Improved phosphorus efficiency of three new wheat genotypes from CIMMYT in comparison with an older Mexican variety

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Dedicated to Prof. Dr. *Brunk Meyer* on the occasion of his 70th birthday

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Summary – Zusammenfassung

In a field trial in Northwest Mexico, the phosphorus efficiency of three advanced bread wheat lines (*Triticum aestivum* L.) from CIMMYT were compared with an older Mexican variety Curinda, under irrigation, on an alkaline clay soil (3.7 mg Olsen-P kg^{-1} soil) without (P-0) and with P-fertilisation (P-35; 35 kg P ha^{-1}). Dry matter, P-content, P-uptake of above ground biomass and root growth (root length densities in different soil depths) were measured at different growth stages, and the net P-uptake rates per unit root length calculated.

All four genotypes responded positively to P-fertilisation. The three new genotypes showed significantly higher grain yields compared with the old variety Curinda, on the average, 54% and 42% higher at P-0 and P-35, respectively. The higher grain yield was mainly due to a larger number of kernels per ear, higher thousand kernel weight as well as a higher harvest index. The old variety Curinda had the same (P-0) or greater (P-35) number of spikes m^{-2} than the new genotypes. In conclusion of this experiment, the three new genotypes could be classified as more P-efficient. The P-uptake at harvest averaged 35% and 24% more than the old variety Curinda at the P-0 and P-35 level, respectively. The improved P-efficiency was mainly due to a more efficient P-uptake. However, there were only small differences in P-utilisation efficiency (kg grain per kg P in shoots) between old and new varieties (8–11%). The differences in the root systems were more decisive in the P-0 treatment than with P-fertilisation. At low P, the improved P-uptake per ha of the advanced lines was due to a higher root length density especially after flowering, while at high P, a higher P-influx rate per unit root length played a more important role than the root length density. The superiority of the new genotypes at both P levels is obviously due to the good adaptation of their root system (root length density, uptake rate per unit root) to variable P availability in soil.

Key words: wheat genotypes / phosphorus uptake efficiency / phosphorus utilization efficiency / phosphorus netto uptake rate / root length density

Verbesserte Phosphateffizienz von drei neuen Weizengenotypen von CIMMYT im Vergleich zu einer alten mexikanischen Sorte

In einem Feldversuch im Nordwesten Mexikos wurde die Phosphateffizienz dreier neuer Weizenzuchtlinien (*Triticum aestivum* L.) von CIMMYT mit der älteren mexikanischen Sorte Curinda verglichen. Die vier Weizengenotypen wurden unter Bewässerung, ohne (P-0) und mit P-Düngung (P-35, 35 kg P ha^{-1}) auf einem alkalischen Tonboden (3–3,7 mg Olsen P kg^{-1} Boden) angebaut. Zu mehreren Vegetationsstadien wurde die Trockenmasse, P-Gehalte und P-Entzüge der oberirdischen Biomasse, sowie das Wurzelwachstum (Wurzellängendichte in mehreren Bodenschichten) bestimmt und die Netto P-Aufnahmeraten pro Wurzellänge berechnet.

Alle vier Weizengenotypen reagierten mit Ertragssteigerungen auf die P-Düngung. Der Kornertrag der drei neuen Genotypen war bei niedrigem wie bei hohem P-Angebot um 54% bzw. 42% höher als bei Curinda. Bei niedrigem P-Angebot besaßen die neuen Genotypen bei gleicher Anzahl Ähren pro m^2 mehr Körner pro Ähre und eine höheres TKG als Curinda; hingegen bei hohem P-Angebot eine signifikant geringere Anzahl Ähren m^{-2}, aber eine viel höhere Kornzahl pro Ähre und tendenziell höheres TKG als die alte Sorte. Der Harvestindex der neuen Genotypen war gegenüber Curinda bei mit und ohne P-Düngung um 21 bzw. 28% erhöht. Die neuen Weizenlinien nahmen ohne P-Düngung 35% und mit P-Düngung 24% mehr P als Curinda auf. Die P-Verwertungseffizienz (kg Korn kg^{-1} P im oberirdischen Spross) der neuen Genotypen war nur leicht höher als die von Curinda (8 bzw. 11%). Bei niedrigem P-Angebot basierte die höhere P-Aufnahme der neuen Zuchtlinien im Wesentlichen auf einer größeren Wurzellängendichte, insbesondere nach der Blüte und bei hohem P-Angebot auf einer effizienteren Netto-P-Aufnahmerate der Wurzel. Die Überlegenheit der neuen Genotypen sowohl bei niedrigerem als auch ausreichendem P-Angebot ist offenbar auf eine gute Anpassungsfähigkeit der Wurzelsysteme (Wurzellängendichte, P-Aufnahmerate) an wechselnde Bedingungen der P-Verfügbarkeit zurückzuführen.

1 Introduction

Phosphorus deficiency is one of the limiting factors for crop production on many tropical and subtropical soils (*Ozanne*, 1980), because of absolute P-deficiency in soils or fixation of P-fertiliser in form of hardly-soluble Fe- or Al- or Ca-phosphate compounds. Therefore, many agricultural soils in the developing countries are P-deficient (*Vlek* and *Koch*, 1992), and have an unfavourable P-dynamics (*Soltan* et al., 1993). The P-supply to crops is often insufficient in many regions of the developing world because of the lack of money or unavailability of P-fertilisers. To increase wheat production without undue degradation of the soil-resource base and the environment requires optimal use of phosphorus in the soil-crop systems. In addition to improving P-efficiency through

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crop management it is appealing to turn to plant breeding to raise phosphorus efficiency. Selection of P-efficient wheat cultivars is also a breeding-goal of the *Centro Internacional del Mejoramiento de Mais y Trigo* (CIMMYT) in Mexico.

The objective of this study was to evaluate the P-efficiency of three new wheat-lines from CIMMYT in comparison with an older Mexican variety under low and high P-conditions, to determine P-uptake and P-utilization, and to analyse related traits.

2 Material and methods

The field trial was conducted on the CIMMYT breeding-station CIANO in the Yaqui Valley, near Obregon, Sonora; Northwest Mexico (27°N 109' W, 40 masl), during the crop cycle Winter 1996/97. Obregon has a semiarid climate, and wheat is grown under intense irrigation during the winter season. With sufficient supply of water and nutrients, this environment with its dry and cool winters and high solar radiation offers ideal conditions for high grain yields in wheat. The soil was a coarse sandy-clay mixed montmorillonitic Typic Calciorthid (Aridisol), with 44–46% clay, 15–20% loam, 36–38% sand and low soil organic matter (0.3 to 1% in the upper soil layer 0–20 cm) and a soil-pH (H_2O) 8.1. Before P fertilisation, the available P (Olsen P) was 3 to 3.7 mg P kg^{-1} soil, indicating P deficiency in this soil accordingly to *Page* (1982).

Four spring wheat genotypes (three new, advanced lines from CIMMYT and the older Mexican variety Curinda) were grown with two P-levels (P-0 = 0 kg P ha^{-1} and P-35 = 35 kg P ha^{-1} applied as Triple Super Phosphate). The three advanced lines originated from following crosses: Chilero/Wuhan (in the text abbreviated as ChilWuh), Bagula/Kauz (BauKauz) and Pagago/Seri (PgoSeri).

The two-factorial (two P-levels, four genotypes) experiment was conducted as a complete randomised block design with four replications. Irrigation water was applied when 50% of the available water in the topsoil was depleted. Mineral fertiliser was broadcast directly before sowing, in addition to the P treatment, 225 kg N ha^{-1} as urea and 25 kg Zn ha^{-1} in the form of zinc sulphate to each plot. The crop was sprayed twice for stem rust (*Puccinia graminis*) and leaf rust (*P. recondita*) with Propiconazole, and the weeds were controlled with Bromoxynil (3.5-dibromo-4hydroxybenzonitrile) and by hand weeding. Wheat was seeded at the optimum sowing dates (November 20, 1996) with a seeding rate of 120 kg ha^{-1}. Plots were 11 m long, with seven rows spaced 20 cm apart, and the harvest area was 3 m^2 (3 m of the 5 centre rows). Plots were harvested at physiological maturity (April 15, 1997). Harvest was done by hand at ground level and total biomass was measured in the field. A subsample of 100 stems was randomly taken from the harvested area and dried in an oven at 75°C for 48 hrs to adjust the moisture of the biomass to 0%. After threshing, fresh grain weight was determined, sub-samples of grain and straw taken, weighed, dried, and weighed again to adjust to 0% moisture. The yield components (spikes per m^{-2}, number of kernels per spike and thousand-kernel-weight) were determined. Representative sub-samples were analysed colorimetrically for P concentration in grain and straw with the vanadate-molybdate method (*Kitson* and *Mellon*, 1944).

During the wheat crop cycle, biomass, P-accumulation, root-length density were determined at three stages of plant development, at tillering (Zadoc's decimal code = DC 23–25), early anthesis (DC 61) and post-anthesis (DC 75). Aboveground biomass was sampled (1 m^2 per plot) and its P concentration determined. Roots from a defined volume of soil were extracted in the form of monoliths from the upper soil layer (0–20 cm soil depth) by driving a metal frame (30 cm length, 20 cm broad and 20 cm depth) into the soil and in the form of soil cores from the deeper soil layer (20–35 cm depth) by a root auger (diameter 8 cm, length 15 cm, volume 750 cm^3 (*Böhm*, 1979). The roots were separated from the soil by hand washing. Total root length was assessed by the line-intercept method of *Tennant* (1975). Root length density (RLD) was calculated by the root length divided by the volume of the monoliths or cores. For each phase of plant development, the average net-P-uptake rate per cm root length was calculated by the P-accumulation in the above ground biomass divided by the total root-length (*Williams*, 1948).

3 Results

Phosphorus fertilisation improved the grain yield of all four wheat genotypes, on the average by 78% (Fig. 1). The application of 35 kg P ha^{-1} was sufficient for this location, because grain yield could not be enhanced by higher P-fertiliser application (data not shown).

The three new wheat lines from CIMMYT showed at both P-levels higher grain yields compared with the old variety Curinda, 54% at P-0 and 42% at P-35, on the average of the three new lines. The higher grain-yield of the new genotypes was primarily related to more kernels per spike (25% and 58% more compared with Curinda at P-0 and P-35, respectively) and higher thousand kernel weight (33% and 12% more, respectively). In contrast, the older variety Curinda produced more spikes per m^{-2} (Fig. 1). The new genotypes translocated much more assimilates from the aboveground biomass into the grains. The

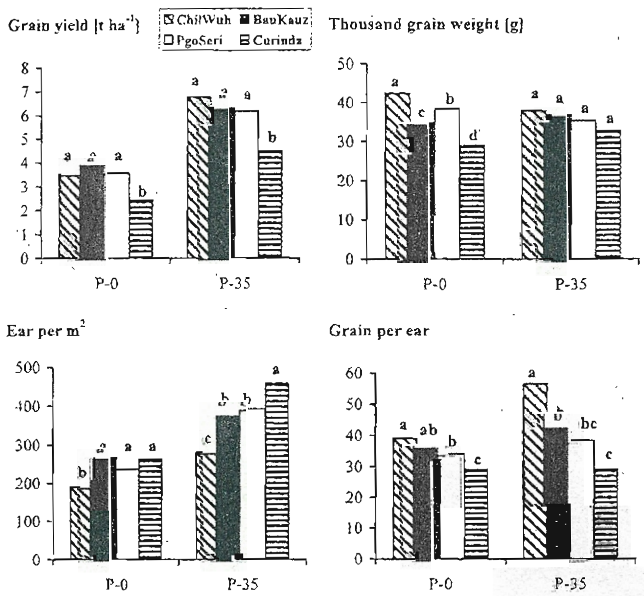

Figure 1: Grain yield and yield components of three new wheat genotypes (ChilWuh, BauKauz and PgoSeri) and the old cultivar Curinda, without (P-0) and with 35 kg P ha^{-1} fertilised (P-35); a > b significant different for P = 0.05, separately calculated for each P level.

Abbildung 1: Kornertrag und Ertragskomponenten von drei neuen Weizengenotypen (ChilWuh, BauKauz und PgoSeri) und der alten Sorte Curinda, ohne (P-0) und mit 35 kg P ha^{-1} gedüngt (P-35); a > b signifikant verschieden für P = 0.05, getrennt für beide P-Stufen.

Table 1: Harvest index, P uptake, P utilization at harvest and grain P-content of four wheat genotypes depending on P fertilization.
Tabelle 1: Harvestindex, P-Aufnahme (Spross), P-Verwertung zur Reife und P-Gehalt der Körner bei vier Weizengenotypen in Abhängigkeit von der P-Düngung.

	Harvest-index[(a)]		P uptake [kg P ha^{-1}]		P utilization [kg grain kg^{-1} P in shoot]		Grain P-content [mg P g^{-1} dry weight]	
Genotypes	P-0	P-35	P-0	P-35	P-0	P-35	P-0	P-35
ChilWuh (new)	34.0	38.7	6.6	18.7	470	320	1.7	2.5
BauKauz (new)	35.4	39.8	6.8	18.3	461	307	1.6	2.6
PgoSeri (new)	37.4	41.3	6.5	17.2	484	320	1.8	2.7
Curinda (old)	29.4	31.1	4.9	14.6	437	283	1.9	2.8
New genotypes (average)	35.6	39.9	6.6	18.0	472	316	1.8	2.7
% relative values of the new genotypes[(b)]	121*	128*	135*	124*	108	111	104	108

(a) Grain dry matter in % shoot dry matter
(b) Old variety = 100%
* Significant at P = 0.05 probability level.

Table 2: Comparison of important plant parameters between the old wheat variety Curinda and the mean values of the three new lines ChilWuh, BauKauz and PgoSeri, without P-fertilization (P-0), at tillering (Zadoc's decimal code = DC 23–25), early anthesis (DC 61) and post-anthesis (DC 75).
Tabelle 2: Mittelwertvergleich wichtiger Pflanzenparameter der drei neuen Zuchtlinien (ChilWuh, BauKauz und PgoSeri) mit der alten Weizensorte Curinda ohne P-Düngung (P-0), zur Ernte, und drei Vegetationsstadien, Bestockung (Zadoc's Dezimalcode = DC 23–25), zur Blüte (DC 61) und nach der Blüte (DC 75).

	Old variety Curinda	Mean of the new lines	% relative values of the new lines[(a)]
Grain yield [t ha^{-1}]	2.4	3.7	154*
Shoot growth rate [kg shoot ha^{-1} day^{-1}]			
Between tillering-anthesis	75	79	105
Between anthesis-postanthesis	147	155	105
Between postanthesis-maturity	156	279	179*
Root length density [cm cm^{-3} soil] in different soil depths			
at tillering: 0–20 cm	3.2	3.2	100
at anthesis: 0–20 cm	6.0	6.8	113
at anthesis: 20–35 cm	2.9	3.2	110
at postanthesis: 0–20 cm	5.0	6.1	122*[(1)]
at postanthesis: 20–35 cm	2.2	3.0	136*[(2)]
P uptake [kg P ha^{-1}]			
at tillering	1.1	1.3	118
at anthesis	3.0	3.3	110
at postanthesis	4.4	4.6	105
at harvest (straw plus grain)	4.9	6.6	135*
Net P-uptake rate [10^{-15} mol P cm^{-1} root length s^{-1}]			
Between tillering-anthesis	1.71	1.67	98
Between anthesis-postanthesis	1.90	1.70	89

(a) Old variety = 100%
* Significant at P = 0.05 probability level
(1) (2) Significant differences between the old variety Curinda and the new lines ChilWuh and PgoSeri, respectively.

difference in harvest index between the new genotypes and Curinda was 21% at P-0 and 28% at P-35 (Tab. 1).

The higher grain yield of the new genotypes was closely related to a higher P-uptake. The P-uptake of the new wheat lines was at P-0 35% and at P-35 24% higher than in Curinda (Tab. 1). The P-utilization efficiency was reduced by the P-fertilisation, from 472 at P-0 to 316 kg grains kg^{-1} P at P-35, which is expected due to the Mitscherlich growth equation. The P-utilization efficiency of the new genotypes was also, although not significant,

Table 3: Comparison of important plant parameters between the old wheat variety Curinda and the mean values of the three new lines ChilWuh, BauKauz and PgoSeri, with 35 kg P ha^{-1} fertilised (P-35), at tillering (Zadoc's decimal code = DC 23–25), early anthesis (DC 61) and post-anthesis (DC 75).

Tabelle 3: Mittelwertvergleich wichtiger Pflanzenparameter der drei neuen Zuchtlinien (ChilWuh, BauKauz und PgoSeri) mit der alten Weizensorte, mit 35 kg P ha^{-1} gedüngt (P-35), zur Ernte, und drei Vegetationsstadien, Bestockung (Zadoc's Dezimalcode = DC 23–25), zur Blüte (DC 61) und nach der Blüte (DC 75).

	Old variety Curinda	Mean of the new lines	% relative values of the new lines[a]
Grain yield [t ha^{-1}]	4.5	6.4	142*
Shoot growth rate [kg shoot ha^{-1} day^{-1}]			
Between tillering-anthesis	165	143	87
Between anthesis-postanthesis	232	237	102
Between postanthesis-maturity	150	296	194*
Root length density [cm cm^{-3} soil] in different soil depths			
At tillering: 0–20 cm	7.0	7.1	101
At anthesis: 0–20 cm	10.7	9.5	89
At anthesis: 20–35 cm	4.7	4.8	102
At postanthesis: 0–20 cm	8.3	7.4	89
At postanthesis: 20–35 cm	4.1	4.0	98
P uptake [kg P ha^{-1}]			
At tillering	7.3	7.3	100
At anthesis	12.0	12.6	105
At postanthesis	14.4	16.4	114*
At harvest (straw plus grain)	14.6	18.1	124*
Net P-uptake rate [10^{-15} mol P cm^{-1} root length s^{-1}]			
Between tillering-anthesis	2.1	2.7	128*[1]
Between anthesis-postanthesis	2.1	3.1	148*

(a) Old variety = 100%
* Significant at P = 0.05 probability level
(1) Significant differences between the old variety Curinda and the new lines BauKauz and PgoSeri.

on the average about 10% superior compared to the old variety. The grain P-content was not different among the genotypes but it increased from 0.19% to 0.28% by P-fertilization (Tab. 1).

The genotypic differences in P-uptake and utilization efficiency were related to differences in shoot-growth rates and morphological and physiological traits. The P-fertilisation enhanced the shoot-growth rates and the root-length densities of all genotypes (Tab. 2 and 3). As expected, the root-length densities increased from the stage of tillering to anthesis and declined afterwards (Tab. 2 and 3). The new genotypes, however, had a higher biomass-production rate connected with a higher root length per plant and P-uptake per unit root length. Without P-fertilisation (P-0), the new genotypes (especially ChilWuh and PgoSeri) had a higher root-length density between anthesis and postanthesis than Curinda, 22% and 36% at 0–20 and 20–35 cm, respectively (Tab. 2). During grain filling, the higher root-length density enabled the new genotypes to absorb more P than Curinda, in spite of the P-uptake rate per unit root length being not different among genotypes. At P-0, the root-length density was important for improved P-uptake, not the P-uptake rate.

The results were different when 35 kg P ha^{-1} were applied. Then, the three new genotypes had slightly lower root length densities than Curinda. In spite of that, the new genotypes showed on the average higher P-uptake in the above ground biomass than Curinda (24% at harvest, Tab. 1). This was related to improved P-uptake rates in the new genotypes, 28% between tillering and anthesis and 48% between anthesis and postanthesis higher compared with Curinda. The improved net-P-uptake rates increased the biomass-production rates and grain yields and P-uptake of the above ground biomass in the new genotypes.

4 Discussion

During the last decades, plant breeding can be made responsible for 15 to 50% of the production increase in wheat (*Feil*, 1990). The results of this study confirm this: the three new genotypes from CIMMYT produced 54% and 42% more grain yield at low and adequate P-supply, respectively. *Horst* et al. (1996) found also higher grain yield in a modern, semidwarf cultivar compared to an older, tall cultivar at different P-levels. In general, higher grain yields in wheat are related to more kernels per m^2, especially from more kernels per spike (*Feil*, 1990). This important yield component had been raised from 30 grains ear^{-1} in Curinda to 40 at P-0, but to 56 at P-35 in ChilWuh (Fig. 1) indicating the importance of an adequate P-supply for the establishment of a high sink capacity. Breeding for higher yield potential in wheat did seldom affect the thousand kernel weight. This was also true for this comparison between three new and one old genotypes, independently of the P-supply. Here, the new genotypes had fewer spikes m^{-2} compared with Curinda. However, this was more than compensated by a much higher kernel number per spike in the new genotypes. The new genotypes showed also significant higher thousand kernel weight at P-0, in contrast to observations made by *Horst* et al. (1996) with the modern, semidwarf variety Cosir, which had lower kernel weights at all levels of P-supply compared with a tall variety. The new genotypes produced more grain yield with less tillers, lower straw weight, and had thus a 21% and 28% higher harvest index at P-0 and P-35, respectively.

In plants, phosphorus efficiency depends on external P-availability and internal P requirements. The latter can be split into P uptake efficiency (*Föhse* et al., 1988) and P utilization efficiency. For economic and agronomic reasons, P efficiency should be based on the cropping area, i.e. hectare (*Sattelmacher* et al., 1994). In this study, the improved P-uptake per ha of the new genotypes was analysed in relation to root length and net-P-uptake rate per unit root length; both are mechanisms to improve P-uptake.

The P utilization efficiency was 8% and 11% at P-0 and P-35, respectively, higher compared with Curinda. More effective translocation of assimilates into kernels may improve P utilization (*Horst* et al., 1996), because developing kernels are strong sinks for assimilates (*Römer*, 1971). More kernels per spike at both P levels and a higher 1000-grain weight at P-0 in the three new genotypes indicate strong sinks for assimilates. If this might be due to phytohormones (*Marschner*, 1995) or altered enzyme activities (*Sonnewald* and *Ebneth*, 1998) remains an open question. But the nearly doubled shoot growth rate of the new genotypes between postanthesis and maturity supports the decisive role of sink capacity (cell division) and duration of sink filling for P utilization efficiency. Any wheat breeding for higher grain yield, be it by conventional or transgenic methods, selects indirectly for improved P-utilization. This approach is especially relevant in regions, where the P availability is low, like on the acid soils in Australia (*Batten* and *Kahn*, 1987) or the calcareous soils in Syria (*Stelling* et al., 1996). But it may also be possible to improve P utilization by the selection for low grain P-content. Selection for wheat genotypes that remove small amounts of P from the soil because of low grain P-concentration contribute to sustainable land use (*Schulthess* et al., 1997). In theory, P concentration in wheat grain could obviously be reduced, because nearly all genotypic variation in seed total P is due to a variation in phytic acid P, non-phytic-acid P tends to remain constant (*Raboy* et al., 1991). Phytic acid is the major storage form of P in wheat seeds (60 to 80% of the seed P), which however, has a negative impact on P-digestibility in monogastric animals. If very low grain P-content (0.1% or less, as suggested by *Batten* and *Kahn* (1987)) would be an appropriate selection criteria for improved P utilisation efficiency, is questionable, because grain-P is important for seed germination and plant establishment. Although phosphorus could under low input conditions be provided through seed coating or P-placement (*Rebafka* et al., 1993), the higher grain yield of all genotypes at P-35 (Fig. 1) shows: a) that P contents in grain < 1.8 mg g^{-1} seem to be suboptimal and b) that the soil must provide a sufficient amount of plant available P to support the shoot growth rate observed at P-35 as compared to P-0 (Tab. 2, 3). In addition, recent data on maize and barley by *Raboy* (1998) indicate that mutations for lower phytate-P are not associated with a decrease of total grain-P, but with a compensatory increase of inorganic P and low-inosits-P.

The differences between the new genotypes and the old Curinda were even more pronounced in P-uptake efficiency than in P-utilization efficiency. Improved P-uptake efficiency leads to improved P-fertiliser recovery and use of soil-P (*Sattelmacher* et al., 1994). Developing shoots and spikes serve as sinks for P, the growth and development of which can be stimulated by the application of gibberelline thus enhancing the P-absorption of roots and P-translocation into spikes (*Römer*, 1985). The spikes of the new genotypes with more kernels per spike may have increased the sink for P, which on the other hand implies also a higher demand for P. The genotypes reacted with different mechanisms under different P-levels in order to satisfy their higher demand for P. Under conditions of P-deficiency, genotypes with larger root systems are more efficient (*Römer* et al., 1989), which was confirmed by the new genotypes ChilWuh and PgoSeri. They had higher root length densities than the old Curinda (Tab. 2). Under conditions of sufficient P-supply, however, the net-P-uptake rate per unit root length of the new genotypes was more important (*Horst* et al., 1996). One can only speculate, which mechanisms may be responsible for increased P-uptake rates per unit root length. The activity of the acid phosphatase in roots as well as the infection with vesicular-arbuscular mycorrhizal fungi, which both could enhance the P-uptake rate per unit root length were not different among genotypes (*Egle*, 1998).

Wheat exhibits a remarkable plasticity in root growth, adjusting to the soil nutrient and water status (*Vlek* et al., 1996). The three new wheat genotypes from CIMMYT reacted with high plasticity to different levels of P-supply, so that they could always accumulate more P than the old variety. To improve P-uptake efficiency in wheat germplasm targeting to P-deficient and P-fixing soils, wheat germplasm has to be selected under the conditions of P-deficiency and P-fixation where improved root traits are genetically best expressed (*Sattelmacher* et al., 1994). However, plasticity in root traits should be not the only criterion and it should also be clear, that targeting for a full exploitation of the higher yield potential of modern genotypes requires screening also under conditions of modern farming.

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