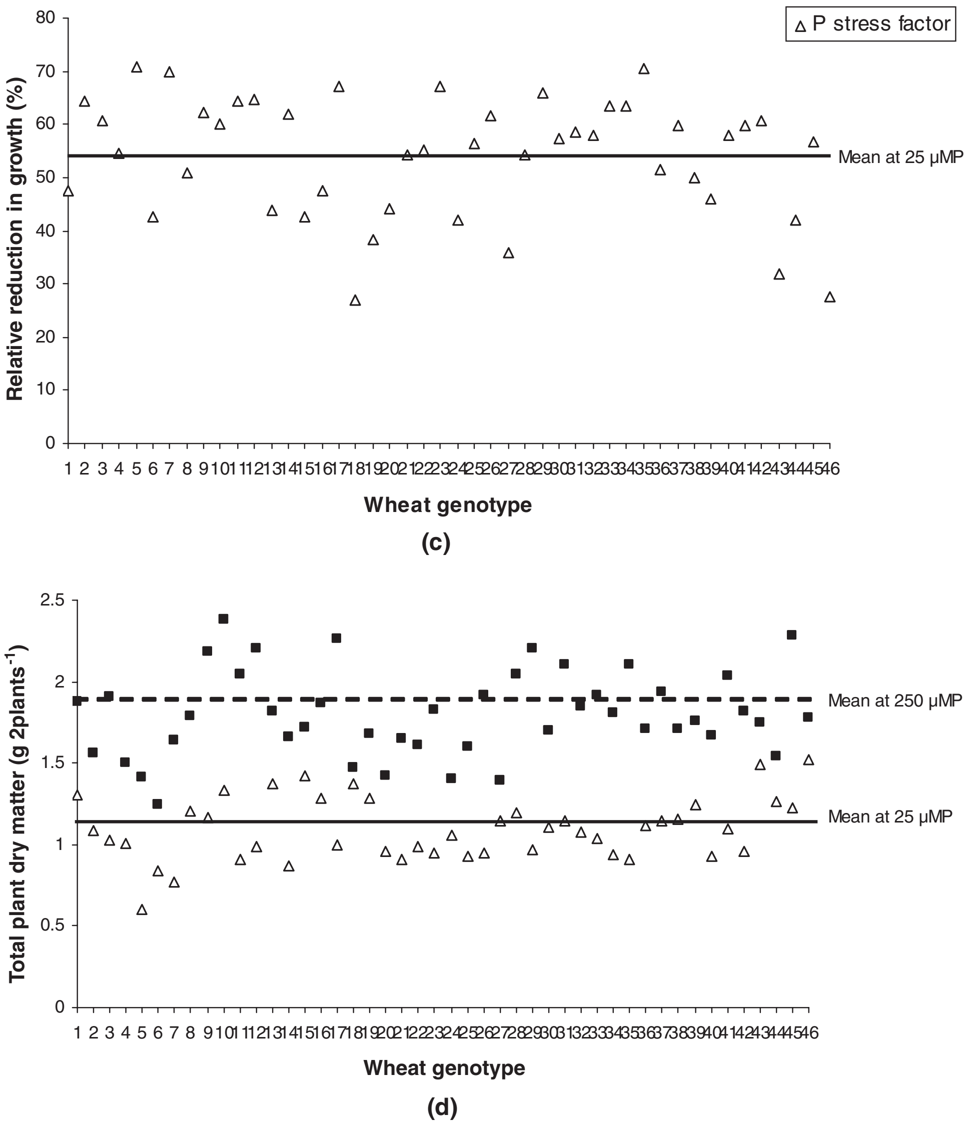
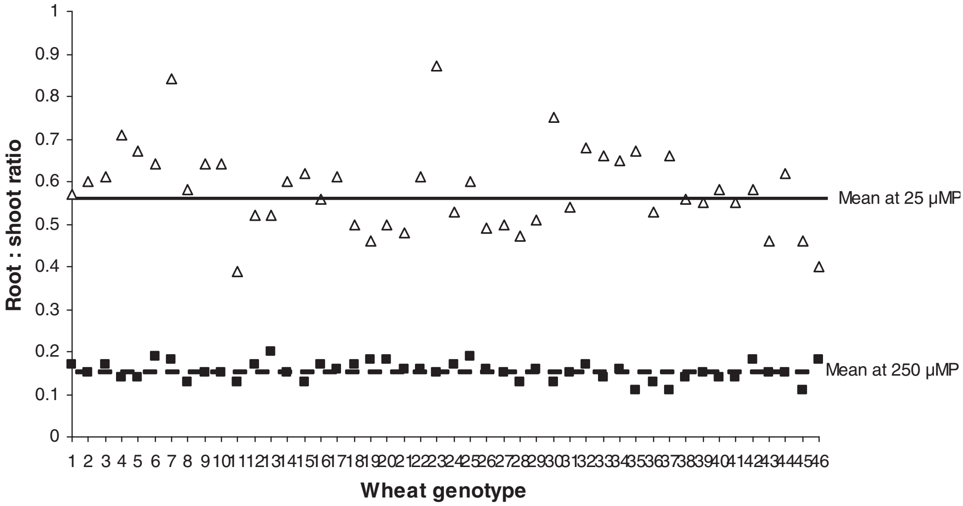


FIGURE 1 (Continued)

Although differential and substantial growth of root was observed at both P levels by increasing the P supply, considerable genotypic variation elucidated the adaptation of wheat genotypes to P stress by increased root growth (Figure 1b). Wheat genotype Lu-26s exhibited significantly the highest and marked increase in RDM in stress P treatment and reverse was observed in adequate P treatment. At stress P level, RDM ranged between 0.24 and 0.55 g 2 plants^{-1}, while at adequate P level it ranged between 0.18 and 0.32 g 2plant^{-1} (Table 3). It was also observed that genotypes with larger RDM at



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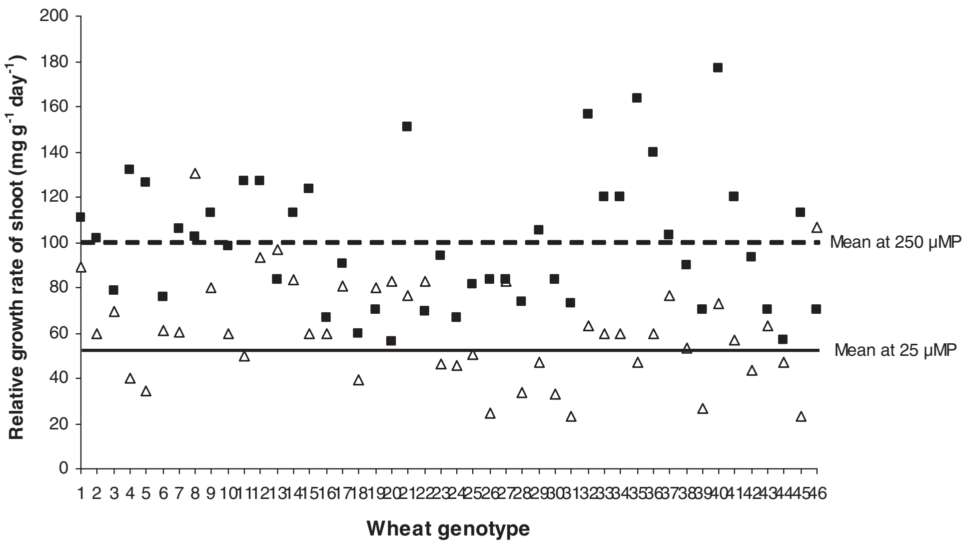

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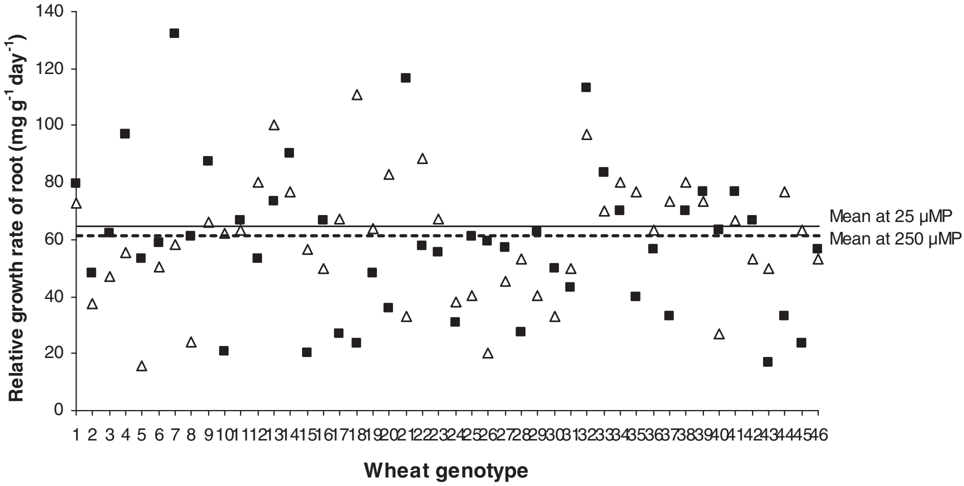
FIGURE 1 (Continued)

stress P level had relatively lower reduction in SDM, indicating one way of adaptation to low P supply and to explore more volume for P acquisition. Response of root biomass to P supply was greater in terms of less root growth and more shoot growth. At the low P supply level, overall genotypes showed significant increase in RDM production. This increase had consequences to identify efficient wheat genotypes, i.e., Lu-26s, Chakwal-86, SARC-II, III and IV, Parvaz-94, Lu-31, 5039, 91109, 89626, 90627, and 91773.



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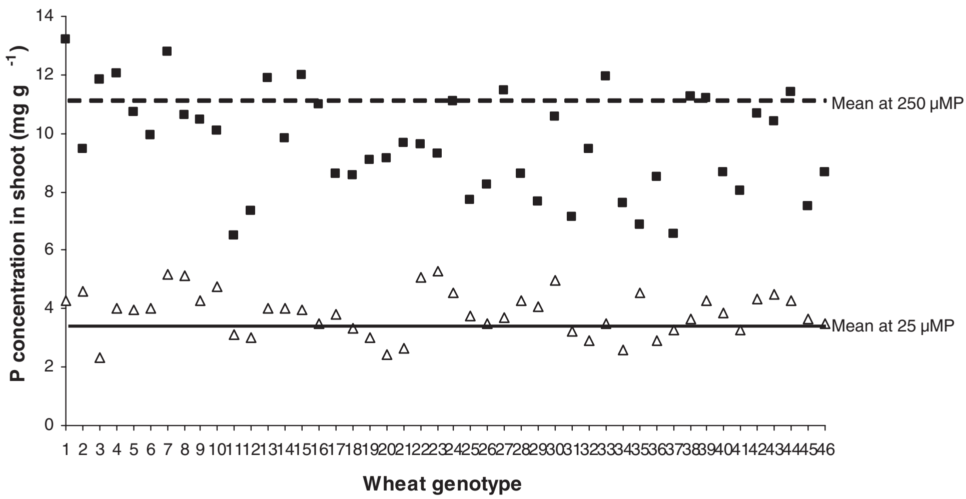

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FIGURE 1 (Continued)

Plant Total Dry Matter

Plant total dry matter (TDM) of 46 wheat genotypes was significantly affected by both stress (25 μM P) and adequate (250 μM P) P levels (Table 2). Plant TDM (averaged over 46 genotypes) was increased 65% when P supply was increased 10 fold from 25 μM P to 250 μM P. Significant genotypes × P level interaction at $P < 0.01$ depicted differential growth of individual genotype and reduction in TDM at stress P level and increase in TDM at adequate P to a varying extent. At stress P level, TDM ranged from 0.60 to 1.52 g 2plants^{-1}, while it ranged between 1.25 to 2.38 g 2plants^{-1} at

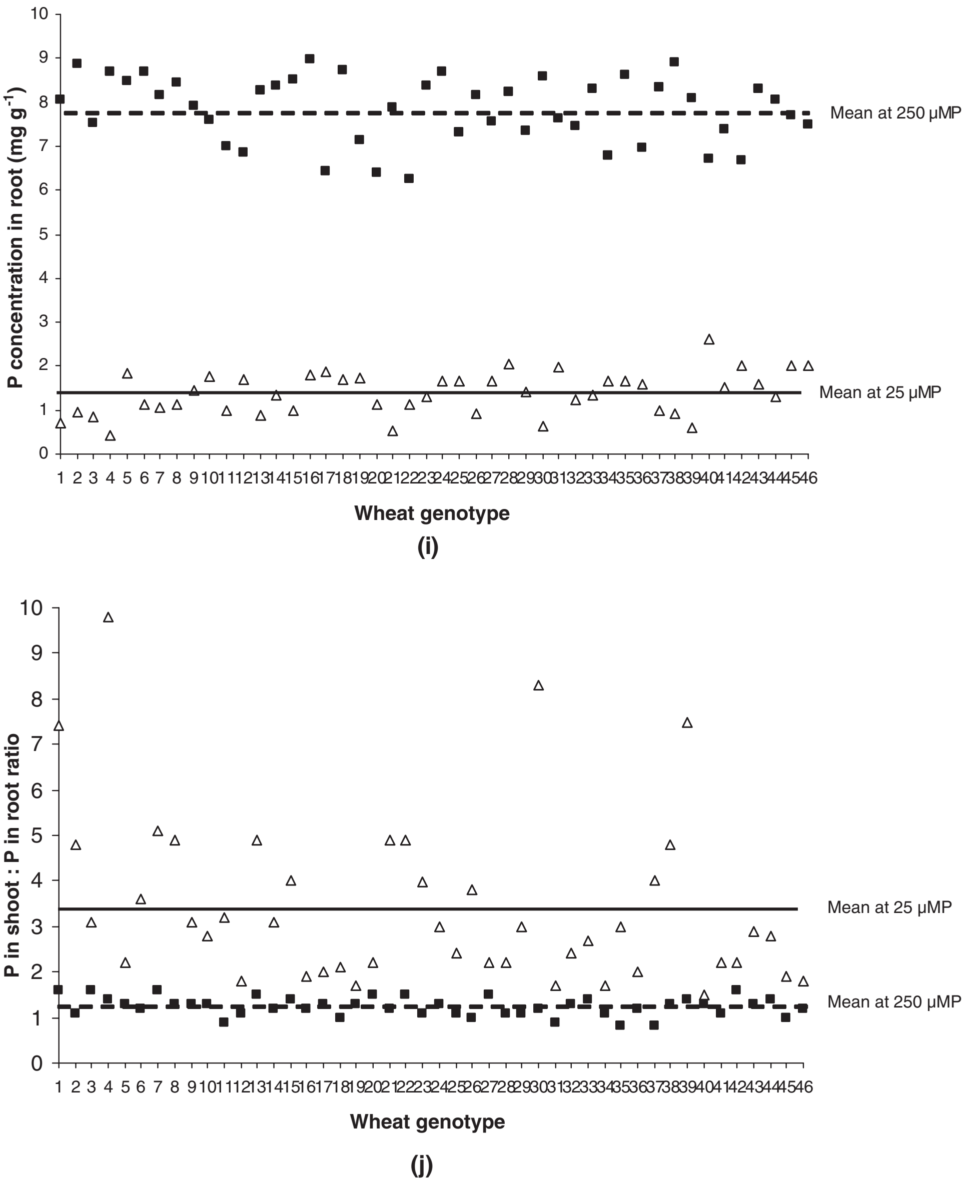
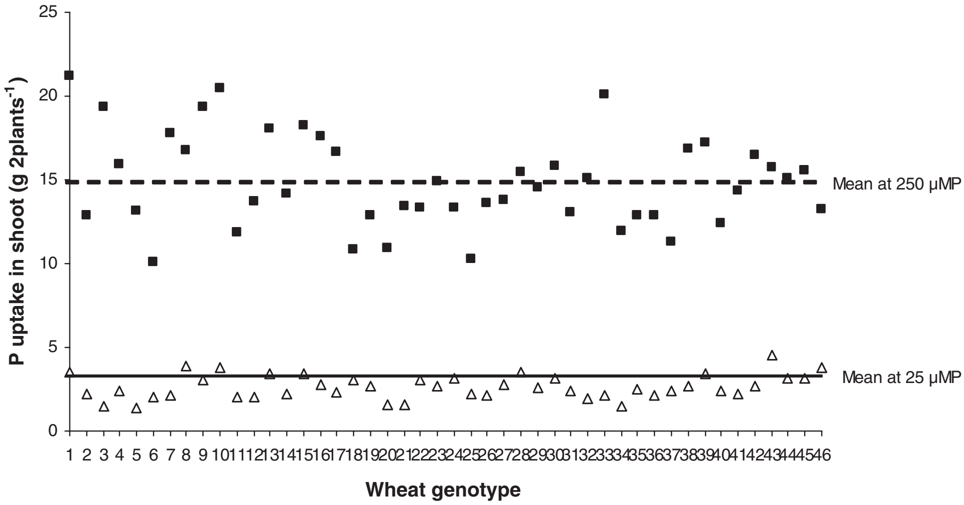


FIGURE 1 (Continued)

adequate P level. Genotypes 91773, 90627, 89626, Lu-31, Lu-26s, Inqlab-91, SHK-95, Parvaz-94, SARC-IV, and Chakwal-86 produced highest TDM at stress P level, while genotype Pato produced lowest TDM (Figure 1d). This varying potential of genotypes to produce dry matter at stress P level indicates the existence of genetic variation among wheat genotypes, and control on nutrient absorption from the growth medium. This differential behavior of



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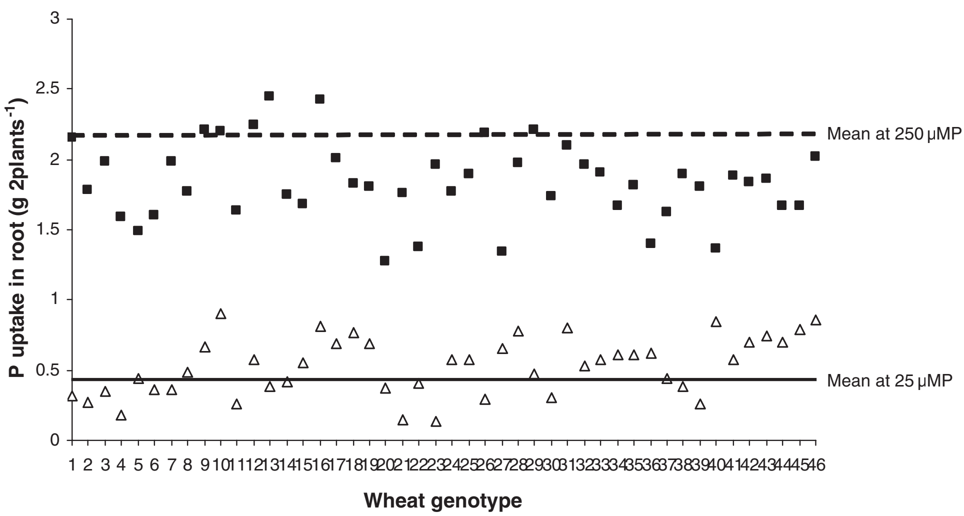

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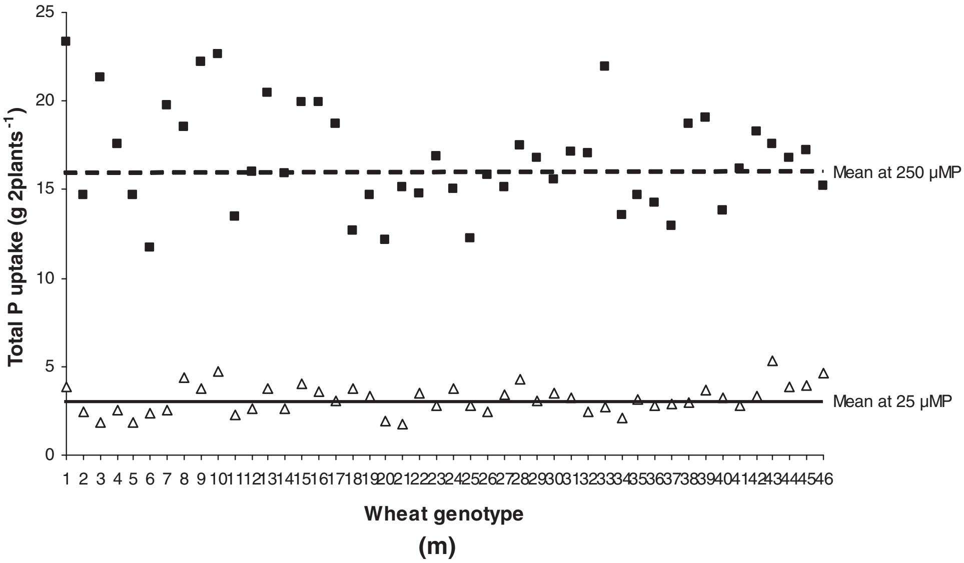
FIGURE 1 (Continued)

wheat genotypes appeared in differential partitioning of total plant biomass between shoots and roots.

Root:Shoot Ratio

All wheat genotypes differed significantly in partitioning of their dry matter in roots and shoots. This difference partly can be attributed to their difference in genetic makeup. Root:shoot ratio was also significantly influenced by genotype, P level, and interaction of genotype × P level (Table 2).



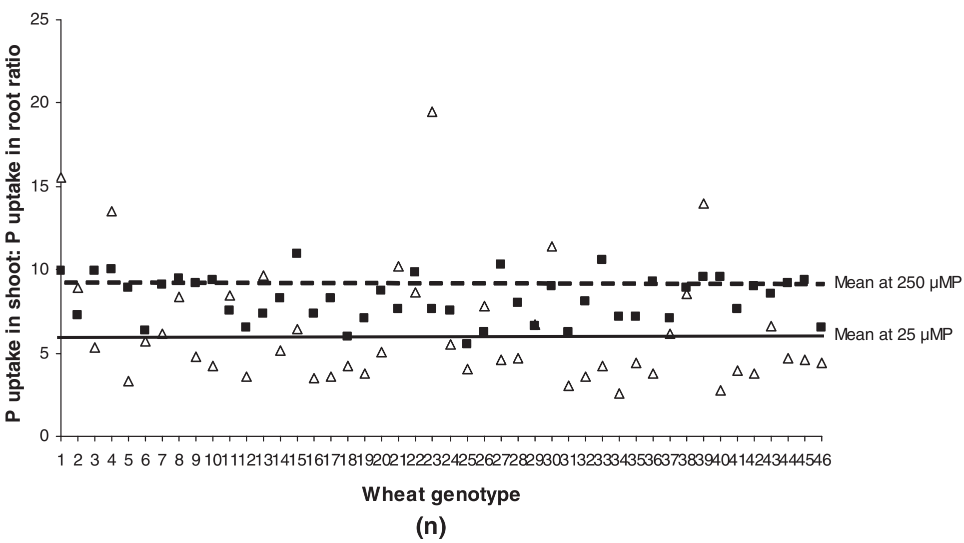
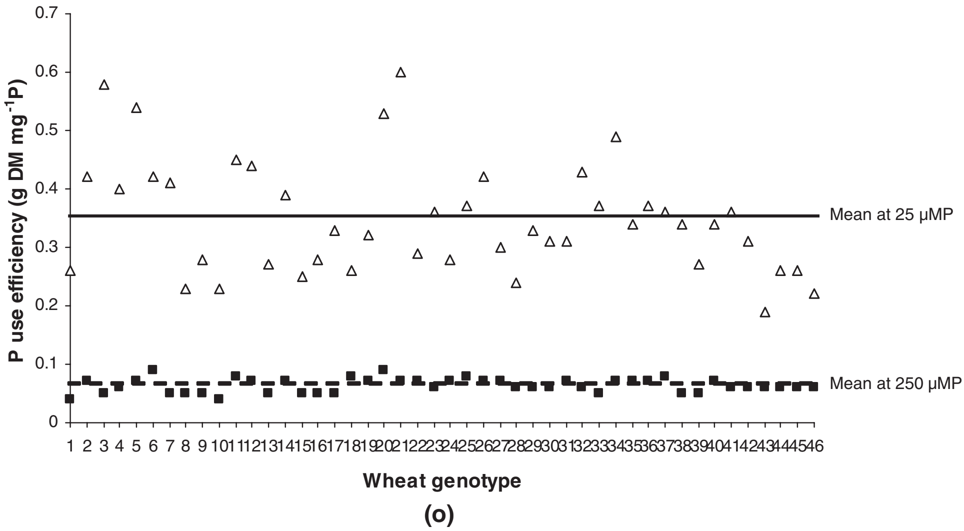


FIGURE 1 (Continued)

This indicates the pattern of distribution of biomass between root and shoot. Significant differences in root:shoot ratio were observed in stress P treatment. These differences were less pronounced and non-significant in adequate P treatment (Figure 1e). Root:shoot ratio was about 4 fold high at stress P level than that at adequate P level. This confirms the conclusion of higher root growth due to P deficiency stress. Root:shoot ratio decreased with increasing P level. It was also observed that wheat genotypes differed in root:shoot ratio to a varying extent. For example, genotype 91773



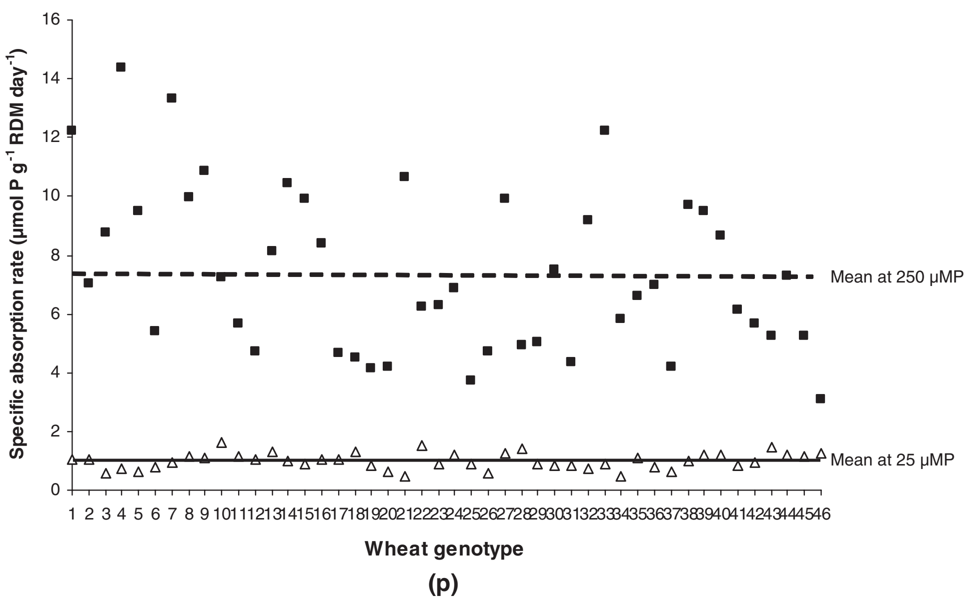
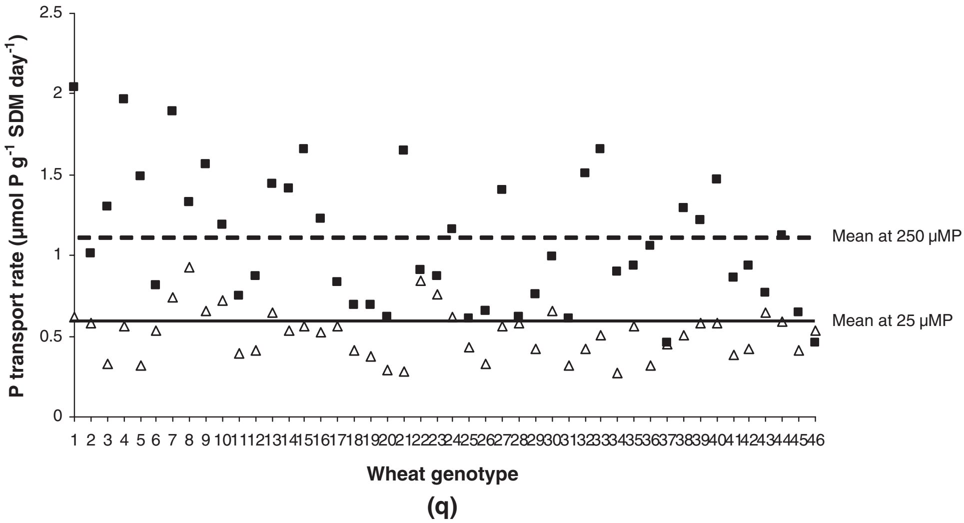


FIGURE 1 (Continued)

obtained significantly minimum, while '4943' had the maximum root:shoot ratio among all the genotypes. Genotypes with higher root:shoot ratios might have more root growth at the expense of shoot growth, however, genotypes with characteristics of low root:shoot ratio and least relative reduction in shoot growth are also desirable for low P conditions.

Non-significant differences in the distribution of dry matter between root and shoot among the genotypes at adequate P supply indicated similar



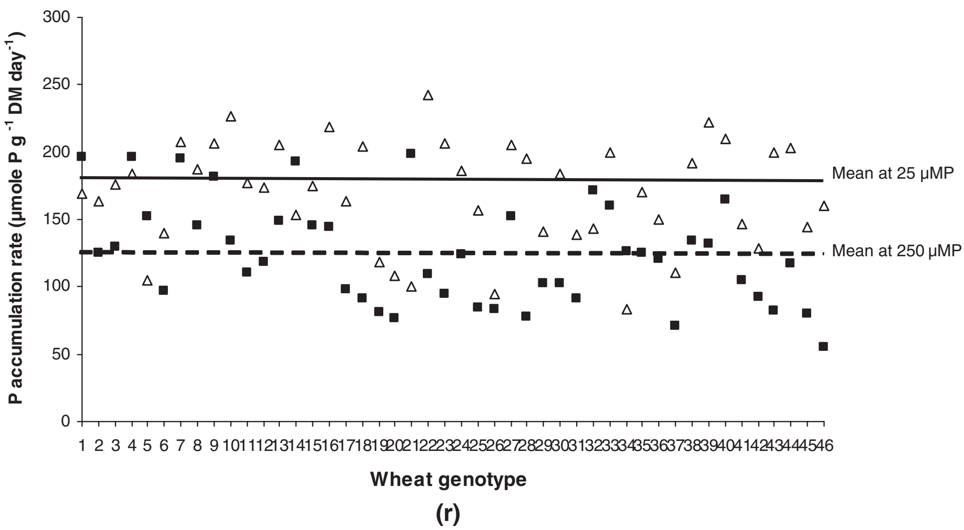


FIGURE 1 (Continued)

utilization efficiency of P and could also be due to the reproductive strategy of genotypes. Genotypes that showed adjustment in poor P conditions had greater RDM and consequently, had high root:shoot ratio. Genotypes 4943, SARC-I and 5039 had significantly the highest root:shoot ratio at stress P level (Figure 1c).

Relative Growth Rate of Shoot

Relative growth rate of shoot (RGR_{shoot}) is the accumulation of SDM per unit plant weight per unit time. Genotypes with faster rate of growth per unit

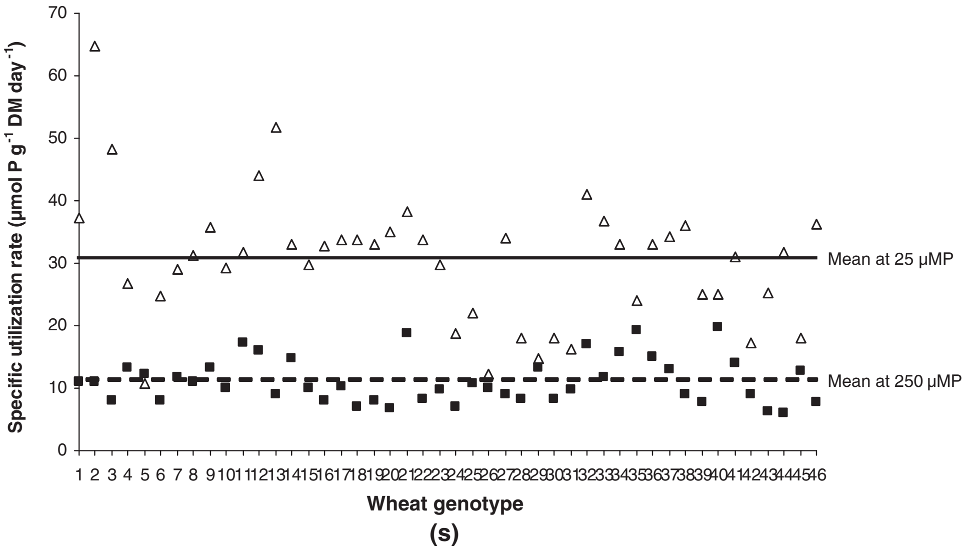


FIGURE 1 (Continued)

time are better adapted to stress conditions as they are able to exploit more volume for nutrient acquisition. Relative growth rate of shoot (RGR_{shoot}) was significantly affected by genotype, P level, and genotype × P level interaction (Table 2). Differences in shoot growth at stress and adequate P levels provided evidence of genotypic efficiency to produce SDM per unit time (Figure 1f). Increase in RGR_{shoot} by increasing the P supply (Table 3) provided information that P responsive wheat genotypes produced greater SDM at adequate P level but to a varying extent, indicating the existence of differences in genetic potential of different wheat genotypes. Differences in RGR_{shoot} are obvious due to wide differences in RGR_{shoot} among the wheat genotypes at both P levels. Highly significant genotype × P level interaction also revealed the presence of such differences. The RGR_{shoot} ranged from 23.3 to 130.3 mg g^{-1} day^{-1} at stress P level and 56 to 176.7 mg g^{-1} day^{-1} at adequate P level (Table 3). Analysis of variance also revealed highly significant ($P < 0.01$) influence of genotype × P level on RGR_{shoot}. This information suggested the presence of genetic differences in the genotypes that respond to the differences in P supply in the growth medium. Genotypes SARC-II, TC-4881, 4926, SHK-95, Inqlab-91, and 91773 had higher RGR_{shoot} at stress P level compared to that at adequate P level. This indicates either the least effect of substrate P, or low P requirement or efficient utilization of substrate P.

Relative Growth Rate of Root

Relative growth rate of root (RGR_{root}) of 46 wheat genotypes differed significantly at both P levels. It was significantly influenced by genotype, and genotype × P levels. However influence of P level on RGR_{root} was non-significant (Table 2), indicating almost no increase in RGR_{root} by increasing P supply. A number of wheat genotypes had a wide range of differences in RGR_{root} at stress P level compared to adequate P level (Figure 1g). Many genotypes attained higher RGR_{root} at stress P level than that at adequate P level. The RGR_{root} ranged from 4.3 to 110.7 at stress P, and from 16.7 to 132.0 mg g^{-1} day^{-1} at adequate P (Table 3). Wide differences in RGR_{root} at both P levels indicated differential response of genotypes in terms of RDM production per unit time in response to growth medium P. It is also obvious from the data (Figures 1f, 1g) that genotypes with least differences in RGR_{root} at both P levels also had least differences for RGR_{shoot}. Genotypes Chakwal-86, Pak-81, Pitic-62, TC-4926, SHK-95, 89053, Inqlab-91, and Lu-31 had least differences in RGR_{shoot} and RGR_{root} at both P levels. Genotypes SARC-IV, TC-4881, TC-4926, 4943, 6500, PB-96, Parvaz-94, SHK-95, 89053, FSD-83, Inqlab-91, Lu-26s, 6529–11, 4770, 89251, 89313, 91109, 91116, 89626, 90640, 90627, and 91773 had higher RGR_{root} at stress P than at adequate P level.

Phosphorus Relations with Plant Growth

Whatever the amount of P is absorbed by root from the growth medium, it is either retained in root for root growth, or different fractions of this absorbed P are transported to shoot for above ground growth. Partitioning of P between root and shoot, or the extent of remobilization of P between root and shoot are considered responsible for differences in the partitioning of plant dry matter between roots and shoots.

Phosphorus Concentration in Shoot

Phosphorus concentration was influenced by genotype, P level, and their interaction (Table 2). At stress P treatment, P concentration of shoot (averaged across the 46 genotypes) was almost 2.5-fold less than that when P supply was increased by 10 fold (Table 3). Wide differences in P concentration in shoot of 46 genotypes when grown at the same P level revealed the existence of genotypic variation among the wheat genotypes. All wheat genotypes differed significantly in shoot P concentration at stress P level (Figure 1h). Many genotypes were able to acquire P $\geq$ 4 mg P g^{-1} in their shoots. Shoot P concentration at this level ranged between 2.35 to 5.26 mg P g^{-1} (Table 3). These differences became wider with the increase in P supply (6.51–13.19 P mg g^{-1}). Overall, high P concentration in shoot was observed compared to root P concentration (Table 3). This indicates mobilization of P from root to shoot. Genotypes × P level interaction also revealed significant differences in the shoot P concentration.

Phosphorus Concentration in Root

Decrease in external P supply from 250 μM P to 25 μM P drastically reduced the root P concentration from 7.85 mg P g^{-1} to 1.38 mg P g^{-1}. It was estimated that P concentration decreased more than 5 fold with decreasing P supply. In spite of low average P concentration at stress P level compared to adequate P level, genotypes differed significantly in root P concentration. Root P concentration at this level ranged from 0.43 to 2.60 mg P g^{-1}. At an adequate P level, this concentration was in between 6.26 and 8.96 mg P g^{-1} RDM (Table 3). This concentration was too high compared to that at stress P level but genotypes did not differ as widely as at stress P level (Figure 1i). Very wide variations in root P concentration among wheat genotypes at stress P level suggested their differential abilities to absorb P from the growth medium and also to P transport to shoot.

Phosphorus Concentration in Shoot:Phosphorus Concentration in Root Ratio

Differences for shoot P:root P concentrations among the 46 wheat genotypes are quite obvious from the data in Table 3. Shoot P:root P concentration ratio indicates the efficiency of wheat genotypes to translocate P from root to shoot. Higher shoot P concentration than root P concentration at both P levels (Figure 1j) provided evidence of translocation of P from root to shoot. Significant differences in shoot P:root P concentration at stress P level also elucidated the significant differences in the efficiency of individual wheat genotype to have high shoot P concentration. These differences in shoot P:root P concentrations were higher at stress P level, indicating variation in adaptation of wheat genotypes to P deficient conditions. Genotypes differed non-significantly in shoot P:root P concentration at adequate P level.

Phosphorus Uptake in Shoot

Shoot P uptake was influenced by genotype, P level, and genotype × P level interaction (Table 2). Shoot P uptake increased about 6 fold with the increase in P supply. Increased shoot P uptake at adequate P level was due to greater SDM at this P level. At low P level (25 μM P) there were significant differences among wheat genotypes for shoot P uptake (Figure 1k). It was also observed that genotypes with the lowest dry matter yields had the highest P concentration and lowest P uptake, and genotypes with the highest dry matter yields had the lowest P concentration and highest P uptake. This was because of dilution, or possibly because of higher P requirements of plants. Total plant P uptake was found coinciding consistently with shoot P uptake. Genotypes with highest shoot P uptake at limited P supply (stress P level) were large in number, and these genotypes had significantly the highest shoot P uptake among all wheat genotypes.

Phosphorus Uptake in Root

Differences in root P uptake of 46 wheat genotypes at stress and adequate P levels were due to differences in RDM yields and root P concentration. Differences in root P uptake at the same P level reflected the diversity found among the wheat genotypes (Figure 1l). Phosphorus level and genotype × P level interaction were found significantly affecting the root P uptake. More than three-fold increases in root P uptake was observed with the increase in P supply from 25 μM P to 250 μM P. Analysis of variance revealed significant influence of genotype × P level interaction on root P uptake (Table 2). At limited P supply, root P uptake ranged from 0.14 to 0.90 mg P 2 plants^{-1} with fourteen wheat genotypes having root P uptake more than 0.62 mg P 2 plants^{-1}, However, reverse trend was observed at adequate P level where root P uptake ranged between 1.28 to 2.45 P mg 2 plants^{-1} with only six wheat genotypes having root P uptake > 2.2 mg P 2 plants^{-1} (Table 3, Figure 1l). Minimum root P uptake was shown by genotypes 4943 and TC-4881 at stress and adequate P levels, respectively.

Total Plant Phosphorus Uptake

Total plant P uptake is the sum of the P taken up by root plus shoot. Reduction in total P uptake was observed at stress P level. Although the extent of P uptake by 46 wheat genotypes was highly variable at both P levels, however, P uptake increased by five-fold with the increase in P supply from 25 to 250 μM P (Table 3). Total P uptake was influenced by genotype, P level, and genotype × P level interaction (Table 2). Highly significant genotype × P level interaction ($P < 0.01$) reveals great differences among wheat genotypes for total P uptake. This differential P uptake might be either due to high dry matter production and low P concentration, or low dry matter and high P concentration. Quite a wide differences in total P uptake between stress P and adequate P levels (Figure 1m) confirmed the role of P in the plant body. However, such differences among wheat genotype at stress P level provided information on the existence genetic differences due to their origin. Total P uptake ranged from 1.73 to 5.31 mg P 2 plants^{-1} at stress P level.

Phosphorus Uptake in Shoot:Phosphorus Uptake in Root Ratio

The amount of P retained in the roots compared to the amount moved to shoot is represented in terms of shoot P uptake: root P uptake ratios (Table 3). Wheat genotypes with greater values of shoot P uptake: root P uptake ratios (Figure 1n) transported more P from root to shoot, and wheat genotypes with lower values have retained more P in their roots. Wheat genotypes varied markedly in the amounts of P taken up by shoot and root. This extent of variation can be read out by shoot P uptake: root P uptake ratio. This ratio was significantly affected by genotype, P level, and genotype × P level interaction (Table 2). Wheat genotypes with high ratios have greater shoot P uptake, indicating greater P accumulation in shoot than in the root. It is also evident from the results that roots transferred most of their P to shoots in these genotypes. Mean shoot P uptake: root P uptake ratios (averaged across 46 wheat genotypes) at stress P level and adequate P level indicated a little effect of growth medium P on the transport of P from root to shoot, and it increased only from 6.31 to 8.26 by increasing the 10 fold P supply.

Highly significant genotype × P level interaction ($P < 0.01$) elucidates considerable differences among wheat genotypes for shoot P uptake: root P uptake. Shoot P uptake: root P uptake ranged between 2.58 to 19.49 and 5.52 to 10.96 at stress and adequate P levels, respectively (Table 3). Wide differences among wheat genotypes (about seven-fold between low and high ratios) elucidated the differential response of the wheat genotypes to P deficiency.

Phosphorus Use Efficiency

Phosphorus use efficiency provides information on the differences in the use of a nutrient within the plant. It is calculated by the reciprocal of the total P uptake. This parameter is particularly good to describe better use of a nutrient within the plant under P deficient condition. Phosphorus use efficiency therefore, describes the most efficient use of a nutrient when its internal supply is lower. It is possible for a plant to appear to be an efficient user of a nutrient merely because it is inefficient in obtaining the nutrient.

Data regarding the PUE in Table 4 elucidate the significant influence of genotype, P level, and genotype × P level interaction (Table 2). No prominent differences among the wheat genotypes were observed in PUE at adequate P level. All wheat genotypes had statistically similar PUE. However, the differences for PUE among wheat genotypes were marked at stress P level (Figure 1o). These marked differences pointed out the differences in the ability of wheat genotypes for internal P use. Wheat genotypes having greater PUE values had comparatively better internal use of P within the plant and vice-versa for genotypes with low PUE values. Genotypes TC-4884, Pak-81, and Pato had the highest PUE, hence had better internal use of P. Genotype 89626 had the lowest PUE (0.19 g DM mg^{-1} P absorbed) among all the wheat genotypes.

TABLE 4 Highest and lowest P efficiency related parameters for 46 wheat genotypes grown at stress P level and at adequate P level with ammonium phosphate in Johnson's modified solution culture experiment

	Average (range) for P efficiency related parameters in P treatments[z]	
Phosphorus efficiency parameter	250 μM P	25 μM P
PUE (g DM mg^{-1} P)	0.06 (0.04–0.09)	0.35 (0.19–0.60)
SAR (μmol P g^{-1} RDM day^{-1})	7.37 (3.11–14.40)	0.99 (0.46–1.65)
PTR (μmol P g^{-1} RDM day^{-1})	1.09 (0.46–2.04)	0.61 (0.27–0.93)
PAR (μmol P g^{-1} RDM day^{-1})	124.4 (55.7–198.0)	169.0 (83.3–242.0)
SUR (μmol P g^{-1} RDM day^{-1})	11.2 (6.0–19.7)	30.4 (10.7–64.7)

*Values outside the parenthesis are mean while values within parenthesis are minimum and maximum attained by genotypes. PUE = Phosphorus use efficiency; SAR = Specific absorption rate of phosphorus; PTR = Transport rate of phosphorus; PAR = Accumulation rate of phosphorus; SUR = Specific utilization rate of phosphorus; RDM = Root dry matter.

Specific Absorption Rate of Phosphorus

Nutrient use efficiency involves the measures of the ability of plants to obtain nutrients. One of them is the rate of uptake of nutrient per unit of root dry weight. Several terms can be used to describe this but more suitable is the specific absorption rate of P (SAR). This term is considered better as the index of uptake efficiency of roots. When measuring SAR, different choices are available to measure the root system such as root length, root volume, and root weight. In this study root weight is preferred as it is easy to measure. Wheat genotypes grown at stress and adequate P levels exhibited significant and substantial influence of genotype, P level, and genotype × P level interaction on SAR (Table 2). The specific absorption rate of P increased more than six-fold by the increase of 10-fold P supply in the growth medium (Figure 1p). Since, this measurement is related to root weight, so marked differences in morphological and physiological root characteristics could influence SAR. At stress P level, though genotypic differences were non-significant for SAR, yet many genotypes had SAR more than the average value of 0.99 μmol P g^{-1} RDM day^{-1} (averaged across 46 means). Since SAR involved the measurement of root growth at two growth stages (30 and 37 days after transplanting, respectively), therefore, smaller values of SAR indicated little difference in root growth between the two growth stages at stress P level. This leads to non-significant differences in SAR of 46 wheat genotypes at this P level. In other words, whatever the root biomass was attained at first growth stage, it was not or little changed at second growth stage.

All wheat genotypes exhibited marked differences in SAR at adequate P level probably it happened as the P levels were maintained again after first harvest and added P might initiated or stimulated further root growth at adequate P level. At adequate P level, SAR ranged between 3.11 to 14.40 μmol P g^{-1} RDM day^{-1} (Table 4). Maximum SAR was attained by Pasban 90 while minimum by genotype 91773.

Phosphorus Transport Rate

As plants grow under P stress condition, an increasing amount of root biomass in response to P deficiency explores more volume of growth medium for P absorption and transports more P from roots to shoot. Generally plants that have such root systems that can effectively transport P to their shoots are able to sustain growth under P stress conditions. Phosphorus transport rate (PTR) was calculated as described by Pitman (1972). This term is related to shoot P concentration and shoot growth rate at two growth stages.

Phosphorus transport rate in wheat genotypes was markedly influenced by genotype, P level, and genotype × P level interaction (Table 2). Phosphorus transport rate generally increased with increasing P supply. Data indicated almost 80% increase in PTR with the increase in P supply from 25 μM P to 250 μM P (Figure 1q). All the genotypes markedly differed in PTR at both P levels. Genotype × P level interaction ($P < 0.01$) also revealed significant differences in PTR among wheat genotypes. At stress P level, genotypes SARC-I, SARC-II, SARC-III, SARC-IV, 4926, 4943, Pak-81, 5039, and 89626 had the maximum PTR ($\geq$0.65 μmol P g^{-1} SDM day^{-1}). Phosphorus transport rate at this level ranged from 0.27 to 0.93 μmol P g^{-1} SDM day^{-1} (Table 4). However, both the lowest and highest values were greater at adequate P level due to more availability of soluble P in the growth medium (0.46 to 2.04 μmol P g^{-1} SDM day^{-1}). Majority of the wheat genotypes had PTR greater than the average PTR (1.09 μmol P g^{-1} SDM day^{-1}). Only two genotypes, Chakwal-86 and Pasban-90, exhibited the greatest PTR.

Phosphorus Accumulation Rate

This term describes the ability of plant to obtain, particularly retain some amount of nutrient in a given time. It is better to say how much plant is efficient in retaining the nutrient in a given time. Plants with good absorption ability per unit time generally have higher accumulation rate. This measurement is well described when plants are grown in nutrient deficient conditions. Phosphorus accumulation rate (PAR) is commonly high under nutrient deficient conditions. Similar results were observed when wheat genotypes were grown at stress and adequate P levels (Table 4). Genotypic response to growth medium P in terms of PAR was markedly affected by genotype, P level, and genotype × P level interaction. Significant genotype × P level interaction ($P < 0.01$) shows marked differences in PAR at stress and adequate P supply (Table 2). Phosphorus accumulation rate decreased from 169.0 to 124.4 μmol P g^{-1} SDM day^{-1}. This means that wheat genotypes showed better PAR at stress P level than at adequate P level. At stress P level, PAR ranged from 83.3 to 242.0 μmol P g^{-1} SDM day^{-1} (Table 4). Wide differences for PAR at this level revealed the existence of wide differential abilities of wheat genotypes to accumulate phosphorus. Twelve genotypes had >200 μmol P g^{-1} SDM day^{-1} and only two genotypes, 88163 and 4770 had <100 μmol P g^{-1} SDM day^{-1}. Rest of the genotypes was fall between these limits. At adequate P level, PAR ranged between 55.7 to 198.0 μmol P g^{-1}SDM day^{-1}. Thirteen wheat genotypes had PAR <100 μmol P g^{-1} SDM day^{-1} (Figure 1r). Comparably narrow and lower ranges of PAR at adequate P than at stress P level advocated higher PAR values and wide differences among wheat genotypes at stress P level.

Specific Utilization Rate of Phosphorus

Hunt (1978) used the term specific utilization rate (SUR) as the reciprocal of concentration of a nutrient in dry matter production with time. In other words, it is the rate of dry matter increment per unit nutrient absorbed. This measure describes the efficiency with which dry matter is produced by mineral nutrient uptake. This measurement is more appropriate under nutrient deficient conditions. Increase in P supply decreased the SUR. Extent of decrease varied with increment in P supply. Specific utilization rate decreased from 30.4 mg DM mg^{-1} P day^{-1} at stress P level to 11.2 mg DM mg^{-1} P day^{-1} at adequate P level by increasing growth medium P supply from 25 μM P to 250 μM P (Table 4). At adequate P level, SUR of wheat genotypes varied non-significantly. Majority of the genotypes had more than the double of SUR at stress P level than at adequate P level (Figure 1s). At stress P level, SUR ranged from 10.7 to 64.7 mg DM mg^{-1} P day^{-1}, indicating wide genotypic variation for SUR.

Categorization of Wheat Genotypes

Based upon the plant characteristics, the 46 wheat genotypes were ranked at stress P level (25 μM P) and position of each genotype is presented in Table 5. The assessed plant characteristics are divided into three levels (I, II, and III). Level-I represents the most efficient/productive genotypes, level-II the average or medium efficient/productive genotypes, and level-III the lowest efficient/productive genotypes. Table 5 lists the 46 wheat genotypes and the distribution of 19 investigated plant characteristics with respect to their performance levels. When the levels are added together for each genotype, the total number is 19. The distribution of these characteristics by levels is used to rank or grade the genotypes.

Wheat genotype Inqlab-91 achieved the highest grade. Thirteen out of the 19 investigated parameters of this genotype were within level-I. Five genotypes (Chakwal-86, SARC-IV, 91141, 89626, and 90627) received grade

TABLE 5 Overview and distribution of 19 investigated plant characteristics for 46 wheat genotypes, grown at stress P level and at adequate P level with ammonium phosphate in a Johnson's modified solution culture experiment, within three performance levels

	Performance levels[z]			
Genotype	I	II	III	Grading
Inqlab-91	13	3	3	1
Chakwal-86	11	5	3	2
SARC-IV	11	5	3	2
91141	11	4	4	3
89626	11	4	4	3
90627	11	4	4	3
SARC-II	10	6	3	4
TC-4926	10	6	3	4
Parvaz-94	10	3	6	5
91773	9	5	5	6
89053	9	4	6	7
SARC-III	8	6	5	8
Lu-26s	7	10	2	9
6500	7	7	5	10
Lu-31	7	6	6	11
90640	7	4	8	12
89044	6	10	3	13
5039	6	7	6	14
SARC-I	6	6	7	15
4943	6	6	7	15
SHK-95	6	6	7	15
91169	5	9	5	16
Pasban-90	5	8	6	17
FSD-83	5	7	7	18
Kohinoor-83	5	6	8	19
91116	4	12	3	20
89251	4	9	6	21
6544-6	4	7	8	22
TC-4881	4	4	11	23
TC-4884	4	3	12	24
PB-96	3	13	3	25
PB-85	3	9	7	26
88678	3	8	8	27
Pitic-62	3	7	9	28
4770	3	5	11	29
Blue Silver	3	4	12	30
4072	2	11	6	31
91173	2	10	7	32
91109	2	9	8	33
6529-11	2	8	9	34
Pak.81	2	7	10	35
88163	2	4	13	36
Pato	2	2	15	37
89313	1	11	7	38
88042	1	8	10	39
89295	1	8	10	39

[z]Level-I = Highly tolerant for low-P, Level-II = Medium tolerant for low-P, Level-III = Very low tolerant for low-P.

11 times higher than that of level I. These genotypes could be identified as having medium to high potential to produce normal yield under P-deficiency stress. Genotypes 88042, 89295, 89313, Pak-81, Pato, 88163, 6529–11, 4072, 91109, and 91173 received the lowest grade as only one or two of their characteristics were in level-I, 2–11 were in level-II and the remainder were in level-III. All the other genotypes could be ranked as medium to low in efficiency.

DISCUSSION

Results clearly show substantial differences among wheat genotypes in their ability to produce biomass at adequate (250 μM P) and stress (25 μM P) P supply levels. Gill et al. (1994a, 1994b), Gahoonia and Nielsen (1996), and Wang et al. (2005) have also reported similar results in wheat. Wheat genotypes differed significantly in dry matter production. The genotypes with the highest SDM yields at stress P level were genotypes 91773, 9626, and Parvaz-94. The genotypes with the lowest SDM yields at stress P level were Pato, Kohinoor-83, SARC-1, Pitic-62, and 89251. Differences among genotypes with respect to highest and lowest SDM, RDM, and TDM (shoot + root) weights ranged from 0.5 to 1.2 fold (Table 3). Genotypes with least or non-significant differences in the SDM weights illustrated that there was no difference in their abilities to produce SDM. This means that once P was located in their shoots, no difference in internal shoot efficiencies took place. Genotypes having minimum relative reduction in their SDM due to P stress (PSF) were less P responsive compared to genotypes with the highest values of PSF. The latter genotypes were highly dependent upon P supply for their shoot biomass production. Genotypes having least relative reduction in SDM could be regarded as P efficient and non-responsive, and vice versa.

Gill and Yaseen (1994), Yaseen et al. (1998) and Yaseen and Malhi (2009) described the usefulness of PSF for the categorization of wheat genotypes for P use efficiency under P deficiency stress. Genotypes with the highest SDM at stress P level had least PSF values and vice-versa. Phosphorus stress factor had a highly significant negative correlation ($r = -0.743^{**}$) with SDM at stress P level and highly positive correlation ($r = 0.522^{**}$) at adequate P level. This suggests that about 55% variability in PSF can be attributed to SDM production at stress P level. This parameter can be used as an indicator of relative performance of different genotypes of wheat under differential nutrient supply in term of their vegetative yield response. Highly significant and substantial differences in PSF value among the genotypes were very useful and may be used as a basis for selecting P efficient wheat genotypes in the field. In a broad sense, heritability ranged between 0.36 and 1.09 g 2 plants^{-1} at stress P level, while it was 1.07 and 2.07 g 2 plants^{-1} at adequate P level for SDM weight.

Significant differences among the wheat genotypes for RDM weights were observed both at low and adequate P levels. The genotypes Lu-26s, SARC-IV, 90627, Lu-31, Chakwal-86, and 89626 had a significantly higher RDM weights among all the wheat genotypes at low P, while differences at adequate P were not so marked. The differences in RDM weights between P rates were decreased with increasing P supply. Due to these differences, RDM increased by 1.6 fold at low P (25 μM P) over that of adequate P (250 μM P). Although differences in RDM weights are determinants of P uptake (Blair and Godwin, 1991), even then P uptake did not appear to consistently follow the pattern of increase in RDM weight. According to Mian et al. (1994), selection of wheat genotypes with larger root system in the hydroponic culture might be capable of producing more roots in the field. The data collected by them had held a promise for initial screening of a large number of genotypes for their relative root growth abilities in the field. The advantage of larger root system in the field for the availability of diffusion limited element such as P is well known (Fawole et al., 1982; Gahoonia and Nielsen, 1996). The increase in root biomass at deficient P supply have apparent advantage to exploit large volume of soil for nutrient, since the size and distribution of roots in soil has a large impact on nutrient uptake particularly P (Van Noordwijk et al., 1990; Fohse et al., 1991). Research has shown that increased root growth (which enhanced P acquisition), increased uptake per unit of root and a high efficiency in internal P use were associated with superior performance under P limited conditions (Gabelman and Gerloff, 1986; Yan et al., 1995). Marked differences in RDM elucidated that relative root growth rate however, showed a marked decline in most of the wheat genotypes with P supply. This indicates that the entire root growth may be enhancing/expanding at a faster rate with decreasing P supply, but relative root growth rate which is the ability of unit root weight to produce a further increment of root weight in unit time, declines with P supply.

Results also revealed that genotypes with the highest relative root growth rate had the lowest relative shoot growth rate at stress P level (Figures 1f, 1g), indicating adaptation mechanism to P deficiency by diverting the photosynthates from top towards roots (Burauel et al., 1990). Significant positive correlation (r = 0.544** and 0.508**, $P < 0.01$) between RDM and SDM at stress and adequate P levels, respectively, defined the well-documented phenomenon that root system development is influenced or dependent upon the shoot development (Fageria et al., 1988). Root dry matter weight differences were also correlated with total growth (r = 0.733** and 0.614**) and P uptake (r = 0.566** and 0.350**) at stress and adequate P levels, respectively. Plants yielding the highest and lowest SDM weights did not necessarily yield the highest and lowest RDM weights. Differences in partitioning of dry matter between root and shoot can be well described by root:shoot ratio. Root:shoot ratio ranged from as high as of 0.87 to as low as of 0.40 at low P level, while non-significant differences were observed at adequate P level.

Wheat genotypes differed in the amount of SDM compared to RDM produced, and this may be important adaptive ability of plants to withstand low P conditions because root:shoot ratio determines the uptake efficiency and ultimately P efficiency in plants (Fohse et al., 1991). Although, average SDM yield of wheat genotypes at 25 μM P (stress level) was almost one-half of that at 250 μM P (adequate P level). Relative response of these genotypes to increased P supply was 54% of the response of these genotypes over the 25 μM P level. Caradus and Dunlop (1978) compared the *Trifolium repens* genotypes at high and low P supply. The reverse response was observed for root where a 1.6 fold RDM production was decreased with increase in P supply.

These variations in shoot and root dry matter production in response to growth medium P resulted in higher root:shoot ratio at low P level than at adequate P level. Haynes et al. (1991), Gill et al. (1994a, 1994b) and Yaseen and Malhi (2009) also observed decrease in root:shoot ratio with P supply. Root:shoot ratio of wheat genotypes at stress P level had highly significantly positive correlation ($r = 0.397^{**}$) with PSF, indicating more partitioning of photosynthates to roots compared to shoots. This caused reduction in SDM at stress P level. Genotypes with the highest ratios (more than 70% RDM) were 4943, SARC-1, 5039, and Pasban-90. Genotypes with the lowest ratios (less than 50%) were 91773, 90640, 89626, 89053, 88163, TC-4884, Blue silver, and SHK-95. The reduced RDM production at high P level (250 μM P) is in accordance to Pigott (1971) who reported that it was the character of P responsive genotypes. Similar results were reported by Romer et al. (1988), Gill et al. (1994a, 1994b), Wang et al. (2005), and Gunes et al. (2006) in wheat. Access of roots to P is important since diffusion and mass flow of P in soils are usually too low to bring adequate P to the root surfaces to meet plant needs. That is why roots need to grow out to where P is located in the soil. If a plant has inadequate roots, it cannot make proper contact with sufficient P needed by the tops, and then P deficiency would be expected. In addition, a plant with a high root:shoot ratio may have few roots but have a sufficient P because it has a greater amount of root mass to that of shoot mass and does not have to provide as much P per root mass as for a plant with a low root:shoot ratio. However, if P accessibility is not limiting, a plant with a low root:shoot ratio may accumulate more P in the shoots and store less in the roots compared to a plant with a high root:shoot ratio. This suggests that the wheat genotypes employed in this study could be grouped according to the differences in their SDM yield response to high and low P supply. Ozturk et al. (2005) and Wang et al. (2000, 2005) used such differences for grouping the genotypes as efficient and inefficient P users. This is also because the abilities of different wheat genotypes for acquisition of P at high and low P levels suggest a possible selection criterion to improve the growth of wheat crop under field conditions. The selection of genotypes that are able to use P efficiently at low soil P levels may represent an alternative to traditional agricultural strategies.

Phosphorus concentration and uptake efficiencies, partitioning of P between root and shoot, and its utilization determine the ability of a genotype to produce biomass and its distribution between roots and shoot. Genotypes with the lowest dry matter yields usually had the highest P concentrations and lowest P uptake, and genotypes with the highest dry matter yields usually had the lowest P concentration and highest P uptake. This is because of dilution or possibly because of higher P requirements. Phosphorus concentrations in shoots were higher than in roots. Shoots had broader range of P concentrations than roots. Phosphorus uptake of shoots was also markedly higher than P uptakes of roots. Except wheat genotypes Pak-81, TC-4884, 6544–6, and 4770, all other genotypes had P concentration > 3 mg P g^{-1} at stress P level, which seems sufficient at this level. All these genotypes had many times more P in shoot than root, indicating better ability in these genotypes for transport of P from root to shoot. The ability of wheat genotypes to maintain higher shoot concentrations of P at low level of P supply may be related to a low shoot sink demand as a result of lower growth rates. This conclusion is in agreement with the findings of Blair and Wilson (1990) who found that a vigorous white clover had lower tissue P levels compared to white clover of lower vigor. This finding may explain in part, differences in shoot P levels among the wheat genotypes in this study at low P supply. This is supported by differences among wheat genotypes in SDM, suggesting that genotypes with low SDM have less structural material per unit of tissue weight, possibly as a result of larger cell size therefore, the differences discussed may be due to genetic control of growth. Caradus (1990); however, reported contrary results, despite the significant and substantial differences in shoot P concentrations; he found no relationship between SDM and P concentration in shoot.

In this study, higher shoot P concentrations do not mean higher SDM because the presence of higher concentration of P in shoot is meaningful only if these genotypes have better internal use efficiencies. Significant and positive correlation between shoot P concentration and RDM and root:shoot ratio ($r = 0.231^{**}$ and 0.410^{**}, respectively) at stress P level also suggest that genotypes with larger root system accumulate higher P in their shoots. Shoot P:root P concentrations ratio describes the partitioning of P between shoots and roots. Partitioning of P to the shoot and root was greater at low P level. As the solution P level was increased from 25 to 250 μM P, average P concentration in the shoots declined from 3.7 to 1.2 mg P g^{-1}. The amount of P retained in the roots compared to the amounts moved to the tops is represented by P concentration and uptake of shoot/root. These values ranged from 1.5 to 16.5 and 2.58 to 19.49 at stress P level, and from 0.8 to 1.6 and 5.52 to 10.96 for P concentration and uptake, respectively, at adequate P level. In the case of genotype 4943, shoot retained more P and had the highest shoot P uptake than that of its own roots as well as the root of many other genotypes. Genotypes SHK-95, 4770, Lu-31, Pato, Pitic-62, SARC-IV, TC-4881, PB-96, Parvaz-94, 88042, 89044, 89053, FSD-83, 6529–11, 6544–6, 4072, 89313, 91173, 88678, 90627, 90640, and 91773 also retained more P and hence had greater P uptake at stress P level than at adequate P. These results indicate that under low P supply a greater proportion of the total P uptake and assimilate was apportioned to shoots than roots. At both P levels, P concentration in the shoot tissue was higher than the root and this was found associated with a higher growth rate. This agrees with the findings of Jones et al. (1989), who indicated that assimilated P is diverted to P rich zones in the plant. At adequate P level, root P concentration had a significantly negative correlation with RDM ($r = -0.369^{**}$) probably due to growth dilution effect or transportation of P from root to shoot.

Plant response to P was also affected by their ability to translocate absorbed P from roots to shoots. Genotypes with higher phosphorus transport rate (PTR) were able to translocate more P from their roots to their shoots than genotypes having least values of PTR. These results are in accordance with the findings of Blair and Cordero (1978) and Paynter (1990). All the genotypes except SARC-I, SARC-II, SARC-III, SARC-IV, TC-4926, 4943, Inqlab-91, 5039, and 89626 (having PTR $> 0.62\ \mu$ mol P g^{-1} SDM day^{-1}) were the least able to translocate P from their roots to shoots at low P level. These genotypes, therefore, appear to be less tolerant of P deficiency, partly because they are less efficient to absorb P from growth medium and partly they have a lower ability to translocate P from their roots to shoots.

Total uptake of P varied widely and was closely related to dry matter production. The correlation coefficient for P uptake and dry matter was $r = 0.682^{**}$ and 0.500^{**} at stress and adequate P levels, respectively, which are significant at 1% level of probability. This means, as the plant size will be bigger in terms of dry matter production, the amount of P required by the plant will also rise, but this efficient use of P by a plant must be related to the economy of P availability. The efficient use of P by plant will, therefore, mean a saving in the fertilizer application. Efficient use of P thus can be defined as the plant capacity to yield higher amount of dry matter per unit of P absorbed, which can be expressed in terms of mg P per g of dry matter. To take the advantage of this definition, wheat genotypes can be grouped into most and less efficient genotypes. Highest and lowest dry matter production per unit P uptake (reciprocal of P uptake) is shown as phosphorus use efficiency (PUE). The amount of plant material produced per unit P was different in different genotypes, and was lower at adequate P than at stress P level. Phosphorus use efficiency (PUE) in wheat genotypes ranged between 0.19 ('89626') to 0.60 g dry matter mg^{-1} P absorbed (TC-4884) at adequate P. This means wheat genotypes showed 5 to 7 fold increases in efficiency of using P at stress P level. Genotypes with the highest g of dry matter per unit P uptake values had about 6 fold higher (on average basis) PUE at stress

P than at adequate P supply. On whole plant basis, the highest production of dry matter per unit P uptake was noted for the genotypes TC-4884, Pato, Pak-81 and TC-4881, and the lowest for 89626, 90627, 90640, 91773, Lu-26s, 89053, Parvaz-94, SARC-II, SARC-IV, and Chakwal-86.

Differences in SDM production can be attributed to differences in shoot P accumulation. Although, P uptake varied widely from 2.64 mg P 2 plants^{-1} (at stress P) to 14.88 mg P 2 plants^{-1} (at adequate P), even then there were 10 wheat genotypes out of 46 with low total P uptake and most of them had high capacity to produce dry matter. This may be associated to a high total P accumulation as it is well correlated to P accumulation ($r = 0.461^{**}$) at stress P level. Genotypic differences in P metabolism may be reflected from the differences in shoot and root growth rates, which affected P uptake, and this effect may cause change in ranking the wheat genotypes for P utilization. Blair and Wilson (1990) also reported differences in white clover accessions in the proportion of various amount of P metabolites. One of the important factors for establishing P efficiency in plants is the efficiency with which P is utilized in metabolic processes. Gerloff (1976) pointed out that if certain strains of plants produce different amounts of SDM from a given amount of P, then the genotypes that produced highest yields must also have lowest P concentrations. These differences in efficiencies of utilization of P for growth of 46 genotypes used in this experiment were attributed to an inherently differing growth rate capacity (Jones et al., 1989, 1992; Blair and Wilson, 1990; Yan et al., 1995). Thus, genotypes with greater efficiency for P utilization in metabolism would be those genotypes with lowest P concentrations. However, a greater P re-transport to the active growing regions of efficient plants could result in the maintenance of similar P concentration in the active regions of both efficient and inefficient genotypes. Gerloff (1976) also pointed out that differential P efficiency being associated with metabolic effectiveness would be evidenced, 1) by large plant growth at a given P level even though the P concentration for both plants were the same, and 2) P concentrations were lower in the top of efficient plants yet they produced more dry matter than P inefficient plants. Many of the genotypes used in this experiment met these criteria and could be considered more P efficient than others.

Another criteria is suggested by Clark (1990) that the genotypes that had the most severe P deficiency symptoms usually had higher dry matter yield, P uptake, and dry matter production per unit P, and lower P concentrations, and should be more P efficient than genotypes with values opposite to these. Using these selection criteria and the grading system used by El-Bassam (1998) for the selection of wheat genotypes for PUE, the most P-efficient genotypes would be Inqlab-91, SARC-II, SARC-IV, Chakwal-86, 90627, 89626 and Parvaz-94, and P-inefficient genotypes would be Pak-81, Pato, 88042, 88163, 89295, 4072, 89313, and 91109. All other genotypes fall in between as these were medium in P use efficiency.

CONCLUSIONS

Phosphorus use efficiency of crop plants depends upon many factors, which are neither understood or clearly defined, nor applicable everywhere. Differences were noted among wheat genotypes for dry matter yield, P concentrations and P uptake, distribution of dry matter, P concentration, and P uptake between shoot and root, and dry matter production per unit P or P use efficiency. Each of these parameters is important and should help to explain differences among wheat genotypes for efficiency of P uptake and utilization.

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