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Importance of P uptake efficiency versus P utilization for wheat yield in acid and calcareous soils in Mexico

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Abstract

There are large agricultural areas in the world where wheat yields are limited by low phosphorus (P) availability. Breeding for P uptake and P utilization efficiency may reduce this problem. This study was conducted to determine the contribution of P uptake and utilization efficiency to grain yield of selected spring wheat genotypes in different environments. Thirty-eight semidwarf spring bread wheat (*Triticum aestivum*) genotypes were grown in two experiments in Mexico, each on an acid Andisol under rainfed conditions and on a calcareous Aridisol with irrigation, without (−P) and with 35 kg P per ha fertilized (+P). Without P fertilization, grain yield ranged from 0.8 to 4.6 t ha^{-1} in the acid soil and from 2.4 to 5.2 t ha^{-1} in the calcareous soil. With P fertilization, this range was even larger. Under conditions of P deficiency, i.e. in the acid soil at −P and +P (high P adsorption) and calcareous soil at −P (P-depleted soil), P uptake explained 71–100% of the variation in grain yield, and was highly correlated with grain yield ($r = 0.79$–0.95). In contrast, at +P in the calcareous soil, P utilization efficiency explained 60–63% of the variation in grain yield. Here, low grain P concentration was related to high grain yield ($r = -0.40$ to -0.59). In the calcareous soil, the harvest index was correlated with grain yield, irrespective of the P level. In the acid soil, post-anthesis P accumulation was important. It was positively correlated with grain yield, whereas in the calcareous soil, no post-anthesis-P accumulation occurred. Here, grain P accumulation at maturity was completely determined by translocation of pre-anthesis shoot P. We conclude that the combination of improved P uptake and P utilization efficiency in the same genotypes requires selection under both high and low-P conditions. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Phosphorus use efficiency; *Triticum aestivum*; P uptake; P utilization; Wheat

1. Introduction

Wheat represents more than a quarter of the world's total cereal output and constitutes the

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main source of calories for over 1.5 billion people. Although the yield potential of spring bread wheat has reached 8 t ha^{-1} in favorable, irrigated subtropical environments, the actual average yield worldwide is less than 3 t ha^{-1} (CIMMYT, 1996). By the year 2030, average yields worldwide must increase to about 6 t ha^{-1} to keep up with a conservative projection of a 1.6% annual increase in demand (CIMMYT, 1997). It is virtually impossible to expand wheat production areas; thus, yields must be increased.

Soil phosphorous (P) deficiency is a major constraint to increased crop yields in tropical and subtropical regions (Stangel and von Uexküll, 1990). Too little P fertilizer is actually used in those parts of the world where P input could have a major effect on food production (Tiessen, 1995). To maintain production levels, P must be added to the soil–plant system as mineral fertilizer to replenish what is removed by harvested grain and straw (Vlek et al., 1997).

The International Maize and Wheat Improvement Center (CIMMYT) in Mexico has organized its wheat breeding work around six mega-environments (MEs) that are relatively homogeneous for biotic and abiotic stresses (Rajaram, 1995). Of these, ME3 (acid, P-fixing soils) is the one where P deficiency and aluminum toxicity are the most important abiotic yield constraints. Mega-environment ME1 (irrigated wheat), with more than 32 million ha of spring bread wheat, about 40% of all produced in the tropics and subtropics, has high-yield potential and is highly responsive to inputs.

The distribution of improved cultivars to farmers is among the most cost-effective means to upgrade crop production (Byerlee, 1994). Thus, it is appealing to breed for P use efficiency (PUE; grain yield per P supply) in addition to improving P efficiency through crop management (Batten, 1992). Three prerequisites are essential to improve PUE in wheat: genetic diversity for PUE in wheat must be present, traits for improved efficiency must be identified, and the environment for selection must have the potential to permit expression of the desired traits.

Genotypic variation and tolerance to P deficiency in wheat have been reported (Rosa and Carmago, 1990; Jones et al., 1992; Gahoonia and Nielsen, 1996). Batten et al. (1984) demonstrated genotypic differences among wheat cultivars in response to P fertilization. Use efficiency of P can be divided into P uptake and P utilization efficiency, analogous to similar terms defined for N use efficiency (Moll et al., 1982). The objectives of this study were to evaluate the contribution of P uptake and utilization and related traits for improved PUE in acid and calcareous soils, under low and high P conditions.

2. Materials and methods

Field trials were conducted from 1993 to 1995 at two locations in Mexico. One location was in the valley of Paso del Muerto in the Central Mexican Highlands near Patzcuaro, Michoacan (19°N 101′W, 2400 masl), and the other in the Yaqui Valley, near Obregon, Sonora, Northwest Mexico (27°N 109′W, 40 masl). According to CIMMYT's classification of targeted wheat breeding MEs, Patzcuaro is representative for ME3 (acid soil), and Obregon for ME1 (irrigated wheat). At both locations, wheat was grown at two P levels — without P fertilization (−P) and with P fertilization (+P, 35 kg P per ha), applied as triple superphosphate at seeding.

Thirty-eight semidwarf spring bread wheat genotypes were tested at both locations; 29 were advanced lines from CIMMYT's wheat program, selected for high yields without P and good response to P fertilization in Patzcuaro, while the remaining were eight CIMMYT or Mexican cultivars (Inia, Turaco, Bacanora, Attila, Genaro, Culiacan and two lines of Irena), and one cultivar from Brazil (Alondra, known for its adaptation to acid soils). Attila and Bacanora are genotypes with high-yield potential, and Inia, Irena, Culiacan and Turaco served as negative checks with low yields at low P.

Two experiments, No. 1 (32 genotypes) and No. 2 (30 genotypes), were conducted at both locations in 1993–1994 and 1994–1995, respectively. There were 11 common entries in both experiments, which allowed a comparison across 2 years and both locations.

2.1. Patzcuaro

The field trials in the acid soil (pH 5.8, Andisol) were rainfed, and wheat was cultivated in the summer during the rainy season. Seasonal rainfall was 800–1000 mm. Summer temperatures were mild and declined near the end of the crop cycle (Fig. 1), which delayed maturity into October and November. Other soil properties were loam texture (sand, loam, clay were 51, 38 and 11%, respectively); high organic matter, i.e. 83 g kg^{-1}; and cation exchange capacity was 4.8 cmol kg^{-1}. The trials in the acid soil were conducted on different fields after two previous summer crops of unfertilized maize and fallow during the dry winter season.

The Andisol was selected for this study because of its relatively low Al concentration and wheat is known to respond to P fertilization (Manske et al., 2000). Genotypic variation of PUE in acid soils is often confounded with aluminum toxicity (Rosa and Carmago, 1990). Concentrations of exchangeable aluminum ranged between 2.1 and 4.0 mg kg^{-1} soil and aluminum saturation was 20% of the cation exchange capacity, which is below the level considered toxic for wheat (Wheeler et al., 1992).

The +P plots were fertilized with the recommended rate of 35 kg P per ha, which was banded with the seed at planting, the recommended technique for soils with a high P-fixation capacity. All plots were additionally fertilized with 130 kg N per ha as urea, 1/3 of the urea was broadcast at seeding and 2/3 at tillering. Wheat was seeded within the optimum sowing dates for the location (around June 20, after initiation of the rainy season) at a seeding rate of 120 kg ha^{-1}. High rainfall and humidity favored fungal diseases, which had to be controlled by intense fungicide spraying, i.e. every 2 weeks after anthesis with thiabendazole (2-[4-thiazolyl]-benzimidazole) for *Fusarium* spp. and with propiconazole (1-[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yi]-1*H*-1,2,4-triazole) for *Septoria nodorum*, *S. nivale* and *S. graminae*. Broadleaf weeds were controlled with bromoxynil (3,5-dibromo-4-hydroxybenzonitrile) at 1 l ha^{-1} applied 20 days after emergence and by hand weeding.

The plots were 6-m long, with six rows spaced 30-cm apart, and the harvested area was 4.8 m^2 (4 m of the four center rows). The spikes of the harvest area were hand-harvested at physiological maturity, which occurred between 10 and 25 November. Total biomass was determined by se-

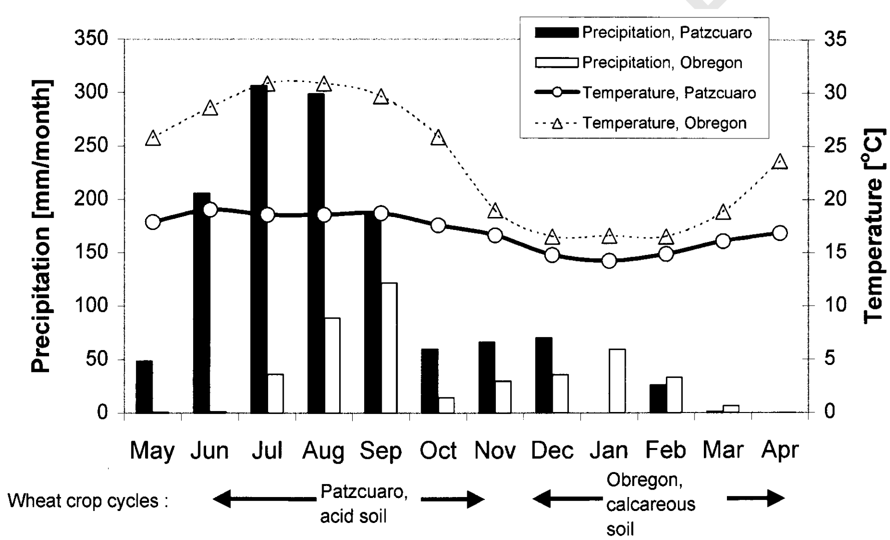

Fig. 1. Monthly mean precipitation and temperature in Patzcuaro (acid soil) and Obregon (calcareous soil), averages measured during experiments 1 and 2 (1993–1995).

Table 1
Olsen P without (−P) and with 35 kg P per ha (+P), measured in topsoil (0–20 cm) before fertilization in calcareous soil, 20 days after fertilization in acid soil, and other nutrients as means of 2 years measured before planting

Olsen P Year	P-level	Patzcuaro Acid Andisol	Obregon Calcareous Aridisol
		(mg kg^{-1})	
1993–1994	−P	3.6	2.9
	+P	6.3	4.1
1994–1995	−P	2.8	2.7
	+P	5.9	3.6
Other nutrients		(g kg^{-1})	
N-kj		0.46	0.05
		(mg kg^{-1})	
Ca		725	4933
Mg		70	635
K		285	370
Fe [a]		14.8	3.9
Mn [a]		1.8	4.8
Zn [a]		0.3	0.5
Cu [a]		0.5	1.2
B [a]		0.03	0.72

[a] Micronutrients by DTPA-method, B by hot water extraction.

lecting 100 stems randomly from the harvest area. The spikes were dried and threshed, straw weight and grain weight calculated at 0% moisture. Harvest index and total biomass per hectare were calculated.

2.2. Obregon

Obregon has a semi-arid climate, and wheat is grown under irrigation during the winter season. Irrigation water was applied when 50% of the available water in the topsoil (0–30 cm) was depleted. With sufficient supply of water and nutrients, cool temperatures and high solar radiation during the winter offer ideal conditions for high grain yields in wheat. High temperatures near the end of the crop cycle in April shortened the phase of grain-filling (Fig. 1). The calcareous soil (pH 8.3) in Obregon was a coarse sandy clay, mixed montmorillonitic, Typic Caliciorthid (Aridisol) (Table 1). Other properties were low organic matter (7 g kg^{-1}) and relatively high cation exchange-capacity (32 cmol kg^{-1}). The wheat experiments were established in the same fields following a rotation with unfertilized summer maize. Two P regimes were established in two adjacent fields. In the low P-treatment field, plant-available P (Olsen P) had been reduced from 4.1 to 2.7 mg P per kg by continuously cropping without P fertilization since the winter of 1991–1992, with a winter wheat and summer maize rotation. Maize biomass was removed to reduce accumulation of residual P. In the high P treatment, 35 kg P per ha was applied as a broadcast treatment to each wheat crop.

Before seeding, 225 kg N per ha as urea and 25 kg Zn per ha in the form of zinc sulfate were applied uniformly, since soil Zn concentration was low (0.5 mg kg^{-1}). The crop was sprayed twice for stem rust (*Puccinia graminis*) and leaf rust (*Puccinia recondita*) with propiconazole; weeds were controlled as in Patzcuaro. Wheat was seeded at 120 kg ha^{-1} within the optimum sowing dates for the location (November 15 to December 15).

Plots were 5-m long, with six rows spaced 20-cm apart, and the harvest area was 2.4 m^2 (3 m of the four center rows). Plots were harvested at physiological maturity (5–15 April). Harvest was done by hand-cutting at ground level, and total biomass was measured in the field. A sub-sample of 100 stems was randomly taken from the harvested area and dried in an oven at 75°C for 48 h. After threshing, fresh grain weight was determined, and sub-samples of grain and straw taken, weighed, dried, and weighed again.

2.3. Pot experiment

In 1994–1995, a pot trial was conducted in Obregon with four wheat genotypes grown in the acid and calcareous soils from both locations, without and with P fertilization (139 mg P per pot), in four replications. The pots (4447 cm^3) were inserted into the field.

2.4. Parameters of P use efficiency

Plant-available P in both soils was assessed by the method of Olsen et al. (1954), inorganic P concentration in soil solution was determined colorimetrically in the displaced soil solution (Adams, 1974).

Representative sub-samples of dry matter of straw and grain were analyzed colorimetrically for P concentration in grain (PCg) and straw (PCs) with the vanado-molybdate method (Kitson and Mellon, 1944). In experiment 2, P accumulation was additionally determined at early anthesis, i.e. Zadok's code 61 (Zadok et al., 1974). For this, above-ground biomass was sampled (0.24 m^2 and per plot in the calcareous and 0.36 m^2 in the acid soil) and its P concentration determined. Pre- and post-anthesis P accumulations in above-ground biomass were calculated. Translocation of pre-anthesis P into grain was calculated by subtracting post-anthesis P accumulation from grain P at maturity, because grain P at maturity is equivalent to P accumulated after anthesis plus net translocation of P stored in the vegetative tissue prior to anthesis as stated by Moll et al. (1982) for nitrogen.

The following parameters were measured or calculated: dry matter of grain yield (GY) and total above-ground biomass (B), harvest index in percent (GY/B × 100), total grain P at maturity (Pg = grain P concentration × GY), total straw P at maturity (Ps = straw P-concentration × straw dry-weight), total P in biomass (Pt = Pg + Ps), P concentration in total biomass (PCt = Pt/B), and P harvest index in percent (PHI = Pg/Pt × 100). Genotypic P fertilizer response was defined as $(GY_{+P} - GY_{-P})/GY_{-P}$ in percent, where +P and −P are the means of the replicated plots with and without P fertilization, respectively. Apparent P fertilizer recovery was $(Pt_{+P} - Pt_{-P})/$ amount of P fertilized.

Phosporus use efficiency (PUE) was defined analogue to the definition of nitrogen use efficiency by Moll et al. (1982) as the grain production per unit P supplied from the soil and fertilizer ($GY/P_{available}$). PUE is the product of P uptake efficiency ($Pt/P_{available}$) and P utilization efficiency (PUTE = GY/Pt). We assumed that the available P for each genotype was indicated by the total P taken up by the genotypes at each P level, the relative differences in PUE and P uptake effiency among genotypes will be the same as the relative differences in GY and Pt, respectively, and PUTE would be the quotient of both. PUE is, therefore, GY = Pt × GY/Pt. The genetic contribution analysis determines the relative contribution of genetic variation of multiplied related parameters to the genetic variation in GY (Moll et al., 1982). This relationship is changed from multiplied to an additive by taking the log of all components, i.e. log(GY) = log(Pt) + log(PUTE). We define $Z =$ log(GY), $X_1 =$ log(Pt), and $X_2 =$ log(PUTE) = log(GY/Pt), so that $Z_k = X_{1k} + X_{2k}$ for the kth genotype mean of GY. After Moll et al. (1982), the sum of cross-products of each term, divided by the sums of squares of GY, estimates the ith component's contribution to the variation of GY ($C_i = \Sigma X_i Z / \Sigma Z^2$). The sum of the contributions of Pt and PUTE to GY totals one.

P utilization efficiency (PUTE) can be divided by simple algebraic transformation in two ways: PUTE = grain yield/total P uptake = harvest index/P concentration in total aboveground biomass, or PUTE = P harvest index/grain P concentration. The relative contribution of genetic variation of these multiplied related parameters to PUTE were also analyzed as described by Moll et al. (1982) for nitrogen.

2.5. Experimental design and statistical analysis

The statistical analysis across locations and years was considered a split-plot design with locations and years as main plots and genotypes as sub-plots. In the calcareous soil (Obregon), the two levels of P had been in two adjacent fields, i.e. main plots with three replications nested within the P levels. This experimental arrangement was necessary to establish the low P treatment by previous cropping without P fertilization. In the acid soil (Patzcuaro), the P deficiency and high P-fixation capacity was sufficient to establish both P levels in sub-plots with six (1993) or four (1994) replications.

Because of the different designs, the combined analysis across locations had to be conducted on the basis of treatment means as described by Cochran and Cox (1992). The mean square errors of the combined analysis on the mean basis were pooled from mean square errors derived from individual analysis of variance on the plot basis for each individual field trial. In the case of different number of replicates in combined trials, the mean square error for the combined analysis was weighted. Analysis of variance was performed with the SAS statistical package (SAS Institute, 1985).

Pearson correlation coefficients for phenotypic correlation were based on individual genotypic means across replications, separately for each P level, location and year. A *t*-test was used to determine the significance of the phenotypic correlation coefficients.

3. Results and discussion

3.1. Influences by soil type and P fertilization

The readily available amount of P measured as the inorganic P concentration in the soil solution (Holford, 1997) was very low in the acid soil and not affected by P fertilization (Fig. 2). This suggests that fertilizer P was rapidly adsorbed in the acid soil. Allophanes, which are the major mineral constituent of Andisols have a unique tendency to adsorb fertilizer P in the form of mineral–organic P complexes (Borie and Zunino, 1983). The soil solution P was higher in the calcareous than in the acid soil regardless of the P level. In the calcareous soil, the soil solution P increased after P fertilization with 35 kg P per ha, but declined again during the crop cycle to below 0.21 mg P per l (Fig. 2). Barraclough (1986) found 0.21–0.42 mg inorganic P per l soil-solution required for 95% maximum grain yield in wheat.

Crops growing on soils low in readily available P are often found to exploit more P from the soil than soil solution measurements and mechanistic models predict (Baldwin et al., 1973; Claassen, 1990). Roots induce changes in the physico-chemical equilibrium in the rhizosphere, which makes exchangeable P fractions and organic P in the soil accessible to the plant roots. The Olsen P, which includes readily available and the exchangeable P-fractions, was higher in the acid Andisol compared with the calcareous Aridisol, and in both soils affected by the P-fertilization (Table 1). In the calcareous soil, even with P applied to each subsequent wheat crop, Olsen P was as low as 4.1 mg P per kg soil. Less than 4 mg plant-available P per kg soil indicate P-deficiency accordingly to Page (1982).

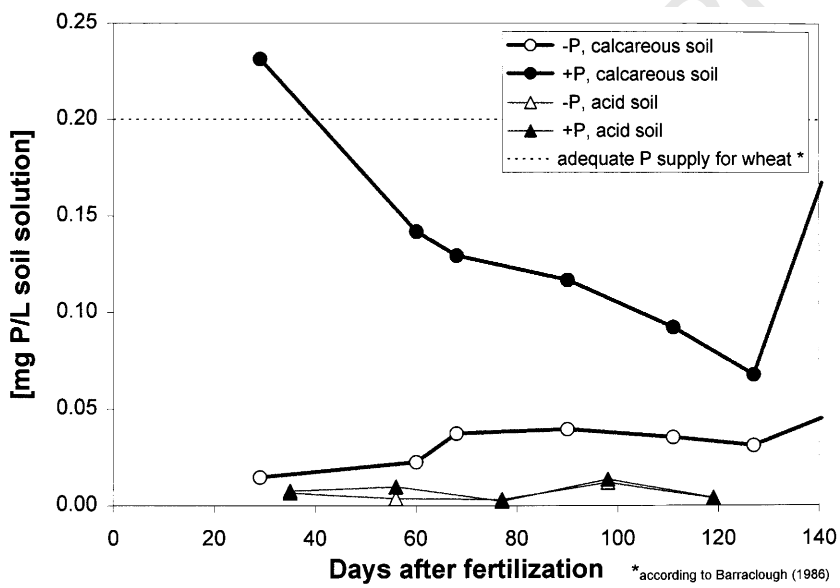

Fig. 2. Change of inorganic P concentration in soil solution during the wheat crop cycles in acid soil (Andisol) and calcareous soil (Aridisol), without (− P) and with P fertilization (+ P, 35 kg P per ha), average of 2 years (1993–1995).

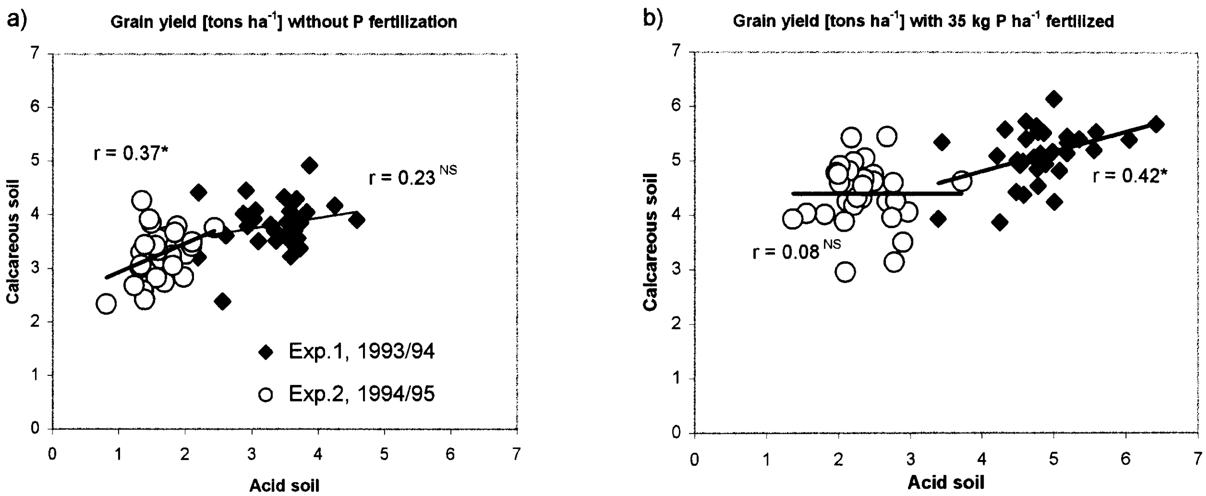

Fig. 3. Grain yield (kg ha^{-1}) of 32 and 30 spring bread wheat genotypes grown in experiments 1 and 2, respectively, in acid and calcareous soil, (a) without and (b) with 35 kg P per ha; phenotypic correlation between locations, *, $P < 0.05$; NS, non-significant.

3.2. Effects by genotypes, location, years and P levels

Under conditions of P deficiency, the tested germplasm showed considerable variability in P use efficiency. Without P fertilization, the grain yield of the wheat genotypes ranged in the acid soil from 2.2 to 4.6 and 0.8 to 2.4 t ha^{-1} in experiment 1 and 2, respectively, and in the calcareous soil from 2.4 to 4.9 and 2.3 to 4.3 t ha^{-1} in experiment 1 and 2, respectively (Fig. 3a). The genotypes varied in their response to P fertilization. With P fertilization, the grain yield ranged in the acid soil from 3.4 to 6.4 and 1.4 to 3.7 t ha^{-1} in experiment 1 and 2, respectively, and in the calcareous soil from 3.9 to 6.2 and 3.0 to 5.5 t ha^{-1} in experiment 1 and 2, respectively (Fig. 3b).

In experiment 1, the combined analysis of variance across locations showed location by P-level interactions for P uptake efficiency and PUTE. In experiment 2, the three-way interaction was significant for grain yield, P uptake and utilization efficiency. In the analysis of common entries in experiments 1 and 2 over 2 years, the three way interaction year–location–P level was significant for grain yield, P uptake and utilization efficiency. Therefore, the analysis of the environmental effects has to be based either on the location–P level or year–location–P level interactions, depending if the experiment was conducted over 1 and 2. The genotypes showed significant interactions by year, location and/or P level, depending on the experiment. The four-way interaction was never significant. Therefore, the analysis of genotypic correlations and genotypic contribution analysis was separated into location–P level or year–location–P level.

The year–location–P level interaction is shown by the means over 11 entries common at both years and both locations (Table 2). Grain yield without and with P fertilization varied among locations and years. Yields were higher on the calcareous soil, with P responses of 33 and 35% for the years 1993–1994 and 1994–1995, respectively. On the acid soil, where the trials were conducted in different farmers' fields, grain yield varied considerably between years, with higher yields in 1993 and lower yields in 1994. In both years, the P-response on the acid soil was with 42% higher than on the calcareous soil (Table 2).

The higher grain yield in Obregon compared with Patzcuaro was also influenced by the more favorable climate in Obregon. In order to separate the effects of soil from those of climate, a pot trial with both soils was performed with four spring bread wheat genotypes in Obregon, with and without P-fertilization. Under the same climatic conditions, wheat plants grown in the calcareous soil yielded twice as much biomass at anthesis as those grown in the acid soil, independently of the P application, which tripled the biomass by the same relative response in both soils.

The results of this pot experiment confirmed the results of the soil-solution analysis, which classified the acid soil as less fertile, more P deficient, and with a higher P adsorption than the calcareous soil. In the acid soil, P deficiency was also yield limiting with P fertilization due to the high P-adsorption capacity. This may explain the lower apparent P fertilizer recovery in the acid soil (Table 2). Phosphorus uptake by the aboveground biomass was highest in the calcareous soil with P fertilization, leading to apparent P-fertilizer recoveries of 19 and 21% in 1993–1994 and 1994–1995, respectively. Under conditions of P deficiency, the wheat plants utilized the adsorbed P more efficiently for grain yield formation. PUTE was higher without P fertilization and higher in the calcareous soil than in the acid soil (Table 2).

3.3. Importance of P uptake versus P utilization efficiency

In both experiments, the location by genotype interaction was the most significant of all genotype interactions. In addition, the phenotypic correlations for grain yield between locations were low or absent at low and high P (Fig. 3). This indicates that the tested germplasm acted differently at the locations, with different crop strategies for P use efficiency.

For the acid soil, grain yield was highly, positively correlated with total P uptake (up to $r=0.95$), but not correlated with P utilization efficiency, independently of the P-level. For the calcareous soil, total P uptake was less correlated with grain yield, especially with P-fertilization (up to $r=0.67$). In this situation, P utilization efficiency was positively correlated with grain yield in both experiments; without P application, only too a lesser degree in experiment 2 (Table 3).

The method of genetic contribution analysis by Moll et al. (1982) revealed distinct differences in the relative importance of P uptake and P utiliza-

Table 2
Wheat grain yield, harvest index and P parameters of 11 wheat genotypes, grown on acid and calcareous soil over 2 years, without (−P) and with 35 kg P per ha (+P)

	1993–1994				1994–1995				LSD[a]
	Acid		Calcareous		Acid		Calcareous		
	−P	+P	−P	+P	−P	+P	−P	+P	
t ha⁻¹									
Grain yield	3.37	4.80	4.11	5.46	1.56	2.20	3.50	4.72	0.76
P response		*42%*		*33%*		*42%*		*35%*	
kg P per ha									
Total P uptake	8.4	14.6	9.8	16.6	5.0	7.7	9.8	17.3	3.1
Apparent P fertilizer recovery		*18%*		*19%*		*8%*		*21%*	
kg P per ha									
P utilization efficiency	408	331	480	396	315	286	364	274	67
%									
Harvest index	44.0	40.2	35.9	35.9	35.2	35.4	38.0	36.0	NS
mg P per kg									
P concentration in total aboveground biomass	1087	1213	850	1094	1118	1241	1056	1323	324

[a] For comparison of means of year–location–P level interaction, TUKEY test, probability level 0.05.

Table 3
Phenotypic correlations of grain yield with P efficiency parameters and harvest index, in acid and calcareous soil, without (−P) and with 35 kg P per ha (+P) [a]

	Experiment 1, 1993–1994				Experiment 2, 1994–1995			
	Acid		Calcareous		Acid		Calcareous	
	−P	+P	−P	+P	−P	+P	−P	+P
Total P uptake	0.92***	0.91***	0.84***	0.67***	0.94***	0.95***	0.79***	0.62***
P utilization efficiency	0.21	0.30	0.03	0.60***	−0.05	0.23	0.44**	0.63***
Harvest index	0.42*	0.53**	0.61***	0.47**	−0.10	0.05	0.46**	0.73***
Total biomass P concentration	0.33	0.49**	0.46**	0.00	−0.11	−0.15	−0.02	0.26
P harvest index	0.17	0.36*	0.26	−0.11	0.05	0.16	0.33	0.60***
Grain P concentration	−0.10	−0.13	−0.11	−0.59***	0.18	−0.15	−0.31	−0.40*

[a] *, $P<0.05$; **, $P<0.01$ and ***, $P<0.001$ by t-test.

tion efficiency between both soils (Table 4), and confirmed the results of the correlation analysis. Using the inorganic P concentration in the soil solution as a criterion, the acid soil was P deficient even with P fertilization (Fig. 2), and the genotypic variation of grain yield was attributed more to the variation in P uptake efficiency. In both experiments in the acid soil, variation in grain yield was almost completely (between 85 and 100%) related to variation in P uptake efficiency, regardless of the P level (Table 4).

P utilization efficiency (PUTE) was better expressed and contributed most to grain yield in the case of adequate P supply such as in the calcareous soil with P fertilization, accounting for 43 and 50% of the variability in yield in experiments 1 and 2, respectively. At low P in the calcareous soil, PUTE played less role. In experiment 1, variation in grain yield at low P was 91% explained by P uptake efficiency, whereas in experiment 2 this was 71% (Table 4).

Thus, P use efficiency (grain yield) was mostly determined by P uptake efficiency under P deficient conditions. P utilization efficiency played a role under good P supply conditions, especially in the calcareous soil. These findings are corroborated by the phenotypic correlations between P levels, separately for each location. In the acid soil, where P was deficient irrespective of the level of P applied, grain yields were positively correlated between −P and +P, with $r=0.65$ and 0.80 for experiments 1 and 2, respectively. Regardless of the P level, the germplasm expressed mainly differences in P uptake. In the calcareous soil, such correlations were weak if present at all. Here, different traits were relevant, P uptake efficiency more at −P and P utilization efficiency more at +P.

3.4. Traits associated with improved P utilization efficiency

Increased harvest index, P harvest index and low P concentration in grain may improve PUTE (Jones et al., 1989; Batten, 1992). On the average of all genotypes, the higher PUTE in the calcareous soil at −P compared with the acid soil was related to lower P concentrations in total aboveground biomass, not to improved harvest index, which was not significantly different among location, years and P levels (Table 2). A decrease of P concentration in total aboveground biomass is equal to an increase in biomass production efficiency, which is defined as biomass divided by total P in biomass (Ortiz-Monasterio et al., 1997). On the average, in the acid soil, P concentration in total aboveground biomass was not or only slightly increased by P fertilization, in contrast to the calcareous soil.

The relative contribution of the variation of harvest index or P harvest index, and P concentrations in total aboveground biomass or grain to the variation of PUTE was influenced by the experiment, soil and P-level (Table 5). In both experiments, the P harvest index contributed more to PUTE than the grain P-concentration, except in experiment 1 in the acid soil, where both parameters were equally important. In the acid soil, the genotypic variation in harvest index had a higher effect on the genotypic variation of PUTE than the P concentration in total biomass. The latter tended to be more relevant in the calcareous soil at low P. At +P in the calcareous soil, the results varied between years; in experiment 2, the harvest index was more important, whereas in experiment 1, both parameters had almost the same effect on the variation of PUTE (Table 5).

These traits for improved PUTE were best correlated with grain yield when PUTE played a role such as in the calcareous soil at +P. In this situation, grain P concentration was negatively and harvest index positively correlated with yield (Table 3). At high P, the P concentration in total biomass was not correlated with grain yield in the calcareous soil, and P harvest index was only positively correlated in experiment 2. In experiment 1, in the calcareous soil at low P, harvest index and P concentration in total biomass were positively correlated with grain yield (Table 3).

In the acid soil, where P utilization efficiency was less important, grain yield was only correlated in experiment 1 with P harvest index and P concentration in total aboveground biomass at +P and with harvest index at both P levels (Table 3). Apparently, under conditions of severe P deficiency such as in this acid soil, higher P concentrations in total aboveground biomass are favorable for improved grain formation.

Batten (1992) found that selection of wheat cultivars under growth conditions with higher yield levels will improve P use efficiency, especially if the yield advantage is due to an improved harvest index. This was the case in the calcareous soil under high P and irrigation. About 80% of the total P in the wheat plants was in the grain at harvest. Therefore, the effect of a decrease in grain P concentration on PUTE is much higher than a decrease in P concentration in the total biomass. Genotypic differences in grain P concentration are reported to be fairly consistent across environments (Schulthess et al., 1997). At both locations, grain P concentration was positively correlated among P-fertilizer levels (in experiment 1 by $r = 0.60$ and 0.70, in the calcareous and acid soil, respectively; in experiment 2 by $r = 0.77$ only in the acid soil). Across locations, grain P concentration was only positively correlated between the calcareous soil at −P and the acid soil ($r = 0.55$ and 0.60, at low and high P, respectively).

Table 4
Relative contribution of variation in P uptake and P utilization efficiency to the variation of grain yield in acid and calcareous soil, without (−P) and with 35 kg P per ha (+P)

	Experiment 1, 1993–1994 [a]				Experiment 2, 1994–1995 [b]			
	Acid		Calcareous		Acid		Calcareous	
	−P	+P	−P	+P	−P	+P	−P	+P
Total P uptake	0.94	0.85	0.91	0.57	1.03	0.95	0.71	0.50
P utilization efficiency	0.06	0.15	0.09	0.43	−0.03	0.05	0.29	0.50

[a] Thirty-two genotypes.
[b] Thirty genotypes.

Table 5
Relative contribution of variation in harvest index 1/P concentration in total above-ground biomass, or P harvest-index and 1/grain P concentration to the variation of P utilization efficiency in acid and calcareous soil, without (−P) and with 35 kg P per ha (+P)

	Experiment 1, 1993–1994 [a]				Experiment 2, 1994–1995 [b]			
	Acid		Calcareous		Acid		Calcareous	
	−P	+P	−P	+P	−P	+P	−P	+P
Harvest index	0.83	1.10	0.16	0.41	1.22	1.14	0.10	0.80
1/P-concentration in total biomass	0.17	−0.10	0.84	0.59	−0.22	−0.14	0.90	0.20
P harvest-index	0.60	0.53	1.19	1.17	0.72	0.82	0.64	0.77
1/P-concentration in grain	0.40	0.47	−0.19	−0.17	0.28	0.18	0.36	0.23

[a] Thirty-two genotypes.
[b] Thirty genotypes.

3.5. Differential P uptake patterns and translocation of P

The pattern of P uptake differed between locations. In the acid soil, post-anthesis P accumulation was important, accounting for 42 and 31% of the total P uptake, at −P and +P, respectively (Table 6). Post-anthesis P uptake was highly positively correlated with grain yield in the acid soil (Table 7). In the calcareous soil, no post-anthesis P accumulation occurred (Table 6). In fact, there was a net loss of P from the aerial parts of the wheat plants during the post-anthesis period, especially under high P, where on the average of all genotypes, 19% of the total shoot P were lost. Similar observations were made by Waldren and Flowerday (1979), who reported a net-P-loss of 39% at maturity in winter wheat. The losses were due to both reductions in aboveground biomass and in its P concentration. P can be translocated to and released by the roots at post-anthesis (Boatwright and Haas, 1961).

In the calcareous soil at both P levels, grain P accumulation at maturity was completely determined by translocation of pre-anthesis shoot P (Table 6). However, at +P, neither pre- nor post-anthesis P uptake nor P translocation were significantly correlated with grain yield (Table 7). This was in contradiction to Moll et al. (1982), who found for nitrogen, that improved nutrient translocation was related to improved nutrient utilization efficiency, because it led to higher nutrient harvest index, if nutrient concentration in the grain was kept constant. Apparently, reduced grain P concentration and higher harvest index reduced the effect of P translocation on grain yield under these conditions. Both were correlated with grain yield (Table 4).

4. Conclusions

In the calcareous soil at high P, P utilization efficiency was the dominant factor explaining variations in grain yield. Further progress in grain yield through higher P utilization efficiency can be achieved by selection for higher harvest index, and P harvest index, and reduced grain P concentration. Selection for wheat genotypes that remove small amounts of P from the soil because of low P grain concentration contribute to sustainable land use (Schulthess et al., 1997). An example of this is the situation of a country such as Australia, which has soil that are poor in available of P and at the same time it is a major exporter of wheat grain to the world. In a wheat-breeding program in Argentina, Calderini et al. (1995) showed that the grain P concentration was significantly decreased over the years by breeding. However, the strategy of reducing the P concentration in grain has a limit. A minimum amount of P in the grain is needed for nutritional reasons and for good germination. Without reduction of the grain P concentration, grain yield can only be increased by improved P uptake, higher harvest index or better translocation of P into the grains. It is unlikely to use the latter two traits for further yield improvement in wheat. P translocation into grains was not correlated with grain yield in this study, and the internal translocation mechanisms for improved P translocation are still unknown. Also, the future improvements in harvest index as a way to increase grain yields in wheat are limited (Fischer, 1981; Calderini et al., 1995).

Given little room to breed for higher harvest index, the selection for high grain yield potential in wheat will further reduce grain P concentration due to an effect of dilution, if P uptake efficiency is not improved. Under conditions of P-deficiency, i.e. in the acid soil at low and high P and calcareous soil at low P, the variation of grain yield was most explained by changes in P uptake efficiency, which was highly correlated with grain yield. Selection pressure for P uptake efficiency is imposed consciously on soils with low P availability. However, genetic progress would be higher with selection is carried out directly for traits for P-uptake improvement (Manske et al., 2000). The plant factors that influence P uptake efficiency are mainly associated with root characteristics. In the acid soil, the genotypic differences in P uptake efficiency were related to root length density, colonization by vesicular arbuscular and arbuscular mycorrhizal fungi and root excretion of phosphatases (Manske et al., 2000).

With P uptake efficiency as a strategy to improve grain yield, we are faced with another dilemma. In the case of resource of poor farmers (unable to purchase fertilizers), the development of wheat cultivars with high P uptake efficiency may accelerate soil nutrient mining. This will not be such a serious problem with phosphorus, because there are many soils in the world that have large reserves of total P, but low levels of available P (Tiessen, 1995). And if P fertilizer is available, improved of P uptake efficiency would increase P fertilizer recovery, especially on soils with high P adsorption capacity.

Nevertheless, in the developing world, P fertilization is not always possible. In this situation, an ideal genotype would be one that has a high adaptation capability to situations of low and high P availability. It should combine both, good response to P fertilization and high yields under P-deficient conditions. Wheat breeding only under high selection pressure of P deficiency will improve mainly P uptake efficiency, but may not lead to germplasm with high-yield potential. Genotypes selected under conditions of low-P supply often have a lower yield potential and response to P fertilization than others when planted in fertile soils (Graham, 1984). Yield potential is best expressed under high input conditions. The combination of improved P utilization and P uptake efficiency may be achieved by selection under both high and low-P conditions. This hypothesis is currently being tested at CIMMYT.

Table 6
Pre- and post-anthesis P accumulation in % of total P in above-ground biomass and translocated preanthesis P into grain as % of total grain P, at maturity in experiment 2, in acid and calcareous soil, without (−P) and with 35 kg P per ha (+P) [a]

	Acid		Calcareous	
	−P	+P	−P	+P
Percent of Pt				
Pre-anthesis	58*c*	69*d*	107*c*	119*d*
Post-anthesis	42*b*	31*a*	−7*b*	−19*a*
Percent of Pg				
Translocated pre-anthesis P into grain	42*a*	58*b*	109*a*	128*b*

[a] $a<b$ For $P<0.05$, separately for each soil, Tukey-test.

Table 7
Phenotypic correlations of wheat grain yield with pre- and post-anthesis P accumulation in aboveground biomass and translocated pre-anthesis P into grain, in experiment 2, in acid and calcareous soils, without (−P) and with 35 kg P per ha (+P) [a]

	Acid		Calcareous	
	−P	+P	−P	+P
Pre-anthesis P	0.25	0.58**	0.52**	0.25
Post-anthesis P	0.86***	0.73**	0.30	0.29
Translocated pre-anthesis P into grain	−0.07	0.32	0.76**	0.29

[a] *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

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