Plant Soil (2012) 357:1–8
DOI 10.1007/s11104-012-1128-4

COMMENTARY

Nature and nurture: the importance of seed phosphorus content

Philip J. White · Erik J. Veneklaas

Received: 13 December 2011 / Accepted: 5 January 2012 / Published online: 25 February 2012

Abstract

Background Low phytoavailability of phosphorus (P) limits crop production worldwide. Increasing seed P content can improve plant establishment and increase yields. This is thought to be a consequence of faster initial root growth, which gives seedlings earlier access to growth-limiting resources, such as water and mineral elements. It can be calculated that seed P reserves can sustain maximal growth of cereal seedlings for several weeks after germination, until the plant has three or more leaves and an extensive root system.

Case study In this issue of Plant and Soil, Muhammad Nadeem and colleagues report (1) that measurable P uptake by roots of maize seedlings begins about 5 d after germination, (2) that the commencement of root P uptake is coincident with the transition from carbon heterotrophy to carbon autotrophy, and (3) that neither the timing nor the rate of uptake of exogenous P by the developing root system is influenced by initial seed P content.

Hypothesis Here it is hypothesised that the delay in P acquisition by roots of maize seedlings might be explained if the expression of genes encoding phosphate transporters is not upregulated either (1) because the plant has sufficient P for growth or (2) because a systemic signal from the shoot, which relies on photosynthesis or phloem development, is not produced, translocated or perceived.

Keywords Arabidopsis · Germination · Maize (*Zea mays*) · Mineral nutrition · Phosphorus use efficiency (PUE) · Sucrose · Seed · Wheat (*Triticum aestivum*)

Responsible Editor: Hans Lambers.

P. J. White (✉)
The James Hutton Institute,
Invergowrie, Dundee DD2 5DA, UK
e-mail: philip.white@hutton.ac.uk

E. J. Veneklaas
School of Plant Biology,
The University of Western Australia,
Crawley, WA 6009, Australia

Phosphorus nutrition of annual crops

Annual crops exhibit a characteristic time course of P acquisition and internal P redistribution during their life cycle (Fig. 1; Hanway and Weber 1971; Hocking and Pate 1978; Hill 1980; Hocking and Steer 1983; Karlen et al. 1988; Feil et al. 1992; Hocking 1994; Manske et al. 2001; Masoni et al. 2007; Rose et al. 2007, 2008, 2010; Fageria et al. 2011). Seed P is the only P source available to sustain the initial growth of seedlings and, upon germination, seed P reserves are rapidly mobilized and translocated to emerging root and shoot tissues. This P source is subsequently supplemented by P uptake by the developing root system. Little is known about the physiological mechanisms controlling the transition between complete reliance on seed P reserves and the initiation of P acquisition

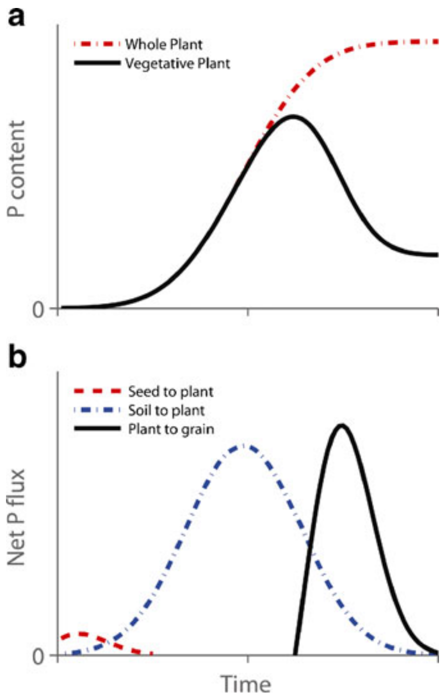

Fig. 1 Schematic time course of (**a**) the phosphorus content of an annual crop plant from germination to maturity and (**b**) net P fluxes from seed and soil to plant tissues and from vegetative tissues to the seed

by roots. Once seed P reserves are exhausted, plant growth must be supported by root P uptake alone, and the P concentrations in plant tissues are determined largely by the ability of the roots to acquire P from the soil and tissue growth rates (Lynch and Brown 2001; Manske et al. 2001; Aráujo and Teixeira 2003; Trehan and Sharma 2005; White et al. 2005; Parentoni and de Souza Júnior 2008; Hammond et al. 2009; Yaseen and Malhi 2009). If root P acquisition is insufficient to meet the P demand for new growth, characteristic biochemical, physiological and morphological responses occur both to improve the P economy of tissues and to increase P acquisition from the soil (Vance et al. 2003; Lynch 2007; White and Hammond 2008). Many of the responses of root tissues to P deficiency are co-ordinated by local and systemic signals involving gibberellins, auxin, cytokinins, ethylene and strigalactones, and the translocation of regulatory miRNAs and excess sucrose from the shoot to the root in the phloem (Hammond and White 2008, 2011; Vance 2010; Yang and Finnegan 2010; Chiou and Lin 2011; Lei et al. 2011). Increased sucrose supply to the root, in particular, is associated with the induction of greater P-uptake capacity in P deficient plants.

The P concentration in seeds of a mature plant varies with the phytoavailability of P in the soil and with environmental factors affecting plant growth and development. It also differs between plant species and between genotypes of the same plant species grown in the same environment (Schultz and French 1978). Chromosomal loci (QTL) affecting seed P concentration have been identified in several plant species including rice (*Oryza sativa*; Stangoulis et al. 2007; Garcia-Oliveira et al. 2009; Norton et al. 2010), common bean (*Phaseolus vulgaris*; Blair et al. 2009; Cichy et al. 2009a, b), *Lotus japonicus* (Klein and Grusak 2009), *Arabidopsis thaliana* (Bentsink et al. 2003; Waters and Grusak 2008), *Brassica rapa* (Zhao et al. 2007, 2008), and oilseed rape (*Brassica napus*; Ding et al. 2010). Between 30% and 90% of seed P occurs in the form of phytate (Table 1; Frossard et al. 2000; Reddy 2002; Raboy 2007, 2009). Phytate concentrations range from about 2 to 70 mg g^{-1} dry matter (DM) in seeds from various cereal and legume crops (Reddy 2002). Significant genetic variation in seed phytate concentration has been observed among commercial varieties of wheat, maize, barley, triticale, oats, rice, pearl millet and sorghum (White and Broadley 2009), and chromosomal loci (QTL) influencing seed phytate concentration have been identified in several plant species including rice (Stangoulis et al. 2007), common bean (Blair et al. 2009; Cichy et al. 2009ab), soybean (Walker et al. 2006; Maroof et al. 2009; Scaboo et al. 2009), *Arabidopsis thaliana* (Bentsink et al. 2003) and *Brassica rapa* (Zhao et al. 2007, 2008). Phytate typically accumulates in seeds as mixed salts of several cations, including K, Mg, Ca, Mn, Fe and Zn (Frossard et al. 2000; Reddy 2002; Raboy 2007, 2009; White and Broadley 2009). The activities of various phosphatases and phytases, already present in dry seeds, or synthesised *de novo* upon germination, effect phytate hydrolysis to provide the principal P source for developing seedlings (Dionisio et al. 2007, 2011).

Although the P contained in a seed contributes little to the final P content of the mature plant it produces, it contributes significantly to the P nutrition of a young seedling. Greater seed P reserves allow seedlings to establish faster and ultimately produce plants with higher yields (Bolland and Baker 1988; De Marco 1990; Zhang et al. 1990; Thompson et al. 1991;

Table 1 Typical phosphorus fractions (mg P g^{-1} FW) and their proportion of total P content (in parentheses) in seeds of various crop plants. Inositol-P is mainly *myo*-inositol hexakisphosphate (phytate) but also includes other inositol phosphates. Cellular-P includes phosphorus in starch, phospholipids and nucleic acids. Data from Hall and Hodges (1966), Lolas and Markakis (1975) and Raboy (2007)

Crop	Total Phosphorus	Inositol-P	Inorganic Phosphate	Cellular-P
Rice (*Oryza sativa*)	3.1	2.33 (75.2%)	0.14 (4.5%)	0.79 (25.5%)
Maize (*Zea mays*)	4.5	3.4 (75.6%)	0.3 (6.7%)	0.8 (17.8%)
Barley (*Hordeum vulgare*)	4.8	2.9 (60.4%)	0.4 (8.3%)	1.5 (31.3%)
Oat (*Avena sativa*)	4.28	2.27 (53.0%)	0.86 (20.1%)	1.15 (26.9%)
Wheat (*Triticum aestivum*)	5.3	4.0 (75.5%)	0.5 (9.4%)	0.8 (15.1%)
Common Bean (*Phaseolus vulgaris*)	5.22	3.91 (74.9%)	0.38 (7.3%)	0.93 (17.8%)
Soybean (*Glycine max*)	7.95	5.68 (71.4%)	0.3 (3.8%)	1.97 (24.8%)

Thomson and Bolger 1993; Ros et al. 1997; Grant et al. 2001; Zhu and Smith 2001). Similarly, increasing seed P, for example by soaking in potassium phosphate solution, often, but not always, accelerates the growth of seedlings in P-deficient soils (Grant et al. 2001; Sekiya and Yano 2010). This is consistent with the beneficial effects of targeted early-season P-fertiliser applications, or the placement of P-fertilizers, on the establishment and yield of arable and horticultural crops (Grant et al. 2001; Burns et al. 2010). It is thought that a greater P supply from the seed promotes rapid root elongation, which gives seedlings earlier access to growth-limiting resources, such as water and mineral elements, thereby promoting resource acquisition and vigorous early growth (Grant et al. 2001).

The length of time that seed reserves can supply the P requirement of a seedling growing at its maximal rate in a particular environment can be calculated theoretically based on knowledge of the P content of the seed, the maximal growth rate, and the critical tissue P concentration required to sustain the maximal growth rate. Assuming a critical tissue P concentration of 2 mg Pg^{-1} DM (White and Brown 2010), a small grain cereal, such as rye (S*ecale cereale*), with a seed P content of 0.151 mg (Broadley et al. 2003; USDA-ARS 2011), a growth function of $1.4^*e^{0.27t}$ mg DM, where t is the number of days after germination, and a leaf appearance rate of 0.284 d^{-1} with an apparent start 1 d after germination at 20°C (White 1993), would have sufficient seed P reserves to support plant growth for 14.8 d, until after the appearance of the third leaf and the first tiller. The longest root might be about 30 cm long at this time (White 1993). For maize, seed P reserves would be sufficient to maintain maximal seedling growth for 17.5 d after germination assuming a similar tissue P requirement of 2 mg Pg^{-1} DM, a seed P content of 0.952 mg (Nadeem et al. 2011b) and a growth function of $29^*e^{0.16t}$ mg DM at 28/25°C day/night (Pérez Leroux and Long 1994). This calculation can be compared with the observations of Nadeem et al. (2011a, b) that, when maize is grown at 25–28°C, (1) the average tissue P concentration has not fallen below 2 mg Pg^{-1} DM even 4 weeks after germination, (2) seed P reserves alone can support maximal seedling growth in a medium lacking P for at least 4 weeks after germination, and (3) seed P is the only source of P for seedlings until about 1 week after germination when root P uptake begins to contribute. Similarly, Spinks and Barber (1948) observed no appreciable uptake of P by roots of wheat seedlings growing in unfertilised soil until they were at least 2 weeks old, and Schjørring and Jensén (1984) reported that seed P reserves could support maximal root growth of oilseed rape, barley and buckwheat (*Fagopyrum esculentum*) seedlings for at least 7 days at 20°C in a medium lacking P.

Relative contributions of seed P reserves and root P uptake to the P nutrition of seedlings

Two informative studies by Muhammad Nadeem and colleagues have been published recently in Plant and Soil (Nadeem et al. 2011a, b) quantifying the relative contributions of seed P reserves and root P uptake to the P requirements of young maize seedlings during establishment.

In the first of these papers, Nadeem et al. (2011a) observed that phytate, which contributed most of the seed P, was rapidly hydrolysed, but that hydrolyzed forms of P were temporarily stored in the seed before being translocated to the developing seedling (Nadeem et al. 2011a). This suggested to the authors that phytate hydrolysis did not limit P redistribution from seed to seedling (Nadeem et al. 2011a). They also observed that roots of seedlings growing at 25–28°C only began to take up significant amounts of P about 5 d after sowing, slightly earlier than the transition from carbon heterotrophy to carbon autotrophy, but seedlings continued to import seed P reserves for approximately 2 weeks until these were exhausted (Nadeem et al. 2011a, b). Thus, they concluded that seed P was the main P source during germination and initial seedling establishment.

In their second paper, Nadeem et al. (2011b) studied the influence of seed P content and exogenous P availability on the mobilisation of seed P reserves and induction of root P uptake by maize seedlings. They observed that the hydrolysis of phytate and the export of P from germinating seeds were both independent of exogenous P supply, but that the absolute rate of phytate hydrolysis was faster in seeds with greater phytate concentrations. They also observed that the amount of P contained in the seed did not influence the onset or rate of uptake of exogenous P by the developing root system. Phosphorus acquisition was determined solely by the P availability in the nutrient solution fed to the roots. They therefore concluded that the remobilization of seed P and the uptake of exogenous P by roots of maize seedlings were controlled independently.

It is often observed that phosphate uptake by roots is regulated systemically by plant P status (White 2012). It has been suggested that sucrose transported in the phloem from the shoot to the root acts as a systemic signal to regulate phosphate uptake by roots (Hammond and White 2008, 2011; Vance 2010; Lei et al. 2011). Thus, the expression of phosphate transporters increases (1) during the day, or under conditions of N or P deficiency, when more sucrose is translocated to the root, (2) when roots are supplied exogenous sucrose, and (3) in mutants overexpressing the *SUC2* gene, which accumulate sucrose in their roots (Hammond and White 2008, 2011; Vance 2010; Lei et al. 2011). It is possible that roots of young seedlings do not take up phosphate either because the plant is P-replete or because there is no systemic sucrose signal. The theoretical calculations presented in the previous section, together with the empirical observations of Nadeem and colleagues, suggest that the P reserves of high-P maize seed (0.952 mg P seed^{-1}) would be sufficient to maintain maximal growth of maize seedlings for 17.5 d, and that even the P reserves of low-P maize seed (0.506 mg P seed^{-1}) would be sufficient to support maximal growth for 13.5 d at 25–28°C. However, it is also noteworthy that commencement of root P uptake was roughly coincident with the transition from carbon heterotrophy to carbon autotrophy (Nadeem et al. 2011a).

Classical studies indicated a basal temperature for leaf appearance in maize of 5–12°C (Duncan and Hesketh 1968; Tollenaar et al. 1979; Warrington and Kanemasu 1983) and a phyllochron of 22–66°C d (Tollenaar et al. 1979; Thiagarajah and Hunt 1982; Warrington and Kanemasu 1983). Assuming a basal temperature for leaf appearance of 10°C, a phyllochron of 60°C d, and an apparent start to leaf appearance after 2 d, the P reserves of high-P seed (0.952 mg P seed^{-1}) and low-P seed (0.506 mg P seed^{-1}) would suffice until the plant had 4.6 and 3.5 leaves, respectively (Fig. 2, line a). If the critical P concentration was greater than 2 mg P g^{-1} DM, then the leaf number at which the plant would begin to suffer from a lack of P (i.e. the critical phyllochron) would be reduced (Fig. 2, line b). For example, if the critical P concentration was 5 mg P g^{-1} DM, P reserves of 0.952 mg P seed^{-1} and 0.506 mg P seed^{-1} would suffice only until the plant had 2.9 and 1.7 leaves, respectively (Fig. 2, line b). If plant relative growth rate was lower, but the leaf production occurred at the same rate, seed P reserves would provide sufficient P for plant growth for a longer period (Fig. 2, line c). For example, if the critical P concentration was 2 mg P g^{-1} DM and the growth function was $29*e^{0.08t}$ mg DM, the leaf number at which the plant would begin to suffer from a lack of P would be 9.9 and 7.5 in plants grown from seeds containing 0.952 mg P seed^{-1} and 0.506 mg P seed^{-1}, respectively (Fig. 2, line c). This would equate to a plant of the same physiological age, but with smaller leaves and roots. Interestingly, P-replete seedlings of plant species from low P environments often have lower growth rates than those originating from high P environments (Bradshaw et al. 1960). Reducing seedling growth rates is, of course, not an agricultural solution for soils with low P availability, since it would result in reduced yields.

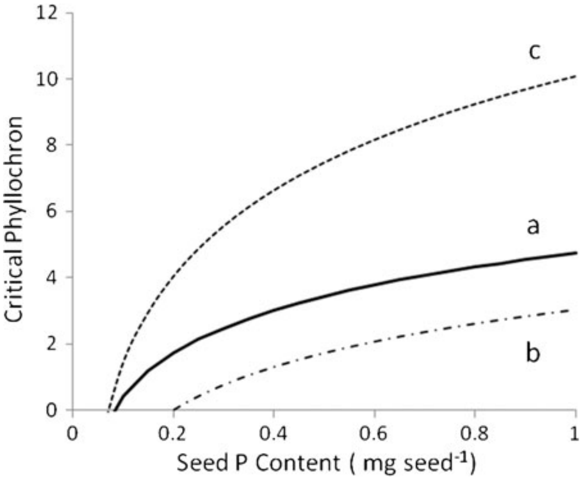

Fig. 2 Leaf number of a maize seedling at incipient P deficiency (critical phyllochron) versus the P content of the seed. Data were calculated for a seedling growing at 28°C, assuming a basal temperature for leaf appearance of 10°C, a phyllochron of 60°C d, an apparent start to leaf appearance after 2 d, and (**a**) a growth function of $29{*}e^{0.16t}$ mg DM and a tissue critical P concentration of 2 mg Pg^{-1} DM, (**b**) a growth function of $29{*}e^{0.16t}$ mg DM and a tissue critical P concentration of 5 mg Pg^{-1} DM and (**c**) a growth function of $29{*}e^{0.08t}$ mg DM and a tissue critical P concentration of 2 mg Pg^{-1} DM

Contribution of seed reserves to the micronutrient nutrition of seedlings

In addition to supplying the seedling with P, seeds are a source of other essential elements required for plant growth, and the length of time that seed reserves can meet the requirements of a seedling growing at its maximal rate can be estimated (Table 2). It would appear that, with the exception of P, a wheat seedling, for example, growing at 20°C rapidly exhausts the supply of macronutrients in the seed. However, there are sufficient amounts of the micronutrients Fe, Zn, Mn, Cu, B, Ni and Mo in the seed to fulfil the requirements of the seedling for at least 2.5 phyllochrons after germination. This is a significant observation since it has been reported that increasing seed concentrations of micronutrient elements, such as Zn, Mn, Cu and Mo, often improves crop establishment and leads to increased yields on soils that have restricted phytoavailability of these elements (Brennan and Longnecker 2001; Brennan and Bolland 2007; Broadley et al. 2007; Malhi 2009). Greater seed reserves of micronutrients with low phytoavailabilty in the soil are likely to assist root system development, faster resource acquisition, and vigorous early growth.

Conclusions

It is evident from the foregoing discussion that seeds of crop plants generally contain sufficient P to support maximal growth of seedlings for several weeks after germination. This allows the development of an extensive root system, which must ultimately acquire the

Table 2 The length of developmental time (expressed in phyllochrons) that seed reserves can meet the requirements of a wheat seedling growing at 20°C with a growth function of $9.73{*}e^{0.128t}$ mg DM, where t is the number of days after germination, and a leaf appearance rate of 0.170 d^{-1} with an apparent start 2.12 d before germination (White et al. 1990, 1991), assuming typical concentrations of essential mineral elements in the grain and the critical concentrations in tissue suggested by Reuter et al. (1997)

Element	Content (μg seed^{-1})	Critical concentration (mg g^{-1} DM)	Critical phyllochron
N	1171	74	1.01
K	224	39	–
P	184	3.1	2.76
S	74	3.0	1.60
Ca	17	2.5	–
Mg	48	1.3	2.14
Cl	26	1.0	1.66
Fe	2.4	0.025	3.38
Zn	1.7	0.015	3.64
Mn	2.0	0.011	4.23
Cu	0.19	0.004	2.45
B	0.13	0.0025	2.58
Ni	0.13	0.000084	7.09
Mo	0.014	0.000075	4.28

P required for continued plant growth. Greater seed P content enables seedlings to establish faster and, ultimately, to produce plants with higher yields. Significant P uptake by roots of several crop plants begins about a week after germination. The reason for this delay in P acquisition by roots is unknown. It might be attributed to limited access to phosphate in the rhizosphere or to a low abundance or activity of phosphate transporters in root epidermal cells. It is possible that the abundance of phosphate transporters in the root is developmentally regulated, or that the expression of genes encoding phosphate transporters is not upregulated in roots of young seedlings either (1) because the plant has sufficient P for growth or (2) because a systemic signal from the shoot, which relies on photosynthesis and phloem development, is not produced, translocated or perceived.

Acknowledgements We thank all participants at the international workshop on "Phosphorus: The Inside Story" held at the University of Western Australia in February 2011. Research by PJW is supported by the Rural and Environment Science and Analytical Services Division (RESAS) of the Scottish Government. We thank Dr Alison Bennett and Dr Paul Hallett for their comments on an original draft of the manuscript.

References

Aráujo AP, Teixeira MG (2003) Nitrogen and phosphorus harvest indices of common bean cultivars: implications for yield quantity and quality. Plant Soil 257:425–433

Bentsink L, Yuan K, Koornneef M, Vreugdenhil D (2003) The genetics of phytate and phosphate accumulation in seeds and leaves of *Arabidopsis thaliana*, using natural variation. Theor Appl Genet 106:1234–1243

Blair MW, Sandoval TA, Caldas GV, Beebe SE, Paez MI (2009) Quantitative trait locus analysis of seed phosphorus and seed phytate content in a recombinant inbred line population of common bean. Crop Sci 49:237–246

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

Bradshaw AD, Chadwick MJ, Jowett D, Lodge RW, Snaydon RW (1960) Experimental investigations into the mineral nutrition of several grass species. III. Phosphate level. J Ecol 48:631–637

Brennan RF, Bolland MDA (2007) Increased concentration of molybdenum in sown wheat seed decreases grain yield responses to applied molybdenum fertilizer in naturally acidic sandplain soils. J Plant Nutr 30:2005–2019

Brennan RF, Longnecker NE (2001) Effects of the concentration of manganese in the seed in alleviating manganese deficiency of *Lupinus angustifolius* L. Aust J Exp Agric 41:1199–1205

Broadley MR, Bowen HC, Cotterill HL, Hammond JP, Meacham MC, Mead A, White PJ (2003) Variation in the shoot calcium content of angiosperms. J Exp Bot 54:1431–1446

Broadley MR, White PJ, Hammond JP, Zelko I, Lux A (2007) Zinc in plants. New Phytol 173:677–702

Burns IG, Hammond JP, White PJ (2010) Precision placement of fertiliser for optimising the early nutrition of vegetable crops—a review of the implications for the yield and quality of crops, and their nutrient use efficiency. Acta Horticult 852:177–187

Chiou T-J, Lin S-I (2011) Signaling network in sensing phosphate availability in plants. Annu Rev Plant Biol 62:185–206

Cichy KA, Blair MW, Mendoza CHG, Snapp SS, Kelly JD (2009a) QTL analysis of root architecture traits and low phosphorus tolerance in an Andean bean population. Crop Sci 49:59–68

Cichy KA, Caldas GV, Snapp SS, Blair MW (2009b) QTL analysis of seed iron, zinc, and phosphorus levels in an Andean bean population. Crop Sci 49:1742–1750

De Marco DG (1990) Effect of seed weight, and seed phosphorus and nitrogen concentrations on the early growth of wheat seedlings. Aust J Exp Agric 30:545–549

Ding G, Yang M, Hu Y, Liao Y, Shi L, Xu F, Meng J (2010) Quantitative trait loci affecting seed mineral concentrations in *Brassica napus* grown with contrasting phosphorus supplies. Ann Bot 105:1221–1234

Dionisio G, Holm PB, Brinch-Pedersen H (2007) Wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) multiple inositol polyphosphate phosphatases (MINPPs) are phytases expressed during grain filling and germination. Plant Biotechnol J 5:325–338

Dionisio G, Madsen CK, Holm PB, Welinder KG, Jørgensen M, Stoger E, Arcalis E, Brinch-Pedersen H (2011) Cloning and characterization of purple acid phosphatase phytases from wheat, barley, maize, and rice. Plant Physiol 156:1087–1100

Duncan WG, Hesketh JD (1968) Net photosynthetic rates, relative leaf growth rates and leaf numbers of 22 races of maize grown at eight temperatures. Crop Sci 8:670–674

Fageria NK, Baligar VC, Jones CA (2011) Growth and mineral nutrition of field crops. CRC Press, Boca Raton

Feil B, Thiraporn R, Geisler G, Stamp P (1992) Yield, development and nutrient efficiency of temperate and tropical maize germplasm in the tropical lowlands. 2. Uptake and redistribution of nitrogen, phosphorus and potassium. Maydica 37:199–207

Frossard E, Bucher M, Mächler F, Mozafar A, Hurrell R (2000) Potential for increasing the content and bioavailability of Fe, Zn and Ca in plants for human nutrition. J Sci Food Agric 80:861–879

Garcia-Oliveira AL, Tan LB, Fu YC, Sun CQ (2009) Genetic identification of quantitative trait loci for contents of mineral nutrients in rice grain. J Integr Plant Biol 51:84–92

Grant CA, Flaten DN, Tomasiewicz DJ, Sheppard SC (2001) The importance of early season phosphorus nutrition. Can J Plant Sci 81:211–224

Hall JR, Hodges TK (1966) Phosphorus metabolism of germinating oat seeds. Plant Physiol 41:1459–1464

Hammond JP, White PJ (2008) Sucrose transport in the phloem: integrating root responses to phosphorus starvation. J Exp Bot 59:93–109

Hammond JP, White PJ (2011) Sugar signaling in root responses to low phosphorus availability. Plant Physiol 156:1033–1040

Hammond JP, Broadley MR, White PJ, King GJ, Bowen HC, Hayden R, Meacham MC, Mead A, Overs T, Spracklen WP, Greenwood DJ (2009) Shoot yield drives phosphorus use efficiency in *Brassica oleracea* and correlates with root architecture traits. J Exp Bot 60:1953–1968

Hanway JJ, Weber CR (1971) Accumulation of N, P, and K by soybean (*Glycine max* (L.) Merrill) plants. Agron J 63:406–408

Hill J (1980) The remobilization of nutrients from leaves. J Plant Nutr 2:407–444

Hocking PJ (1994) Dry-matter production, mineral nutrient concentrations, and nutrient distribution and redistribution in irrigated spring wheat. J Plant Nutr 17:1289–1308

Hocking PJ, Pate JS (1978) Accumulation and distribution of mineral elements in annual lupins *Lupinus albus* L. and *Lupinus angustifolius* L. Aust J Agric Res 29:267–280

Hocking PJ, Steer BT (1983) Uptake and partitioning of selected mineral elements in sunflower (*Helianthus annuus* L.) during growth. Field Crops Res 6:93–107

Karlen DL, Flannery RL, Sadler EJ (1988) Aerial accumulation and partitioning of nutrients by corn. Agron J 80:232–242

Klein MA, Grusak MA (2009) Identification of nutrient and physical seed trait QTL in the model legume *Lotus japonicas*. Genome 52:677–691

Lei M, Liu Y, Zhang B, Zhao Y, Wang X, Zhou Y, Raghothama KG, Liu D (2011) Genetic and genomic evidence that sucrose is a global regulator of plant responses to phosphate starvation in Arabidopsis. Plant Physiol 156:1116–1130

Lolas GM, Markakis P (1975) Phytic acid and other phosphorus compounds of beans (*Phaseolus vulgaris* L.). J Agric Food Chem 23:13–15

Lynch JP (2007) Roots of the second green revolution. Aust J Bot 55:493–512

Lynch JP, Brown KM (2001) Topsoil foraging—an architectural adaptation to low phosphorus availability. Plant Soil 237:225–237

Malhi SS (2009) Effectiveness of seed-soaked Cu, autumn- versus spring-applied Cu, and Cu-treated P fertilizer on seed yield of wheat and residual nitrate-N for a Cu-deficient soil. Can J Plant Sci 89:1017–1030

Manske GGB, Ortiz-Monastério JI, Van Ginkel M, González RM, Fischer RA, Rajaram S, Vlek PLG (2001) Importance of P uptake efficiency versus P utilization for wheat yield in acid and calcareous soils in Mexico. Eur J Agron 14:261–274

Maroof MAS, Glover NM, Biyashev RM, Buss GR, Grabau EA (2009) Genetic basis of the low-phytate trait in the soybean line CX1834. Crop Sci 49:69–76

Masoni A, Ercoli L, Mariotti M, Arduini I (2007) Post-anthesis accumulation and remobilization of dry matter, nitrogen and phosphorus in durum wheat as affected by soil type. Eur J Agron 26:179–186

Nadeem M, Mollier A, Morel C, Vives A, Prud'homme L, Pellerin S (2011a) Relative contribution of seed phosphorus reserves and exogenous phosphorus uptake to maize (*Zea mays* L.) nutrition during early growth stages. Plant Soil 346:231–244

Nadeem M, Mollier A, Morel C, Vives A, Prud'homme L, Pellerin S (2011b) Maize (*Zea mays* L.) endogenous seed phosphorus remobilization is not influenced by exogenous phosphorus during germination and early growth stages. Plant Soil. doi:10.1007/s11104-011-1111-5

Norton GJ, Deacon CM, Xiong LZ, Huang SY, Meharg AA, Price AH (2010) Genetic mapping of the rice ionome in leaves and grain: identification of QTLs for 17 elements including arsenic, cadmium, iron and selenium. Plant Soil 329:139–153

Parentoni SN, de Souza Júnior CL (2008) Phosphorus acquisition and internal utilization efficiency in tropical maize genotypes. Pesq Agropec Bras 43:893–901

Pérez Leroux HAJ, Long SP (1994) Growth analysis of contrasting cultivars of *Zea mays* L. at different rates of nitrogen supply. Ann Bot 73:507–513

Raboy V (2007) Seed phosphorus and the development of low-phytate crops. In: Turner BL, Richardson AE, Mullaney EJ (eds) Inositol phosphates: linking agriculture and the environment. CABI, Wallingford, pp 111–132

Raboy V (2009) Approaches and challenges to engineering seed phytate and total phosphorus. Plant Sci 177:281–296

Reddy NR (2002) Occurrence, distribution, content, and dietary intake of phytate. In: Reddy NK, Sathe SK (eds) Food phytates. CRC Press, Boca Raton, pp 25–51

Reuter DJ, Edwards DG, Wilhelm NS (1997) Temperate and tropical crops. In: Reuter DJ, Robinson JB (eds) Plant analysis: an interpretation manual, 2nd edn. CSIRO Publishing, Collingwood, pp 81–285

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

Rose TJ, Rengel Z, Ma Q, Bowden JW (2007) Differential accumulation patterns of phosphorus and potassium by canola cultivars compared to wheat. J Plant Nutr Soil Sci 170:404–411

Rose TJ, Rengel Z, Ma Q, Bowden JW (2008) Post-flowering supply of P, but not K, is required for maximum canola seed yields. Eur J Agron 28:371–379

Rose TJ, Pariasca-Tanaka J, Rose MT, Fukuta Y, Wissuwa M (2010) Genotypic variation in grain phosphorus concentration, and opportunities to improve P-use efficiency in rice. Field Crops Res 119:154–160

Scaboo AM, Pantalone VR, Walker DR, Boerma HR, West DR, Walker FR, Sams CE (2009) Confirmation of molecular markers and agronomic traits associated with seed phytate content in two soybean RIL populations. Crop Sci 49:426–432

Schjørring JK, Jensén P (1984) Phosphorus nutrition of barley, buckwheat and rape seedlings. I. Influence of seed-borne P and external P levels on growth, P content and $^{32}P/^{31}P$ fractionation in shoots and roots. Physiol Plant 61:577–583

Schultz JE, French RJ (1978) The mineral content of cereals, grain legumes and oilseed crops in South Australia. Aust J Exp Agric Anim Husb 18:579–585

Sekiya N, Yano K (2010) Seed P-enrichment as an effective P supply to wheat. Plant Soil 327:347–354

Spinks JWT, Barber SA (1948) Study of fertilizer uptake using radioactive phosphorus: II. Sci Agric 28:79–87

Stangoulis JCR, Huynh BL, Welch RM, Choi EY, Graham RD (2007) Quantitative trait loci for phytate in rice grain and their relationship with grain micronutrient content. Euphytica 154:289–294

Thiagarajah MR, Hunt LA (1982) Effects of temperature on leaf growth in corn *(Zea mays*). Can J Bot 60:1647–1652

Thompson BD, Bell RW, Bolland MDA (1991) Low seed phosphorus concentration depresses early growth and nodulation of narrow-leafed lupin (*Lupinus angustifolius* cv gungurru). J Plant Nutr 14:1355–1367

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

Tollenaar M, Daynard TB, Hunter RB (1979) Effect of temperature on rate of leaf appearance and flowering date in maize. Crop Sci 19:363–366

Trehan SP, Sharma RC (2005) Differences in phosphorus use efficiency in potato genotypes. Adv Hortic Sci 19:13–20

U.S. Department of Agriculture, Agricultural Research Service [USDA-ARS] (2011) USDA National Nutrient Database for Standard Reference, Release 24. Nutrient Data Laboratory Home Page, http://www.ars.usda.gov/ba/bhnrc/ndl. Accessed 1 November 2011

Vance CP (2010) Quantitative trait loci, epigenetics, sugars, and micro-RNAs: quaternaries in phosphate acquisition and use. Plant Physiol 154:582–588

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

Walker DR, Scaboo AM, Pantalone VR, Wilcox JR, Boerma HR (2006) Genetic mapping of loci associated with seed phytic acid content in CX1834-1-2 soybean. Crop Sci 46:390–397

Warrington IJ, Kanemasu ET (1983) Corn growth response to temperature and photoperiod. II. Leaf initiation and leaf appearance rates. Agron J 75:755–761

Waters BM, Grusak MA (2008) Quantitative trait locus mapping for seed mineral concentrations in two *Arabidopsis thaliana* recombinant inbred populations. New Phytol 179:1033–1047

White PJ (1993) Relationship between the development and growth of rye (*Secale cereale* L.) and the potassium concentration in solution. Ann Bot 72:349–358

White PJ (2012) Ion uptake mechanisms of individual cells and roots: short-distance transport. In: Marschner P (ed) Marschner's mineral nutrition of higher plants, 3rd edn. Academic, London, pp 7–47

White PJ, Broadley MR (2009) Biofortification of crops with seven mineral elements often lacking in human diets—iron, zinc, copper, calcium, magnesium, selenium and iodine. New Phytol 182:49–84

White PJ, Brown PH (2010) Plant nutrition for sustainable development and global health. Ann Bot 105:1073–1080

White PJ, Hammond JP (2008) Phosphorus nutrition of terrestrial plants. In: White PJ, Hammond JP (eds) The ecophysiology of plant-phosphorus interactions. Springer, Dordrecht, pp 51–81

White PJ, Cooper HD, Earnshaw MJ, Clarkson DT (1990) Effects of low temperature on the development and morphology of rye (*Secale cereale*) and wheat (*Triticum aestivum*). Ann Bot 66:559–566

White PJ, Cooper HD, Clarkson DT, Earnshaw MJ, Loughman BC (1991) Effects of low temperature on growth and nutrient accumulation in rye (*Secale cereale*) and wheat (*Triticum aestivum*). Ann Bot 67:23–31

White PJ, Broadley MR, Greenwood DJ, Hammond JP (2005) Proceedings of the international fertiliser society 568. Genetic modifications to improve phosphorus acquisition by roots. IFS, York, UK

Yang XJ, Finnegan PM (2010) Regulation of phosphate starvation responses in higher plants. Ann Bot 105:513–526

Yaseen M, Malhi SS (2009) Differential growth performance of 15 wheat genotypes for grain yield and phosphorus uptake on a low phosphorus soil without and with applied phosphorus fertilizer. J Plant Nutr 32:1015–1043

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

Zhao J, Paolo MJ, Jamar D, Lou P, van Eeuwijk F, Bonnema G, Vreugdenhil D, Koorneef M (2007) Association mapping of leaf traits, flowering time, and phytate content in *Brassica rapa*. Genome 50:963–973

Zhao J, Jamar DCL, Lou P, Wang Y, Wu J, Wang X, Bonnema G, Koorneef M, Vreugdenhil D (2008) Quantitative trait loci analysis of phytate and phosphate concentrations in seeds and leaves of *Brassica rapa*. Plant Cell Environ 31:887–900

Zhu Y-G, Smith SE (2001) Seed phosphorus (P) content affects growth, and P uptake of wheat plants and their association with arbuscular mycorrhizal (AM) fungi. Plant Soil 231:105–112