Importance of Early Season Phosphorus Nutrition

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Phosphorus is critical in the metabolism of plants, playing a role in cellular energy transfer, respiration, and photosynthesis. It is also a structural component of the nucleic acids of genes and chromosomes and of many coenzymes, phosphopro-

teins and phospholipids. Early season limitations in P availability can result in restrictions in crop growth, from which the plant will not recover, even when P supply is increased to adequate levels. An adequate supply of P is essential from the earliest stages of plant growth.

A growing plant may experience different stages in mineral nutrition, based on the balance among internal and external nutrient

supplies and crop demand for nutrients. Initially, plants will live on their seed reserves, with external supply having little effect on plant growth. A second stage occurs when growth rate is determined by nutrient supply through a dynamic balance between internal plant factors and external (soil) supply. In a final stage, the relative growth rate may decline for reasons other than inadequate nutrition. At this point, the growth rate of deficient and sufficient plants may converge, since the factor most limiting to growth is not nutrient supply.

The length of time required for a P deficiency to show an effect on plant processes depends on the extent of P reserves in the plant. In tissues of most higher plants, the majority of the P is present as inorganic P.

Phosphorus (P) fertilization is a major input on the Great Plains, as many soils lack sufficient P to optimize crop production. Effective nutrient management requires that nutrients be available in adequate amounts when needed by the plant. Ensuring that P is plant available early in the growing season is of particular importance.

Concentrations of stored inorganic P tend to vary to a great extent with external P availability, while concentrations of metabolically active organic P tend to be more stable. Only a small amount of the P present in the plant is actively involved in metabolism. If P

> supply is adequate, most of the inorganic P pool is nonmetabolic and stored within the vacuole as orthophosphate. Under P stress, the inorganic reserves are depleted, while the metabolic levels remain essentially unaffected. Therefore, high concentrations of stored P from the seed, or from luxury uptake early in the season, form reserves of available P that can buffer against short-term fluctuations in P supply later

in the plant's life cycle.

Effect of P Deficiency on Plant Development

Moderate P stress may not produce obvious deficiency symptoms. However, with a more severe deficiency, plants become dark green to purplish in color. Phosphorus deficiency can reduce both respiration and photosynthesis, but if respiration is reduced more than photosynthesis, carbohydrates will accumulate, leading to dark green leaves. A deficiency can also reduce protein and nucleic acid synthesis, leading to the accumulation of soluble nitrogen (N) compounds in the tissue. Ultimately, cell growth is delayed and potentially stopped. As a result, symptoms of P deficiency include decreased plant height, delayed leaf emergence, and reductions in tillering, secondary root development, dry matter yield, and seed production.

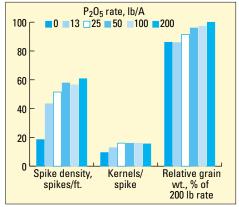
Plants respond to P deficiency by adaptations that maximize the likelihood of producing some viable seed. Generally, P stress decreases the number of seeds produced more than seed size. For example, in cereal crops the reduction in seed number occurs through reduced numbers of fertile spikes and reduced numbers of kernels per spike (**Figure 1**). Reducing the number of seeds formed increases nutrient supply per seed and enhances the likelihood of producing viable seed for successful reproduction.

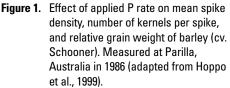
Phosphorus Supply during Early Plant Growth Is Critical

A large number of studies in many plant species have shown that early season P supply is critical for optimum crop yield. Withholding P during early plant growth will limit crop production and cause a restriction in crop growth from which the plant may not recover. Phosphorus limitation later in the season has a much smaller impact on crop production than do limitations early in growth.

Research with spring wheat and intermediate wheatgrass found that maximum tiller production was obtained when P was supplied in the nutrient culture for the first four weeks of growth (**Table 1**).

If P was withheld for the initial four or more weeks, final tiller production was less than maximum. Secondary





to a P-deficient medium during different portions of the first five weeks of growth (**Table 2**). Supplying P for the first three to four weeks of growth led to reduced dry matter yields. In addition, withholding P for the first two to three weeks led to lower dry matter yields. Although both crops absorbed only small quantities of P during the first two weeks of growth (15 percent of maximum for wheat and 5 percent for intermediate wheatgrass), this early accumulation of P was extremely important for maximum dry matter and grain yields at maturity.

(tiller) root development followed the same pattern as tiller d e v e l o p m e n t . Available P is required early in plant growth for maximum root development. Final dry matter yields of spring wheat and intermediate wheatgrass were reduced to some extent when plants were exposed

TABLE 1. Average tiller and secondary root development of wheat as influenced by the absence of P during various intervals (adapted from Boatwright and Viets, 1966).							
Weeks without P in a 10-week growth period	Tillers/6 plants at week 10	Secondary roots/6 plants at week 10					
0-control	27.7	120.0					
First 2 weeks	22.3	76.2					
Last 2 weeks	23.0	123.6					
First 4 weeks	10.3	21.6					
Last 4 Weeks	24.0	106.2					
First 6 weeks	9.4	19.8					
Last 6 weeks	24.0	66.0					

TABLE 2. Influence of P supply in nutrient medium on the dry matter accumula- tion of spring wheat and intermedi- ate wheatgrass. Results presented as a percentage of the check (1 to 5 weeks). Adapted from Boatwright and Viets, 1966.							
P supp	-		Intermediate				
perio	al Sp	ring	wheat-				
weeks	of w	heat	grass				
growt	h C)ry matter, %	of check				
1-5		100	100				
1-4		80	66				
1-3		50	25				
3-5		80	59				
4-5		30	19				

A number of reasons have been proposed as to why early season P is so critical for later plant growth and development. However, the most likely effect is that a process in the plant leads to an irreversible response that impairs later growth, even if the plant receives adequate nutrients later. The mechanism for growth impairment by early season P deficiency may relate to restrictions in carbon (C) nutrition of the plant. In field-grown corn, P deficiency slows the rate of leaf appearance and leaf size, particularly in the lower leaves. The effects of reduced leaf growth and solar radiation interception on C nutrition of the plant caused by P deficiency may reduce subsequent nodal root emergence, which would have an additional impact on P uptake capacity.

Yield response of corn to seed-placed P is related to the P concentration at the fourto five-leaf stage, or possibly earlier. It has been suggested that a mechanism relating seedling P nutrition to kernel number in corn might be due to the effects of P on early ear size. A P deficiency during ear formation, which occurs by the six- or seven-leaf stage, could decrease ear size, leading to fewer initiated kernels per ear. A similar mechanism may occur in other species, as evidenced by the reductions in seed number with P deficiency in a variety of crops.

Requirement for P Supply during Grain Fill/Flowering

Although P supply during early development has a dominant effect on crop yield potential, there may also be a requirement for an external supply of P later in crop growth. It has been suggested that spring wheat normally attains maximum uptake of P by heading, and P accumulation in the grain is largely due to redistribution from the leaf and stem tissue. However, in studies of hard red spring wheat under irrigation, only 45 percent of the total above-ground P had been accumulated by flowering. As the plant developed, P was removed from the leaves and stems and moved to the grain. At maturity, the distribution of P among the leaves, stems, heads, and grain was approximately 3, 8, 9, and 80 percent, respectively. Adequate P had been absorbed by winter wheat at the first node stage to ensure maximum P concentration levels in the mature grain, but a small supply of P was required through the ripening stage to allow carbohydrate translocation mechanisms to function for maximum mature grain vield. Phosphorus in the head of wheat may be supplied from post-anthesis soil uptake, as well as internal redistribution of nutrients accumulated during early growth.

Differences among Plants in P Uptake Strategies and Effectiveness

The importance of P for plant survival has supported the development of plant adaptations to improve the access of the crop to P supplies. Concentration of P in the soil solution is usually low since it is rapidly adsorbed onto soil surfaces as well as precipitated as calcium (Ca), magnesium (Mg), iron (Fe), and aluminum (Al) phosphates. Most P moves to the plant by diffusion rather than mass flow. As movement through the soil to the root is restricted, diffusion is generally considered to be the rate-limiting factor in P absorption by plants. It is estimated that, on average, P can only diffuse approximately 0.004 in., thus only P within 0.004 in. of a plant root is positionally available for absorption.

Uptake of P by the plant is proportional

to the root density, so enlargement of the root surface area increases the ability of the plant to access and absorb P from the soil. Therefore, many plants respond to low soil P concentrations by enlarging the root system and developing highly branched roots with abundant root hairs to enhance their ability to explore new soil reserves of P and efficiently extract P from the soil when areas of high P are encountered. Many plants will form associations with mycorrhizal hyphae, which also increase the ability of the crop to access and absorb P.

It has been reported that the root:shoot ratio was increased with early season P deficiency. Growth reduction was generally greater in the shoot than in the root, allowing the plant to maintain root growth and encounter and extract P from the soil. Growth of tops and roots closely paralleled the distribution of P between the plant parts. Where P supply was low, the proportion of P held in plant roots was higher than where the P supply was moderate. At higher P status, there was also a relative increase in root P as compared to shoot P. This may imply P retention by the root to meet its requirements at low concentration, P export to the shoot at sufficient concentrations, and P retention by the root at high concentration to avoid P toxicity in the shoot.

While increased rooting is an important factor in improved P access under conditions of a limited P supply, there are other plant responses to restricted P supply that can increase the accumulation of P in the plant. Some plants release phosphatases into the growth medium to break down organic phosphates, increasing the supply of available P. Plants such as canola can acidify the rhizosphere through secretion of organic acids to increase P availability. Some plants may also respond to P deficiency by increasing their ability to accumulate the P that they contact. In corn, a decrease in P level in the plant appears to signal the roots to absorb P more rapidly. Plants which have experienced P stress show a great increase in rate of P uptake when they come in contact with P as compared to plants that have not experienced P stress. The higher rate of



Early-season response of spring wheat to seedplaced P is shown at right in the photo, compared to wheat with no P at left.

uptake leads to higher P concentration in the tissue in the initially P-stressed plants as compared to those with an adequate P supply.

Phosphorus-deficient plants may lose the ability to regulate P uptake, leading to unrestricted uptake of P when P supply in the nutrient solution is re-established. It has been suggested that normal plants have a regulatory mechanism that limits excessive P uptake or accumulation, with the mechanism being ineffective in P-deficient plants. Therefore, P-deficient plants may accumulate toxic amounts of P on exposure to levels of solution P that, when continuously available, are non-toxic. A high ratio of organic to inorganic P in the plant seems to signal a transport system to increase the influx rate. The restoration of an external inorganic P supply appears to be regulated by inorganic P concentration in the plant, which could help to protect plants against P toxicity.

Soil Temperature and P Supply

When considering P supply early in the growing season, soil temperature is of particular importance, as annual crops on the Great Plains are frequently planted in cold soil. Therefore, temperature may influence the ability of the plant to access P during the early stages of crop growth, with slower diffusion of P in soil and lower soil P solubility. This may be of particular relevance where cold soil temperatures at seeding may enhance the need for P application near the seed row.

The simplest effect of soil temperature is on P solubility, with less P being soluble at lower temperatures. However, the effect of temperature is not necessarily the same among different soils. In research on soils where root growth was least affected by low temperature, plant uptake of P was most affected by temperature. Clearly, solubility of soil P was affected, regardless of the effect on root growth.

Temperature also has an influence on the rate of reaction of fertilizer P with soil. Fertilizer P reacts and transforms rapidly when first applied to soil, but continues to transform for months afterward. The transformation is generally to less-soluble forms, with lower temperatures slowing the process. Obviously, this effect of temperature can be important in early season and is opposite to the effect on the solubility of native soil P. The result is that with cold soil, native soil P will be less available to the plant, and fertilizer P will remain more available. This increases the relative value of fertilizer P for cold soils.

Banding of fertilizer P is a common practice because the plant uses P in the band more effectively than broadcast P. Temperature can affect plant use of banded P by influencing root proliferation in the fertilizer band compared to adjacent unfertilized soil. In one study, at warm soil temperatures, wheat showed little root proliferation in the band, but at 50°F, root mass was up to 3.6-fold greater in the P band than in the adjacent soil volume. However, at soil temperatures above 68°F, banded P became more toxic and decreased growth. As a result, plants were able to exploit the differences between the availability of soil and fertilizer P brought about by cold soil temperatures.

Phosphorus Concentration in Seed

Enhanced P concentration in the seed may be used to improve early season P supply and increase subsequent plant growth. Many plants can subsist on the P contained in the seed for about two weeks. Under greenhouse conditions, wheat grown from seed of the same size but with increasing P concentrations (0.14 to 0.37 percent), produced higher dry matter yields up to 35 days after seeding. In the field, the increases in wheat dry matter yield persisted until 67 days after seeding. Similarly, with wheat seeds that varied in P concentration by 40 percent, higher P concentration seedlings emerged more rapidly than low P seedlings. The high P seedlings had greater early growth, higher leaf numbers, and higher leaf area. Increasing P status of the seed increased root length, but the effect of P was greater on shoot than root growth. Increasing seed weight had similar effects to increasing seed P concentration, with the effects of seed weight and P status on leaf area appearing to be additive.

Fertilizer source	4	weeks	7 week	s (heading)	9 weeks	(soft dough)	13 wee	eks (mature)	Grain
	Total	Fertilizer	Total	Fertilizer	Total	Fertilizer	Total	Fertilizer	yield,
	••••••		Р, I	mg	••••••	g/pot			
Monoammonium							•••••	••••••	•••••
phosphate ²	27.0	12.5	177.0	75.5	195	77.0	281	101.0	78.0
Dicalcium									
phosphate plus									
Ca nitrate	19.7	1.9	126.0	15.1	182	19.0	241	22.0	63.3
Unfertilized	18.8	_	95.0		146	_	188		49.0

Fertilizer Management

If P supplied from the soil and seed reserves is inadequate to support optimum crop yield, fertilizer applications can supply P to the plant. Phosphorus supply during the first two to six weeks of growth tends to have a large impact on final crop yield in most crops; therefore, it is important that P fertilizer applications are managed in a way that ensures early season access to the fertilizer by the growing crop.

Relative uptake of P from soil and fertilizer sources will differ with crop type and growth stage. Research showed that rate of uptake of soil P increased in the four- to sixweek period of wheat growth and that as the root area expanded, an increasing proportion of the P in the plant was derived from the soil, rather than from fertilizer application (Table 3). The total amount of P and the amount of fertilizer P taken up by wheat plants increased with increasing rates of P fertilization, with the percentage of the total P coming from the fertilizer increasing with increasing fertilizer rate. Therefore, the amount of soil P used decreased with increasing rates of applied P.

Phosphorus is relatively immobile in the soil and so remains near the site of fertilizer placement. It will react with Ca and Mg present in high pH soils to form sparingly soluble Ca and Mg phosphate compounds. These compounds are less available to the plant than fertilizer P and become increasingly less available over time. In acid soils, similar reactions occur with Fe and Al oxides. Band placement of P reduces contact with the soil and should result in less fixation than broadcast application. In P-deficient soils with a high P fixation capacity, the best means of supplying P for early crop growth is generally by banding the fertilizer near to or with the seed (i.e. use of starter P). In soils where the soil P levels are not extremely low (e.g. soils with a history of P fertilization), P fertilizer may be effectively applied in a deep-band, dual-banded with the N.

While precision placement of P is one

strategy to optimize early season uptake of P, an alternate approach may be to develop and maintain high concentrations of P in the soil. In Manitoba, a single broadcast application of 400 or 800 lb P_2O_5/A increased crop yields and maintained soil P at levels above those where a response to application of additional P would be expected, even after eight years of cropping. Continued assessment of the availability of P to crops early in the season on soils with high residual P levels, whether from previous fertilization or manure applications, is required in order to determine the likelihood of a response to applications of additional fertilizer P.

Summary

Crops require an adequate P supply during the early stages of growth to optimize crop yield. It is important to recognize P deficiency and to manage cropping systems to ensure adequate levels of available P are provided to the young, developing crop. This requires recognition of the potential effects of management practices on soil physical and biological characteristics that can influence the early season availability of P to crops. Band placement of P fertilizer in or near the seed row and maintenance of soil levels of P through long-term fertilizer management are among the practices that should be adopted to optimize P nutrition.

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Interested in more detail on this topic? A review paper from which this article was developed has been published in the Canadian Journal of Plant Science. Copies of the journal manuscript reprint are also available from Dr. Adrian Johnston, PPI/PPIC Western Canada Director, located at Saskatoon, SK Canada; e-mail: ajohnston@ppi-ppic.org.