

## 2.0 Role of P in Crop Production

### Key Messages:

- Phosphorus is required for energy transfers, photosynthesis, and cell division; it plays a critical role in all stages of crop growth
- Phosphorus is taken up from the soil solution as orthophosphate through an active uptake system in the plant root cell membrane
- The ability of the plant to absorb P from the soil will depend on the concentration of P ions in the soil solution at the root surface, the area of absorbing surface in contact with the solution and the rate of P ion movement through the soil to the root surface
- Plant-available soil P over the season will be affected by the concentration of P in the soil solution and the ability of the soil to replenish the soil solution from other organic and inorganic soil P pools
- Plants' mechanisms to improve their ability to access P when deficiencies occur include increased root growth, secretion of compounds to mobilize P in the solution and formation of associations with mycorrhizal fungi to increase soil exploration for P
- Phosphorus deficiency symptoms are often subtle, but plants may develop dark green or purple coloration of leaves and stems, and be shorter with delayed leaf emergence, slower development, reduced tillering, lower dry matter yield and reduced seed production.

### Summary

Phosphorus is an essential plant nutrient and, after nitrogen, is the nutrient most frequently limiting to crop production in the Northern Great Plains. Phosphorus is required for photosynthesis as a component of ATP, ADP, NADP and NADPH, the molecules that capture the energy harvested from sunlight in the chloroplasts. The chemical energy stored in these phosphate-based molecules is used to convert CO<sub>2</sub> and water to carbohydrates and to drive other energy-requiring reactions of plant metabolism. Phosphorus is also a structural component of the nucleic acids of DNA, RNA, genes and chromosomes and of many coenzymes, phosphoproteins and phospholipids. Phosphate compounds are also intermediate metabolites in a wide range of metabolic processes. The concentration of inorganic P present in the cell affects enzyme regulation and the control of starch synthesis. Dissociation of phosphoric acid plays a role in buffering of cellular pH and maintenance of homeostasis.

The importance of P in all energy transfers, photosynthesis, and cell division means that P plays a critical role from the initial reactions in the germinating seed, throughout plant growth, to formation of crop yield. Each time a cell divides, P is required to provide energy for reactions, to replicate the genetic material that is passed to the new cell, to form the phospholipids of the cell membranes, and to form a wide range of enzymes and other cellular components. Therefore, an adequate supply of P is essential from the earliest stages of plant growth. 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.

Phosphorus is taken up by the plant as the inorganic orthophosphate ion ( $\text{H}_2\text{PO}_4^-$  or  $\text{HPO}_4^{2-}$ ), with the greatest uptake rate occurring when the P is in the monovalent  $\text{H}_2\text{PO}_4^-$  form. Therefore, plant uptake rates of P are greatest between soil pH levels of 5 and 6, where the monovalent form dominates. Uptake of P by the plant from the soil solution occurs mainly through actively growing cells just behind the root cap, where root hair density is high. A series of active carriers transports the P across the cell membranes of the various cells and organelles to move it into the root and distribute it throughout the plant to where it is needed. The concentration of phosphate ions in the soil solution is many times lower than that in the plant, so uptake of P from the soil to the plant requires energy to move the P against the concentration gradient.

The ability of the plant to absorb P from the soil will depend on the concentration of P ions in the soil solution at the root surface, the area of absorbing surface in contact with the solution, and the movement of P ions in the soil to the root surface. The P ions in solution are absorbed quickly by the active transporter system on the root cell membranes, leading to a depletion zone of low concentration at the root surface. Phosphorus ions will move through the soil water to the root surface by mass flow and diffusion, with diffusion along the concentration gradient being the most important mechanism. Movement of P will increase with increasing concentration of P in the soil solution, partly because there will be more P in the water moving towards the plant in mass flow, but mainly because the concentration gradient for diffusion will increase as the P concentration in the bulk soil solution increases.

Plant roots can directly take up only dissolved inorganic P ( $\text{P}_i$ ) in the soil solution, but at any time the solution  $\text{P}_i$  contains only a small amount of the total soil P. Most of the soil P is present in a range of organic and inorganic forms that can be viewed as being “pools” of P that vary in availability. Phosphorus can move from pool to pool along concentration gradients that result from P being added or removed from the soil solution. Labile P is the pool that will rapidly move in and out of the soil solution in the short-term, while non-labile P is more stable, slowly retaining and releasing P over the long-term. When plants remove P from solution, most of the P that is removed can be replenished from the labile pool of P. When fertilizer P is added to the soil solution, most of the added P will move out of solution and replenish the labile pool. The P will also move between the labile and non-labile pools, but these reactions take longer to occur. Phosphorus supply to a crop will be influenced by the ability of the soil to replenish the P in the soil solution at the root surface from the P present in the other soil pools. Therefore, plant-available soil P over the season will be affected both by the concentration of P in the soil solution (the intensity factor, I) and the amount and rate of release P from other soil pools (the quantity factor, Q).

Phosphorus concentration in the plant will be affected by the amount of P that the plant can take up from the soil solution. Most of the P in the plant is present as inorganic phosphate with only a small portion being metabolically active. This small amount of active P remains relatively constant with changes in P supply while the concentrations of inorganic P may vary substantially, being stored or mobilized as external supplies increase or decrease. Surplus phosphate can be stored in the vacuoles of plant cells, to be used as a reserve source if P supplies

become limited. Mobilization of the plant's "luxury" reserves of stored P helps to maintain the metabolically active P to support plant growth if external P becomes deficient.

The importance of P for plant growth has led plants to develop strategies to improve their ability to access P when deficiencies occur. The ability of the plant to take up P depends on the P in solution at the soil surface and the amount of root surface area. If P supply is low, plants will increase root development at the expense of shoot growth, producing finer and more abundant roots and root hairs to improve their ability to explore the soil and take up P. Deficient plants will also release organic acids and acid phosphatases that increase P availability in the rhizosphere. Low P concentrations in plant tissue will encourage mycorrhizal colonization in many plants, a symbiosis that increases the soil volume explored for P uptake.

Phosphorus deficiency symptoms are often subtle, and moderate P deficiency may not produce obvious symptoms ("hidden hunger"). Plants may develop dark green or purple coloration of leaves and stems. Plants may be shorter, leaf emergence and development can be delayed, and there can be less tillering and root development, lower dry matter yield and reduced seed production. Seed number will be reduced but usually the seed size will be maintained.

Deficiency generally occurs at P concentrations below approximately 0.2% in the plant tissue, depending on the crop stage and portion sampled, but the thresholds for sufficiency will vary with different crops. The P in plant tissue will usually decline as the plant ages and matures; therefore, the critical P concentrations required for optimum growth decrease as plants age. Phosphorus is generally mobile in the crop and will re-translocate from vegetative tissue to reproductive organs such as seeds. As a result, most of the P taken up by the crop will be removed in the harvested material.

## **Detailed Information**

### **2.1 Functions of P in plants**

Phosphorus is one of the 17 essential plant nutrients. It is critical for plant metabolism and an adequate amount of P is required for a plant to grow and reproduce. Phosphorus is needed in nearly all energetic reactions in a plant because of its role as a component of adenosine triphosphate (ATP), adenosine diphosphate (ADP), nicotinamide adenine dinucleotide phosphate (NADP) and NADPH (Glass et al. 1980; Hopkins 2015; Raven et al. 2005; Sultenfuss and Doyle 1999). The ATP molecule is composed of a unit of adenine, a sugar and three phosphate groups, with the last two phosphates linked to the molecule by a high-energy bond (Figure 1). The NADP and NADPH molecules also contain phosphate groups (Figure 2).

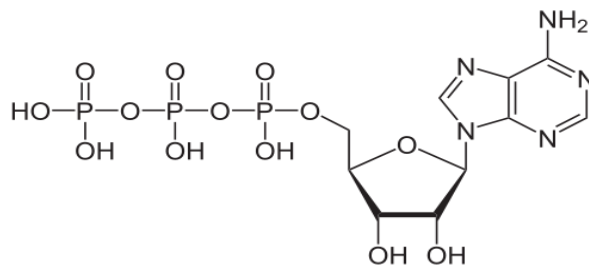


Figure 1. Structure of adenosine triphosphate (ATP)

[https://en.wikibooks.org/wiki/Structural\\_Biochemistry/ATP#/media/File:Adenosintriphosphat\\_proniert.svg](https://en.wikibooks.org/wiki/Structural_Biochemistry/ATP#/media/File:Adenosintriphosphat_proniert.svg)

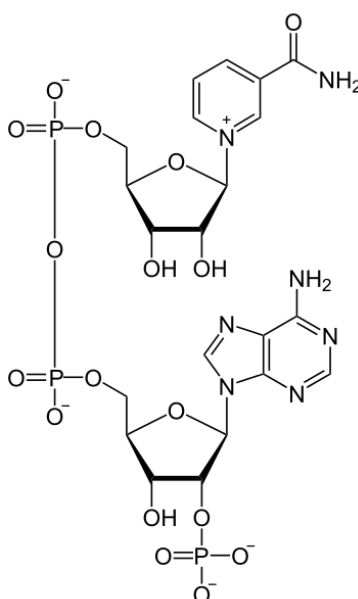
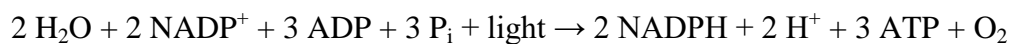


Figure 2. Structure of NADP (NEUROtiker - Own work, Public Domain,

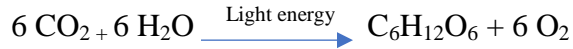
<https://commons.wikimedia.org/w/index.php?curid=2326143>).

Phosphorus plays a key role in photosynthesis. The light energy absorbed by chlorophyll during photosynthesis is stored in adenosine triphosphate (ATP) and serves as the primary source of energy for all energy-requiring biological processes. Light energy captured by the chlorophyll molecule during photosynthesis causes the chlorophyll to lose an electron. In non-cyclic reactions in photosystem II, the electron passes down an electron transport chain, reducing NADP to NADPH and creating an energy gradient across the chloroplast membrane that is used to synthesize ATP (Raven et al. 2005).



In the cyclic reaction, which takes place only in photosystem I, no NADPH is generated, and the displaced electron returns to photosystem I from which it was emitted. Through the action of

these two photosystems, light energy is converted to stored chemical energy that can be used to power plant metabolism. The NADPH and ATP formed using the energy captured during the light reactions are used to reduce carbon dioxide to carbohydrates during the dark reactions of photosynthesis.



When the phosphate is transferred from the ATP to another molecule by hydrolytic enzymes, the high energy bond is broken, and the energy is released. The ATP hydrolysis can be coupled with other energy-requiring reactions to power their progress.

Phosphorus is a structural component of the nucleic acids (e.g., DNA and RNA) of genes and chromosomes and of many coenzymes, phosphoproteins and phospholipids (Figure 3) (Raven et al. 2005). Phosphate compounds are also intermediate metabolites in a wide range of metabolic processes (Raven et al. 2005). The concentration of inorganic P present in the cell is involved in enzyme regulation and in the control of starch synthesis (Mills and Jones 1996). Dissociation of phosphoric acid plays a role in buffering cellular pH and maintenance of homeostasis (Mills and Jones 1996).

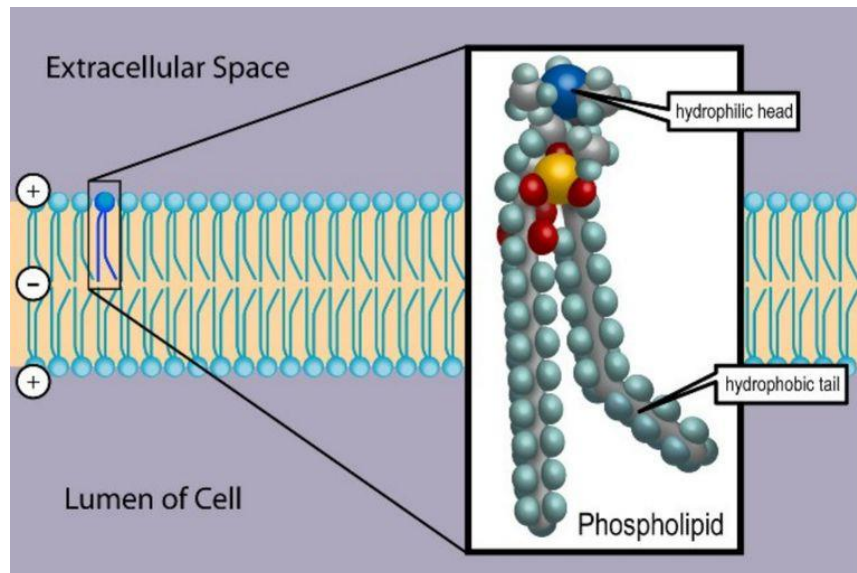


Figure 3. The phospholipid bilayer is an important component of cell membranes (<https://www.thoughtco.com/phospholipids-373561>)

The importance of P in all energy transfers, photosynthesis, and cell division means that P plays a critical role from the initial reactions in the germinating seed, throughout plant growth, to formation of crop yield. Each time a cell divides, P is required to provide energy for reactions, to replicate the genetic material that is passed to the new cell, to form the phospholipids of the cell membranes, and to form a wide range of enzymes and other P containing cellular components.

Therefore, an adequate supply of P is essential from the earliest stages of plant growth. Studies conducted at Melfort, SK showed that about half of the P accumulation in wheat occurred by about 41 days after emergence, with maximum uptake of P attained by full flowering to late milk or ripening, depending on the environmental conditions during the growing season (Malhi et al. 2006). The maximum rate of P accumulation and the maximum total P uptake occurred earlier than the corresponding values for biomass accumulation, a pattern similar to that of N and other macronutrients, indicating that P uptake preceded biomass accumulation and that the supply of nutrients must be adequate in early stages to support biomass production. However, P accumulation continued until as late as the early ripening stages. A similar pattern of nutrient accumulation preceding biomass accumulation occurred for pulse crops (Malhi et al. 2007b) and oilseed crops (Malhi et al. 2007a). The P present in the seed of cereal grains is largely provided by redistribution of nutrients accumulated in the vegetative tissue during the early stages of growth. As the plant develops, P is transported from leaves and stems to the grain until 75 to 80% of the plant P is present in the grain at maturity (Mohamed and Marshall 1979). Although uptake of P by the plant continues until as late as the ripening phase, the supply in the early growth stages has a great effect on plant response. 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 (Grant et al. 2001).

## **2.2 Phosphorus accumulation in plants**

Phosphorus is taken up by the plant root as inorganic P ( $P_i$ ). The major location for P uptake by plants is in the area of actively growing cells just behind the root cap, where root hair density is high (Hopkins 2015). Uptake of  $P_i$  requires energy since  $P_i$  concentration in the soil solution is as much as 1000-fold lower than that in the plant (Schachtman et al. 1998; Vance et al. 2003). The  $P_i$  is transported across the plasma membranes of the root cells and moved in the symplasm from the root surface to the xylem. The  $P_i$  travels in the xylem from the root and is distributed throughout the plant, again by passing through the membranes of other cells and organelles (Rouached et al. 2010; Schachtman et al. 1998). Movement from the xylem to the cell cytoplasm is also against a steep concentration gradient, so it requires active transport. The movement of  $P_i$  across cell membranes uses a suite of primary orthophosphate transporter proteins, with both low- and high-affinity transporters involved in phosphate uptake (Schroeder et al. 2013). The high affinity system tends to function when  $P_i$  concentrations are low, improving the plant's ability to transport the orthophosphate across the root membranes when P supply is restricted. Phosphate transporters also function in the distribution of  $P_i$  throughout the plant and from source to sink tissues and in regulating phosphate homeostasis within the plant. Since P is transported as an anion, co-transport requires a counterion. The cytoplasm is acidified when P is added to deficient cells, indicating that  $H^+$  is likely the counterion (Vance et al. 2003). Surplus  $P_i$  will be stored in the vacuole, where it can be a reserve for future deficiencies (see Section 2.4). The concentration in the vacuole tends to be lower than that in the cytoplasm, so movement from the cytoplasm to the vacuole does not need an input of energy, although there is evidence of active transport in some cases (Yang et al. 2017). Phosphorus deficiency can trigger

an active movement of  $P_i$  from the vacuole to the cytoplasm to meet the metabolic requirements of the plant (Yang et al. 2017).

The ability of the plant to absorb P from the soil will depend on the concentration of P ions in the soil solution at the root surface (the intensity factor or I), the area of absorbing surface in contact with the solution, and the movement of P ions through the soil. The inorganic P in the soil solution is present as orthophosphate P ions, usually  $H_2PO_4^-$  and  $HPO_4^{2-}$ , with most  $P_i$  being present as  $H_2PO_4^-$  if the pH is below 6 (Figure 4). Uptake rates of  $P_i$  by plants tend to be greatest between pH of 5 and 6, indicating that  $P_i$  is primarily taken up by the plant in the monovalent form,  $H_2PO_4^-$  (Schachtman et al. 1998). The P ions in solution are absorbed quickly by the active transporter system on the root cell membranes, leading to a depletion zone of low concentration at the root surface (Bagshaw et al. 1972). Phosphorus ions will move through the soil water to the root surface by mass flow and diffusion (Barber 1980; Barber et al. 1963). However, because the concentration of P in the soil solution is very low, the total amount of P that will move to the plant root via mass flow will also be very low, in the order of 2-3% of the total amount required for optimum crop growth (Johnston et al. 2014). Therefore, most P movement towards the root surface occurs through diffusion down the concentration gradient created by the active uptake of P by plant roots (Barber 1995). Movement of P will increase with increasing concentration of P in the soil solution, partly because there will be more  $P_i$  in the water moving towards the plant in mass flow and mainly because the concentration gradient for diffusion will increase as the  $P_i$  concentrate in the bulk soil increases. However, the speed of diffusion of phosphate ions through the soil solution is very slow and the path of movement through the soil moisture films around the soil particles is long and crooked, or “tortuous”. Therefore, the net movement of P through the soil is small, in the range of 0.13 mm per day.

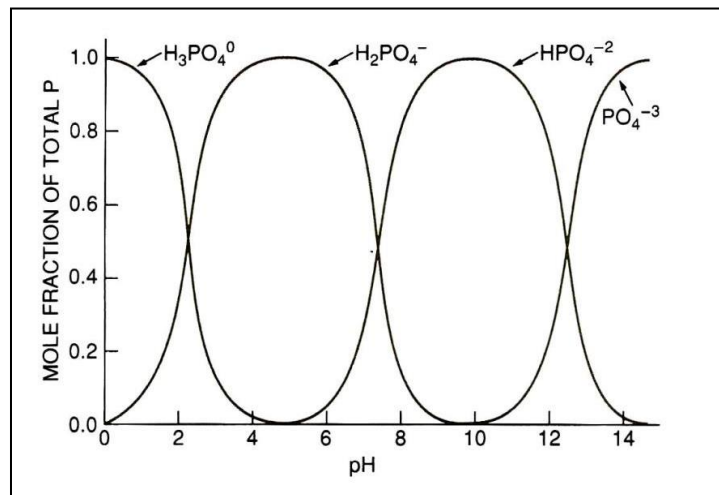


Figure 4. Influence of pH on the distribution of orthophosphate forms in solution (Havlin et al. 2014).

While the P ions in soil solution are the immediate source for uptake by the plant, the soluble  $P_i$  in solution at any given time generally represents less than 1% of P taken up by crops during a growing season, with approximately 99% of P that plants use over time being bound to soil constituents prior to uptake. Phosphorus in the soil is present in organic and inorganic forms of

varying availability (Figure 5). As the phosphate ions in the soil solution are depleted they are replenished from the organic and inorganic reserves of P that are present in soil solids or on soil surfaces. These reserves are broadly divided into “Labile” and “Non-Labile” forms. Labile P will rapidly equilibrate with the soil solution and become available in the short-term, while non-labile P equilibrates more slowly and will replenish the labile reserves and the soil solution in the long-term (Figure 5) (Johnston et al. 2014; Syers et al. 2008).

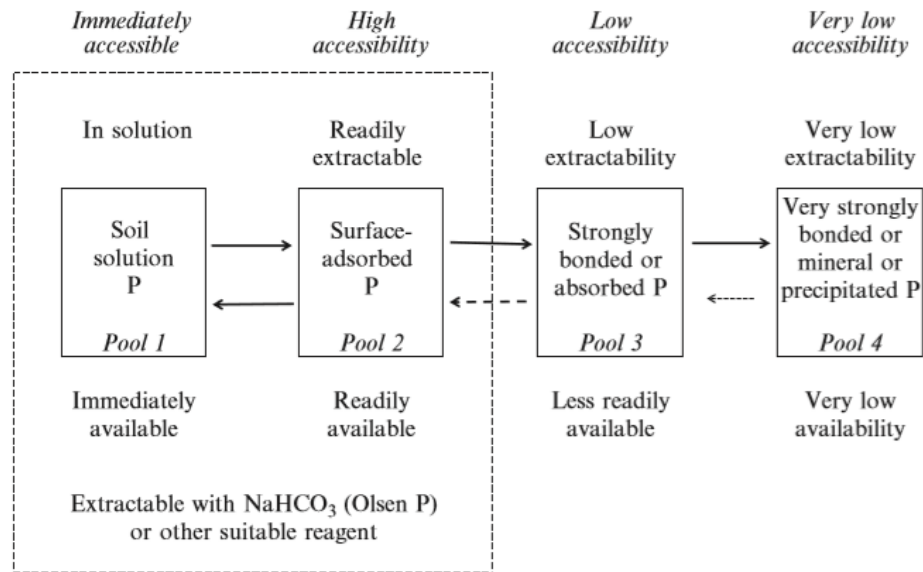


Figure 5. Conceptual diagram for the forms of inorganic P in soils categorized in terms of accessibility, extractability and plant availability (Johnston et al. 2014)

The ability of the soil to replenish the P in the soil solution is referred to as the quantity factor (Q) or the P buffering capacity. The depletion of the P ion concentration of the solution at the root surface though plant uptake will drive the movement of P by diffusion to the root surface and the movement of inorganic P into solution from the labile pools. Conversely, addition of soluble forms of P such as fertilizers will shift the equilibria towards the less available pools. The movement of P among the various phases varies with time and the gradient of P ion concentration (Morel and Plenchette 1994; Morel et al. 2000; Schneider and Morel 2000). Phosphorus supply to a crop will be influenced by the ability of the soil to replenish the depletion zone at the root surface from the P present in the soil in the other pools, especially the labile P pool. During periods of peak P demand, the P in the soil solution at the root hair surface must be replenished at least 10 to 20 times per day (Syers et al. 2008). Therefore, plant-available soil P over the season will be affected both by the concentration of P in the soil solution (the intensity factor, I) and the amount and rate of release P from other soil pools (the quantity factor, Q) (Morel et al. 2000).



### 2.3 Effects of phosphorus deficiency

In tissues of most of the higher plants, phosphate is mainly present as inorganic phosphate. More than 75% of the P moving in the xylem is inorganic phosphate, while that moving in the phloem is generally present as proteins, RNA, enzymes and ATP (Bielecki 1973; Glass et al. 1980; Lefebvre and Glass 1982). With an adequate supply of P, much of the inorganic P is stored in cell vacuoles as orthophosphate or present in storage compounds such as phytic acid or polyphosphate. In seeds, P is stored in a myoinositol-P form, for example as a Mg or K salt of phytic acid in cereals and legumes. For the first few days of growth, a plant will rely on its seed reserves and external P supply will have little effect on growth. Only a small amount of the P in plants is metabolically active and much of the metabolically active portion is involved in cyclical processes such as the cycle between ATP and ADP. The metabolically active P will be held relatively constant by the plant and so will vary much less with changing external P supply than will the concentration of stored inorganic P. When the external P supply falls, the plant remobilizes the stored inorganic reserves while the metabolically active forms are maintained (Ozanne 1980). Therefore, luxury uptake of P early in the season, or high P concentration from the seed can help the plant to maintain metabolic activity when external P supply becomes restricted.

Plants respond to P deficiency by implementing strategies to increase their ability to access P from the soil. One strategy used by plants to increase access to P is enlargement of the root surface area. Plants preferentially retain P in the root, over moving it to the shoot when P supply is limited to meet the metabolic requirements for root growth to access soil P (Loneragan and Asher 1967; Schjørring and Jensén 1984; Sutton et al. 1983). With P deficiency, many plants will also allocate more carbohydrate to roots than shoots (Marschner et al. 1996), increasing the root:shoot ratio to improve their ability to access P from the soil (Brenchley 1929; Schjørring and Jensén 1984). Under low-P conditions, plants develop enlarged root systems, with highly branched roots, numerous and long root hairs, and a greater root length per unit mass to increase the soil volume explored (Barber 1977; Brenchley 1929; Hodge 2004; Ozanne 1980; Schjørring and Jensén 1984; Tomaszewicz 2000; Vance et al. 2003). In addition, many plants such as canola and buckwheat will increase root density when they encounter a region of high P concentration such as a fertilizer reaction zone, increasing the ability of the plant to extract P from that area (Drew and Saker 1978; Foehse and Jungk 1983; Strong and Soper 1974a; Strong and Soper 1974b). Uptake of P by roots is proportional to both the concentration of the P at the root surface and the area of absorbing root surface that contacts the P, so root proliferation in a zone of high P concentration increases the ability of the plant to take up P. Other plants, such as flax and soybean, are less able to proliferate roots in a high-P zone and are more reliant on P in the bulk soil.

Plants can also implement physiological changes in response to P deficiency to enhance the ability of the root to absorb P from the solution (Hodge 2004). Uptake rate per unit of root can be increased in P-deficient plants (Anghinoni and Barber 1980; Borkert and Barber 1983; Drew et al. 1984; Green et al. 1973; Hodge 2004; Jungk and Barber 1974). Many plants will secrete low molecular weight amino acids that acidify the rhizosphere, compete with phosphate ions for

sorption sites, and complex cations bound to phosphate ions, thus increasing P availability (Hinsinger 1998; Hinsinger 2001; Hinsinger and Gilkes 1995; Hoffland et al. 1989; Jungk et al. 1993). Some plants can also excrete phosphatases into the rhizosphere to release P from organic forms (Ashworth and Mrazek 1995; Hinsinger 2001; Lefebvre and Glass 1982). Plants can also excrete compounds that encourage development of P-solubilizing microorganisms in the rhizosphere (Kucey et al. 1989; Richardson 2001; Richardson et al. 2009).

Another strategy used by most plant species to improve access to soil P is to form mycorrhizal associations (Bolan 1991; Grant et al. 2005; Hamel and Strullu 2006; Jakobsen 1986; McGonigle et al. 2011; Miller 2000; Monreal et al. 2011; Ryan and Graham 2002; Ryan et al. 2000; Smith et al. 2011). In return for fixed carbon from the host, mycorrhizal fungi capture P, water and some other nutrients from the soil and transfer it to the plant. The mycorrhizal hyphae are finer than plant root hairs and will extend both further from the root and into finer soil pores, greatly increasing the effective volume of soil that can be accessed by the mycorrhizal association. Plants vary substantially in their reliance on mycorrhizal colonization for P access, with some crops such as flax relying heavily on mycorrhizal associations and other crops such as canola, having no mycorrhizal associations.

Phosphorus deficiency symptoms are often subtle, and moderate P deficiency may not produce obvious symptoms. If P deficiency becomes severe, the plant may develop dark green or purple coloration of leaves and stems (Hopkins 2015; Hoppo et al. 1999). Both photosynthesis and respiration can decline with P deficiency, but if respiration falls more than photosynthesis, carbohydrates will accumulate producing a dark green colour. Anthocyanins may accumulate because of a blockage in metabolic pathways, leading to purpling or reddening of the tissue (Close and Beadle 2003). With severe P deficiency, nitrate reduction may proceed normally but the synthesis of proteins and nucleic acids may be restricted, so that soluble N compounds accumulate in the tissue. Metabolic processes in the cell will be slowed because of the lack of protein catalysts, so cell growth can be impaired by P deficiency (Elliott et al. 1997a; Glass et al. 1980). Restrictions in cell growth leads to shorter plants, delayed leaf emergence, delayed development, reduced tillering and secondary root development, decreased dry matter yield and reduced seed production (Elliott et al. 1997a; Glass et al. 1980; Grant et al. 2001; Hoppo et al. 1999; Konesky et al. 1989). Plants will respond to P deficiency in a way that will increase the probability of producing viable seed. For example, in cereal crops, P stress will reduce seed number by reducing the number of fertile tillers and the number of grains per tiller, but seed size will be maintained. (Hoppo et al. 1999). In soybean, P deficiency will reduce the number of pods and seeds, but will not decrease seed size (Crafts-Brandner 1992). The restricted plant resources are distributed among fewer seeds, increasing the likelihood that the remaining seeds will be viable.

Deficiency generally occurs at P concentrations in plant tissue below 0.2%, but the sufficiency thresholds will vary with crop stage and with different crops (Table 1). The P in plant tissue will usually decline as the plant ages and matures because of a declining proportion of metabolically active tissue and an increasing proportion of low-P structural and storage tissue (Bélanger and Richards 1999; Elliott et al. 1997a; Racz et al. 1965). Therefore, the critical P concentration

required for optimum growth decreases as plants age (Elliott et al. 1997a; Elliott et al. 1997b; Tomasiewicz 2000). Phosphorus is generally mobile in the crop and will re-translocate from vegetative tissue to storage organs such as seeds. As a result, most of the P taken up by the crop will be removed in the harvested material (Table 2).

Table 1. Sufficiency ranges for phosphorus tissue concentrations in selected crops of the Northern Great Plains. (Adapted from Mills and Jones (1996)).

Species	Latin Name	Plant Part Sampled	Timing	P Concentration %
Alfalfa	<i>Medicago sativa</i> L.	12 tops 15 cm new growth	Prior to flowering	0.26 to 0.70
Barley	<i>Hordeum vulgare</i> L.	25 whole tops	emergence of head from boot	0.20 to 0.50
Beans	<i>Vicia faba</i> L.	50 leaf blades without petiole from uppermost mature leaves	summer	0.32 to 0.42
Brome	<i>Bromus inermis</i> L.	25 fully developed stems with leaves	Summer, midway between mowings	0.25 to 0.35
Canola	<i>Brassica napus</i> L.	50 mature leaves (5th from the top) without petioles	Rosette to pod development	0.28 to 0.69
Corn	<i>Zea mays</i> L.	15 whole tops	Plants 30 cm tall	0.30 to 0.5
Oats	<i>Avena sativa</i> L.	25 whole tops	Head emerging from boot	0.20 to 0.50
Potato	<i>Solanum tuberosum</i> L.	25 most recent fully-developed leaves	Plants 30 cm tall	0.20 to 0.50
Rye	<i>Secale cereale</i> L.	25 whole tops	Panicle initiation	0.52 to 0.65
Sorghum	<i>Sorghum bicolor</i> L.	25 whole tops	seedlings < 30 cm tall, 23 to 39 days old	0.30 to 0.60
Soybean	<i>Glycine max</i> Merr.	25 mature leaves from new growth	Prior to pod set	0.25 to 0.50
Spring wheat	<i>Triticum aestivum</i> L.	25 whole tops	As head emerges from boot	0.20 to 0.50
Sugar Beet	<i>Beta vulgaris</i> L.	25 leaves	50 to 80 days after planting	0.45 to 1.10
Sunflower	<i>Helianthus annuus</i> L.	25 mature leaves from new growth	summer	0.25 to 0.60
Winter Wheat	<i>Triticum aestivum</i> L.	50 leaves, top two leaves	Just before heading	0.20 to 0.50

Table 2. Phosphorus uptake and removal (lbs per unit of yield) for a range of crops<sup>a</sup>.

Crop	Unit for Yield	Uptake			Removal		
		Min	Max	Prairies	Min	Max	Prairies
		----- lb P <sub>2</sub> O <sub>5</sub> -----					
Spring wheat	Bushel	0.73	0.88	0.68	0.53	0.65	0.51
Barley	Bushel	0.50	0.61	0.33	0.38	0.46	0.29
Oats	Bushel	0.36	0.45	0.27	0.26	0.28	0.23
Canola	Bushel	1.31	1.63	0.87	0.94	1.14	0.68
Faba Beans	Bushel	1.78	2.19	-	1.10	1.34	-
Flax	Bushel	0.75	0.92	0.71	0.58	0.71	0.64
Lentil	Bushel	0.76	0.92	-	0.60	0.66	-
Peas	Bushel	0.76	0.92	0.53	0.62	0.76	0.44
Corn	Bushel	0.57	0.69	0.46	0.39	0.48	0.39
Sunflowers	CWT	1.15	1.40	1.90	0.70	0.90	1.20
Soybeans	Bushel	1.10	1.32	1.37	0.80	1.00	1.17
Dry Beans	CWT	-	-	1.39	1.40	1.40	1.12
Potatoes	CWT	0.15	0.18	0.18	0.08	0.10	0.16

<sup>a</sup> Low and high values are estimates from the Canadian Fertilizer Institute (CFI 2001) and values for Canadian Prairie crops are from Heard and Hay (2006). Values for lentils and faba bean are from [https://saskpulse.com/files/general/160401\\_Phosphorus\\_management\\_for\\_pulses2.pdf](https://saskpulse.com/files/general/160401_Phosphorus_management_for_pulses2.pdf), accessed March 25, 2019). It is important to note that these values are strongly affected by crop yield potential, genetics and environment. Much of the data contributing to this table was collected using older cultivars and management practices. Efforts are currently underway to update uptake and removal values using more current information.

### Gaps in Knowledge

More information is needed on:

- nutrient requirements and removals for current high-yielding crop cultivars.
- the development of crop varieties and hybrids with the ability to mobilize P from the soil through rhizosphere modification or improved rooting. Such cultivars could be more productive than current cultivars, when grown on soils with low levels of P fertility. This would not necessarily save on crop inputs of P in the long term, since the rates of crop P removal must eventually be balanced with rates of P application. However, P-efficient cultivars could enable farmers to maintain crop productivity at lower levels of soil test P, which could reduce P loss to surface water due to runoff and erosion.
- more refined information on threshold tissue concentrations required for optimum yield in current, high-yielding crop cultivars.

## References

- Anghinoni, I. a. and Barber, S. 1980.** Phosphorus influx and growth characteristics of corn roots as influenced by phosphorus supply. *Agronomy Journal* 72(4):685-688.
- Ashworth, J. and Mrazek, K. 1995.** “Modified Kelowna” test for available phosphorus and potassium in soil. *Communications in Soil Science and Plant Analysis* 26(5-6):731-739.
- Bagshaw, R., Vaidyanathan, L. V. and Nye, P. H. 1972.** The supply of nutrient ions by diffusion to plant roots in soil - V. Direct determination of labile phosphate concentration gradients in a sandy soil induced by plant uptake. *Plant and Soil* 37(3):617-626.
- Barber, S. 1995.** *Soil Nutrient Availability. A Mechanistic Approach.* 2nd ed. Wiley, New York.
- Barber, S. A. 1977.** Application of phosphate fertilizers: Methods, rates and time of application in relation to the phosphorus status of soils. *Phosphorus in Agriculture* 70:109-115.
- Barber, S. A. 1980.** Soil-plant interactions in the phosphorus nutrition of plants. *The Role of Phosphorus in Agriculture*:591-615.
- Barber, S. A., Walker, J. M. and Vasey, E. H. 1963.** Mechanisms for the movement of plant nutrients from the soil and fertilizer to the plant root. *Journal of Agricultural and Food Chemistry* 11(3):204-207.
- Bélanger, G. and Richards, J. E. 1999.** Relationship between P and N concentrations in timothy. *Canadian Journal of Plant Science* 79(1):65-70.
- Bieleski, R. L. 1973.** Phosphate pools, phosphate transport, and phosphate availability. *Annu Rev Plant Physiol* 24:225-252.
- Bolan, N. S. 1991.** Critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. *Plant and Soil* 141:1-11.
- Borkert, C. and Barber, S. 1983.** Effect of supplying P to a portion of the soybean root system on root growth and P uptake kinetics. *Journal of Plant Nutrition* 6(10):895-910.
- Brenchley, W. E. 1929.** The phosphate requirement of barley at different periods of growth. *Annals of Botany* 43:89-112.
- CFI. 2001.** Nutrient uptake and removal by field crops - western Canada. Canadian Fertilizer Institute, Ottawa, Ontario, Canada.
- Close, D. C. and Beadle, C. L. 2003.** The ecophysiology of foliar anthocyanin. *The Botanical Review* 69(2):149-161.
- Crafts-Brandner, S. J. 1992.** Significance of leaf phosphorus remobilization in yield production in soybean. *Crop Science* 32:420-424.
- Drew, M. and Saker, L. 1978.** Nutrient supply and the growth of the seminal root system in barley: III. Compensatory increases in growth of lateral roots, and in rates of phosphate uptake, in response to a localized supply of phosphate. *Journal of Experimental Botany* 29(2):435-451.
- Drew, M. C., Saker, L. R., Barber, S. A. and Jenkins, W. 1984.** Changes in the kinetics of phosphate and potassium absorption in nutrient-deficient barley roots measured by a solution-depletion technique. *Planta* 160(6):490-499.
- Elliott, D. E., Reuter, D. J., Reddy, G. D. and Abbott, R. J. 1997a.** Phosphorus nutrition of spring wheat (*Triticum aestivum* L.). 2. Distribution of phosphorus in glasshouse-grown wheat and the diagnosis of phosphorus deficiency by plant analysis. *Australian Journal of Agricultural Research* 48(6):869-881.
- Elliott, D. E., Reuter, D. J., Reddy, G. D. and Abbott, R. J. 1997b.** Phosphorus nutrition of spring wheat (*Triticum aestivum* L.). 4. Calibration of plant phosphorus test criteria from rain-fed field experiments. *Australian Journal of Agricultural Research* 48(6):899-912.

- Foehse, D. and Jungk, A. 1983.** Influence of phosphate and nitrate supply on root hair formation of rape, spinach and tomato plants. *Plant and Soil* 74(3):359-368.
- Glass, A. D. M., Beaton, J. D. and Bomke, A. 1980.** Role of P in plant nutrition. *Proceedings of the Western Canada Phosphate Symposium*:357-368.
- Grant, C., Bittman, S., Montreal, M., Plenchette, C. and Morel, C. 2005.** Soil and fertilizer phosphorus: Effects on plant P supply and mycorrhizal development. *Canadian Journal of Plant Science* 85(1):3-14.
- Grant, C. A., Flaten, D. N., Tomasiewicz, D. J. and Sheppard, S. C. 2001.** The importance of early season phosphorus nutrition. *Canadian Journal of Plant Science* 81(2):211-224.
- Green, D. G., Ferguson, W. S. and Warder, F. G. 1973.** Accumulation of toxic levels of phosphorus in the leaves of phosphorus-deficient barley. *Canadian Journal of Plant Science* 53:241-246.
- Hamel, C. and Strullu, D.-G. 2006.** Arbuscular mycorrhizal fungi in field crop production: potential and new direction. *Canadian Journal of Plant Science* 86(4):941-950.
- Havlin, J. L., Tisdale, S. L., Nelson, W. L. and Beaton, J. D. 2014.** Soil fertility and fertilizers: An introduction to nutrient management. 8th ed. Pearson, Inc., Upper Saddle River, NJ, USA.
- Heard, J. and Hay, D. 2006.** Typical nutrient content, uptake pattern and carbon: nitrogen ratios of prairie crops. Designing cropping systems that prosper in variable weather: *Proceedings of the 7th Manitoba Agronomists Conference, Winnipeg.*
- Hinsinger, P. 1998.** How do plant roots acquire mineral nutrients? Chemical processes involved in the rhizosphere. *Advances in Agronomy* 64:225-265.
- Hinsinger, P. 2001.** Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: A review. *Plant and Soil* 237(2):173-195.
- Hinsinger, P. and Gilkes, R. 1995.** Root-induced dissolution of phosphate rock in the rhizosphere of lupins grown in alkaline soil. *Soil Research* 33(3):477-489.
- Hodge, A. 2004.** The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* 162(1):9-24.
- Hoffland, E., Findenegg, G. R. and Nelemans, J. A. 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.
- Hopkins, B. G. 2015.** Phosphorus. Pages 65 -126 in A. V. Barker, D. J. Pilbeam, eds. *Handbook of plant nutrition.* CRC press, Boca Ratan, FL.
- Hoppo, S. D., Elliott, D. E. and Reuter, D. J. 1999.** Plant tests for diagnosing phosphorus deficiency in barley (*Hordeum vulgare* L.). *Australian Journal of Experimental Agriculture* 39(7):857-872.
- Jakobsen, I. 1986.** Vesicular-arbuscular mycorrhiza in field-grown crops. III. Mycorrhizal infection and rates of phosphorus inflow in pea plants. *New Phytologist* 104:573-581.
- Johnston, A. E., Poulton, P. R., Fixen, P. E. and Curtin, D. 2014.** Phosphorus: its efficient use in agriculture. Pages 177-228 *Advances in Agronomy.* Elsevier.
- Jungk, A. and Barber, S. A. 1974.** Phosphate uptake rate of corn roots as related to the proportion of the roots exposed to phosphate. *Agronomy Journal* 66:554-557.
- Jungk, A., Seeling, B. and Gerke, J. 1993.** Mobilization of different phosphate fractions in the rhizosphere. *Plant and Soil* 155-156(1):91-94.

- Konesky, D., Siddiqi, M., Glass, A. and Hsiao, A. 1989.** Wild oat and barley interactions: varietal differences in competitiveness in relation to phosphorus supply. *Canadian Journal of Botany* 67(11):3366-3371.
- Kucey, R., Janzen, H. and Leggett, M. 1989.** Microbially mediated increases in plant-available phosphorus. Pages 199-228 *Advances in Agronomy*. Elsevier.
- Lefebvre, D. D. and Glass, A. D. M. 1982.** Regulation of phosphate influx in barley roots: Effects of phosphate deprivation and reduction of influx with provision of orthophosphate. *Physiol Plant* 54:199-206.
- Loneragan, J. F. and Asher, C. J. 1967.** Response of plants to phosphate concentration in solution culture: II. Rate of phosphate absorption and its relation to growth. *Soil Science* 103(5):311-318.
- Malhi, S. S., Johnston, A. M., Schoenau, J. J., Wang, Z. H. and Vera, C. L. 2006.** Seasonal biomass accumulation and nutrient uptake of wheat, barley and oat on a Black Chernozem soil in Saskatchewan. *Canadian Journal of Plant Science* 86(4):1005-1014.
- Malhi, S. S., Johnston, A. M., Schoenau, J. J., Wang, Z. H. and Vera, C. L. 2007a.** Seasonal biomass accumulation and nutrient uptake of canola, mustard, and flax on a black chernozem soil in Saskatchewan. *Journal of Plant Nutrition* 30(4):641-658.
- Malhi, S. S., Johnston, A. M., Schoenau, J. J., Wang, Z. H. and Vera, C. L. 2007b.** Seasonal biomass accumulation and nutrient uptake of pea and lentil on a black chernozem soil in Saskatchewan. *Journal of Plant Nutrition* 30(5):721-737.
- Marschner, H., Kirkby, E. A. and Cakmak, I. 1996.** Effect of mineral nutritional status on shoot-root partitioning of photoassimilates and cycling of mineral nutrients. *Journal of Experimental Botany* 47(SPEC. ISS.):1255-1263.
- McGonigle, T. P., Hutton, M., Greenley, A. and Karamanos, R. 2011.** Role of mycorrhiza in a wheat-flax versus canola-flax rotation: A case study. *Communications in Soil Science and Plant Analysis* 42(17):2134-2142.
- Miller, M. H. 2000.** Arbuscular mycorrhizae and the phosphorus nutrition of maize: A review of Guelph studies. *Canadian Journal of Plant Science* 80(1):47-52.
- Mills, H. A. and Jones, J. B., Jr. 1996.** *Plant analysis handbook II*. MicroMacro Publishing, Inc., Jefferson City, MO. 422 pp.
- Mohamed, G. E. S. and Marshall, C. 1979.** The pattern of distribution of phosphorus and dry matter with time in spring wheat. *Annals of Botany* 44(6):721-730.
- Monreal, M. A., Grant, C. A., Irvine, R. B., Mohr, R. M., McLaren, D. L. and Khakbazan, M. 2011.** Crop management effect on arbuscular mycorrhizae and root growth of flax. *Canadian Journal of Plant Science* 91(2):315-324.
- Morel, C. and Plenchette, C. 1994.** Is the isotopically exchangeable phosphate of a loamy soil the plant-available P? *Plant and Soil* 158(2):287-297.
- Morel, C., Tunney, H., Pleynet, D. and Pellerin, S. 2000.** Transfer of phosphate ions between soil and solution: Perspectives in soil testing. *Journal of Environmental Quality* 29(1):50-59.
- Ozanne, P. G. 1980.** Phosphate nutrition of plants - A general treatise. *The Role of Phosphorus in Agriculture*:559-589.
- Racz, G. J., Webber, M. D., Soper, R. J. and Hedlin, R. A. 1965.** Phosphorus and nitrogen utilization by rape, flax and wheat. *Agronomy Journal* 57:335-337.
- Raven, P. H., Evert, R. F. and Eichhorn, S. E. 2005.** *Biology of plants*. Macmillan.

- Richardson, A. E. 2001.** Prospects for using soil microorganisms to improve the acquisition of phosphorus by plants. *Functional Plant Biology* 28(9):897-906.
- Richardson, A. E., Hocking, P. J., Simpson, R. J. and George, T. S. 2009.** Plant mechanisms to optimise access to soil phosphorus. *Crop & Pasture Science* 60(2):124-143.
- Rouached, H., Arpat, A. B. and Poirier, Y. 2010.** Regulation of phosphate starvation responses in plants: signaling players and cross-talks. *Molecular Plant* 3(2):288-299.
- Ryan, M. H. and Graham, J. H. 2002.** Is there a role for arbuscular mycorrhizal fungi in production agriculture? *Plant and Soil* 244(1-2):263-271.
- Ryan, M. H., Small, D. R. and Ash, J. E. 2000.** Phosphorus controls the level of colonisation by arbuscular mycorrhizal fungi in conventional and biodynamic irrigated dairy pastures. *Australian Journal of Experimental Agriculture* 40(5):663-670.
- Schachtman, D. P., Reid, R. J. and Ayling, S. M. 1998.** Phosphorus uptake by plants: From soil to cell. *Plant Physiology* 116(2):447-453.
- Schjørring, J. K. and Jensen, P. 1984.** Phosphorus nutrition of barley, buckwheat and rape seedlings. I. Influence of seed-borne P and external P levels on growth, P content and P/P-fractionation in shoots and roots. *Physiologia Plantarum* 61:577-583.
- Schneider, A. and Morel, C. 2000.** Relationship between the isotopically exchangeable and resin-extractable phosphate of deficient to heavily fertilized soil. *European Journal of Soil Science* 51(4):709-715.
- Schroeder, J. I., Delhaize, E., Frommer, W. B., Guerinot, M. L., Harrison, M. J., Herrera-Estrella, L., Horie, T., Kochian, L. V., Munns, R. and Nishizawa, N. K. 2013.** Using membrane transporters to improve crops for sustainable food production. *Nature* 497(7447):60.
- Smith, S. E., Jakobsen, I., Grønlund, M. and Smith, F. A. 2011.** Roles of arbuscular mycorrhizas in plant phosphorus nutrition: Interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. *Plant Physiology* 156(3):1050-1057.
- Strong, W. M. and Soper, R. J. 1974a.** Phosphorus utilization by flax, wheat, rape, and buckwheat from a band or pellet-like application. I. Reaction zone proliferation. *Agronomy Journal* 66:597-601.
- Strong, W. M. and Soper, R. J. 1974b.** Phosphorus utilization by flax, wheat, rape, and buckwheat from a band or pellet-like application. II. Influence of reaction zone phosphorus concentration and soil phosphorus supply. *Agronomy Journal* 66:601-605.
- Sultenfuss, J. and Doyle, W. 1999.** Functions of phosphorus in plants. *Better Crops* 83(1):6-7.
- Sutton, P. J., Peterson, G. A. and Sander, D. H. 1983.** Dry matter production in tops and roots of winter wheat as affected by phosphorus availability during various growth stages. *Agronomy Journal* 75:657-663.
- Syers, J., Johnston, A. and Curtin, D. 2008.** Efficiency of soil and fertilizer phosphorus use., *FAO Fertilizer and Plant Nutrition Bulletin* No. 18.(FAO: Rome).
- Tomasiewicz, D. J. 2000.** Advancing the understanding and interpretation of plant and soil tests for phosphorus in Manitoba Ph.D. Thesis, University of Manitoba, Winnipeg, MB.
- Vance, C. P., Uhde-Stone, C. and Allan, D. L. 2003.** Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytologist* 157(3):423-447.



**Yang, S.-Y., Huang, T.-K., Kuo, H.-F. and Chiou, T.-J. 2017.** Role of vacuoles in phosphorus storage and remobilization. *Journal of experimental botany* 68(12):3045-3055.