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REGULAR ARTICLE

Seed P-enrichment as an effective P supply to wheat

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Abstract Most fertilizer phosphorus (P) is sorbed by soil rather than being taken up by crops. We hypothesize enriching wheat seed with P before sowing the crop will reduce requirement of fertilizer P for subsequent wheat production. We produced P-enriched wheat (*Triticum aestivum* L.) seed by soaking the seed in different concentrations of potassium phosphate solution. We found that ~0.35 M potassium phosphate was the most effective concentration for P-enrichment of the seed. In pot and field experiments we found that the P-enriched seed required ~60% less fertilizer P than seed not soaked with potassium phosphate before sowing. Increases in shoot P content could not be explained only by the increase of seed P-enrichment, suggesting that P acquisition from soil was also enhanced. Under hydroponic conditions we found that root length was greater in seedlings grown from P-enriched seed with higher specific root length than in seedlings grown from non-P-enriched seed. We conclude P-enrichment of wheat seed before sowing reduces fertilizer P requirements of plants.

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Introduction

Phosphorus (P) deficiency limits crop production in more than 30% of the world's arable land, where the application of fertilizer P to soils is often necessary to achieve sufficient yields (Runge-Metzger 1995; Vance et al. 2003). Terrestrial ecosystems accumulate P at an annual rate of 10.5–15.5 Tg; this build-up occurs mostly in agricultural soils as a consequence of fertilizer application in excess of crop needs (Bennett et al. 2001; Carpenter 2005). There is a serious concern that we might exhaust deposits of phosphate rock, which is the raw material for fertilizer P, within the present century (Runge-Metzger 1995). Indeed, its price is currently rising due to increased demands for food and, hence, for fertilizer. Moreover, excessive P input from agricultural fields into aquatic ecosystems through runoff or soil erosion is responsible for eutrophication (Bennett et al. 2001; Carpenter 2005; Sharpley 1995; Tilman 1999). We are therefore faced with the challenge of reducing P input into farmland without impairing current sustainable crop yields.

Plants take up inorganic phosphate (Pi) from soil solution. The Pi concentrations in soil solutions are usually very low (typically less than 1 μM) because most Pi is heavily bonded with the relatively abundant cations aluminum (Al), calcium (Ca), and iron (Fe) (Raghothama and Karthikeyan 2005). Although fertilizer P application can temporarily increase the Pi concentration in soil solution, it is immobilized almost immediately due to sorption of P by soil (Stevenson and Cole 1999). Soil interference only allows plants to acquire P within a few millimetres of root surfaces, and acquisition is determined by the volume of soil explored by plant roots, which is normally less than 1% and rarely reaches 5% (Barber 1995). As a result, most fertilizer P, often more than 90%, is not taken up by plants with the remainder being retained by soil in sparingly soluble forms (Stevenson and Cole 1999). Hence there is the need to develop systems to improve use of soil and fertilizer P for crop production.

One way of achieving this may be to enrich crop seed with P before sowing the crop which may reduce the need for fertilizer P in subsequent crop growth. To examine the hypothesis, we attempted to soak seeds of wheat (*Triticum aestivum* L.) in potassium phosphate solution just before sowing. This solution drastically reduced fertilizer P in maize growth when applied to the seedlings (Watanabe et al. 2005). Previous studies have shown that nutrient enrichment by soaking seeds in macronutrient solutions had little or even a negative effects on subsequent plant production (e.g. Scott 1989). We think that failure in the previous studies of seed soaking might be due to inappropriate P concentrations in the solutions. We therefore firstly attempted to determine the optimum P concentration of the soaking solution for P-enrichment of wheat seed. We then compared shoot production responses of untreated and P-enriched wheat seed when rates of fertilizer P were applied to soil. In this study, we aimed to clarify whether or not the seed P-enrichment is an effective way to reduce P input without growth depression of wheat.

Materials and methods

Seed treatment

Potassium phosphate solutions were prepared by dissolving mixtures of KH_2PO_4 and K_2HPO_4 (3:1) at different concentrations in distilled water (Watanabe et al. 2005). Each solution was aerated with a pump, and wheat (cv. Norin 61) seeds placed within net bags were dipped into the solutions and were incubated in the solutions at 30°C for 24 h. Seeds used in the experiments were not rinsed, except when measuring P concentration in the seed using procedures described below.

Optimizing P concentration in hydroponic and soil experiments

Two separate hydroponic experiments were conducted in a glasshouse between Jul. and Sep. 2004. Seeds were P-enriched as described in solutions of 0, 0.1, 1, and 5 g L^{-1} potassium phosphate (low P concentration) in the first batch, and in solutions of 0, 10, 50, and 100 g L^{-1} (high P concentration) in the second batch. Seeds were sown in growth containers with deionized water, and were grown for six days. Five representative seedlings grown at each concentration were then transplanted into growth containers holding quarter-strength Hoagland solution (pH 5.8) without P. The solutions were replaced by new ones every two days. Shoots were harvested 40 days and 35 days after transplanting from the first and second batch, respectively. The harvested shoots were dried at 80°C for 48 h before weighing to provide yields of dried shoots (DM_{shoot}).

The pot experiment was conducted in a glasshouse from Sep. to Dec. 2004. A plastic pot (132 mm height×82 mm diameter) was filled with 400 g Andisol containing 96 mg ammonium sulphate, 36 mg potassium chloride, and 0, 20, or 200 mg super-phosphate. Before sowing, seeds were treated in solutions of 0, 0.1, 1, 10, and 50 g L^{-1} potassium phosphate. Each of the fifteen treatments (five levels of soaking solution concentrations and three levels of fertilizer P) was replicated three times. Ten seeds were sown in each pot, and the seedlings were thinned to six stands. The pots were placed in trays, and water was applied from the bottom of each pot so as to maintain a water depth of approximately 8 mm in the tray throughout the experiment. Shoots were harvested 70 days after sowing, dried at 80°C for 48 h, and weighed to determine DM_{shoot}.

Reduction of P input in pot and field conditions

An additional pot experiment was conducted in a growth chamber illuminated with natural light (30°C and 70% relative humidity (RH) during the 14 h light period, and 25°C and 70% RH during the 10 h dark period). The same plastic pot used in the previous experiment was filled with 400 g Andisol containing 96 mg ammonium sulfate, 36 mg potassium chloride, and 0, 40, 80, or 240 mg super-phosphate. Seeds were treated in 50 g L^{-1} potassium phosphate solution as the P-enrichment treatment and in distilled water as the control. Each of the eight treatments (four levels of fertilizer P and two levels of solution concentration) was replicated six times. Five seeds were sown in each pot, and the seedlings were thinned to two stands. The pots were placed in trays, and water was applied as described above. Shoots were harvested 80 days after sowing, dried at 80°C for 48 h, and the DM_{shoot} was measured by weighing. Samples were then dry-ashed at 550°C for 5 h and dissolved in hydrochloric acid. The P concentrations in the extract solutions were determined using a colorimetric method (Murphy and Riley 1962), and the shoot P content was calculated by multiplying the DM_{shoot} by the P concentration.

A field experiment was conducted from Nov. 2005 until May 2006 at Nagoya University, Japan (35° 9′ N and 136° 58′ E). During this period, the total rainfall was 557 mm, and the monthly mean temperature ranged between 3.4 and 18.7°C. The soil in the field was loamy sand, with a pH (H_2O) of 5.8, and an EC level of 3.0 $\mu S\ cm^{-1}$. Before the experiment, a dense maize crop was grown between Jun. and Oct. 2005, in order to achieve a homogeneous soil nutrient distribution. The soil was tilled to a depth of 0.2 m, and plots $1.5 \times 0.5 \times 0.1$ m (length × width × height) were created. On each plot, two ditches 0.05×0.15 m (width × depth) were produced 0.2 m apart. Fertilizer containing 36 g ammonium sulfate, 10 g potassium chloride, and 0, 12, or 36 g super-phosphate was applied into the ditches, and covered with soil. The seeds were then soaked in solutions of 50 g L^{-1} potassium phosphate solution as the P-enrichment treatment and in distilled water as the control. Holes were made 0.15 m apart above the ditches, and 15 seeds were sown in each hole. The six treatments (three levels of fertilizer P and two levels of solution concentration) were replicated four times. Plot allocation followed the randomized block method. Seedlings were thinned to five plants per hole 49 days after sowing, and all shoots were harvested 169 days after sowing. The shoots were air-dried for 2 weeks, and the DM_{shoot} was determined.

Seed P content and root morphology evaluation between treatments

Seeds were soaked in 50 g L^{-1} potassium phosphate solution as the P-enrichment treatment and in distilled water as the control. Half of the seeds from the P-enrichment treatment were rinsed with tap water for 10 min to remove the potassium phosphate solution adhering to their surfaces. They were then dried at 80°C for 48 h and weighed. The seed P concentration was determined using the method described above, and the seed P content was calculated by multiplying the seed weight by the P concentration.

An analysis of root morphology was conducted in a growth chamber (30°C and 50% RH during the 12 h light period with 500 mol $m^{-2}\ s^{-1}$ light, and 25°C and 50% RH during the 12 h dark period). The seeds were soaked in 50 g L^{-1} potassium phosphate solution as the P-enrichment treatment and in distilled water as the control. Five seeds were sown in a seed-pack growth pouch (Mega International, St Paul, MN). Four holes (5 mm diameter) were made on both sides of each pouch, 30 mm from the bottom. The pouches were then left to stand in a container of quarter-strength Hoagland solution (pH 5.8) with P (+P) and without P (−P), which supplied the roots through the holes. Each of the four treatments (two levels of nutrient solution and two levels of solution concentration) was replicated four times. The solutions were replaced at two day intervals. The seedlings were thinned to one plant 6 days after sowing, and the shoots were harvested 53 days after sowing. The roots were gently removed from the pouch and spread on a transparent sheet, without overlap. Digitized images were produced using a scanner with a resolution of 300 dpi and an output format of 256 grey-scales. The image capture took less than 10 min. The root length (RL) was determined by the diameter class, using a macro-program developed by Kimura et al. (1999) on NIH Image software (version 1.60). The shoot and root samples were dried at 80°C for 48 h, and the DM_{shoot} and root dry-matter weight (DM_{root}) were determined. The specific RL or SRL was calculated by dividing the RL by the DM_{root}.

Statistical analyses

Analysis of variance (ANOVA) was used to compare treatment means. Data were analyzed by a two-factor factorial ANOVA, with sources of variation consisting of P-enrichment and P fertilizer in the pot and field experiments, P-enrichment and P nutrients in the growth pouch experiments, and treatment and diameter in the analysis of RL by diameter class. Data in the hydroponic experiments and the seed P content were analyzed by a one-factor ANOVA.

Results

Optimizing P concentration in hydroponic and soil experiments

The effect of soaking seeds in potassium phosphate solutions (P-enrichment) on the shoot growth of wheat plants was examined in a hydroponic experiment (Fig. 1). P-enrichment had a significant effect on DM_{shoot} ($p < 0.001$), and the effect was particularly distinct using the 50 g L^{-1} solution. However, P-enrichment in solutions with lower P concentrations (0.1, 1 and 5 g L^{-1}) exhibited no significant effect ($p=0.29$).

To confirm the effect of P-enrichment on the shoot growth of wheat plants, a soil experiment was also conducted (Fig. 2). As expected, the P fertilizer application to the soil significantly increased the DM_{shoot}. The effect of P-enrichment on the DM_{shoot} was also significant, and was particularly noticeable in treatment where the seeds soaked in 10 and 50 g L^{-1} solutions were grown in the soil with no super-phosphate, and when those soaked in 50 g L^{-1} solution were grown in the soil with 20 mg pot^{-1} super-phosphate. Both the hydroponic and the soil experiments indicated that the 50 g L^{-1} solution was most effective for P-enrichment under all experimental conditions, so this was used in the following experiments.

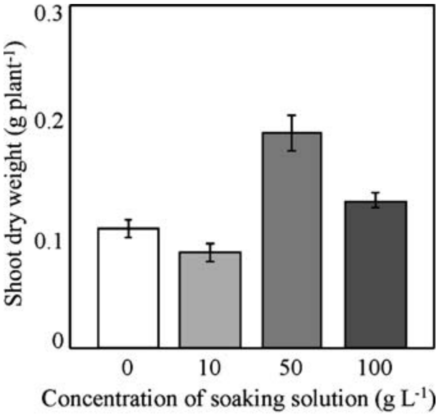
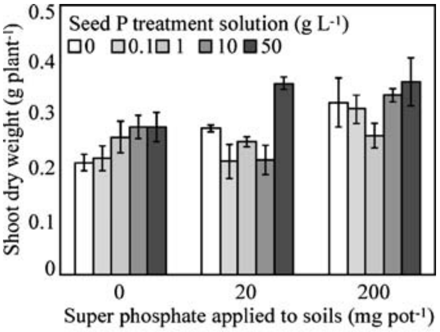


Fig. 1 DM_{shoot} of wheat plants grown from seeds soaked in solutions of different concentrations (0, 10, 50, and 100 g L^{-1}) of potassium phosphate (KH_2PO_4:K_2HPO_4=3:1). Plants were grown in quarter-strength Hoagland solutions without P. Each bar represents the mean ± standard error (SE; $n=5$)



Probabilities according to ANOVA

P-enrichment	$p = 0.004$
P fertilizer	$p < 0.001$
Interaction	$p = 0.094$

Fig. 2 DM_{shoot} of wheat plants grown from seeds soaked in solutions of different concentrations (0, 0.1, 1, 10, and 50 g L^{-1}) of potassium phosphate (KH_2PO_4:K_2HPO_4=3:1). Plants were grown in pots of 400 g Andisol with 0, 20, or 200 mg super-phosphate pot^{-1}. Each bar represents the mean ± SE ($n=3$)

Reduction of P input in pot and field conditions

P-enriched seeds were grown in soil containing four different levels of P fertilizer in the pot experiment (pot experiment in Fig. 3). As a control, seeds that had been soaked in distilled water instead of 50 g L^{-1} P solution were sown. Again, the DM_{shoot} was significantly increased by both the P fertilizer application and P-enrichment. We observed that the DM_{shoot} from P-enriched seeds grown with 80 mg pot^{-1} P fertilizer was equivalent for those of control seeds grown with 240 mg pot^{-1} P fertilizer. The shoot P content was also significantly increased by both treatments (Table 1). The mean shoot P content across the P fertilizer levels was 1.3 times higher in the P-enriched plants than in the control plants.

A separate field experiment was conducted in which the soil contained three different levels of P fertilizer (field experiment in Fig. 3). There were intermittent snowfalls from 19 to 30 days after sowing, and the snow remained on the field until 40 days after sowing. Interestingly, seedlings from the P-enriched seeds emerged through the remaining snow, while those from the control seeds only grew

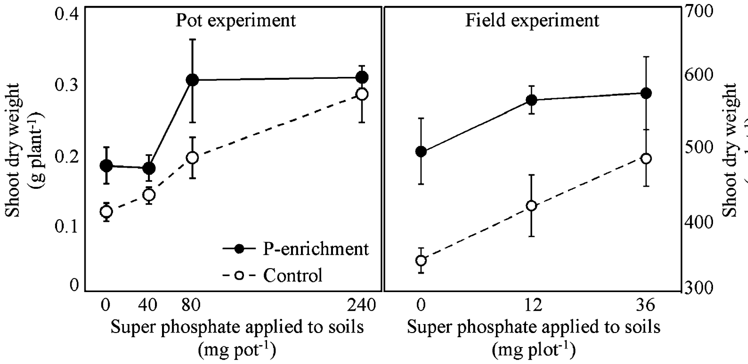


Fig. 3 DM$_{shoot}$ of wheat plants grown from seeds soaked in distilled water (control) and 50 g L^{-1} potassium phosphate solutions (P-enrichment). Plants were grown in pots filled with 400 g Andisol with 0, 40, 80, or 240 mg super-phosphate pot^{-1}, and in field plots with 0, 12, or 36 g super-phosphate plot^{-1}. Each data point represents the mean ± SE (n=6 for the pot experiment; n=4 for the field experiment)

Probabilities according to ANOVA

	Pot experiment	Field experiment
P-enrichment	$p = 0.004$	$p = 0.002$
P fertilizer	$p < 0.001$	$p = 0.042$
Interaction	$p = 0.486$	$p = 0.707$

once the snow had melted completely. At harvest, the DM$_{shoot}$ was significantly increased by both the P fertilizer application and P-enrichment. As a result, the DM$_{shoot}$ from P-enriched seeds grown with 0 g plot^{-1} and 12 g plot^{-1} P fertilizer equaled those from control seeds grown with 36 g plot^{-1} P fertilizer.

Seed P content and root morphology evaluation between treatments

The P contents of seeds soaked in distilled water and 50 g L^{-1} P solution were 0.12 mg seed^{-1} and 0.19 mg seed^{-1}, respectively. However, when P-enriched seeds were rinsed with tap water, this figure fell to 0.15 mg seed^{-1}. These values were shown by one-factor ANOVA to be significantly different (p<0.001), suggesting that the increase of the seed P content as a result of P-enrichment was achieved by accumulation of solution P into the seed and onto the outside of the seed.

Table 1 P contents of wheat shoots

P fertilizer (mg pot^{-1})	Shoot P content (mg plant^{-1})	
	P-enrichment	Control
0	0.4±0.1	0.18±0.03
40	0.34±0.1	0.28±0.1
80	0.8±0.2	0.53±0.1
240	1.0±0.1	0.89±0.1
mean	0.62±0.1	0.46±0.2
ANOVA	P-enrichment	p=0.039
	P fertilizer	p<0.001
	Interaction	p=0.748

Data represent the P contents of wheat shoots grown from seeds soaked in distilled water (control) and 50 g L^{-1} potassium phosphate solutions (P-enrichment). The plants were grown in pots filled with 400 g Andisol with four levels (0, 40, 80, and 240 mg pot^{-1}) of super-phosphate. Each value represents the mean ± SE (n=6)

In the growth-pouch experiment, P-enrichment significantly increased the DM$_{shoot}$ under both +P and −P conditions (Table 2). In addition, the DM$_{root}$ was significantly increased by P-enrichment. This was paralleled by an increase in the root length (RL) and specific root length (SRL). The analysis of RL by root diameter showed that the effects of treatment and diameter were significant (Fig. 4), indicating that P-enrichment increased the RL of each diameter under both +P and −P conditions. There was also a significant interaction between treatment and diameter, showing that fine roots with diameters of 0.08 −0.6 mm were particularly enhanced by each treatment. Evidently, P-enrichment induced the development of more fine roots.

Discussion

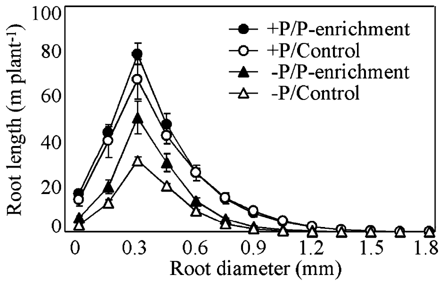
We determined the appropriate P concentration in the soaking solution to enrich wheat seed with P for optimum subsequent production of wheat plants. The P-enrichment of wheat seed reduced requirement of fertilizer P for shoot production. A fertilizer P reduction of approximately 65% was achieved by this

Table 2 DM_{shoot}, DM_{root}, root length (RL), and specific root length (SRL) values of wheat plants

P fertilizer	Seed treatment	DM_{shoot} (g plant^{-1})	DM_{root} (g plant^{-1})	RL (m plant^{-1})	SRL (m g^{-1})	S/R ratio (g g^{-1})
+P	P-enrichment	0.76±0.05	0.15±0.01	26.7±1.3	181±0.6	5.13±0.1
	Control	0.58±0.07	0.14±0.01	22.4±2.6	164±0.9	4.29±0.3
−P	P-enrichment	0.17±0.02	0.07±0.01	13.1±1.7	178±1.1	2.36±0.1
	Control	0.13±0.01	0.06±0.003	8.3±0.4	157±0.4	2.38±0.1
ANOVA	P-enrichment	$p=0.028$	$p=0.05$	$p=0.02$	$p=0.04$	$p=0.038$
	P fertilizer	$p<0.001$	$p<0.001$	$p<0.001$	$p=0.552$	$p<0.001$
	Interaction	$p=0.17$	$p=0.652$	$p=0.876$	$p=0.774$	$p=0.031$

Data are from wheat plants grown from seeds soaked in distilled water (control) and 50 g L^{-1} potassium phosphate solutions (P-enrichment). The plants were grown in seed-pack growth pouches supplied with quarter-strength Hoagland solutions +P and −P. RL is a combined length of all the roots determined following Kimura et al. (1999). SRL is a specific RL calculated by dividing the RL by DM_{root}. Each value represents the mean ± SE ($n=4$)

technique in the pot experiment without sacrificing yield of dried shoots (Fig. 3). This effect was also confirmed under field conditions (Fig. 3). Previous studies showed that nutrient enrichment by soaking seeds in macronutrient solutions had little or even a negative effect on subsequent plant growth (Scott 1989; Guttay et al. 1957; Ros et al. 2000). We hypothesised that the outcome of these previous studies was due to the use of inappropriate P concentrations in the solution to enrich the seed with P. By testing a wide range of P concentrations, we found that the 50 g L^{-1} potassium phosphate solution (approximately 0.35 M) was optimal for seed P-enrichment for production of subsequent wheat shoots (Figs. 1 and 2). Higher concentrations (1 M P) were reported to be necessary for oat growth (Roberts 1948). By contrast, Ros et al. (2000) were unable to find the optimum concentration between 0.3 and 1.5 M P for rice growth. In the study, rice growth was enhanced when a larger amount of P was coated onto the seed with P-containing adhesives, implying that rice growth might require a far greater concentration for seed P-enrichment. Maize growth was suppressed when seeds were soaked in solutions that exceeded 1.8 M P (Guttay et al. 1957), probably due to osmotic stress; hence, lower concentrations should have been considered. These previous and the present studies indicate that P-enrichment of seed requires soaking the seed in solutions of different P concentrations to achieve the optimum effect for different crop species.



Probabilities according to ANOVA

Treatment	$p < 0.001$
Diameter	$p < 0.001$
Interaction	$p < 0.001$

Fig. 4 Root length distribution along the root diameter of wheat plants grown from seeds soaked in distilled water (control) and 50 g L^{-1} potassium phosphate solutions (P-enrichment). Plants were grown in seed-pack growth pouches with quarter-strength Hoagland solutions +P and −P. Each data point represents the mean ± SE ($n=4$)

The extent by which seed P-enrichment reduces the amount of fertilizer P required for subsequent crop growth appears to be affected by the availability of P already present in soil. In the pot experiment, a fertilizer application of at least 80 mg pot^{-1} was required for the P-enriched plant to achieve the maximum level of plant growth reached by the control plant (Fig. 3). However, this level of growth was obtained by the P-enriched plant even without the application of P fertilizer in the field experiment (Fig. 3). The Andisol used in the pot experiment was known to have a high capacity to sorb P and to contain a very low level of available P (0.1 mg Truog-P kg^{-1} of dry soil). By contrast, the loamy sand used in the field experiment contained a relatively high level of available P (12 mg Truog-P kg^{-1} of dry soil). Thus, it was likely that the pot experiment required fertilizer P application in order for seed P-enrichment to perform effectively, while the high P availability of the field experiment enhanced the performance of seed P-enrichment, even without fertilizer P application. Therefore, soil testing for P and a measure of the capacity of soil to sorb P is required to estimate the likely extent to which seed P-enrichment can reduce the need for fertilizer P for subsequent crop production.

Seed P analysis showed that seed P-enrichment increased the P content both inside the seeds and on the seed surfaces. It has been reported that an inherently higher content of seed P leads to better establishment of seedlings (Bolland and Baker 1988; Zhang et al. 1990; Thomson and Bolger 1993; Ros et al. 1997). Moreover, the adhesion of the P source to seed surfaces also reportedly promotes seedling growth (Scott and Blair 1988; Scott 1989; Ros et al. 2000; Peltonen-Sainio et al. 2006). However, the observed differences in the shoot P content between P-enriched and control treatments could not be explained only by the increase of seed P content. The mean shoot P contents in the P-enriched and control plants were 0.62 mg plant^{-1} and 0.46 mg plant^{-1}, respectively (Table 1). The difference was much greater than that observed in the seed P contents (0.19 mg seed^{-1} in the P-enriched and 0.12 mg seed^{-1} in the control seeds). This suggests that plant P uptake from soil was greater in the P-enriched treatment than in the control treatment.

Plant P uptake is strongly dependent on the rooting volume in contact with the soil due to immobility of P in soil (Barber 1995). The growth-pouch experiment demonstrated that seed P-enrichment increased the RL as well as the DM$_{\mathrm{root}}$ (Table 2). The increase in RL by seed P-enrichment is associated with the development of many more fine roots (Fig. 4). This is reflected in the larger SRL (that is, the RL produced at a given DM cost), which is generally greater in fine roots than in coarse roots (Table 2). This suggests that the RL-dependent P-uptake capacity at a given DM cost is also increased by seed P-enrichment, such that P-enriched plants cope with the DM cost of P uptake more efficiently than control plants. This might also contribute to the improved growth of P-enriched plants.

The mechanism behind the increase in SRL caused by seed P-enrichment requires further study. However, Koide and Lu (1995) demonstrated that seeds with high P reserves collected from mycorrhizal plants develop roots with larger SRL values compared with seeds with low P reserves from non-mycorrhizal plants. Our results, in combination with the findings of Koide and Lu (1995), suggest that seed P content is important for the determination of SRL. Furthermore, it has been pointed out that the SRL increases under productive conditions, as fast growth requires rapid and efficient acquisition of resources (Ryser 2006). This implies that the increased seed P content achieved in the present study by seed P-enrichment induced wheat plants to increase the SRL for greater acquisition of nutrients from soil.

Conclusions

To achieve optimal seed P-enrichment performance, the appropriate P concentration of the soaking solution needs to be determined for each crop species. Seed P-enrichment can reduce requirement of fertilizer P for subsequent production of wheat shoots. This is due to an improved seedling growth caused by increased seed P content, and an improved P-uptake capacity caused by increased root production with relatively less investment of dry matter, particularly fine roots. Although the present study focused only on wheat, future work should examine other major crop species such as maize, rice, and legumes. Potentially, more-efficient P fertilizer use could be achieved in a less-expensive and simpler way by combining seed P-enrichment with techniques such as the patchy application of fertilizer P (Kume et al. 2006; Yano and Kume 2005).

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References

Barber SA (1995) Soil nutrient bioavailability, 2nd edn. Willey, New York

Bennett EM, Carpenter SR, Caraco NF (2001) Human impact on erodable phosphorus and eutrophication: a global perspectives. Bioscience 51:227–234. doi:10.1641/0006-3568(2001)051[0227:HIOEPA]2.0.CO;2

Bolland MDA, Baker MJ (1988) High phosphorus concentrations in seed of wheat and annual medic are related to higher rates of dry matter production of seedlings and plants. Aust J Exp Agric 28:765–770. doi:10.1071/EA9880765

Carpenter SR (2005) Eutrophication of aquatic ecosystems: bistability and soil phosphorus. Proc Natl Acad Sci USA 102:10002–10005. doi:10.1073/pnas.0503959102

Guttay JR, Stritzel JA, Englehorn AJ, Black CA (1957) Treatment of corn seed with phosphate. Agron J 49:98–101

Kimura K, Kikuchi S, Yamasaki S (1999) Accurate root length measurement by image analysis. Plant Soil 216:117–127. doi:10.1023/A:1004778925316

Koide RT, Lu X (1995) On the cause of offspring superiority conferred by mycorrhizal infection of *Abutilon theophrasti*. New Phytol 131:435–441. doi:10.1111/j.1469-8137.1995.tb03080.x

Kume T, Sekiya N, Yano K (2006) Heterogeneity in spatial P-distribution and foraging capability by *Zea mays*: effects of patch size and barriers to restrict root proliferation within a patch. Ann Bot (Lond) 98:1271–1277. doi:10.1093/aob/mcl216

Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta 27:31–36. doi:10.1016/S0003-2670(00)88444-5

Peltonen-Sainio P, Kontturi M, Peltonen J (2006) Phosphorus seed coating enhancement on early growth and yield components in oat. Agron J 98:206–211. doi:10.2134/agronj2005.0141

Raghothama KG, Karthikeyan AS (2005) Phosphate acquisition. Plant Soil 274:37–49. doi:10.1007/s11104-004-2005-6

Roberts WO (1948) Prevention of mineral deficiency by soaking seed in nutrient solution. J Agric Sci 38:458–468. doi:10.1017/S0021859600006250

Ros C, Bell RW, White PF (1997) Effects of seed phosphorus and soil phosphorus application on early growth of rice (*Oryza sativa* L.) cv. IR66. Soil Sci Plant Nutr 43:499–509

Ros C, Bell RW, White PF (2000) Phosphorus seed coating and soaking for improving seedling growth of *Oryza sativa* (rice) cv. IR66. Seed Sci Technol 28:391–401

Runge-Metzger A (1995) Closing the cycle: obstacles to efficient P management for improved global food security. In: Tiessen H (ed) Phosphorus in the global environment: transfers, cycles and management. Wiley, New York, pp 27–42

Ryser P (2006) The mysterious root length. Plant Soil 286:1–6. doi:10.1007/s11104-006-9096-1

Scott JM (1989) Seed coatings and treatments and their effects on plant establishment. Adv Agron 42:43–83. doi:10.1016/S0065-2113(08)60523-4

Scott JM, Blair GJ (1988) Phosphorus seed coatings for pasture species. I effect of source and rate of phosphorus on emergence and early growth of phalaris (*Phalaris aquatica* L.) and lucerne (*Medicago sativa* L.). Aust J Agric Res 38:437–445. doi:10.1071/AR9880437

Sharpley AN (1995) Soil phosphorus dynamics: agronomic and environmental impacts. Ecol Eng 5:261–279. doi:10.1016/0925-8574(95)00027-5

Stevenson FJ, Cole MA (1999) The phosphorus cycle. Cycles of soil: carbon, nitrogen, phosphorus, sulfur, micronutrients. Wiley, New York

Thomson CJ, Bolger TP (1993) Effects of seed phosphorus concentration on the emergence and growth of subterranean clover (*Trifolium subterraneum*). Plant Soil 155/156:285–288. doi:10.1007/BF00025038

Tilman D (1999) Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. Proc Natl Acad Sci USA 96:5995–6000. doi:10.1073/pnas.96.11.5995

Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol 157:423–447. doi:10.1046/j.1469-8137.2003.00695.x

Watanabe K, Murayama T, Niino T, Nitta T, Nanzyo M (2005) Reduction of phosphatic and potash fertilizer in sweet corn production by pre-transplanting application of potassium phosphate to plug seedlings. Plant Prod Sci 8:608–616. doi:10.1626/pps.8.608

Yano K, Kume T (2005) Root morphological plasticity for heterogeneous phosphorus supply in *Zea mays* L. Plant Prod Sci 8:427–432. doi:10.1626/pps.8.427

Zhang M, Nyborg M, Mcgill WB (1990) Phosphorus concentration in barley (*Hordeum vulgare* L.) seed: Influence on seedling growth and dry matter production. Plant Soil 122:79–83. doi:10.1007/BF02851912