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Plant strategies and cultural practices to improve the uptake of indigenous soil P and the efficiency of fertilization

VFRC Report 2013/4



A.L. Smit, M. Blom-Zandstra, A. van der Werf and Prem S. Bindraban



Plant strategies and cultural practices to improve the uptake of indigenous soil P and the efficiency of fertilization

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List of acronyms and abbreviations

AP	Ammonium phosphate
DAP	Diammonium phosphate
DAS	Days after sowing
GPS	Global positioning system
K	Potassium
LAI	Leaf Area Index
N	Nitrogen
P	Phosphorus
PPC	Phosphatase-polyresorcinol complex
Pw	Soil P fertility level expressed as water extractable P (mg P ₂ O ₅ L ⁻¹ after extraction in a 1:60 v/v ground:water solution)
S	Sulfur
SMK	Sound mature kernel
TKC	Total kernel P content
UAN	Urea ammonium nitrate
VFRC	Virtual Fertilizer Research Center

1 Introduction

This study verifies the hypothesis whether enhancing early plant growth leads to a better use of P from indigenous soil resources and fertilizer P.

Phosphorus (P) availability is limiting crop production nearly everywhere in the world. Annual input of mineral P fertilizer in global food production is about 17 Mton P, which corresponds to approximately 10 kg P ha⁻¹ arable land. The application rate varies however significantly between continents from about 3 kg P ha⁻¹ in Africa to over 25 kg P ha⁻¹ in Europe (Liu et al., 2008). Total P input on cropland (so including manure and organic recycling) was estimated globally between 15 and 19 kg P ha⁻¹, indicating that a yearly input of mineral P of 10 kg P ha⁻¹ is essential for food production (Liu et al., 2008; Smit et al., 2009a). Global offtake (crops and crop residues) was estimated at 7-9 kg P ha⁻¹. So, worldwide the input of fertilizer exceeds already the takeoff.

Also, the global estimate for the efficiency of “conversion” of P from fertilizer to consumed P in food is only about 20% (Cordell 2010; Cordell et al., 2011). Losses throughout the production chain can explain this apparent low efficiency, erosion being the most important one. In addition application of P in excess to the crops’ offtake actually lead to accumulation of P in soils. Also soil accumulation in various parts of the world can explain the apparent low efficiency of fertilizer to consumed food.

As P resources are finite, remaining deposits should be used as efficiently as possible. Boosting efficiencies should apply to the remaining mining deposits of P but also and importantly, to the already accumulated P in agricultural soil. In order to efficiently exploit accumulated P in soils and to stimulate the efficient uptake of newly applied P fertilizers, plant uptake ability should be significantly improved. This report analyses the impact of early root growth to boost plant P uptake irrespective of soils with high or low P.

2 Background

Experiments show that the *recovery of mineral P- fertilizer* (i.e. the fraction of the applied fertilizer that is taken up by the crop) is at least on the short term rather low, usually much less than 30% (Syers et al., 2008). At many sites much of the applied fertilizer is bound firmly to the soil complex into Al, Fe and Ca phosphates and not readily available for plant uptake. Soil chemical processes in general lead to very low P concentrations in the soil solution, often in the order of 10 µM, as compared to concentrations in root that are over 1000 times higher. In developing countries P deficiency of soils (e.g. on the entire continent of Africa and in Brazil) often results in low crop yields. To improve the yield on these soils the P concentration in the soil solution needs to be increased or plants should have the ability to better extract the P from the soil complex.

However, increasing the P availability on these soils requires the application of substantial amounts of P; *much* more than the yearly uptake by the crop and should be applied during a large number of years (Römer 2009). This “loading” of soil with P is sometimes intentionally done to improve the fertility of the soil but sometimes unintentionally. The latter occurs in regions with nutrient surpluses due to the concentration of livestock; here the production of manure leads to an excess application on the surrounding arable fields. This can occur even at a farm scale in Africa where much of the manure is applied in the vicinity of stables or settlements.

These fertile soils contain over 2500 kg P ha⁻¹ and sometimes even exceed 7000 kg P ha⁻¹. These are excessive amounts as comparing to the annual uptake of a high yielding arable crop of approximately 25 kg P ha⁻¹. In less fertile soil the amount of total soil P will be less, but so is the off take with the crop. In both cases soil reserves of P are abundant, and if all of it would be available to the crop, it would suffice to sustain agricultural production for more than hundred years or several hundred years (W. Europe).

An example for Africa was based on two tables (Total P soil content and Effect of placed fertilizer P on maize grain yield) of van der Eijk et al. (2006), data from their experiments on several sites in Kenya. Figure 1 shows that maize yield increases with increasing total soil P content (blue diamonds). When assuming a P content for the maize of 3 kg P tonne⁻¹ then the ratio between soil pool and yearly offtake would indicate the number of years the total soil P pool would sustain production if it were plant available. The figure shows that even at the lowest fertility level total P content would be sufficient for more than hundred years at the current yield level, and probably even longer because the P concentration in the maize dry matter would be lower at these sites than the assumed 3 kg P tonne⁻¹.

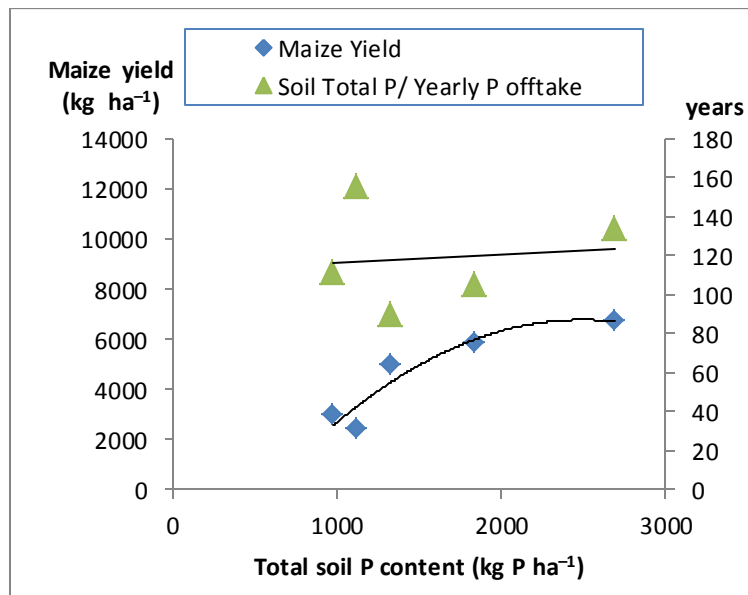


Figure 1. Relationship between total soil P content and maize yield and the ratio between total Soil P and yearly offtake (~ number of years total soil P would suffice to sustain production if it were fully plant available). Calculated from Tables 2 and 4 from van der Eijk et al. (2006)

So, while soils contain large amounts of “indigenous soil P” and/or applied fertilizer P, it is hardly accessible to the crops.

The challenge is to understand why accessibility of these large soil P pools is so low for plants and how it can be improved.

We observed in the Netherlands that there is no positive correlation between the recommended P supply for various crops and the amount of P taken up. On the contrary, a negative relationship was suggested (Smit et al., 2009b). This is unlike nitrogen where crops taking off large amounts of nitrogen require more nitrogen according to prevailing recommendations.

A crop like oilseed rape takes up large amounts of P, but the P fertilizer recommendation rate is very low, if not zero, whereas some vegetable crops take up small amounts of P but are recommended to be heavily fertilized. Why are low or even negative correlation found between recommended phosphorus application rates and phosphorus uptake?

Due to the immobile character of the phosphate ion and the low concentration in the soil solution, *root length* determines to a large extent the potential phosphorus uptake capacity (de Willigen and van Noordwijk 1987). Obviously a crop like (winter) oilseed rape with an extensive root system can easily exploit the soil to obtain its required P from the soil P reserves *without* additional P fertilizer. Autumn sown winter oil seed rape has the additional advantage of a functioning root system already in early spring before growth starts with rising temperature. In this way, from the beginning onwards this crop can fully exploit the P soil reserves without additional P fertilization. Many other crops in spring have to build up “from scratch” such a root system.

Therefore, as a logical follow up, it can be hypothesized that sufficient root length for P uptake will be a crucial factor *particularly in the juvenile phase of growth*. This is corroborated by the observation that P-deficiency is particularly visible in the younger plant stages. If the plant cannot realize the required P uptake already at this early stage, it will remain detrimental for the crops growth during its entire cycle, especially for short duration crops like most vegetable crops.

Long-term experiments with a range of P input rates with maize showed that slower development of the crop caused by a P deficiency takes place in the first part of the growing season (Plénet et al., 2000) and *not*, which would make more sense, after closure of the canopy when growth rate (*and daily P-uptake rate*) would be much higher (Figure 2Figure 2).

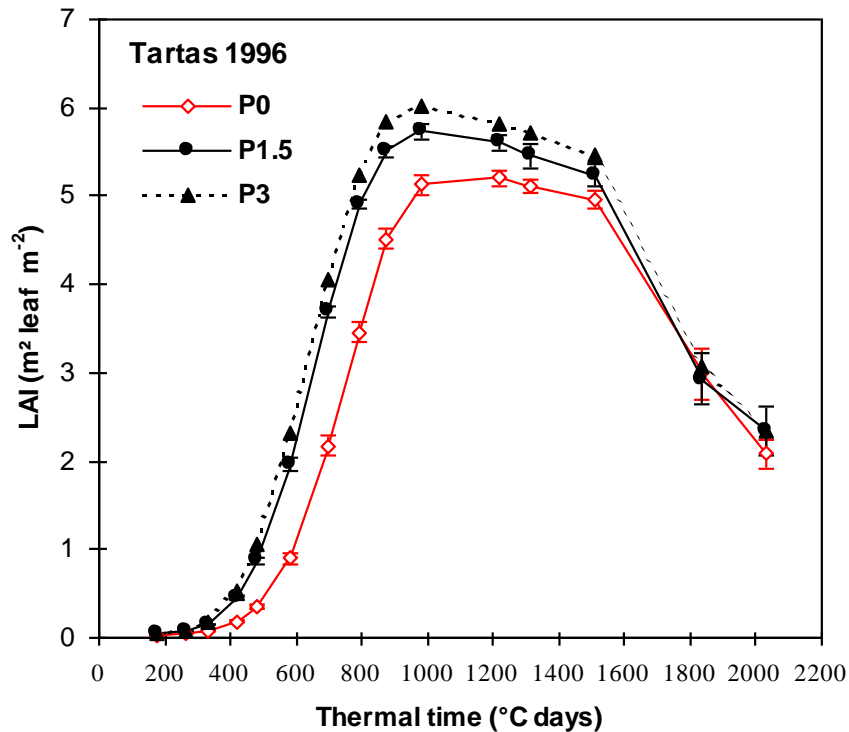


Figure 2. The effect of P application rate on Leaf Area Index (LAI) of maize. P0, P1.5 and P3 are yearly P application rates of 0, 52 en 111 kg P ha⁻¹ respectively. From Plénet et al. (2000)

The consequence of the above could also be that for a good yield and quality a relative high phosphorus status of the soil is needed *for the sole purpose* to help the plant through the early growth phase when root length is limiting phosphorus uptake.

When considering that during this period only slight amounts of P are taken up and also taking into account that a high soil fertility status requires large inputs of (organic) fertilizer, it seems likely that every factor that can improve the P acquisition during this period would lead to a more efficient use of fertilizer and, even more important, to a better exploitation of the indigenous soil P reserves and applied fertilizer P in subsequent periods when root length is not limiting any longer.

Plant characteristics and agronomic practices helpful to bridge the vulnerable period would include:

- Plant traits:
 - Root and root hair architecture (branching, length, density).
 - Root exudation rates (especially carboxylates) and enzymes (phosphatases).
- Cultural practices:
 - P fertilizer placement.
 - Foliar application of P.
 - Seed coating with P or enzymes.

In the following we reviewed the literature to corroborate the hypothesis mentioned above thereby focusing on mitigation possibilities to prevent early stress in crop production, resulting in an improvement of the efficiency of P fertilizers.

3 Mitigation possibilities to bridge the vulnerable early growth period

3.1 Fertilizer placement

Relatively small amounts of P fertilizer are placed in close vicinity of the germinating seed. Even with a small root length the high concentration of P in the soil solution then warrants sufficient P uptake as the maximum uptake rate of roots is not met under field conditions (de Willigen and van Noordwijk 1987). In later stages root length is sufficient to take over and utilize the larger amount of the soil P reserves. In general, placement of P is a proven technique and the comparison between broadcasted P and placed P often shows that a reduction of sometimes more than 90% in fertilizer application can be realized.

The effect of P placement is especially large under drought conditions, as drought strongly counteracts the diffusion of P towards the plant roots. Because the phosphate ion is much more immobile than the nitrate ion, placement will be especially beneficial for P uptake (de Willigen and van Noordwijk 1987), more than for N uptake. The effect of P placement is also expected to be larger in sown crops than in planted crops because sown crops need more time to proliferate their root system. A positive effect of placement is shown to be more effective when the growth period of a crop is shorter, as a longer growth period allows for more compensation of the slow growth earlier in the season.

Ehlert et al. (2002) identified on the basis of a literature review, low temperature and a large plant distance as factors to increase the fertilizer saving effect of placement vs. broadcasting. They categorized vegetables such as onion, lettuce, carrots as positive reacting to placement, but in cauliflower less effect was to be expected. The latter is very probably related to the strong rooting characteristics of Brassica species.

Stone (1998) experimented with NPK “starter” solutions in various vegetable crops. He found a stimulation of early growth and often higher yields in the end, even at sites with a high soil fertility level. At lower fertility levels small amounts of fertilizer could influence growth in such a way that the difference with high fertility sites were small or absent. The author concluded that with placement it would be possible to lift the low fertility sites to the level of sites with a high soil fertility.

Also Stone (2000) mentioned that placement is especially effective in crops with a large row distance. Experiments with starter solutions, which were applied in close vicinity of the seed, showed that diammonium phosphate (DAP) stimulated early growth and the final yield of onion. The effect was attributed entirely to P and not to N as solutions with only N did not show an effect. The combination of DAP placement with broadcasted N however was successful because N recovery was increased and yield and quality could be maintained with decrease N fertilizer rates. Stone states in his article: “It is likely that, following the boost to early growth provided by a high P starter fertilizer, the root systems of the larger plants can extract mineral N from a larger volume of soil and consequently the requirement for fertilizer N is likely to be less.” In his experiments the author did not apply a complete dose-response trial for both nitrogen and phosphorus so the foregoing statement could refer to fertilizer P as well. Figure 3 shows the positive effect in lettuce of a starter gift with ammonium phosphate (around 25 kg P) on the response curve for nitrogen, keeping in mind that also 100 kg P was given as maintenance application (however broadcasted).

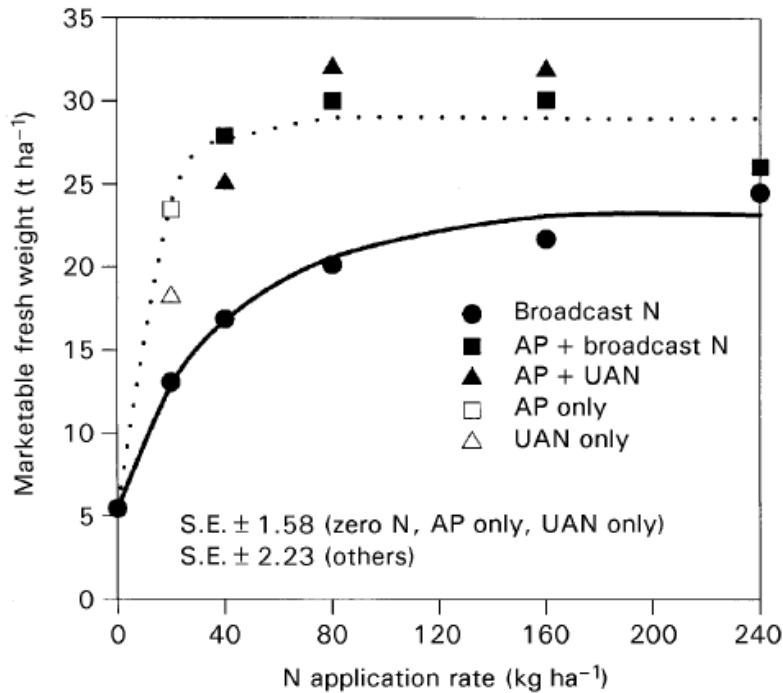


Figure 3. The effect of starter fertilizer with ammonium phosphate starter (AP) with or without urea ammonium nitrate (UAN). From Stone (2000)

Van der Eijk et al. (2006) investigated P placement on phosphorus-fixing soils in southwest Kenya. Total P content varied on the various experimental sites between 490 and 1681 mg P/kg soil, which would correspond assuming a soil profile depth of 20 cm with a total P content of more than 1000 and 4000 kg P ha⁻¹ or 2200 and 8800 kg P₂O₅ ha⁻¹. Olsen P varied between 1.6 and 59 mg/kg respectively. The comparison between placed and broadcasted P in maize on these P-fixing soils revealed that the advantage of placement over broadcasting is seen especially at low application rates of fertilizer P and also at sites with lower yields. An additional advantage of placement was the observation that weed growth was much less than when fertilizer P is incorporated in the whole topsoil where weeds could benefit also.

Van der Eijk et al. (2006) also concluded that yearly small amounts of P fertilizer are much more effective than larger amounts at longer intervals; in the latter case obviously more P is fixed at binding sites in the soil (Fe and Al hydroxides).

Much earlier, Prummel and Barnau Sijthoff (1975) showed some data on the efficiency of placement at low P fertility levels. With placement of only 1/6 of the amount of broadcasted P fertilizer, the same yields were obtained with *Phaseolus* and *Faba* beans, crops known to be sensitive to P fertilization. At higher fertility levels, crops did not respond to broadcasted or placed P fertilizer.

Smit et al. (2010) explored the effects of P-placement using a simulation model (a combination of a plant growth model and a soil model) to study the interactions between P-fertility status, rooting characteristics and P-demand. The simulation confirmed that in the early stages of growth P-uptake is strongly constrained by the length of the root system, although small amounts of P are involved (sometimes < 1 kg P ha⁻¹).

At a low fertility level (Pw 25¹), P uptake was less than the crop demand, especially for crops which were defined to have a low rooting density and a high demand. However, when increasing the fertility level from Pw 25 to 35 the fraction uptake to demand increased only by 10% whereas the application of *placed* P at a rate of only 6 kg P ha⁻¹ was sufficient to realize uptake to meet the demand. However, to increase the fertility level from Pw 25 to 35 would require large amounts of P. For Germany (Römer 2009) concluded that within the recommended range of P fertilities, to bring the soil from the lowest to the highest recommended fertility level, already 500 kg P ha⁻¹ was needed.

On a hectare basis, daily P-uptake, expressed as kg P (ha.day)⁻¹, is initially very low and will increase with the development of the crop. However, the model showed – assuming a realistic development pattern of root length and P uptake in time – that if uptake of P is expressed as kg P (km root length.day)⁻¹ then the opposite is true: the uptake rate decreases with time (see Figure 4). This emphasizes the role of the root system in the early stages of growth, especially for sown vegetable crops with a short growing period as elaborated by Smit et al (2009b).

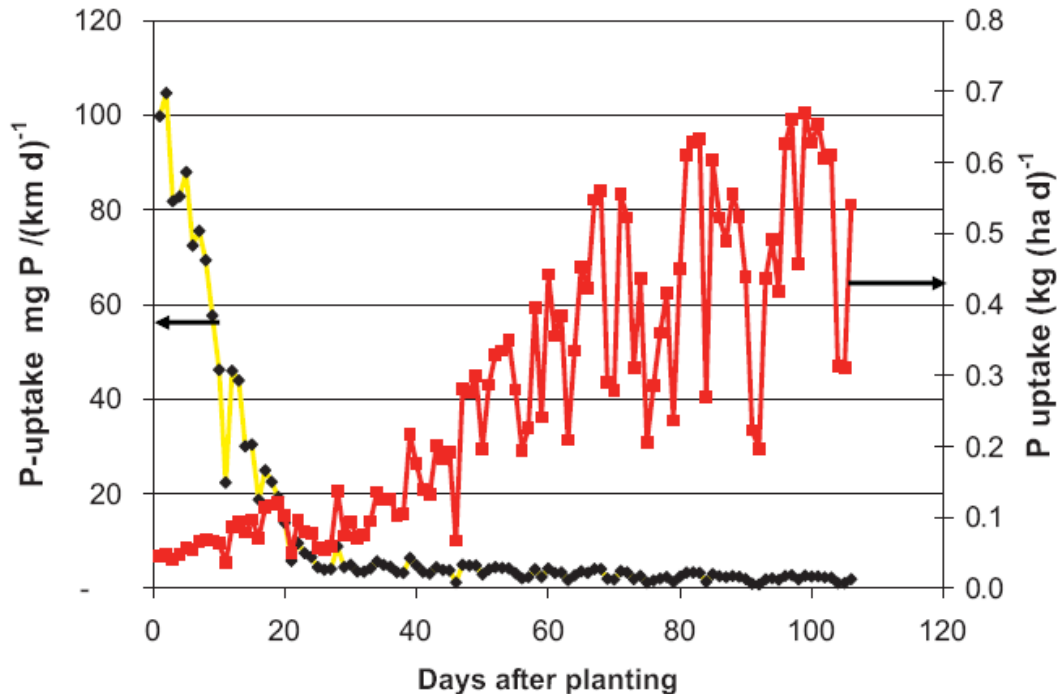


Figure 4. The simulation of a P uptake vs. time in kg P.ha⁻¹.day⁻¹ (red) and expressed as mg P.rootlength⁻¹.day⁻¹(yellow). From Figure 8, Smit et al. (2009b)

In addition Smit and colleagues (2010) carried out an experiment in a climate chamber to observe the effect of P-placement on early growth of several vegetable crops. Next to a non-fertilized control (treatment P1, see Table 1), P was added in only 3% of the pot soil volume in a cylinder shape immediately under the germinating seed at two rates of 58 and 175 mg P kg⁻¹ soil (treatment P2 and P3), equivalent to 4.4 and 13.4 kg P ha⁻¹.

¹ Pw: Soil P fertility level expressed as water extractable P (mg P₂O₅ L⁻¹ after extraction in a 1:60 v/v ground:water solution. In the Netherlands a Pw of 25 is at the lower limit of the recommended range of P fertility levels.

These treatments were compared to a treatment with 35 mg P kg⁻¹ soil added homogeneously to the entire pot's soil volume (Treatment P4), equivalent to 84 kg P ha⁻¹. Table 2 shows that the smallest amount of placed P at 4.4 kg P ha⁻¹ for most characteristics came close to the broadcasted amount of 84 kg P ha⁻¹. The fertility status increased in the broadcasted P treatment from Pw 24 to 31, which was comparable to the rise from PW 25 to 35 in the model simulation, corroborating that placement of small amounts of P led to the same or better P uptake and growth than raising the overall P-fertility of the soil. Although the results of the simulation as well as the pot experiment are quite in line with each other, they should be verified under field conditions.

In general we think that especially in the early growth stages, the balance between sufficient root length and actual P-uptake is very fragile and may be strongly influenced by environmental conditions like soil and air temperature, soil moisture and radiation. This may explain why placement studies in the field often have conflicting and variable results.

Table 1. *Treatments in climate chamber experiment (Smit et al., 2010)*

Treatment	P-Fertilization in kg P ha ⁻¹	P Added as mg P/kg Soil	Average P-Status (Pw) During the Experiment
P1	0	0	24
P2	4.4	58 in 3% of the soil volume	–
P3	13.4	175 in 3% of the soil volume	–
P4	84	35 homogeneously	31

Table 2. *The effect of P fertilization (by placement and broadcasted) on some plant characteristics in spinach, onions and carrots in a climate chamber pot experiment (Smit et al., 2010)*

Variable	Crop	P Fertilization in kg P ha ^{-1a}			
		Placement		Broadcast	
		0	4.4	13.1	87
Leaf area (cm ²)	Spinach	90	123	196	113
	Onion	6	5	9	7
	Carrots	5	7	17	7
Dry matter (mg/pot)	Spinach	603	828	1,070	715
	Onion	115	123	160	135
	Carrots	48	70	123	62
P-content (mg/kg)	Spinach	1.6	2.0	2.8	2.5
	Onion	1.1	1.1	1.5	1.1
	Carrots	2.1	2.3	2.8	2.5

a. The P-rates in the table are scaled up to kg P ha⁻¹ assuming a topsoil of 20 cm (the height of the pots). The effects of P-fertilization were significant (ANOVA) for all crops and all variables.

Table 3. Factors that will lead to strong or minor response by the crop in terms of P uptake and growth upon placement of P

Expected strong effect of placement	Minor effect of placement
Sown crops	Planted crops
Slow root development rate	Fast development rate
Short growth period	Longer growing period
Less root branching per root hair	More branching per root hair
Sites with lower (P) fertility	Sites with a high (P) fertility
Lower application rates	Higher application rates
Low (soil) temperature	High temperature
Large plant distance per row width	Small row width per plant distance

The early growth phase could be critical for the reasons mentioned above. In addition, plants take up about 50% of their seasonal P requirements by the time they have accumulated only 25% of their final dry matter (Black 1968, as cited by Chien et al. (2010)). The fact that P uptake is ahead of dry matter production tends to be valid for a wide range of crops, it was already mentioned by van Itallie in 1937 (cited by de Willigen and van Noordwijk [1987] on p.35 of their thesis). It corroborates the hypothesis that early in crop production, P requirements are critical.

Finally, based on examples in the West African countries of Niger, Burkina Faso and Togo, Buerkert et al. (2001) concluded that P placement is a promising strategy to overcome P deficiency being the strongest regional growth limiting nutrient constraining cereal yield. They carried out experiments with pearl millet (*Pennisetum glaucum* L.), sorghum (*Sorghum bicolor* (L.) Moench) and maize (*Zea mays* L.) either continuously or in rotation with cowpea (*Vigna unguiculata* Walp.) and groundnut (*Arachis hypogaea* L.). Across the eight sites, NPK placements at 0.4 g P per hill raised average cereal yields between 26 and 220%. This was confirmed in 119 on-farm trials.

Based on the above findings in literature with experiments in pots and field and simulation models we conclude that placement of P:

- Can prevent that a large fraction of applied P is fixed to soil binding sites.
- Could subsequently lead to a better utilization of soil P reserves.
- Can lead to a better utilization of other nutrients, like nitrogen.

See Table 3 for a summary of the conditions influencing the success of placement.

To maintain soil fertility, however, total P input in a rotation should be at least meet total P offtake. Yet, placement creates the possibilities for the saved P to be applied in P sensitive crops where placement is not possible.

3.2 Rooting characteristics

In their thesis de Willigen and van Noordwijk (1987) concluded that especially for P-uptake, enough root length is important as more length decreases the transport distances from the soil solution to the roots. They proved that transport distances in the soil are the main limiting factor for P uptake and *not the physiological capacity* of the root for P uptake.

Root proliferation, root architecture, branching and development, root hairs, etc. all can have a significant influence in the extent to which the plant can utilize the available P reserves in the soil. Much is known about the strategies a plant can pursue to respond to P-deficient conditions. In their review article, Richardson et al. (2009) mention more adventitious roots, smaller root diameter, shallower basal roots, more dispersed lateral roots and also longer and denser root hairs; the latter can be seen as an extension of the root system.

Also in a recent review article, Niu et al. (2013) mention root architecture development in response to low P availability as crucial to cope with P stress. The paper describes how plants adjust their root architecture to low-P conditions through inhibition of primary root growth, promotion of lateral root growth, enhancement of root hair development and cluster root formation, which all promote P acquisition by plants. Most of these strategies consist of using root dry matter as efficiently as possible to produce more length per volume soil, thereby stimulating the possibility to scavenge the soil volume for the scarce P ions.

The development of root hairs might be an especially interesting strategy as it increases the length of the root system considerably without much investment of dry matter. A drawback might be the short longevity of root hairs, but it could be argued that after exploring and exhausting a certain volume of soil for phosphorus, the maintenance of these root hairs is no longer needed. Indeed, Brown et al. (2013) concluded based on a cost-benefit analysis of various root traits that root hair development has the greatest potential for P acquisition relative to their cost of production. Moreover, in a modelling approach they argued that the greatest gains in P-uptake efficiency would be made through increased length and longevity of root hairs rather than by increasing their density. They formulated six potential ideotypes to improve crop P acquisition. The conclusion that an investment in more root hair length is more important than root hair density was also drawn by Zygalkis et al. (2011) based on a model approach as well.

Could breeders select for root hair traits and thus improve P efficiency of their varieties?

Yan et al. (2004) investigated the combination of root hair traits and organic acid root exudation traits and the relationship with phosphorus uptake in common bean (*Phaseolus vulgaris* L.). Substantial genotypic variability was observed for these traits as well as for the response to P availability. A P efficient genotype had a greater root hair density, longer root hair length and greater exudation of H⁺ and total acid than the P inefficient genotype in the study. P uptake in the field was found to be correlated to these characteristics. Also from the data given by Hoffland et al. (1989) a relation between root hairs and root exudates could be deduced. They mention that organic anion efflux varies between different parts of root systems but the efflux of organic anions tends to be greater in young regions near the root tip than older parts of lateral roots of rapeseed, which coincides with the region where root hairs are active.

We therefore conclude that the desired root properties for P uptake are well described in literature, but not specifically for the early stages of growth. To our knowledge, any improvement in traits which could enhance P uptake for the young plant could lead to a better use of P soil reserves and to a better use of fertilizer P in later stages. Selection and breeding for these traits in young plants (root hairs – in particular hair length, longevity, root branching, etc.) could be relatively simple and not time consuming, as breeders do not have to wait for the final yield.

3.3 Soil P binding capacity and plant P-uptake in relation to exudates

As a solution, phosphorous is taken up by plants either in the form of H_2PO_4^- or HPO_4^{2-} (Raghothama 1999). However, when applied to acidic soils, P tends to bind very strongly on iron and aluminum hydroxides, thereby decreasing P fertilizer use efficiency (van der Zee and Riemsdijk 1988). Similar effects are observed in calcareous soils when inorganic P fertilizers such as triple superphosphate are applied; for instance calcium phosphate is instantly formed and makes the phosphorus relatively unavailable for plant uptake (Marschner 1995).

Over time plants have developed several mechanisms to overcome the P-binding capacities of several types of soils (Richardson et al. (2011) and references therein): (1) root foraging strategies geared towards enhanced P-uptake, including fine root hair formation, cluster roots, top soil foraging; (2) soil P mining strategies via excretion of carboxylates such as oxalate, malate, citrate; and (3) improved internal P-utilization efficiency. Hard evidence for increased P solubility with increased excretion of carboxylates is scarce however (Richardson et al., 2011), because citrate efflux is difficult to separate from other exudates such as protons and secondary metabolites. Still it is to be expected that carboxylates play a role in solubilizing P, as several incubation experiments have shown that addition of carboxylates to the soil increased water soluble P concentrations. Root born carboxylates have been shown to have the capability of forming bonds with metals such as Fe and Al, and thus decreasing the P sorption capacity of the soil.

The question now arises whether chemically produced chelating agents or organic acids that are mechanically applied to the soil will increase water soluble P concentration, resulting in higher plant P uptake and eventually higher productivity. In a laboratory incubation experiment Edwards (2013) showed that P binding to metals decreased when chelating agents were applied to two acid types of soil, resulting in an increased concentration of water soluble P. Adding chelating agents in a pot experiment with corn, however, did not increase productivity or decrease soil binding P capacity. Guertal and Howe (2013) compared two commercially available P-solubilizing products and concluded that “results are not definitive, but indicate that both products have the potential to improve plant available forms of P in the soil.” Andrade et al. (2007) reported positive effects on productivity of corn when organic acids were supplied to the soil, and that the effect depended on the time of application, i.e., either before or simultaneously with P fertilizing. From a field trial with corn, McGrath and Binford (2012) concluded that starter P fertilizer increased early growth, but that only on 2 sites out of 8 was an increased grain yield observed (this could be an example of compensation mentioned above; i.e. no apparent impact on crops with long growth periods). In the same experiment a simultaneous supply of a commercially available P-solubilizing agent did not have any effect on productivity in the early growth phase or grain yield. In a pot experiment, Khademi et al. (2010) analyzed the effect of carboxylates added on P uptake in wheat and concluded that oxalate was far more effective than citrate in stimulating P uptake, as citrate mineralization by microorganism proceeded at a far higher rate.

Even though there seems to be sufficient evidence that carboxylates by themselves have a P solubilizing effect and therefore will increase P-availability for plants, it is still very uncertain that direct application of carboxylates or analogues to the field will have the desired effect in high P binding soils.

Based on information given in Gerke et al., 2000a and Gerke et al., 2000b we here calculate the absolute minimum amount of Trisodium citrate required per hectare to be effective in solubilizing P. Based on measurements, Gerke et al. (2000a) concluded that concentrations of at least 10 μmol citrate adsorbed g^{-1} soil

are required for P to become soluble. Soil P-solubility increased exponentially in the range of 10 to 50 $\mu\text{mol citrate g}^{-1}$.

This suggests that 6.7-33.5 tons of Trisodium citrate are required per hectare for P-solubilization. A quick scan revealed a sales price of approx. 800€/ton Trisodium citrate, i.e. 5300-27000 € ha^{-1} , excluding machinery and labor costs. In this financial calculation we assume that the top 20 cm of soil is then fully saturated with carboxylates. Large amounts of carboxylates will be necessary as it is paramount for the action of exudates to be in close vicinity of (all the) roots at sites where P can be solubilized. This is quite in contrast to placement of P, where a small volume of higher P concentration leads to a higher diffusion rate of P to the roots, thereby in addition making use of the large P uptake capacity of the roots in the vicinity of the higher P concentration.

We therefore conclude that exudation of organic acids is important to utilize the soil P reserves but it is not feasible to apply these compounds exogenously on a large scale. A possible research area might be to test the activity in the very first phase of growth (e.g. the germination phase), then the input of exudates could perhaps be limited to affordable amounts and applied in the vicinity of roots. In a crop rotation it could be worthwhile to integrate certain crops that are known to have high exudation rates. These crops could make some P available for subsequent crops in the rotation, provided the crop residues are ploughed under.

3.4 Seed coating with P and enzymes

3.4.1 Coating with P

Seed coating with nutrients could be a practical measure to provide the emerging plant with small amounts of P. Although the amounts are small it could help the plantlet to bridge the first stages of growth, phosphorus being right on the spot for uptake. Seed coating would therefore be an effective means to stimulate early P uptake; some promising results have been reported in practice. Several companies have engaged in the production of seeds coated with fertilizers (e.g. www.innoseeds.nl).

Rebafka et al. (1993) conducted experiments with millet on an acid sandy and P deficient soil in Niger. Seeds of pearl millet were coated with different rates of P and with different fertilizer types, including superphosphate, ammonium phosphate and ammonium dihydrogen phosphate (AHP). However, seedling emergence was reduced at rates higher than 5 mg P per seed. The most favorable effect on plant growth and P content was obtained with AHP as seed coating. This was attributed to the enhancement effect of ammonium on P uptake. Compared to the untreated control, dry matter production at 20 days after planting was increased by 280%, plant P content by 330%, total biomass at maturity by 30% and grain yield by 45%. They concluded that seed coating with AHP may be harmful to seedling emergence, but with a large ability to enhance early growth and increase yield of pearl millet.

Karanam and Vadez (2010) stress that phosphorus is one of the main limiting nutrients in the semi-arid regions where pearl millet is grown; its deficiency leads to poor seedling establishment and eventually poor crop yield. They experimented with seed *priming*, i.e. soaking the seed with (nutrient) solution, and seed *coating* with P in three hybrid varieties of pearl millet in a low P Alfisol (soils that have a clay-enriched subsoils and a relatively high native fertility but usually deficient in P). Overall, seed *priming* did not increase shoot biomass at two and four weeks after sowing. In pots, *seed coating* at a rate of approximately 400 g P ha^{-1} increased vegetative biomass over 400% at early stages, and panicle yield by about 50%, over the non-coated treatment, with genotypic

variation in the magnitude of the response. According to the authors, a seed P coating treatment appears a valid option to promote pearl millet seedling establishment and then to boost yield under low soil P conditions.

Mašauskas et al. (2008) mention for malting barley that coating with P sometimes decreased emergence, also the positive effects on seed yield were not convincing with only a positive effect when conditions enabled a grain yield over 6 t ha⁻¹.

Experiments with oat (Peltonen-Sainio et al., 2006) showed that seed coating with P resulted in alterations to many plant stand structure traits. All significant changes represented improvements over the non-coated control but were not consistent. Most often, enhanced biomass accumulation (up to 22%) and grain set (up to 15%) occurred. This was not, however, associated with increased grain yield in any of the experiments. The authors concluded that P seed coating promoted early oat growth however without increasing economic yield.

Ros et al. (2000) investigated the effect of soaking and coating rice with various P fertilizer, including rock phosphate, in view of the large influence that phosphorus can have on early seedling growth and the fact that many rice growing soils are P deficient. However, seedling emergence was reduced by 40-60% when seeds were coated or soaked in solutions (priming). By contrast, seed coating with rock phosphate did not affect final emergence compared to the untreated control but did delay seedling emergence by 2-3 days. At 20 and 40 days after sowing (DAS), no remaining significant effects of soaking in P solutions was found on plant growth. At 20 DAS, coating increased shoot dry weight but decreased root dry weight of plants. The effect of coating treatments persisted up to 40 days after sowing, and at this stage, seed coating increased root length and dry weight and increased shoot dry weight by 400-870%. Although plant growth responded to coating seeds, these seed treatments initially reduced seed emergence and may therefore not be acceptable to farmers. They concluded that coating rice seeds with rock phosphate may be more promising for stimulating early rice growth on low P soils. Rock phosphate when applied at 1.2 mg P per seed or 0.5 kg rock per kg of seed was not harmful to final seedling emergence but quadrupled shoot and root growth of rice.

3.4.2 Coating with phosphatase

A large part of soluble P from fertilizer reacts with soil components, forming chemical compounds that are on the short term not easily taken up by the plants. Eventually in many places in the world this leads to accumulation of P in soils and environmental problems such as eutrophication of surface water. The sometimes large amounts of this P in the soil profile can be in organic as well as in inorganic forms. The fraction of organic P can range between 20 and 80% (Fransson and Jones 2007; Richardson et al., 2011). Especially under P deficient conditions both plant roots and soil microorganisms can release phosphatase enzymes into the soil that have the potential to mobilize at least some of this organic P reserve in soils. Mineralization of organic P is essential because only phosphate ions can pass the barriers in the root system. This mineralization occurs through the activity of phosphatase enzymes in the rhizosphere. The enzymes can be of plant or microbial origin. In their review (Richardson et al., 2011) mention that the root phosphatase activity is enhanced under P-deficient conditions, and is considered a key component of the general response of plants to P starvation. Enhancing this activity may assist in increasing P-use efficiency. Seed coating with the enzymes can therefore be a possibility to increase the use of the organic P pool in the soil.

Rhizosphere microbial inoculants with a specific interest in their ability to increase the availability for P have also been proposed. In their review Richardson et al., 2011 mention some positive responses and even development of commercial inoculants, but mention that often positive responses in a laboratory are not reproduced under field

conditions and concluded more or less that still much work has to be done to arrive at application under field conditions.

However, Pilar-Izquierdo et al. (2012) and Pilar et al. (2009) coated barley seeds with free and immobilized alkaline phosphatase. Two coating techniques were studied: film-coating and pelleting. The highest phosphatase activity retention in the coating layer was observed when seeds were film-coated with phosphatase-polyresorcinol complex (PPC). Under pot culture conditions, an increase in the soil inorganic P was detected when the seeds were film-coated with phosphatase. Moreover, the film-coating significantly increased the P uptake by plants between 25% and 31% at 35 days after planting. The study showed that the seed film-coating with free and immobilized phosphatase increased the phosphatase activity in the rhizosphere and the P uptake by plant.

We therefore conclude that seed coating with P seems a promising technique, but the lower rate of emergence may be problematic. Based on the review so far, there seems to be merit in investigating the effect of a phosphatase coating in combination with coating seeds with fertilizer P or phosphate rock.

3.5 Foliar spraying of phosphorus

The question arises whether foliar spraying of P can be a practice to promote the early vigor of plants in P deficient situations. Here we summarize literature on this subject.

At sites that contain enough soil P to supply the plants till maturity no effect of foliar P is observed (Noack et al., 2010). However, foliar P fertilization may allow an adequate alternative for P supply when P content in the soil is insufficient, when soils have a high capacity of P fixation, and when they are poor in native P (Natale et al., 2002). Roots may also have limited access to P in soils with a low soil moisture content (dos Santos et al., 2006). In a review, Noack et al (2010) present many studies in which foliar P application results in positive plant responses and significant increases of yield at P insufficiency in the soil.

A number of studies have investigated the physiology of foliar P fertilizer uptake under controlled conditions, using single droplets applied to the leaf or sprayed on the crop (Koontz and Biddulph 1957; Bouma 1969). It appears that a spray application method proved superior to droplet methods (Koontz and Biddulph 1957).

3.5.1 Uptake mechanisms

The mechanisms of P uptake through the leaves differ considerably from P uptake through plant roots. After spraying of the foliar P fertilizer, the P-containing solution must first penetrate the leaf surface before entering the cytoplasm of a cell within the leaf. There are several processes required for leaf penetration of solutes:

1. The solute must adhere to the leaf surface and must be retained to allow sufficient time to penetrate.
2. The solute must diffuse through the leaf surface.
3. The P has to be transported as molecule or as complex through different cells or cell layers into the phloem to be transported further to high growth areas in different plant organs (Kirkwood 1999).

Penetration of foliar P fertilizer can occur through the cuticle (Figure 5), cuticular pores, the stomata, leaf hairs (Figure 6) and other specialized epidermal cells (Franke 1967), although not all traverse routes have the same accessibility. There is ongoing debate as to which of these penetration pathways plays the most important role in nutrient uptake (Wittwer and Teubner 1959; Buick et al., 1992), (Kirkwood 1999; Fernández and Eichert 2009). Plant leaves have thick cuticles that are coated with a waxy layer, making penetration of solutes difficult (Currier

and Dybing 1959). Almost all plant surface waxes are hydrophobic and repel water-based sprays. The cuticle itself is a lipid layer making it wettable by oils but remaining only slightly permeable to both water and oils. So, epicuticular waxes are a barrier to the retention and penetration of foliar fertilizers into plant organs (Jenks and Ashworth 2010).

Penetration through stomata appear to be a more important pathway for plants to absorb solutes in foliar sprays. Although measuring stomatal uptake of chemicals applied to leaves has proven to be difficult, Currier and Dybing (1959) provided early evidence for stomatal penetration of P. They described it as quick and rapid with respect to the slower cuticular penetration. Indeed, it has been shown that pretreatment of broad bean leaves with abscisic acid to close stomata resulted in diminished absorption of foliar-applied solution (Buick et al., 1992). Other studies (Field and Bishop 1988; Eichert et al., 1998) also identified stomatal penetration as an important path for nutrient absorption. On the other hand, some researchers suggest that stomatal uptake plays a minor or negligible role compared with cuticle penetration of foliar applied (Schönherr and Mérida 1981; Schönherr 2006). They mention the cuticle, and the cuticle layer that partially extends across the stomatal cavity forming cuticle ledges (Figure 6), as the first route available for penetration of solutes into leaves upon contact with the leaf.

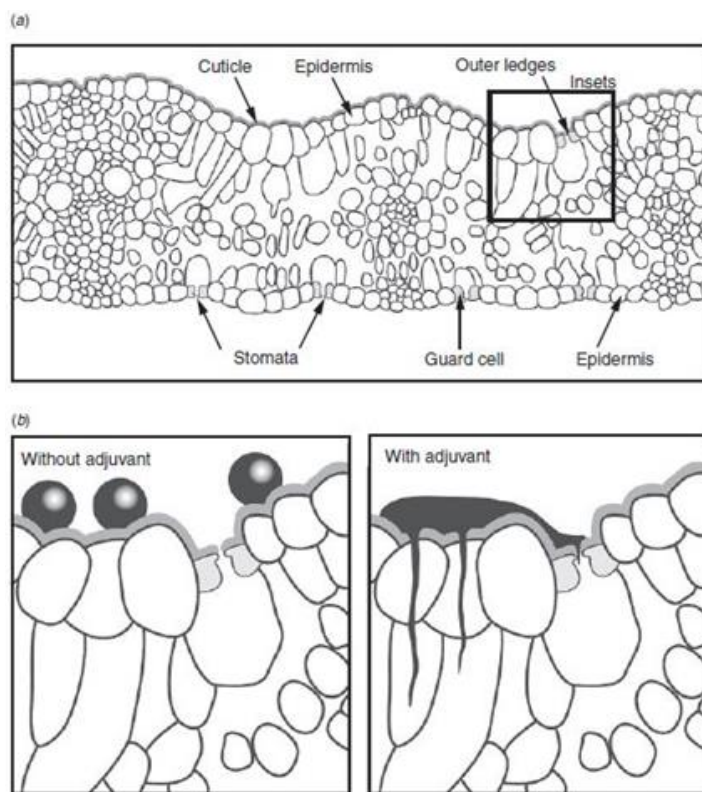


Figure 5. Cross-section (a) of wheat leaf and (b) diagrammatic representation of foliar fertilizer dispersion and penetration with and without adjuvant. From Figure 1, Noack et al. (2010)

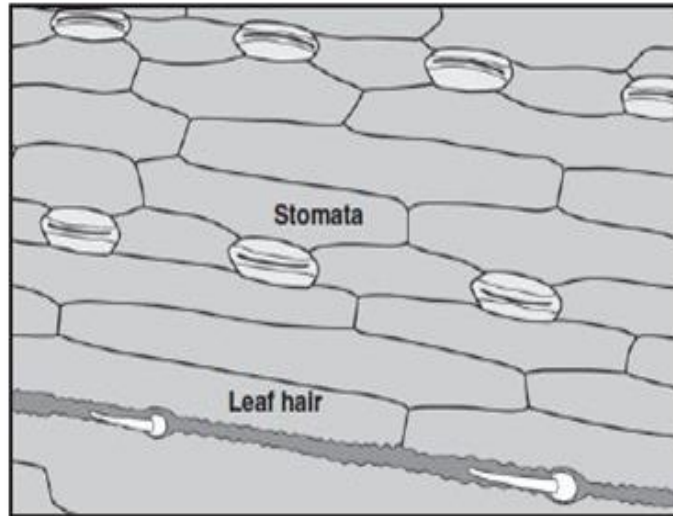


Figure 6. Surface of wheat leaf showing stomata and leaf hairs (redrawn from Scanning Electron Microscopy image). From Figure 2, Noack et al. (2010)

3.5.2 Translocation through the plant

After foliar P uptake, P is translocated from the leaf to other plants organs within a 24-hour period as measured with ^{32}P , and this translocation increased when the concentration of the applied P increased (Koontz and Biddulph 1957).

Translocation of applied phosphorus is greatest with NaH_2PO_4 and decreases with the following compounds (Koontz and Biddulph 1957): $\text{K}_2\text{HPO}_4 > \text{K}_3\text{PO}_4 _ \text{Na}_2\text{HPO}_4 _ \text{NH}_4\text{H}_2\text{PO}_4 _ = (\text{NH}_4)_2\text{HPO}_4 > \text{H}_3\text{PO}_4$ (injury) $> \text{KH}_2\text{PO}_4 \text{ Na}_3\text{PO}_4$. It is shown that the two compounds for which translocation is the highest, NaH_2PO_4 and K_2HPO_4 , do not crystallize on the leaflet as rapidly as the other formulations (Noack et al., 2010) and so they attributed to the effectiveness of supplying P. Wittwer and Teubner (1959) suggested that, when the mono-ammonium salt $[(\text{NH}_4)_3\text{PO}_4]$ is applied to leaves at low pH values, it can maximize P absorption.

The amount of P translocated, appears to be directly related to the time for the solution to dry on the leaf (Noack et al., 2010). It has been shown that absorption of applied phosphorus (NaH_2PO_4) falls off markedly after about 30 hours, but then 60 % is absorbed and 34.5 % translocated out of the treated leaflet in 96 hours. The amount of phosphorus that moved downward from a treated leaf in the stem is initially greater than the amount that moved upward, but after 48 hours accumulation in the upper part exceeds that in the lower. Barrier and Loomis (1957) used ^{32}P to track the movement of P into soybean leaves and found that 16% of the ^{32}P applied to the leaf was even absorbed within 2 hours. Of the absorbed ^{32}P , 66% remained in the leaf and the remainder was concentrated in the bud, in young growing leaves in the stem above the leaves treated, and in the roots.

Natale et al. (2002) studied the effectiveness of foliar P spraying in guava and reported that P was quickly absorbed by leaves, and redistributed quite well through the plants because of its phloem mobility. They also showed that the foliar application of P affected the uptake of other nutrients from the soil, but did not affect the production of fruits.

Translocation rate within the plant appeared to be independent of the leaf area treated, independent on the time of the day and irrespective of whether the upper or lower leaf surface was treated. However, translocation rate

was found to really depend on the stage of leaf maturation: more P was translocated from older leaves positioned lower in the canopy than from younger upper leaves, while very young leaves did not export P from the leaf surface at all. We infer from the above that the application of foliar P fertilization therefore may have limited perspectives at early growth to be translocated for root growth, but the effect should be tested under field conditions also with other crops.

Pawar et al. (2003) showed in a study on sugar cane that foliar P application significantly increased enzyme activities of sucrose synthase and sucrose phosphate synthase. As a result mean commercial cane sugar content was increased to 14.5 % as compared to the control containing 13.7%.

3.5.3 Increasing yield and quality

Foliar applications of P have been tested on various agricultural crops such as soybeans (Garcia and Hanway 1976; Barel and Black 1979; Syverud et al., 1980; Haq and Mallarino, 2005), clover (Bouma 1969; Bouma and Dowling 1976), wheat (Mosali et al., 2006; McBeath et al., 2011) and corn (Harder et al., 1982; Giskin and Efron 1986; Girma et al., 2007). Many researchers demonstrate that foliar applied P fertilizers are more effective as compared to soil-applied P. They show that foliar supply can increase photosynthetic efficiency by delaying the onset of leaf senescence and by increasing net returns from the production of assimilates, because of a higher P uptake efficiency (Noack et al., 2010). The use of a tracing technique with ^{32}P enables measurement of the partitioning of foliar P fertilizer between different plant organs.

For many crops significant increases in crop yield and an increase in the accumulation of valuable compounds upon side foliar P spraying were reported. Results are summarized in **Table 4**.

Table 4. Effects of foliar P spraying on yield and quality of different cash crops.

Crop	Effects on Yield	Effects on quality	Ref
Rapeseed-Mustard	Improved yield (shoot length, leaf number, leaf area, LAI, fresh weight, dry weight, pod number (up to 100% increase), seed number, 1000-seed weight	Increase oil yield and fatty acid composition in oil	Siddiqui et al. (2008)
Spanish Peanut	Increased yield	Total kernel P content (TKC), percent sound mature kernel (% SMK)	Sistani and Morrill (1989)
Soybean	Increase yield higher number of pods, number of seeds pods per seed index and higher grain yield		Vinoth Kumar et al. (2013)
Cowpea		Higher contents of protein, nitrogen, phosphorus and potassium	Yadav and Choudhary (2012)
Maize	Increase plant height, flag leaf length, grain and biological yield		Yosifi et al. (2011)
Wheat	Increase grain P uptake		McBeath et al. (2011); Benbella and Paulsen (1998)
Apple		Fruit color, postharvest firmness	(Wojcik and Wojcik 2007).
Cotton	Increase cotton seed yield, seed index, protein yields	Increase seed oil on saponifiable matter and total unsaturated fatty acids (oleic, linoleic); decrease oil acid value	Sawan et al. (2007)

3.5.4 Risks of foliar spraying

One of the major problems associated with foliar P nutrition has been the limited amount of a given P compound that can be applied without damaging the leaf through high nutrient loading (Koontz and Biddulph 1957; Gray 1977; Barel and Black 1979). The appearance of leaf burn at the spots where foliar droplets have been applied, has been observed in many studies (Barel and Black 1979; Parker and Boswell 1980). Some studies have resulted in leaf burn so severe that part or all of the leaf died, causing a lower yield for foliar-applied treatments. However, the detrimental effect clearly depends on the formula in which the phosphate is added and foliar P spraying does not need to be detrimental to the plant. A study by Barel and Black (1979) showed that more P can be added in polyphosphate compounds compared with the orthophosphate form: The maximum concentration of P tolerated in solutions of tri- and polyphosphates as sprays was 1.3% compared with 0.5% orthophosphate on corn leaves. The most successful compound tested on maize was ammonium triphosphate followed by ammonium polyphosphate and phosphoryl triamide.

The sensitivity to leaf burn also varies between plant species (Noack et al., 2010). The leaf structure for each crop species varies (cuticle thickness, leaf hairs, etc.) and this will influence the sensitivity to P formulations, i.e., soybean appears to be more sensitive to scorch, tolerating 60%–75% less compound than corn.

Possibilities to improve the effectiveness of foliar P spraying

There are different factors that affect the effectiveness of the foliar P spraying:

1. Water status of the soil and the leaves
2. The timing of the application.
3. Facilitation of the foliar P uptake.
4. Formulation of the foliar P by making a mixture with other anions and/or addition of adjuvents.

Ad 1. Alston (1979) investigated the effects of soil water content on the effectiveness of foliar P fertilization on wheat yield. He commented that increasing grain yield after heading can be obtained by applying foliar P fertilizer while keeping the soil wet to enable the uptake of other nutrients. When bean plants were put under severe water stress, their photosynthetic rate was significantly reduced and there was only a small effect of foliar applied P on yield (dos Santos et al., 2006). However, data from Mosali et al. (2006) showed increases in grain yield that resulted from foliar P application in seasons of water stress. Noack et al. (2010) argues in their review that this is likely due to reduced root-soil contact for nutrient exchange, which enhances the benefits of foliar P in lower rainfall areas and/or years. The timing of the application of foliar nutrients under water stress conditions requires careful consideration of stomatal opening and rate of fertilizer drying on the leaf before penetration is possible. The results from Ekelöf et al. (2012) confirmed the importance of the soil water status for the responsiveness to foliar P application. They also emphasized on the importance of a good water status of the leaves, which is related to soil water status, to enable an adequate diffusion of P through the leaf cells. In their study the P use efficiency was significantly improved after foliar P spraying in combination with soil irrigation while only adding P to the soil decreased the P use efficiency.

Ad 2. Key factors that control optimal timing of foliar P applications during the growing season are (Noack et al., 2010): (1) The physiological age of the crop: the potential for yield improvement will decrease with increasing crop age, most likely diminishing beyond anthesis; (2) The degree of P deficiency at the moment of spraying: a crop that is very P deficient already will have limited potential to overcome deficiency at low foliar P application rates, while a crop that is P sufficient will not be responsive; and (3) Leaf area of the crop: the area determines foliar P-uptake potential and photosynthetic potential for grain filling.

The most appropriate timing to apply this in-season 'top-up' P to increase growth rate and yield varies between plant species (Noack et al., 2010) from early pod development in soybeans (Gray 1977), from canopy closure to anthesis in cereal crops (Benbella and Paulsen 1998; Mosali et al., 2006; Girma et al., 2007; Zadoks et al., 1974; Römer and Schilling 1986) and early tasseling in maize/corn (Harder et al., 1982; Giskin and Efron 1986; Girma et al., 2007). In mature apple trees, the influence of the foliar PK-application on photosynthesis of leaves was observed only late in the season (Veberic et al., 2002). While yield was unaffected by foliar application, the P content of the corn grains was increased by 4.7% due to the foliar fertilization.

Ad 3. Hydration of the plant cuticle can improve penetration and conversely water stress can decrease penetration (Kirkwood 1999). When a leaf is hydrated, the stomata are open (Eichert and Burkhardt 2001), and this could allow the foliar spray to be transported across the epidermis at a faster rate, while the opposite effect is expected under water stress. As a penetration of foliar spraying via the stomata has been proved (see above; Noack et al., 2010) it is important to consider the factors that control stomatal opening, like light and water availability when applying foliar P fertilizers.

The effect of high temperature causes the foliar spray to have an increased viscosity that decreases surface tension and increases diffusion across the cuticle and stomata (Kirkwood 1999). However, at high temperatures the solute may evaporate more quickly and so there would be a decrease in the available penetration time. A high temperature in the presence of increased humidity delays the drying of the applied droplets, prevents water stress and favors stomatal opening (Clor et al., 1962; Kirkwood 1999).

For the effectiveness of the cuticular uptake, drop sizes of the foliar sprays are also important: Schönherr (2006) showed that the radius of cuticular pores ranged from 0.45 to 1.18 nm, with most having a diameter of less than 1 nm. Foliar sprays with drop sizes smaller than 1 nm therefore have the capacity to penetrate the cuticular pores. The permeability of cuticles for ions depends on their electric characteristics: The pores are lined with a fixed negative charge and consequently cation movement along this diffusion potential is enhanced whereas anions are repelled from the pores (Tyree et al., 1990). Phosphorus formulations containing anions are not soluble in lipids as they are charged and cannot pass through the lipophilic pathway. The pH has an important effect on the electric characteristics of solutes. A P-fertilizer formulation with a low pH of 2–3 has been shown to facilitate more rapid uptake by leaves, compared with formula with a higher pH (Tukey et al., 1961; Bouma 1969). Low pH will suppress the dissociation of H_3PO_4 and so facilitate absorption due an increased permeability of the epidermal and adjacent tissues (Swanson and Whitney 1953). Bouma (1969) sprayed P-deficient clover plants every 2–3 days with 10–300mM P solutions of H_3PO_4 , with a solution pH adjusted to 2.5 and 5.0. The resulting leaf analysis 7 days after application showed that 23% of the pH 5.0 solution and 72% of the pH 2.5 solution was absorbed by the first trifoliolate leaf. Similarly, H_3PO_4 (pH 2–3) had better penetration than other phosphate salts (pH 4–5) on bean leaves (Tukey et al., 1961).

Ad 4. As reviewed by Noack et al. (2010) a range of P formulations have been examined as potential foliar fertilizers (Silberstein and Wittwer 1951; Garcia and Hanway 1976; Alston 1979; Barel and Black 1979; Parker and Boswell 1980; Harder et al., 1982; Haq and Mallarino 2005). These studies demonstrated that the salt load, pH and mixture with other nutrients all had important effects on the efficacy of foliar P fertilizer.

Giskin and Efron (1986) found in field experiments that foliar applications of N, P, K and sulfur (S) resulted in a significant uptake of P, giving a 16.6% increase in grain yield.

Ahmed (2006) applied a foliar nutrient solution containing 9% P with 12% N, 8% K, 1% zinc, 2% iron, 1.5% manganese, 3% magnesium, 1.4% copper, 2.3% S and 0.05% boron at three different rates to two different wheat cultivars compared with a control treatment with no fertilizer. In all treatments plants had a higher P concentration than the control. When orthophosphoric acid (0.5%) was sprayed with or without urea (2%) on the mango (*Mangifera indica* L) cv. Langra trees, it appeared that the urea given along with P improved the utilization of P in the fruits (Eswara Reddy and Majmudar 1983). Sistani and Morrill (1992) evaluated the effect of foliar P spraying in Spanish peanuts and the residual effect of gypsum and demonstrated a significant increase in yield and total kernel content, although the foliar spray P did not significantly increase the percentage sound matured kernels.

Inclusion of sucrose in the solution applied to soybean (*Glycine max* L. merr.) leaves greatly reduced the severity of the damage to the leaves from application of urea and, to a lesser extent, from application of P as orthophosphoric acid (Barel and Black 1979). Sucrose had no evident effect on P absorption. Addition of adjuvants to foliar P fertilizer are effective to facilitate the P uptake and/or to reduce the effect of leaf burn (Noack et al., 2010). The most common adjuvant cited in research is Tween 20 (Clor et al., 1962; Bouma 1969; Barel and Black 1979; Syverud et al., 1980; Reuveni et al., 1996; Ahmed 2006). Generally this adjuvant is added to foliar fertilizers at a concentration of 0.1% v/v. The majority of studies have considered it a suitable adjuvant because it does not solubilize the lipid-lipid and lipid-protein interactions in the membranes (Helenius et al., 1979). Silicone-based non-ionic surfactants are recommended because to their ability to reduce surface tension and the contact angle of the spray solution (Knoche 1994; Singh and Singh 2008). Stein and Storey (1986) tested 46 adjuvants for leaf burn and foliar absorption of N and P by soybean leaves. The adjuvants were added at 0.05% (v/v) with foliar fertilizer N, P, K, S to the middle adaxial surface of the leaf. Glycerol was the only adjuvant that significantly

increased leaf P concentration over the unsprayed controls at 90 L ha⁻¹. If treatments were applied at the 470 L ha⁻¹ numerous adjuvant/fertilizer combinations increased the P penetration. However, by increasing the spray rate, the phytotoxicity rating also increased with many adjuvants causing total cell necrosis. Therefore, identification of the optimal spray volume requires consideration of the most efficient uptake with minimal leaf damage. Stein and Storey (1986) found that the adjuvants Lecithin and Pluronic L-121 significantly increased percentage of P and chlorophyll content over the control and foliar (no adjuvant) treatments.

Scanning Electron Microscopy images showed that Ferti-Vant, which are fertilizers coated with an adjuvant containing emulsified oils, surfactants and food grade polysaccharides, had a greater spread of P fertilizer across citrus leaves: it increased P % in the dry weight by 0.9% at day 6 compared with the control. While there have been a number of studies on the effect of adjuvants, the findings suggest (Noack et al., 2010) that no single adjuvant, rate of adjuvant, or spray volume will simultaneously increase spread, delay drying and increase the permeability of the cuticle or the plasma membrane for all foliar fertilizer-plant combinations. The adjuvant and/or combination of adjuvants to be used requires careful consideration when developing a foliar fertilizer application plan.

Conclusion: Foliar application of P seems to have effect under conditions of P deficiency. Whether it would be effective in young plant stages is not clear, one reference mentions that only older leaves translocate the P taken up. Experimental evidence of a positive effect of foliar P application in young stages would require new field experiments. Application in a non-closed canopy would also require special precautions and arrangement for a precision application due to the small leaf area. A small LAI would not be a problem per se as also P requirements in this stage are small.

4 Conclusions and a possible research approach

In the preceding paragraphs several indications can be found which support the hypothesis that plant properties and cultural measures can stimulate P uptake in early plant stages and could lead to a better use of indigenous soil P as well as a higher efficiency of mineral P inputs.

With respect to plant properties, it seems worthwhile for breeders to focus on *rooting characteristics* (especially root hair characteristics) in the early plant stages. This would not be time consuming as a selection for these characteristics can be done in a short period of plant growth. It would be worthwhile to explore the present genetic variation for these traits in specific crops and measure the effects in the field. A selection in breeding programs has not been done to our knowledge.

Placement of P is a promising technique with a large potential to increase the efficiency of mineral P fertilizer and possibly also for nitrogen fertilizer (the word efficiency is used here in the sense that at the same yield level input of fertilizer can be reduced by placement vs. broadcasted fertilizer). Questions remain to specify in more detail under which conditions and for which crops placement is a viable option and which techniques should be used (placement in bands, row, spot or plant) and in combination with fertilizer type (solid/liquid etc.) and other nutrients.

As far as placement techniques are concerned, the combination with Global Positioning Systems (GPS) could be feasible, especially in non-tillage systems (widespread in South America for instance). In these systems it would be possible to establish with GPS high-P fertility zones solely on places where plants are grown or planned to be grown. Placement can stimulate early growth and consequently the recovery of P in the rest of the profile. The ultimate effectiveness of this approach would have to be investigated experimentally. In tillage systems (plows or chisels) creating areas of improved P-fertility would be restricted to one season only, as the main tillage would disturb the areas of high fertility. But even in these systems GPS can have possibilities as time of sowing/planting can be decoupled from the time of fertilization.

Seed coating with P and phosphatases seems a promising technique but the often resulting lower emergence rate is still a problem. It would be interesting to investigate the effect of a phosphatase coating in combination with a P (or phosphate rock) coating. In the Netherlands there is now some experience with coating of seed potatoes with P; potatoes have the advantage of a large surface (compared to a seed) to which nutrients can be attached. Possibilities for similar planted crops seem to be present.

Although the *exudation of organic acids* is important to utilize the soil P reserves, it is not feasible to apply these compounds exogenously on a large scale. A possible research area might be to test the activity in the very first phases of growth (e.g. the germination phase); this would limit the input of exudates to affordable amounts.

Crops which are known for high exudation rates could be used at the level of crop rotation, provided the P rich residues are plowed under and made available for subsequent crops.

Finally, *foliar application* of P is found to have a favorable effect on growth under P deficient conditions. It is unclear whether it would be effective in young plant stages as one reference mentions only older leaves to translocate the P that is absorbed through leaves. A positive effect of foliar P application in young stages therefore needs verification. Foliar P would have to be precisely applied in an open canopy because of the small leaf area. The use of detection equipment and GPS could support precision application. Although P foliar application in young stages could be less effective than in a closed canopy in terms of uptake and translocation of P, the positive impact on growth could still be large as P requirements in this stage are small also.

Summarizing it would be worthwhile to combine some or all of the strategic interventions mentioned above and research their impact on yield formation and yield quality and stability. Prior to testing, a thorough evaluation would be needed to find out for which crops this approach is likely to be effective, taking into account the conditions and application techniques. Fine-tuning to crop characteristics and environmental conditions such as climate, soil type, soil fertility etc. is essential as these factors each determine to a great extent the effect of the proposed measures and may also interact.

5 References

- Ahmed, A.G., M.S. Hassanein, and M.M. El-Gazzar, 2006.
Growth and yield response of two wheat cultivars to complete foliar fertilizer compound "Dogoplus". *Journal of Applied Sciences Research* 2:20-26.
- Alston, A, 1979.
Effects of soil water content and foliar fertilization with nitrogen and phosphorus in late season on the yield and composition of wheat. *Australian Journal of Agricultural Research* 30(4):577-585.
- Andrade, F.V., E.S. Mendonça, I.R. Silva and R.F. Mateus, 2007.
Dry-matter production and phosphorus accumulation by maize plants in response to the addition of organic acids in oxisols. *Communications in Soil Science and Plant Analysis* 38(19-20):2733-2745.
- Barel, D. and C.A. Black, 1979.
Effect of neutralization and addition of urea, sucrose, and various glycols on phosphorus absorption and leaf damage from foliar-applied phosphate. *Plant and Soil* 52(4):515-525.
- Barrier, G.E. and W.E. Loomis, 1957.
Absorption and Translocation of 2,4-Dichlorophenoxyacetic Acid and P32 by Leaves. *Plant Physiology* 32(3):225-231.
- Benbella, M. and G.M. Paulsen, 1998.
Efficacy of treatments for delaying senescence of wheat leaves: I. Senescence under controlled conditions. *Agronomy Journal* 90(3):329-332.
- Bouma, D., 1969.
The response of subterranean clover (*Trifolium subterraneum* L.) to foliar applications of phosphorus. *Australian Journal of Agricultural Research* 20(3):435-445.
- Bouma, D. and E. Dowling, 1976.
The relationship between the phosphorus status of subterranean clover plants and the dry weight responses of detached leaves in solutions with and without phosphate. *Australian Journal of Agricultural Research* 27(1):53-62.
- Brown, L.K., T.S. George, L.X. Dupuy and P.J. White, 2013.
A conceptual model of root hair ideotypes for future agricultural environments: What combination of traits should be targeted to cope with limited P availability? *Annals of Botany* 112(2):317-330.
- Buerkert, A., A. Bationo and H.P. Piepho, 2001.
Efficient phosphorus application strategies for increased crop production in sub-Saharan West Africa. *Field Crops Research* 72(1):1-15.
- Buick, R.D., B. Robson and R.J. Field, 1992.
A mechanistic model to describe organosilicon surfactant promotion of triclopyr uptake. *Pesticide Science* 36(2):127-133.
- Chien, S.H., L.I. Prochnow, S. Tu and C.S. Snyder, 2010.
Agronomic and environmental aspects of phosphate fertilizers varying in source and solubility: an update review. *Nutrient Cycling in Agroecosystems*: 1-27.
- Clor, M.A., A.S. Crafts and S. Yamaguchi, 1962.
Effects of High Humidity on Translocation of Foliar-Applied Labeled Compounds in Plants Part: I. *Plant Physiology* 37(5):609-617.

- Cordell, D., 2010.
The Story of Phosphorus: Sustainability implications of global phosphorus scarcity for food security, Doctoral thesis. Collaborative PhD between the Institute for Sustainable Futures, University of Technology, Sydney (UTS) and Department of Water and Environmental Studies, Linköping University, Sweden. Linköping University Press, ISBN 978-91-7393-440-4, Linköping.
- Cordell, D., A. Rosemarin, J.J. Schröder and A.L. Smit, 2011.
 Towards global phosphorus security: A systems framework for phosphorus recovery and reuse options. *Chemosphere* 84(6):747-758.
- Currier, H.B. and C.D. Dybing, 1959.
 Foliar Penetration of Herbicides: Review and Present Status. *Weeds* 7(2):195-213.
- de Willigen, P.D. and M. van Noordwijk, 1987.
Roots, plant production and nutrient use efficiency. PhD thesis, LU Wageningen, 282 pp.
- dos Santos, M.G., R.V. Ribeiro, R.F. de Oliveira, E.C. Machado and C. Pimentel, 2006.
 The role of inorganic phosphate on photosynthesis recovery of common bean after a mild water deficit. *Plant Science* 170(3):659-664.
- Edwards, C. L., 2013.
Effects of synthetic chelating agent application to soils on phosphorus availability. Master Thesis. Blacksburg, Virginia State University.
- Ehlert, P.A.I., C.A.P. v. Wijk and P.D. de Willigen, 2002.
 Fosfaatbehoefte van vollegrondsgroentegewassen 3. *Precisiebemesting*. PPO-Projectrapport nr. 1125232: 27 pp.
- Eichert, T. and J. Burkhardt, 2001.
 Quantification of stomatal uptake of ionic solutes using a new model system. *Journal of Experimental Botany* 52(357):771-781.
- Eichert, T., H.E. Goldbach and J. Burkhardt, 1998.
 Evidence for the uptake of large anions through stomatal pores. *Botanica Acta* 111(6):461-466.
- Ekelöf, J.E., H. Asp and E.S. Jensen, 2012.
 Potato yield response to foliar application of phosphorus as affected by soil moisture and available soil phosphorus. *Acta Agriculturae Scandinavica Section B: Soil and Plant Science* 62(7):637-643.
- Eswara Reddy, S. and A.M. Majmudar, 1983.
 Response of mango (*Mangifera indica* L) to foliar application of phosphorus. *Fertilizer Research* 4(3):281-285.
- Fernández, V. and T. Eichert, 2009.
 Uptake of Hydrophilic Solutes Through Plant Leaves: Current State of Knowledge and Perspectives of Foliar Fertilization. *Critical Reviews in Plant Sciences* 28(1-2):36-68.
- Field, R.J. and N.G. Bishop, 1988.
 Promotion of stomatal infiltration of glyphosate by an organosilicone surfactant reduces the critical rainfall period. *Pesticide Science* 24(1):55-62.
- Franke, W., 1967.
 Mechanisms of foliar penetration of solutions. *Annual Review of Plant Physiology* 18:281-&.
- Fransson, A.M. and D.L. Jones, 2007.
 Phosphatase activity does not limit the microbial use of low molecular weight organic-P substrates in soil. *Soil Biology and Biochemistry* 39(5):1213-1217.
- Garcia, R.L. and J.J. Hanway, 1976.
 Foliar fertilization of soybeans during seed-filling period. *Agronomy Journal* 68(4):653-657.

- Gerke, J., L. Beißner and W. Römer, 2000a.
The quantitative effect of chemical phosphate mobilization by carboxylate anions on P uptake by a single root. I. The basic concept and determination of soil parameters. *Journal of Plant Nutrition and Soil Science* 163(2):207-212.
- Gerke, J., W. Römer and L. Beißner, 2000b.
The quantitative effect of chemical phosphate mobilization by carboxylate anions on P uptake by a single root. II. The importance of soil and plant parameters for uptake of mobilized P. *Journal of Plant Nutrition and Soil Science* 163(2):213-219.
- Girma, K., K.L. Martin, K.W. Freeman, J. Mosali, R.K. Teal, W.R. Raun, S.M. Moges and D.B. Arnall, 2007.
Determination of Optimum Rate and Growth Stage for Foliar-Applied Phosphorus in Corn. *Communications in Soil Science and Plant Analysis* 38(9-10):1137-1154.
- Giskin, M. and Y. Efron, 1986.
Planting date and foliar fertilization of corn grown for silage and grain under limited moisture. *Agronomy Journal* 78(3):426-429.
- Gray, R.C., 1977.
Foliar fertilization with primary nutrients during the reproductive stage of plant growth. *Proceedings of the Fertilizer Society* 164: 23.
- Guertal, E. A. and J. A. Howe, 2013.
Influence of phosphorus-solubilizing compounds on soil P and P uptake by perennial ryegrass. *Biology and Fertility of Soils* 49(5):587-596.
- Haq, M.U. and A.P. Mallarino, 2005.
Response of soybean grain oil and protein concentrations to foliar and soil fertilization. *Agronomy Journal* 97(3):910-918.
- Harder, H. J., R. E. Carlson and R. H. Shaw, 1982.
Corn grain-yield and nutrient response to foliar fertilizer applied during grain fill. *Agronomy Journal* 74(1):106-110.
- Helenius, A., D.R. McCaslin, E. Fries and C. Tanford, 1979.
[63] Properties of detergents. *Methods in Enzymology*. L. P. Sidney Fleischer, Academic Press. Volume 56: 734-749.
- Hoffland, E., G.R. Findenegg and J.A. Nelemans, 1989.
Solubilization of rock phosphate by rape – II. Local root exudation of organic acids as a response to P-starvation. *Plant and Soil* 113(2):161-165.
- Jenks, M.A. and E.N. Ashworth, 2010.
Plant Epicuticular Waxes: Function, Production, and Genetics. *Horticultural Reviews*, John Wiley & Sons, Inc.: 1-68.
- Karanam, P. V. and V. Vadez, 2010.
Phosphorus coating on pearl millet seed in low P Alfisol improves plant establishment and increases stover more than seed yield. *Experimental Agriculture* 46(4):457-469.
- Khademi, Z., D. L. Jones, M. J. Malakouti and F. Asadi, 2010.
Organic acids differ in enhancing phosphorus uptake by *Triticum aestivum* L. – effects of rhizosphere concentration and counterion. *Plant and Soil* 334(1):151-159.
- Kirkwood, R.C., 1999.
Recent developments in our understanding of the plant cuticle as a barrier to the foliar uptake of pesticides†. *Pesticide Science* 55(1):69-77.

- Knoche, M., 1994.
Organosilicone surfactant performance in agricultural spray application: a review. *Weed Research* 34(3):221-239.
- Koontz, H. and O. Biddulph, 1957.
Factors affecting absorption and translocation of foliar applied phosphorus. *Plant Physiology* 32(5):463-470.
- Liu, Y., G. Villalba, R.U. Ayres and H. Schroder, 2008.
Global phosphorus flows and environmental impacts from a consumption perspective. *Journal of Industrial Ecology* 12(2):229-247.
- Marschner, H., 1995.
Mineral Nutrition of Higher Plants. 2nd ed Academic Press, London, England.
- Mašauskas, V., A. Mašauskiene, R. Repšiene, R. Skuodiene, Z. Braziene and J. Peltonen, 2008.
Phosphorus seed coating as starter fertilization for spring malting barley. *Acta Agriculturae Scandinavica Section B: Soil and Plant Science* 58(2):124-131.
- McBeath, T.M., M.J. McLaughlin and S.R. Noack, 2011.
Wheat grain yield response to and translocation of foliar-applied phosphorus. *Crop and Pasture Science* 62(1):58-65.
- McGrath, J.M. and G.D. Binford, 2012.
Corn response to starter fertilizer with and without AVAIL. *Crop Manag. Online*: doi: 10.1094/CM-2012-0320-02-RS.
- Mosali, J., K. Desta, R.K. Teal, K.W. Freeman, K.L. Martin, J.W. Lawles and W.R. Raun, 2006.
Effect of foliar application of phosphorus on winter wheat grain yield, phosphorus uptake, and use efficiency. *Journal of Plant Nutrition* 29(12):2147-2163.
- Natale, W., E. L. M. Coutinho, D. A. Banzatto and A. E. Boaretto, 2002.
Phosphorus foliar fertilization in guava trees. *Acta Horticulturae* 594:171-177.
- Niu, Y.F., R.S. Chai, G.L. Jin, H. Wang, C.X. Tang and Y.S. Zhang, 2013.
Responses of root architecture development to low phosphorus availability: a review. *Annals of Botany* 112(2):391-408.
- Noack, S.R., T.M. McBeath and M.J. McLaughlin, 2010.
Potential for foliar phosphorus fertilisation of dryland cereal crops: a review. *Crop and Pasture Science* 61(8):659-669.
- Parker, M.B. and F.C. Boswell, 1980.
Foliage injury, nutrient intake, and yield of soybeans as influenced by foliar fertilization. *Agronomy Journal* 72(1):110-113.
- Pawar, M.W., S.S. Joshi and V.T. Amodkar, 2003.
Effect of Foliar Application of Phosphorus and Micronutrients on Enzyme Activities and Juice Quality in Sugar Cane. *Sugar Tech* 5(3):161-165.
- Peltonen-Sainio, P., M. Kontturi and J. Peltonen, 2006.
Phosphorus seed coating enhancement on early growth and yield components in oat. *Agronomy Journal* 98(1):206-211.
- Pilar-Izquierdo, M.C., N. Ortega, M. Perez-Mateos and M.D. Busto, 2012.
Barley seed coating with free and immobilized alkaline phosphatase to improve P uptake and plant growth. *Journal of Agricultural Science* 150(6):691-701.
- Pilar, M. C., N. Ortega, M. Perez-Mateos and M. D. Busto, 2009.
Alkaline phosphatase-polyresorcinol complex: Characterization and application to seed coating. *Journal of Agricultural and Food Chemistry* 57(5):1967-1974.

- Plénet, D., S. Etchebest, A. Mollier and S. Pellerin, 2000.
Growth analysis of maize field crops under phosphorus deficiency: I. Leaf Growth. *Plant and Soil* 223(1-2):117-130.
- Prummel, J. and P.A. v. Barnau Sijthoff, 1975.
Rijenbemesting met fosfaat bij stamslabonen en tuinbonen. *Bedrijfsontwikkeling* 6:173-175.
- Raghothama, K.G., 1999.
Phosphate acquisition. *Annual Review of Plant Biology* 50:665-693.
- Rebafka, F.P., A. Bationo and H. Marschner, 1993.
Phosphorus seed coating increases phosphorus uptake, early growth and yield of pearl millet (*Pennisetum glaucum* (L.) R. Br.) grown on an acid sandy soil in Niger, West Africa. *Fertilizer Research* 35(3):151-160.
- Reuveni, R., M. Reuveni and V. Agapov, 1996.
Foliar sprays of NPK fertilizers induce systemic protection against *Puccinia sorghi* and *Exserohilum turcicum* and growth response in maize. *European Journal of Plant Pathology* 102(4):339-348.
- Richardson, A.E., P.J. Hocking, R.J. Simpson and T.S. George, 2009.
Plant mechanisms to optimise access to soil phosphorus. *Crop & Pasture Science* 60:124-143.
- Richardson, A.E., J.P. Lynch, P.R. Ryan, E. Delhaize, F.A. Smith, S.E. Smith, P.R. Harvey, M.H. Ryan, E.J. Veneklaas, H. Lambers, A. Oberson, R.A. Culvenor and R.J. Simpson, 2011.
Plant and microbial strategies to improve the phosphorus efficiency of agriculture. *Plant and Soil* 349(1-2):121-156.
- Römer, V.W., 2009.
Concepts for a more efficient use of phosphorus based on experimental observations (Ansätze für eine effizientere Nutzung des Phosphors auf der Basis experimenteller Befunde). *Berichte über Landwirtschaft* 87(1):5-30.
- Römer, W. and G. Schilling, 1986.
Phosphorus requirements of the wheat plant in various stages of its life cycle. *Plant and Soil* 91(2):221-229.
- Ros, C., R.W. Bell and P.F. White, 2000.
Phosphorus seed coating and soaking for improving seedling growth of *Oryza sativa* (rice) cv. IR66. *Seed Science and Technology* 28(2):391-401.
- Sawan, Z.M., S.A. Hafez, A.E. Basyony and A.E.E.R. Alkassas, 2007.
Cottonseed: Protein, oil yields, and oil properties as influenced by potassium fertilization and foliar application of zinc and phosphorus. *Grasas y Aceites* 58(1):40-48.
- Schönherr, J., 2006.
Characterization of aqueous pores in plant cuticles and permeation of ionic solutes. *Journal of Experimental Botany* 57(11):2471-2491.
- Schönherr, J. and T. Mérida, 1981.
Water permeability of plant cuticular membranes: the effects of humidity and temperature on the permeability of non-isolated cuticles of onion bulb scales. *Plant, Cell & Environment* 4(5):349-354.
- Siddiqui, M.H., F. Mohammad, M.N. Khan and M.M.A. Khan, 2008.
Cumulative effect of soil and foliar application of nitrogen, phosphorus, and sulfur on growth, physico-biochemical parameters, yield attributes, and fatty acid composition in oil of erucic acid-free rapeseed-mustard genotypes. *Journal of Plant Nutrition* 31(7):1284-1298.
- Silberstein, O. and S.H. Wittwer, 1951.
Foliar Application of Phosphatic Nutrients to Vegetable Crops. *Proceedings of the American Society for Horticultural Science* 58(DEC):179-190.

- Singh, D. and M. Singh, 2008.
Absorption and translocation of glyphosate with conventional and organosilicone adjuvants. *Weed Biology and Management* 8(2):104-111.
- Sistani, K.R. and L.G. Morrill, 1989.
Benefit of foliar spray phosphorus on peanuts in relation to gypsum and phosphorus application to soil. *Journal of Environmental Science and Health - Part A Environmental Science and Engineering* 24(4):429-436.
- Sistani, K.R. and L.G. Morrill, 1992.
Foliar application of phosphorus and residual effect of gypsum on peanuts. *Journal of Environmental Science and Health - Part A Environmental Science and Engineering* 27(2):317-327.
- Smit, A.L., P. Bindraban, J.J. Schröder, J.G. Conijn and H.G. v.d. Meer, 2009a.
Phosphorus in agriculture: global resources, trends and developments. *Plant Research International* (Report 282):36 pp.
- Smit, A.L., P. De Willigen and A.A. Pronk, 2009b.
Plaatsing als strategie voor een efficiëntere fosfaatbemesting 1. Literatuur en modelonderzoek. PRI rapport nr. 216, 28pp.
- Smit, A.L., A.A. Pronk and P. De Willigen, 2010.
Placement of phosphate leads to a more efficient use of a finite resource. *Acta Horticulturae* 852:189-194.
- Stein, L.A. and J.B. Storey, 1986.
Influence of adjuvants on foliar absorption of nitrogen and phosphorus by soybeans. *Journal of the American Society for Horticultural Science* 111(6):829-832.
- Stone, D.A., 1998.
The effects of "starter" fertilizer injection on the growth and yield of drilled vegetable crops in relation to soil nutrient status. *Journal of Horticultural Science and Biotechnology* 73(4):441-451.
- Stone, D.A., 2000.
The effects of starter fertilizers on the growth and nitrogen use efficiency of onion and lettuce. *Soil Use and Management* 16(1):42-48.
- Swanson, C.A. and J.B. Whitney, Jr., 1953.
Studies on the Translocation of Foliar-Applied P32 and Other Radioisotopes in Bean Plants. *American Journal of Botany* 40(10):816-823.
- Syers, J.K., A.E. Johnston and D. Curtin, 2008.
Efficiency of soil and fertilizer phosphorus use. Reconciling changing concepts of soil phosphorus behaviour with agronomic information. Food and Agriculture Organization of the United Nations Bulletin (Rome) 18:108 pp.
- Syverud, T.D., L.M. Walsh, E.S. Oplinger and K.A. Kelling, 1980.
Foliar fertilization of soybeans (*glycine-max* L). *Communications in Soil Science and Plant Analysis* 11(6):637-651.
- Tukey, H.B., S.H. Wittwer and M.J. Bukovac, 1961.
Absorption of Radionuclides by Aboveground Plant Parts and Movement within the Plant. *Journal of Agricultural and Food Chemistry* 9(2):106-113.
- Tyree, M.T., T.D. Scherbatskoy and C.A. Tabor, 1990.
Leaf Cuticles Behave as Asymmetric Membranes: Evidence from the Measurement of Diffusion Potentials. *Plant Physiology* 92(1):103-109.
- van der Eijk, D., B.H. Janssen and O. Oenema, 2006.

- Initial and residual effects of fertilizer phosphorus on soil phosphorus and maize yields on phosphorus fixing soils. *Agriculture ecosystems and environment* 116(1-2):104-120.
- van der Zee, S.E.A.T.M. and W.H. v. Riemsdijk, 1988.
Model for long-term reaction kinetics in soil. *J. Environ. Qual.* 17: 35-41.
- Veberic, R., F. Stampar and D. Vodnik, 2002.
Influence of the foliar application of phosphorus and potassium on the photosynthetic intensity in apple trees (*Malus domestica* Borkh.). 594:165-170.
- Vinoth Kumar, C., K. Vaiyapuri, M.M. Amanullah and G. Gopaldaswamy, 2013.
Influence of foliar spray of nutrients on yield and economics of soybean (*Glycine max* L. Merrill). *Journal of Biological Sciences* 13(6):563-565.
- Wittwer, S.H. and F.G. Teubner, 1959.
Foliar Absorption of Mineral Nutrients. *Annual Review of Plant Physiology* 10(1):13-30.
- Wojcik, P. and M. Wojcik, 2007.
Response of mature phosphorus-deficient apple trees to phosphorus fertilization and liming. *Journal of Plant Nutrition* 30(10):1623-1637.
- Yadav, L.R. and G.L. Choudhary, 2012.
Effect of fertility levels and foliar nutrition on profitability, nutrient content and uptake of cowpea [*Vigna unguiculata* (L.) Walp]. *Legume Research* 35(3):258-260.
- Yan, X., H. Liao, S. E. Beebe, M. W. Blair and J. P. Lynch, 2004.
QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. *Plant and Soil* 265(1-2):17-29.
- Yosefi, K., M. Galavi, M. Ramrodi and S.R. Mousavi, 2011.
Effect of bio-phosphate and chemical phosphorus fertilizer accompanied with micronutrient foliar application on growth, yield and yield components of maize (Single Cross 704). *Australian Journal of Crop Science* 5(2):175-180.
- Zygalakis, K. C., G. J. D. Kirk, D. L. Jones, M. Wissuwa and T. Roose, 2011.
A dual porosity model of nutrient uptake by root hairs. *New Phytologist* 192(3):676-688.

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