IDENTIFICATION OF PHOSPHORUS EFFICIENT POTATO CULTIVARS

By

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To my family

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LIST OF ABBREVIATIONS

$^{\circ}C$	Degrees Celsius
A	Atlantic
Al	Aluminum
cm^2	Square centimeters
DAP	Days after planting
g	Gram
GWS	Genome-wide selection
HB	Harley Blackwell
IFAS	Institute of Food and Agricultural Sciences
kg	Kilograms
kg/ha	Kilograms per hectares
LC	La Chipper
M	Marcy
MAS	Marker-assisted selection
mg	Milligrams
mL	Milliliters
P	Phosphorus
Pn	Photosynthetic rate
ppm	Part per million
PSB	Phosphorus solubilizing bacteria
PUE	Phosphorus use efficiency
RB	Relative biomass
RL	Red LaSoda
Rubisco	Ribulose bisphosphate carboxylase

S	Satina
SLW	Specific leaf weight
TCP	Tri-Calcium Phosphate
WAP	Weeks after planting
YG	Yukon Gold

Abstract of Thesis Presented to the Graduate School
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As a nonrenewable mineral resource, mineable phosphate rock will be depleted in a few decades across the world. Efficient use of Phosphorus (P) becomes imperative for sustainable crop production. Use of P-efficient cultivars can lead to reduced P fertilizer consumption and is an important priority to adapt to the dwindling P resource worldwide and to sustain food security. This research included a two-year pot experiment, one-year field experiment, and hydroponics trial. Seven potato (*Solanum tuberosum* L.) cultivars (‘Atlantic’, ‘Harley Blackwell’, ‘La Chipper’, ‘Marcy’, ‘Satina’, ‘Red LaSoda’, and ‘Yukon Gold’) widely grown in Florida were tested in this study. In pot and field experiments, potatoes were grown on a low P sandy soil without or with 59 kg/ha P to compare the cultivars’ ability for P utilization and mobilization. Plant photosynthetic rate, SPAD reading, specific leaf weight, P concentration, P utilization efficiency, rhizosphere P concentration were measured in this study. The hydroponics trial was conducted in green house to understand the relationship between root: shoot ratio and P supply.

The pot and field experiments demonstrated that ‘Harley Blackwell’ and ‘Satina’ were P efficient cultivars with greater P mobilization ability as compared to the other

tested cultivars, because of their great relative biomass and P accumulation. ‘Harley Blackwell’ and ‘Satina’ performed as well in the soil without supplemental P as the soil with P application. ‘Red LaSoda’ showed as a P responsive cultivar, which shoot and tuber yield increased as P rate increased but the growth was significantly reduced without P application as compared to the other cultivars. The result in the hydroponics trial was agreed with those of the pot and field experiments.

The biodiversity of potato germplasm in mobilizing insoluble phosphate and utilizing limited bioavailable P was demonstrated in this study; however, further studies are needed to evaluate this trial using a large pool of germplasm. This genetic diversity for P-use efficiency provides great opportunities for us to mitigate the potential P crisis in potato production.

CHAPTER 1
LITERATURE REVIEW

Potato (*Solanum tuberosum* L.) is an important food crop worldwide, with an annual production of 295 million Mg (National Potato Council, 2011). In 2010, total potato production in the USA was 18 million Mg, ranked fifth in the world (Vanderzaag and Horton, 1983). Potato is also one of the major winter/spring crops grown in Florida. St. Johns, Putnam and Flagler counties are the main production area in the state. (USDA National Agricultural Statistics Service, 2011). The warm and long day length winter in Florida has allowed the potato season start earlier than other areas, which in favor of the better price for Florida potatoes. There is about 33,000 to 37,000 acres of potato grown in Florida annually (National Potato Council, 2013). Potato is a high nutrient demand crop, which responds to Phosphorus (P) fertilization vigorously and is not tolerant to low-P soil (Alvarez-Sanchez et al., 1999; Dechassa et al., 2003). Institute of Food and Agricultural Sciences (IFAS) P recommendation rate is 120 lbs/acre, i.e. the annual P use for Florida potato production is approximately 2,100 tons. However, Florida's soil for potato production area is usually rich in P. The high P application rate is necessary because the P in soil is fixed and unavailable to potato plants. Potato production is distributed throughout a wide geographic area (47°S-65°N) (Hijmans, 2001). With adaption to such a range of growing conditions, there is a considerable biodiversity in potato germplasm, which provides a useful source for selecting P efficient genotypes.

The Importance and Limitation Of Phosphorus

Along with nitrogen (N) and potassium (K), P is one of the major nutrients essential for plant growth and development. Phosphorus plays an irreplaceable role in several key functions, including photosynthesis, respiration, energy transfer, sugar and starch transformation and nutrient translocation. 82 % of world P production is used on crop production (Al-Abbas and Barber, 1964), since modern agriculture mainly uses P fertilizers to meet the plant P demand. To ensure food security of the growing world population, crop production has significant increase in P consumption.

The major resources of profitable phosphate mines can categorize into three groups: Sedimentary P deposits, Igneous P deposits, and Biogenic P deposits. Among the three groups, sedimentary P deposits are the most common on the earth, it can be found on every continent and with varied ranges of age. Around 80% of commercial phosphate mines are obtained from marine sedimentary deposits (Follmi, 1996). About 80 % of world P production comes from nonrenewable sedimentary reserves.

Due to the global population growth and the food demand and P fertilizer requirement both increase. However, the economically exploitable P reserves will be depleted within 50 years (Cisse and Mrabet, 2004). Because no P substitute exists, the increased the cost for mining P and the depletion of P reserves may seriously threaten the global food security. According to the World Bank, rock phosphate price got a major leap during 2007, and hit the highest price to US $430 per metric ton, in Aug, 2008 (The World Bank, 2013). In 2013, the price of rock phosphate was around US $170 per metric ton, which was 4.5 times more than ten years ago. In US, phosphate rock ore was mainly mined in Florida and North Carolina. US imports rock phosphate mainly from Morocco, which provides more than 80% of the import.

In addition to the limitation of the reserve, the efficiency of applied P fertilizer is usually lower than 20% (Shenoy and Kalagudi, 2005). Soil usually contain sufficient amount of P compounds, which ranging from 200 to 3000 mg/kg, averaged at 1200 mg/kg (Harrison, 1987). For those cultivated soil, the soil P concentration was even greater because of the routine P fertilizer application, but the rapid transformation from the applied P fertilizer to unavailable forms to plants is the main obstacle for keeping plants from uptake. The form of P present in the soil is depended on soil pH. There are many different forms of P occur in soil, and that can be categorize into three pools, which are water soluble P, active P, and fixed P. The soluble P pool is the smallest, only few pounds of P per acre (Mardamootoo et al., 2013). The soluble P is most common in orthophosphate form, but some organic P may exist as well. Orthophosphate form is the only P form that count as plant available. Orthophosphate include H_3PO_4, $H_2PO_4^-$, HPO_4^{2-}, and PO_4^{3-}. In the pH range from 4 to 10, $H_2PO_4^-$ and HPO_4^{2-} would be dominant. Plants would deplete the orthophosphate within the rhizosphere rather rapidly if no replenishment for soluble P pool occurs in time. The active P pool is composted by the solid phase of P which is relatively easy to be released into soil solution. The active P pool serves as the source for soluble P pool. Since the size of soluble P form is so small, the active P form is the actual main source of plant available P. The fixed P pool is where most of P in the soil locates, it contains very insoluble inorganic P compounds and hardly mineralizable organic P compounds. The formation of insoluble inorganic P compounds is determined by the soil pH. In weathered acidic soils (mainly ultisols and oxisols), P tends to bind with aluminum (Al) and Iron (Fe), and form Aluminum phosphate ($AlPO_4$) ($K_{sp}=9.84\times10^{-21}$) and Iron (III) phosphate ($FePO_4\cdot2H_2O$) ($K_{sp}=1.0\times10^{-22}$). In calcareous and alkaline calcareous soils (mainly aridisols), P tends to bind with calcium (Ca) and magnesium (Mg), and the form calcium phosphate ($Ca_3(PO_4)_2$)

(K_{sp}= 2.07×10^{-33}) and magnesium phosphate ($Mg_3(PO_4)_2$) (K_{sp}=1.04×10^{-24}). Because the K_{sp} is so small, those fixed P compounds have minimum contribution to crop growth in the soil. One of the challenges of modern agriculture is to figure out how we can increase the solubility of these compounds and mobilize the fixed P to plant available form. So far, we rely on great amount of P fertilizer application to sustain crop production. However, not only the limitation of P reserve, the runoff from excess P applied agricultural soil may also pollute surface water resulting in contamination of water quality, which is also called-eutrophication (Carpenter, 2008). To alleviate the situation of potential P crisis and environmental risk, scientists have been working on the strategy to enhance plant Phosphorus use efficiency.

Phosphorus Deficiency Symptoms

Phosphorus deficiency has great impact on crop production, and that including potato (Hegney and McPharlin, 1999; Hegney et al., 2000). Phosphorus is an essential component in many structures and enzyme activities for plant; including nucleic acids, phospholipids, phosphoproteins, sugar phosphates, enzymes, energy-rich phosphate compounds, any phosphorylation required enzyme activity, and carbon metabolism (Sinclair and Vadez, 2002). The sufficient concentration of inorganic P (Pi) in plant cytoplasm is usually falling in the range of 5-10 mM (Bieleski, 1973). Stable cytoplasmic Pi concentration is vital for several enzyme activities and synthesis, which including ribulose bisphosphate carboxylase (Rubisco). Studies have found that P and Rubisco's concentration were positively related (Brooks et al., 1988; Warren and Adams, 2002). Inorganic P in plants may present as different forms, which is depended on the physical compartments (cytoplasm, vacuole, apoplast and nucleus) Pi locates, and the pH of these compartments (Schachtman et al., 1998). In cytoplasm where pH is 7.2, Pi is approximately equally partitioned between the ionic forms $H_2PO_4^-$ and HPO_4^{2-}. In the more acidic compartments, vacuole and apoplast, $H_2PO_4^-$ will be the dominant species. Phosphorus is relative mobile within the plant, there were many studies focusing on P acquisition , endogenous P pool size, and P exchange between different compartments (Bieleski, 1973; Jain et al., 2012; Lei et al., 2011; Pratt, j.,Boisson,A.M.,Gout,E., Bligny,R.,Douce,R.,Aubert,S., 2009; Schachtman et al., 1998). Cytoplasm Pi concentration and homeostasis are considered most important to enzyme regulation and signal transduction (Mimura, 1999; Rausch,C., Bucher,M., 2002; Shin et al., 2004). Despite the short term fluctuation of external P availability, cytoplasm Pi concentration tends to remain relatively constant at the expense of the Pi in vacuole (Lee et al., 1990; Lee and Ratcliffe, 1993). Long term P deprivation will significantly reduce cytoplasm P concentration (Gout et al., 2011). In that case, plant photosynthesis and carbon fixation will decrease significantly (Cakmak, 2002; Qiu and Israel, 1994; Rao and Terry, 1995).

Phosphorus is a key substrate and modulator for multiple photosynthetic and carbohydrate metabolism enzymes, including Rubisco, phosphoribulokinase, fructose 1,6-bisphosphatase, sucrose phosphate synthase and ADPglucose pyrophosphorylase (Hurry et al., 2000; Nielsen et al., 1998; Paul and Stitt, 1993; Paul and Pellny, 2003). The deficiency of P leads to the inhibition of photosynthesis at several levels. The exchange of Pi and triose phosphate between the chloroplast and cytoplasm is crucial on regulation of photosynthetic and carbohydrate metabolism (Winter and Huber, 2000). Both Rubisco activity and the capacity for ribulose bisphosphate regeneration are affected by P deficiency for several plant species (Jacob and Lawlor, 1991; Lewis et al., 1994; Reich and Oleksyn, 2009; Warren and Adams, 2002). RuBP regeneration capacity can be reduced if the availability of fixed carbon, the initial activity of the Calvin cycle enzymes, and the supply of ATP and NADPH are limited (Rodriguez et al., 1998).

Generally speaking, plant growth is more affected by P limitation than the rate of photosynthesis per unit of leaf area (Jacob and Lawlor, 1991; Terry and Rao, 1991). Increasing specific leaf weight (SLW) is usually accompanied with P deficiency (Field and Mooney, 1986; Schlesinger and Chabot, 1977; Witowski and Lamont, 1991). It is common to find smaller and thicker leaf on P deficient plant. In previously study, photosynthesis per unit of leaf area has been positively correlated to specific leaf weight for several species (Nelson and Schweitzer, 1988), and the high SLW can be explained by the greater concentration of the photosynthate accumulation. However, it is also been reported that phosphate and potassium, which are essential for photosynthesis, were negatively related to SLW (Luquet et al., 2005; Pettigrew, 1999; Zia-ul-Hassan and Arshad, 2010). The availability of carbon assimilates in leaf might not be the major responsible factor for the inhibition of leaf area expansion and plant growth (Schlesinger and Chabot, 1977; Sobrado, 2012). Cell expansion is driven by turgor pressure (Lockhart, 1965), which is extremely sensitive to water deficit (Tardieu et al., 2011; Thomas et al., 1989). Plant P status can positively affected by plant water status (Gutiérrez-Boem and Thomas, 1998); P deficiency could reduce leaf turgor and stomatal conductance on many plant species include cotton, cassava, wheat, rice, soybean, strawberry and corn (Chen and Lenz, 1997; Gutiérrez-boem and Thomas, 1999; Radin and Eidenbock, 1984; Sato et al., 1996). Therefore, increasing SLW under P limited condition can be better explained by the water deficit rather than greater photosynthesis per unit of leaf area.

In a low P condition, increase root shoot ratio is common on many crops (Cakmak et al., 1994; Ciereszko and Barbachowska, 2000; Fernandes and Soratto, 2011; Muller et al., 2007). The P uptake efficiency could be enhanced by a greater root shoot ratio (Machado and Furlani, 2004; Schenk, 2006). Another common plant P deficient symptom is purple leaf/stem, which is the result of anthocyanin accumulation. Low phosphate status in plant induced the expression of the genes that regulate the secondary metabolism of anthocyanin biosynthesis (Hammond et al., 2003). Anthocyanins are red or purple flavonoid, which can protect nucleic acids from UV damage and chloroplasts from photoinhibitory damage caused by P-limited photosynthesis (Hoch et al., 2001; Nilsson et al., 2012; Zeng et al., 2010).

Mechanism of Phosphorus Efficiency in Plants

Phosphorus efficiency is the ability of plant species or cultivars to maintain high yield under P-limiting condition (Gourley et al., 1993). In P limited environment, plants have developed several mechanisms to overcome P deficiency, such as improving the ability of a plant to take up more P in alow P condition, and the ability of a plant to produce greater biomass per unit P taken up. The mechanisms that enhancing plant P uptake efficiency including modification of root architecture (Balemi and Schenk, 2009), development of large and shallow root system (Rubio et al., 2001), more secondary root (Zhu and Lynch, 2004), more root hairs and thinner roots(Bates and Lynch, 2000; Fohse et al., 1991), increasing root exudates (low molecular weight organic acids, protons, chelators and enzymes) (Bhattacharyya et al., 2013), association with mycorrhiza (Miyasaka and Habte, 2001), production of cluster roots and expression of high affinity P transporters. All of which contribute to increased P uptake efficiency of the plant. There are several mechanisms have been reported related to enhancing P utilization efficiency: alternative P-independent enzymes, glycolytic pathways, efficient cytoplasmic P homeostasis and better ability to translocate P from other plant parts (Czarnecki et al., 2013). Enhancing the above morphological, physiological, biochemical, and molecular adaptation mechanisms expression in P deficiency condition through plant breeding can greatly increase P use efficiency in crop production.

Root morphology

To overcome the low-P stress and increase P uptake, plant species may develop various adaptation mechanisms to access any available P or mobilize every insoluble P in soil; one of the most common morphological adaptations is enhancing root surface area to increase root soil interface. Since P is highly immobile in soil, unlike nitrogen and potassium which readily taken up by root via both mass flow and diffusion, only small amount (1-5%) of P is driven by mass flow, and the amount growing roots intercepted is even lower. Most of the plant P demand is delivered via diffusion by physically contact with root surface, but phosphate diffusion coefficients in soil is generally low, which range from 0.3 to 3.3×10^{-13} m^2s^{-1} (Clarksib and Scattergood, 1982). Increasing root length, root hair density, and decreasing root radius resulting in a higher ratio of surface area to volume soil are commonly observed on P deficient plant, and those changes are consider P efficient traits (Foehse and Jungk, 1983; Gahoonia and Nielsen, 1998; Jungk, 2001; Schenk and Barber, 1979).

Because of the immobility of P in soil, cultivated topsoil usually hold most of P compare to other layers. Plant would alter the gravitropism of basal root, and increase the proportion of carbon allocation to adventitious root growth and respiration to explore extended area in topsoil (Bai et al., 2013; Bonser et al., 1996; Nielsen et al., 1998). The response of root gravitropism to Phosphorus availability varies among genotypes, and genotypic adaptation to low Phosphorus availability is correlated with the ability to allocate roots to topsoil under P stress (Bonser et al., 1996; Liao et al., 2001).

Root hair is differentiated from root epidermis cells, which is responsible for most of the ion absorption. Also, the fine root hair has allowed it to penetrate into void, cracks, and pores of the ambient soil (Misra and Gibbons, 1996). Hence, root hairs get more effectively contact with soil. The presence of root hair could greatly increase ions uptake by many fold, especially for those sparingly soluble nutrients, such as P (Datta et al., 2011; Gahoonia and Nielsen, 1997; Keyes et al., 2013). A wide variation exist in root hairs within plant varieties (Krasilnikoff et al., 2003), and advances in genetics provide the capability to breed plants with improved root hairs trait, by manipulation of length and density to provide potential enhance P uptake efficiency (Gahoonia and Nielsen, 2004; Jungk, 2001; Lambers et al., 2013; Zhu et al., 2005).

The advance of sampling device on root study, the root system is no longer considered the 'hidden half' of a plant (Bohm and Kopke, 1977; Nakano et al., 2012; Vogt et al., 1998), and the scientists are able to observe and evaluate the interaction between fertilizer rate and root parameter. More studies have been focus on the root development and nitrogen rates interaction rather than P rates (Munoz-Arboleda et al., 2006). Previous study had reported potato root system and its interaction with fertilizer placement (De Roo and Waggoner, 1961; Weaver, 1926), but no information about the root development with different P rates for potato. In a greenhouse experiment, Dechassa et al have found that though potato had long and dense root hair as cabbage, and potato's P efficiency was much lower than cabbage (Dechassa et al., 2003). This study revealed that there were other major factors to influence P efficiency besides morphological root characteristics such as long root hairs. Despise the advance of root sampling device; there are still many obstacles to observe root development. Also, root development may vary with soil type, irrigation and microorganisms in the soil. All the above challenges need to be overcome to further understand potato root development and P rates relationship.

Proteoid root is another lateral root structure that has been reported relevant to plant P uptake efficiency. The term ‘proteoid’ is because proteoid roots were first discovered in the Proteaceae (Purnell, 1960).Watt and Evans (1999) define proteoid root as an entire root from any species that forms one or more clusters along its length. Plant species with proteoid roots usually do not form mycorrhizal symbioses, and can grow in soils with sparsely soluble nutrients (Skene, 1998). Phosphate compounds which bonded with Fe, Al, and Ca bonded P, in soil are relative readily to be mobilized by proteoid roots, because proteoid roots exude large quantities of organic acid, such as malate and citrate under P stress (Shane et al., 2013; Zeng et al., 2013; Zhu et al., 2005). Nutrition’s availability does affect proteiod root formation. Most of the plant only form proteoid root in P deficient condition (Campbell and Sage, 2002; de Campos et al., 2013; Keerthisinghe et al., 1998). Not all the plant species equipped with proteoid root. So far, 28 species from the Betulaceae, Casuarinaceae, Eleagnaceae, Leguminosae, Moraceae, and Myricaceae families have been reported with proteoid root (Watt and Evans, 1999). Researchers are studying on genetic regulation for proteoid root formation, and we may manipulate proteoid root to form in the other plant family by the advanced bioengineering technology.

Root exudates

Plant roots have the remarkable ability to secrete both low- and high-molecular-weight molecules into the rhizosphere in response to biotic and abiotic stresses (Bertin et al., 2003). To study root exudates require the suitable and accurate sampling procedures which allow non-destructive and repetitive sampling from soil-grown roots to enhance our understanding of the dynamics of related rhizosphere processes; scientists found that amino acid exudation rates were more affected by growth conditions and sampling procedures than organic acid exudation (Oburger et al., 2013).

Plant root exudates including a complex mixture of organic acid anions (citric, oxalic, malic, fumaric, succinic, acetic, butyric, valeric, glycolic, piscidic, formic, aconitic, lactic, pyruvic, glutaric, malonic, aldonic, erythronic, and tetronic acid)(Fox and Comerford, 1990; Lipton et al., 1987), amino acid, inorganic acid (HCO_3^-, OH^-, H^+), gaseous molecules (CO_2,H_2), enzymes (phosphatase), sugars, vitamins, purines/nucleosides(Fries and Forsman, 1951), root border cells, and mucilage (Dakora and Phillips, 2002; Eltrop and Marschner, 1996; Rovira, 1969) which direct or indirect facilitate the acquisition of mineral nutrients in rhizosphere required for plant growth, especially for P acquisition (Gardner et al., 1983; Ohwaki and Hirata, 1992). Plant available form of inorganic P in the soil is related to the soil pH which can be adjusted by the acid root exudates. Also, the organic P in the soil needs to be digested by microorganisms or phosphatase to become plant available form. The indirect effects are the influence on rhizosphere microflora. The soil microorganisms present in the rhizosphere that capable of solubilizing inorganic P were benefit from the root exudates (Kucey et al., 1989; Lambers et al., 2013; Wang et al., 2005). Therefore, root exudates indirectly effects the P mobilization by effects those microorganisms in the rhizosphere.

Root exudates not only enhance the availability of sparingly soluble P in the soil, it sometime also involve in heavy metal tolerance, such as aluminum and cadmium (Ward et al., 2011; Xu et al., 2012; Zoghlami et al., 2011). In acid soil, aluminum (Al) toxicity and P deficiency often coexist. Though the underlying mechanism for crop to adapt this condition is still poorly understood, recent research on cereals and legumes have found that P addition to acid soils could enhance Al tolerance, especially for the P-efficient genotype which release more malate, citrate, and oxalate in different level under acid soils condition (Arunakumara et al., 2013; Kikui et al., 2007; Klug and Horst, 2010; Liang et al., 2013; Liu et al., 2009). Among all the root exudates, organic acid is the major one involve in P mobilization (Kania et al., 2003). Study on P solubilizing bacteria (PSB) also found that most of the PSB solubilize mineral phosphates by secreting a variety of organic acids. And among these organic acids, citrate and malate are the most effective one on P mobilization (Chen et al., 2006; Gietl, 1992; Gyaneshwar et al., 1998; Kochuan, 1995; Martinoia and Rentsch, 1994; Schulze et al., 2002).

Under P stress, the synthesis of malate and citrate in proteoid roots requires the aid of enzymes phosphoenolpyruvate carboxylase, malate dehydrogenase, and citrate synthase (Yu et al., 2012). Manipulation of the expression of these enzymes could result in plants with greater P accumulation and improved tolerance to Al (Chen et al., 2011; Johnson et al., 1994; Johnson et al., 1996; Johnson et al., 1996; Liang et al., 2013). Studies on barley, wheat and lupin have shown that P efficient cultivars have greater root citrate or malate secretion induced by P deficiency and excess of Al (Kania et al., 2003; Li et al., 2000). It showed that lupin root exudates contained high concentration of citrate compared with wheat, and lupin has better Phosphorus acquisition efficiency while rock phosphate as the only P source (Akhtar et al., 2008; Sepehr et al., 2012). All the above findings confirmed that root organic acid secretion is playing an important role on enhancing crop P acquisition efficiency.

Current studies have focused on using molecular genetic technique to improve crop root exudation of organic acid (Gao et al., 2010; Nilsson et al., 2007; Wang et al., 2013; Zhou et al., 2008). How we apply the technique to increase potato root exudates will require more genetic research.

P Utilization Efficiency

Besides improving P acquisition, Plants also increase the efficiency of P use during P starvation via up-regulation of a wide array of P-starvation inducible hydrolases that scavenge and recycle P from intra- and extracellular organic P compounds (Plaxton and Tran, 2011). Phosphorus utilization efficiency is the ability of a plant to produce higher dry matter per unit of P absorbed (Richardson et al., 2011). The details regarding the mechanism of greater P utilization efficiency is not clearly understood, but it could be related to the ability of a plant in releasing Pi from the vacuole to the cytoplasm (cytoplasmic P homeostasis) or to selective allocation of P between cytoplasm and vacuole in favor of cytoplasm that ensure sufficient Pi concentration in metabolically active compartments for normal functioning of plant metabolism (Balemi and Negisho, 2012). Also, using alternative P-independent enzymes, metabolic pathways, and energy sources could also increase plant internal P utilization.

Identification of P Efficient Genotypes

Using P efficient cultivars in agricultural industry could greatly reduce the consumption of P resource and upgrade crop production (Byerlee, 1996). How to select the P efficient cultivars become critical to ensure our food security. Hydronponics system is often used in plant nutrition research; because it allows us to manipulate the growing conditions as designed, such pH, temperature, electrical conductivity, nutrient composition, and aeration. It also allows scientist to analyze and monitor the growth solution relatively easy and without disrupting plant growth (Kim et al., 2013). However, hydroponics condition may have impact on plant root morphology or general plant growth, field experiment is still needed to conform the finding. Several studies have used hydroponics system with different supply of P to select P efficient cultivars or examine the morphological and physiological responses (Beebe et al., 2006; da Silva et al., 2008; da Silva and Maluf, 2012; Sain et al., 1994; Wang et al., 2008; Wang et al., 2013). Rock phosphate or tri-calcium phosphate are often used as sparingly soluble P source in nutrient solution to mimic the low P availability in the soil, and to exam cultivars P mobilization ability. In phosphate-plant study, plant biomass, P concentration, root shoot ratio, specific leaf weight, root exudates, root-mycorrhiza association, root morphology (root length, diameter, angle, density, root hair and proteoid root) were often used as an index to evaluate P efficiency. Generally, P efficient cultivars show greater root shoot ratio, total biomass, root exudates, root hair density, shallower and thinner root system under P limited environment. Phosphorus concentration in plant is measured to calculate P uptake, P-utilization efficiency (PUE) and P efficiency ratio (PER), specific P uptake (SPU) were as follow:

P uptake (mg plant^{-1}) = $\mathrm{P\ concentration\ (mg/g)} \times \mathrm{dry\ matter\ (g/plant)}$ (1)

(Akhtar et al., 2008)

$$\text{PUE} = \frac{\text{Shoot dry matter (g plant}-1)}{\text{P (mg } plant^{-1})} \text{(2) (Elloitt and White, 1994)}$$

$$\text{PER} = \frac{\text{Total dry matter (g plant}-1)}{\text{Total dry matter}} \text{(3) (Blair and Godwin, 1991)}$$

$$\text{SPU} = \frac{\text{Total P in plant (mg)}}{\text{root dry weight (g)}} \text{ (4) (Zhu et al., 2001)}$$

Among those P efficiency evaluation index, which index or trait may best predict potato cultivars P efficiency to tuber production is not clearly understood. Greenhouse experiment alone with field trial is necessary to help us better understand potato P use efficiency. After identify P efficient potato cultivars and the elite traits associate to it, one can apply molecular technique to further accelerate the breeding process.

Marker-assisted selection (MAS) is an important technique for P efficient cultivars genome-wide selection (GWS). MAS could have two times more genetic gain over phenotypic selection, maintain recessive alleles, speed up the backcrossing process, and be more accurate for those traits that are difficult to manage through phenotypic selection, such as root traits (Xu and Crouch, 2008). Marker development require previous knowledge of the given crop genome. Identification and fine mapping regarding P efficient QTL on different plant species is still developing. The study on P efficient gene expression are focusing on those major crop, such as maize, wheat, lupin, soy bean (Beebe et al., 2006; Chen et al., 2009; Liao et al., 20064; Yan et al., 2004; Zhu et al., 2005; Zhu et al., 2005). Several P efficiency proteoid root formation related markers been identified, but how to apply it on potato will required our effort on further genetic study. So far, only little information regarding potato P efficient traits gene expression has been reported (Hammond et al., 2003).

Summary

Developing P efficient cultivars is very important to world food security. Several traits contribute to plant P efficiency. Identifying the P efficient trait that is objective and consistent for potato crop production is needed. Combining the knowledge of physiological and morphological responses to P deficiency may lead us to select elite cultivars that better adapt to P limited conditions. As soils are rich in mineral P in Florida, the cultivar equipped with outstanding P mobilization ability is desirable for Florida's sustainable potato production. Researches in green house and in field are required to understand the most effective trait to potato P efficiency.

CHAPTER 2
POT EXPERIMENT

Introduction

Since the Green Revolution and environmental movement of the 1960s and 1970s, new constraints, such as rapid raise in fertilizer price, environmental regulations and mineral depletion, have had serious impacts on the crop production. Repeated application of excess P fertilizers has increased the demand for P fertilizers (Sharpley and Withers, 1994), hence the need for additional mining. The above practice also contributes to P loading to adjacent water bodies and related environmental quality impacts (Ticconi and Abel, 2004). One estimate of worldwide annual usage of P fertilizers is 39 million tons (Heffer, 2009). Current projections indicate that the annual P fertilizer need for worldwide agricultural production by 2050 will be 83.7 million tons (Tilman et al., 2001). Depletion of available P reserves is estimated to occur in 69-100 years, assuming that P fertilizer usage would increase at a rate of 0.7 to 2.0% per year till 2050, and no increase beyond 2050 (Smit et al., 2009). The high-grade P reserve in the USA is expected to be depleted in 2033 (USGS, 2009).

Phosphorus is a nutrient element essential for plant growth and development. The deficiency of P leads to retardation of terminal growth, poor root and vine growth, delayed maturity, poor yield and quality (Alvarez-Sanchez et al., 1999; Fleisher et al., 2013; Grewal and Singh, 1976; Locascio and Rhue, 1990; Mccollum, 1978; Pursglove and Sanders, 1981; Singh, 1987). Depending on the application methods, crops, irrigation and soil types, current P-use efficiency ranges from 15 to 30% (Syers, J.K., Johnston A.E., Curtin, D., 2008). Phosphorus application rates for different crops have increased globally during the last few decades, particularly since 1990 (Buckingham and Jasinski, 2010). The increasing demand of P, in turn, accelerates the depletion of P reserve. The expected increase of P fertilizer cost in future years may impact global food security because of the continued high demand for P fertilizers and depletion of P reserves. Therefore, there is an urgent need to explore options to enhance P-use efficiency. There are two farming systems that can enhance P-use efficiency: high-input and high-output farming system and low-input and high-output farming system (Murphy et al., 2005; Van Alphen and Stoorvogel, 2000).To achieve low-input and high-output, an elite genotype with enhanced P-use efficiency is needed. Conventional farming systems are basically high-input and high-output. As nonrenewable mineral resources continue to be depleted, low-input systems become increasingly important.

Several strategies have been evaluated to improve phosphate mineral solubility to increase P availability. Use of rhizosphere bacteria to improve P solubility has not been successful because of poor ecological fitness, low metabolite production, variability in inoculant-delivery systems, and inconsistent performance in field applications (Shenoy and Kalagudi, 2005). Phosphate in soils is present in insoluble forms and only sparingly available to plants in highly weathered soils of the tropics and subtropics, as well as in calcareous/alkaline soils. The morphological characteristics are different among plant genotypes and play a key role in P acquisition when grown on low P soils.

Potato is an important food crop worldwide, with an annual production of 295 million ton (National Potato Council, 2011). In 2010, total potato production in the USA was 18 million ton, ranked as the fifth in the world. Inspecting the germplasm for P-use efficiency could potentially increase the future potato yield without excess P application.

The evaluation of wheat cultivars has shown that in low-P stress growing conditions, the grain yields of the P-efficient wheat genotypes were 72 to 88% greater than those of the P-inefficient genotypes (Li et al., 1995; Wang et al., 2005). Poor management of P fertilization in agricultural production contributes to degradation of surface water quality in addition to low P-use efficiency. One approach to minimize the above problems is to explore the current germplasm resources to identify P-efficient genotypes that can be used in the potato variety improvement program. The objectives of this study were to: (i) identify P-efficient potato cultivars and (ii) explore the physiological traits (photosynthetic rate, shoot biomass, leaf greenness) that contribute to enhanced P mobilization from the soil P reserve and increase P uptake.

Materials and Methods

Tuber Growing Condition and Nutrients Management

Certified potato seeds of most commonly grown cultivars in Florida (‘Atlantic,’ ‘Harley Blackwell’, ‘La Chipper’, ‘Marcy’, ‘Satina’, ‘Red LaSoda’, and ‘Yukon gold’) were obtained from USDA, Beltsvillle, Maryland. One seed piece (approximately 85 g) was planted in a plastic pot (21.6 cm diameter and 20.3 cm deep) filled with 12 kg air-dried sandy loam soil collected from top 30 cm from an area located in Hastings, FL in 2012 and Gainesville, FL in 2013. The soil used in this experiment was Ellzey fine sand (sandy, siliceous, hyperthermic, Arenic Endoaqualf) (Soil Survey Staff, 1999; Acharya and Mylavarapu, 2011) form Hastings for both experiments. The bulk soil was amended with N and K at rates equivalent to 224 and 168 kg/ha (Zotarelli et al., 2013), using ammonium nitrate, and potassium sulfate, respectively. The treatments included: (i) no P applied, and (ii) IFAS recommended P application rate 59 kg/ha for low soil P concentration using triple superphosphate.

The experiment was conducted using a randomized complete-block design with three replicates. Each pot was irrigated by drip system with one emitter per pot to deliver 400 to 500 mL water every other day to reach field capacity. Plants were harvested 84 days after planting. Shoot and tuber were washed and chopped into slices then oven-dried at 70 °C till constant weight was achieved.Plant Tissue P Content Analysis

The oven-dried plant shoots were ground to pass a 40 mesh stainless steel sieve, and dry ashed (Kalra, 1998). Ground tissue sample was weighed (0.3±0.05g) into porcelain crucibles and placed in a Thermolyne Muffle Furnace (Cole-Parmer North America,Vernon Hills, IL). The temperature was increased at 10°C/min till 250°C, which was maintained for 30 min, and then increased to 550°C for 6 hours. The ash was cooled and 2.25 mL 6N HCl was added, 15 min later filtered through No.41 filter paper, and diluted to 50 mL with de-ionized water. P concentration was analyzed by Automated Discrete Analyzer (AQ2, SEAL Analytical, Hanau, Germany) based on US EPA Method 365.1 (U.S. environmental Protection Agency, 1993).

Photosynthetic Rate Measurement

Apparent photosynthetic rate (APR) was measured using Li-COR 6400 XT (LI-COR Inc, Lincoln, NE) under saturated photosynthetic photon flux density from an LED light source during 9 to 11 a.m. Flow rate was set at 500 $\mu mol \cdot mol^{-1}$ CO_2, relative humidity of the air in the leaf chamber was maintained at 70% and leaf temperature at 25 °C. The constant values of apparent photosynthetic rate and intercellular CO_2 concentration of each sample leaf were recorded after the monitor value stabilized.

Leaf greenness Measurement

SPAD meter (Konika Minolta, made in Japen, SPAD-502PLUS) was used to measure leaf chlorophyll content and measurements were made on 30, 36, 41, 44, 52, 58, 63, 70 days after planting. Shoots were harvested and dried in oven at 70 °C for 72 h and dry weights were recorded.

Soil P Extraction and Analysis

Root zone soil was collected by shaking off the soil from the roots. Soil samples were air dried and 2±0.2 g soil sample extracted with 20 mL Mehlich 3 extratant (Mehlich, 1984). The suspension was shaken for 5 min, filtered, and P concentration was analyzed by AQ2 (SEAL Analytical, Hanau, Germany).

Relative Biomass Calculation

Relative biomass (RB) was calculated as follows

$$RB = \frac{DM_t}{\overline{DM}_{ck}}$$

Where DM_t is the dry weight of tissue in a given treatment and $\overline{DM}_{ck}$ is the mean of dry weight at zero P applied.

Statistical Analyses

All data were subjected to analysis of variance using Statistical Analysis software JMP version 10 (SAS Institute Inc.). Student t test was used for evaluation of significance between the two means.

Results

The first pot experiment conducted in Hastings showed that cultivars and P application had significant impact on shoot biomass (Table 2-1). 'Yukon Gold' showed the least shoot biomass in both P and –P treatments (Figure 2-1A). Relative shoot biomass was greater in ‘Harley Blackwell’ and ‘Satina’ as compared to the other cultivars, while that of ‘Marcy’ and ‘Red LaSoda’ were the least (Figure 2-1B). Since the heavy rain at the end of the season, we were not able to collect the tuber yield data in this experiment.

The following year experiment was repeated in Gainesville, FL. The tuber yield was significantly influenced by P treatments, the cultivar differences were non-significant (Table 2-2). Most of the cultivars showed greater tuber yield with P application, except for ‘Yukon Gold’ and ‘Atlantic’ (Figure 2-2A). ‘Yukon Gold’ and ‘Atlantic’ showed greater relative tuber biomass while ‘Red LaSoda’ and ‘La Chipper’ were lower than the other cultivars (Figure 2-2B).

For the experiment conducted in Hastings, a significant difference in shoot P concentration of plants between -P *vs.* P-amended soil, and between cultivars was found (Table 2-3). In the non-P-amended soil, there were no significant differences among the cultivars with respect to shoot P concentration (Figure 2-3). In P-amended soil, however, the shoot P concentration of ‘La Chipper’ and ‘Red LaSoda’ was significantly greater than the other cultivars except ‘Marcy’. Shoot PUE was significantly influenced by cultivar (Table 2-4). In both with and without P application, ‘Harley Blackwell’ and ‘Satina’ showed greater or equal PUE than the other cultivars, while ‘Yukon Gold’ showed the least PUE.

The experiment in Gainesville showed that only P rate significantly influenced the tuber P concentration and no cultivar effect was found (Table 2-5). Also, tuber PUE was only influenced by P rate (Table 2-6). In non P treatment, though ‘Yukon Gold’ showed greater or equal tuber P concentration as compared to the other cultivars in non P treatment, its tuber PUE was the least (Figure 2-5, 2-6).Without P application, 'Satina' showed greater or equal tuber PUE as compared to the other cultivars.

Photosynthetic rate (Pn) of potato canopy in Hastings and Gainesville experiments were significantly affected by cultivar, time of measurement, and the interaction between cultivar and P application (Table 2-7, 2-8). In Hastings, 'Atlantic' and 'La Chipper' Pn were significantly greater or equal in P-amended soil as compared with that in the non-P-amended soil throughout the entire growth period (Table 2-7). In the early growing season (36 DAP), 'Red LaSoda', 'Satina' was significantly greater in the plants grown in P amended soil as compared to that of the plants in P-unamended soil. This difference was non-existent in the subsequent measurements, i.e. 48 and 64 DAP. At 48 DAP, no difference was found between P and no P amended treatment for all cultivars' Pn, but most of the cultivars showed greater or equal Pn without P application. At 64 DAP, only 'Atlantic' showed greater Pn with P application than without P application, and no difference was found for other cultivars between treatments.

The Pn response in the Gainesville experiment was not significantly affected by P application but by the cultivar, interaction between cultivar*P and P*time (Table 2-8). At 37 DAP, most of the cultivars, except 'Marcy' and 'Satina', showed no difference between P and -P treatment. No P treated 'Marcy' Pn was greater or equal to other cultivars regardless the P treatment at both 37 and 46 DAP. 'Harley Blackwell' also showed greater Pn without P than with P application at 46 DAP.

The SPAD readings for a given cultivar was similar regardless of the P treatments (Table 2-9). In both -P and P treatment, 'Harley Blackwell' was the greatest in SPAD, and 'Yukon Gold' was the least.

In the first and second pot experiment, P rate and the interaction between P and cultivars showed significant influence on root zone P concentration (Table 2-10, 2-11). In the first and second pot experiment of the non P treated pot, ‘Satina’ and ‘Yukon Gold’ showed greater or equal root zone P concentration as compared to the other cultivars (Figure 2-8). In the second experiment of the non P treated pot, ‘Yukon Gold’ showed greater or equal root zone P concentration, while ‘Atlantic’ showed the least as compared to the other cultivars.

Discussion

Potato response to P deficiency in the soil was cultivar dependent and the differences could be an index for us to identify the P efficient cultivars. The low relative biomass of ‘Red LaSoda’ for both shoot and tuber. However, ‘Red LaSoda’ showed high tuber yield and tuber P concentration with P application. This phenomenon suggested that ‘Red LaSoda’ was not able to adapt in the soil without P application, but it well responded to P fertilization. ‘Red LaSoda’ may be considered a P responsive cultivar, as evident from this cultivar’s high response to P amendment and poor performance under P stress.

Diffusion is the main mechanism for plant P uptake, and mass flow only account for only 1- 5% of the actual P uptake (McLaughlin et al., 1992). Thus, the depletion of P in rhizosphere is common for various plant species (Bhat and Nye, 1973; Jungk, 1996; Kraus et al., 1987; Owusubennoah and Wild, 1979). However, studies also showed that increase rhizosphere P concentration while sparingly soluble phosphate as the P source because of P stress triggered root exudates secretion dissolve the P from sparingly soluble phosphate (Bhattacharyya et al., 2013; Hoffland et al., 1989; Neumann and Romheld, 1999; Sepehr et al., 2012). Phosphorus deficiency can induce the release of root exudates (Kucey et al., 1989; Lambers et al., 2013; Wang et al., 2005), which can enhance the solubility of the fixed P in the rhizosphere, and increase extractable P concentration within the root zone. Dechassa et al (2003) found that potato P efficiency was more likely due to other major factors (ex. root exudates, P transporter) besides morphological root characteristics such as long root hairs. In this study, the soil we used was from Hastings potato field, which was constantly fertilized with P, the total P concentration in soil was 85 and 97 ppm for Hastings and Gainesville experiment, respectively. But those P in the soil was mostly in plant un-available form, in other word-sparingly soluble P. We supposed that the cultivars with better P mobilization ability should show greater P concentration in rhizosphere, but those with greater P-uptake efficiency should have lower P concentration. In both experiments, 'Yukon Gold' showed high root zone P concentration in non-P amended treatment. And the tissue P concentration in 'Yukon Gold' was also high. But due to the low PUE, 'Yukon Gold' was not considered as a P efficient cultivar.

SPAD reading is correlated to leaf chlorophyll content, and it is been reported to be highly related to nitrogen rate (Giletto and Echeverria, 2013).Among the tested seven genotypes, the leaf chlorophyll content showed a similar trend for both P and -P treatments. The genetic variations could be the main factor while nitrogen application was the same. 'Harley Blackwell' had the highest chlorophyll content while 'Yukon Gold' had the lowest on SPAD reading. The SPAD result positively correlated to the result of shoot and tuber biomass in first and second experiment. Since SPAD is very easy to measure, it could be used as an index to evaluate potato cultivars productivity, but it's not able to distinguish cultivar's P efficiency.

Cultivar, and Cultivar*P interaction effects on Pn were significant in both experiments. We were not able to find the significant correlation for Pn to P rate, and the result from two experiments was not consistence. Unlike the reports of showing there is a positive relation between P and Pn (Cakmak, 2002; Qiu and Israel, 1994; Rao and Terry, 1995), our study did not support the above relationship.

Summary

By comparing the physiological and morphological responses of the seven potato cultivars, we considered ‘Red LaSoda’ as a P responsive cultivar, while ‘Satina’ was considered as a P-efficient cultivar based on its responses in non P amended soil, high productivity and PUE for both shoot and tuber. Because of ‘Satina’s ability to utilize fixed P in non-P control, it could be an elite cultivar for the soil that rich in plant P but in plant unavailable form. Potato leaf greenness (SPAD) could be used as an index for general cultivar evaluation, but cannot be used to evaluate differences in cultivar’s P efficiency. Though ‘Yukon Gold’ lack of P utilization ability, its great P mobilization ability is worth for further study on the root exudates production.

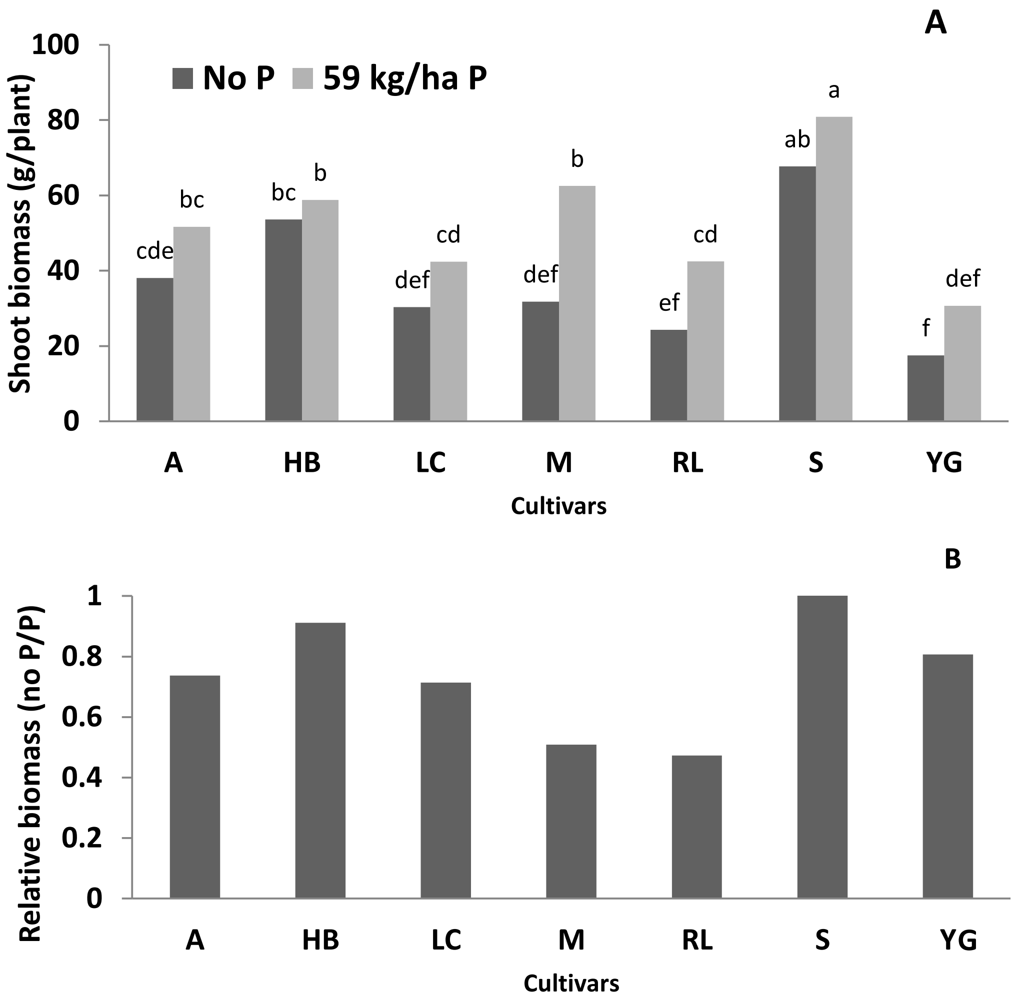

Figure 2-1. Shoot biomass A) and relative biomass B) of seven cultivars (84 days after planting) grown in a sandy soil with no-P or with 59 kg/ha P application of the pot experiment conducted in Hastings, FL. A-‘Atlantic’, HB-‘Harley Blackwell’, LC-‘La chipper’, M-‘Marcy’, RL-‘Red LaSoda’, S-‘Satina,,,’ and YG-‘Yukon Gold’. Means followed by similar letters are not significantly different at P≤0.05.

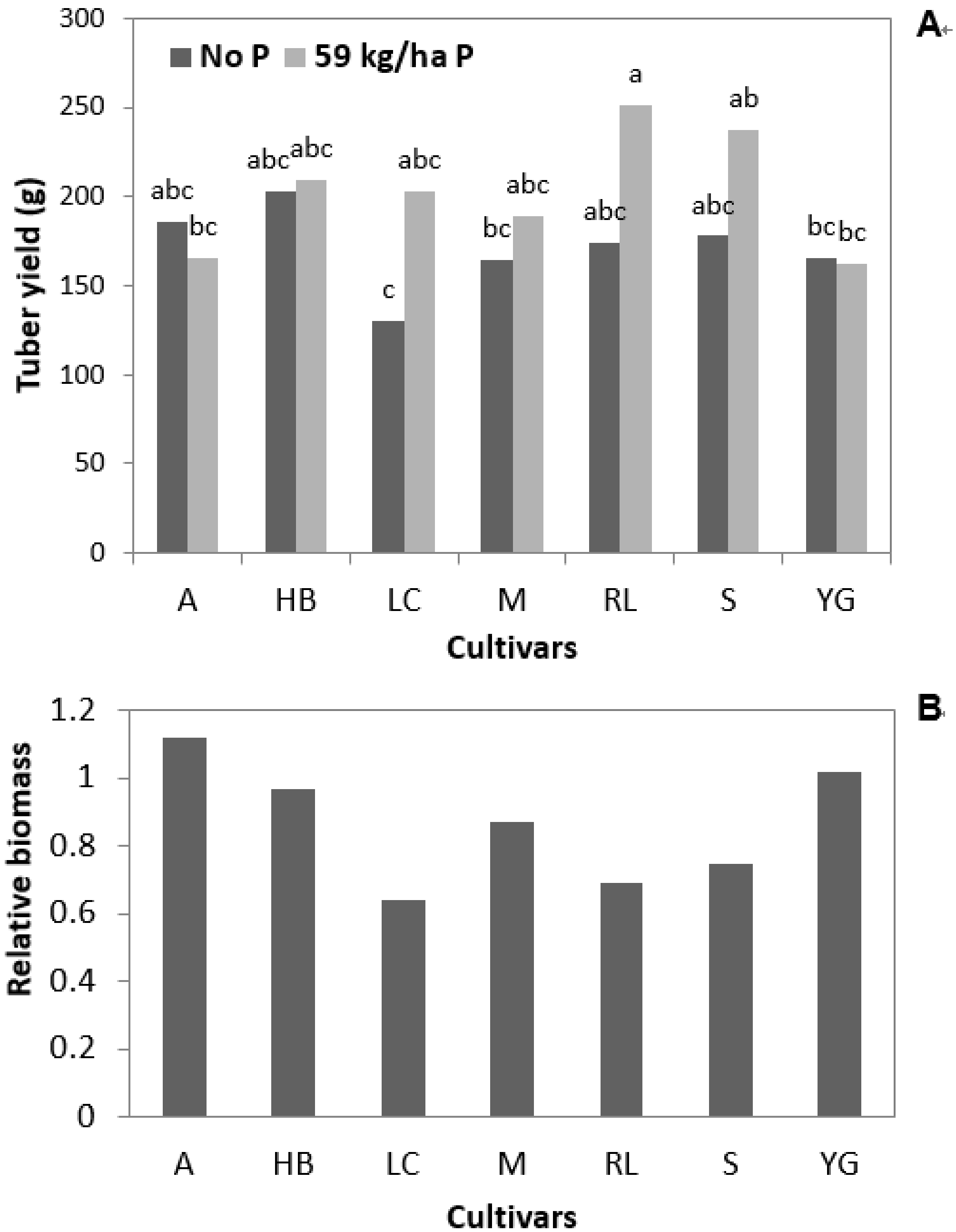

Figure 2-2. Tuber biomass A)and relative biomass ($DW_{no\ P}/DW_{P}$) B) of seven cultivars (84 days after planting) grown in a sandy soil with no-P or with 59 kg/ha P application in a pot experiment conducted in Gainesville, FL. A-‘Atlantic’, HB-‘Harley Blackwell’, LC-‘La chipper’, M-‘Marcy’, RL-‘Red LaSoda’, S-‘Satina,’ and YG-‘Yukon Gold’. Means followed by similar letters are not significantly different at P≤0.05.

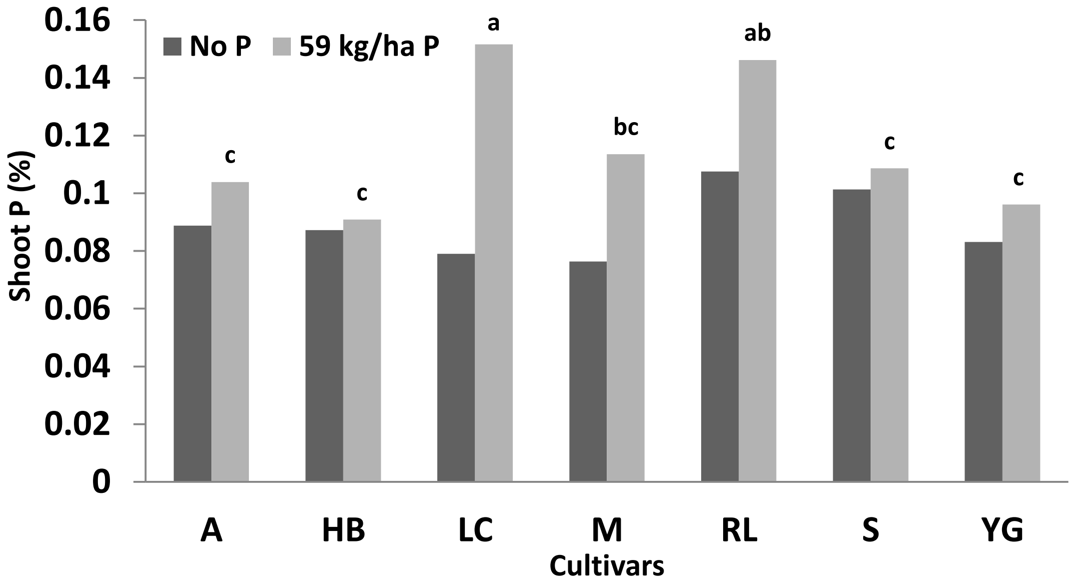

Figure 2-3. P concentrations in shoot of different cultivars grown in a sandy soil with no P and 59 kg/ha P in a pot experiment conducted in Hastings, FL. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina', and YG-'Yukon Gold'. Means followed by similar letters are not significantly different at P≤0.05.

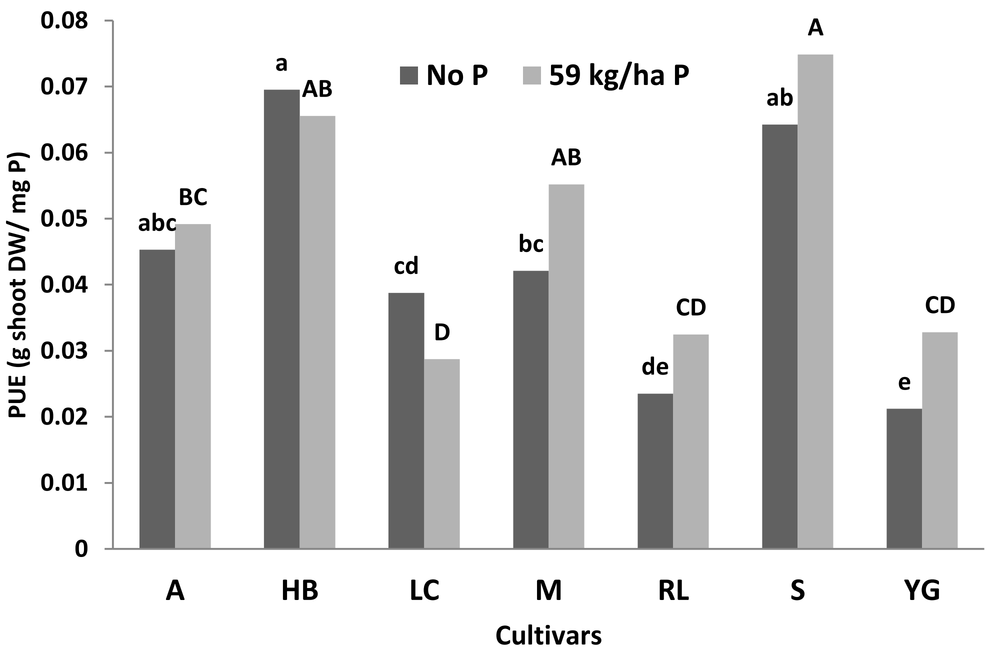

Figure 2-4. Shoot Phosphorus use efficiency with no-P or 59 kg/ha P application in a pot experiment in Hastings, FL. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina', and YG-'Yukon Gold'. Means followed by similar letters are not significantly different at P≤0.05.

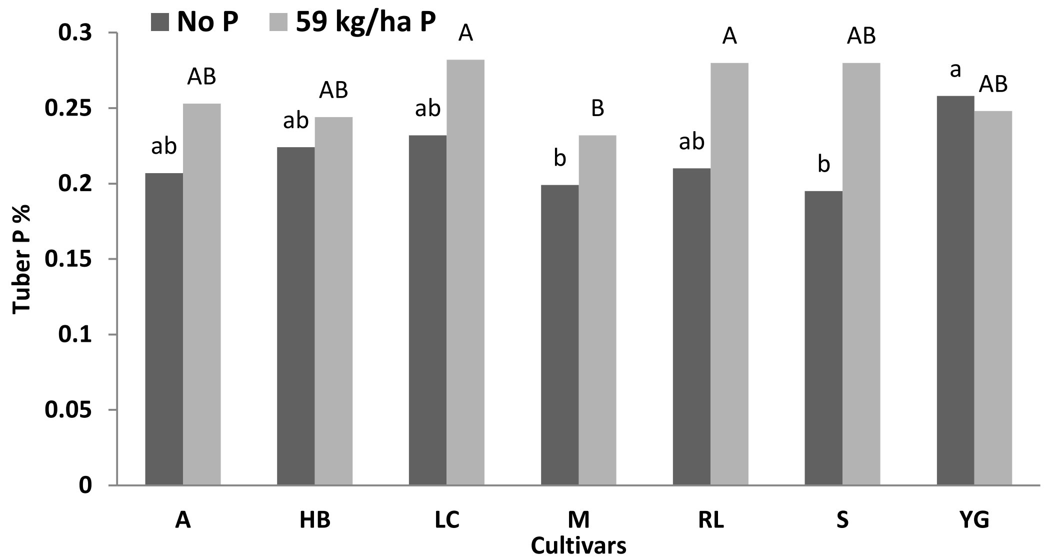

Figure 2-5. Tuber P concentration with no-P or 59 kg/ha P application in a pot experiment in Gainesville, FL. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina', and YG-'Yukon Gold'. Means followed by similar letters are not significantly different at P≤0.05.

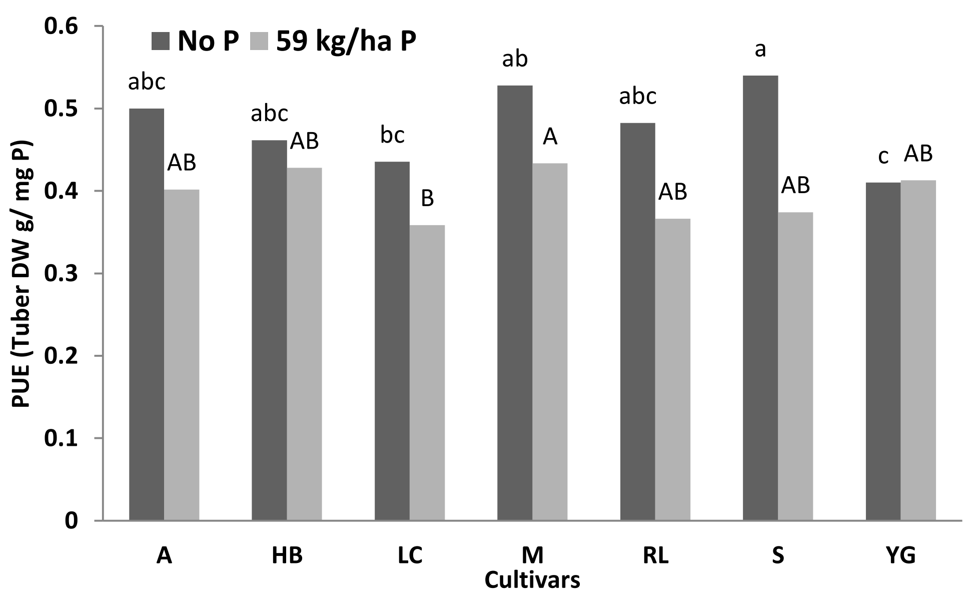

Figure 2-6. Tuber Phosphorus use efficiency with no-P or 59 kg/ha P application in a pot experiment in Gainesville, FL. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina', and YG-'Yukon Gold'. Means followed by similar letters are not significantly different at P≤0.05.

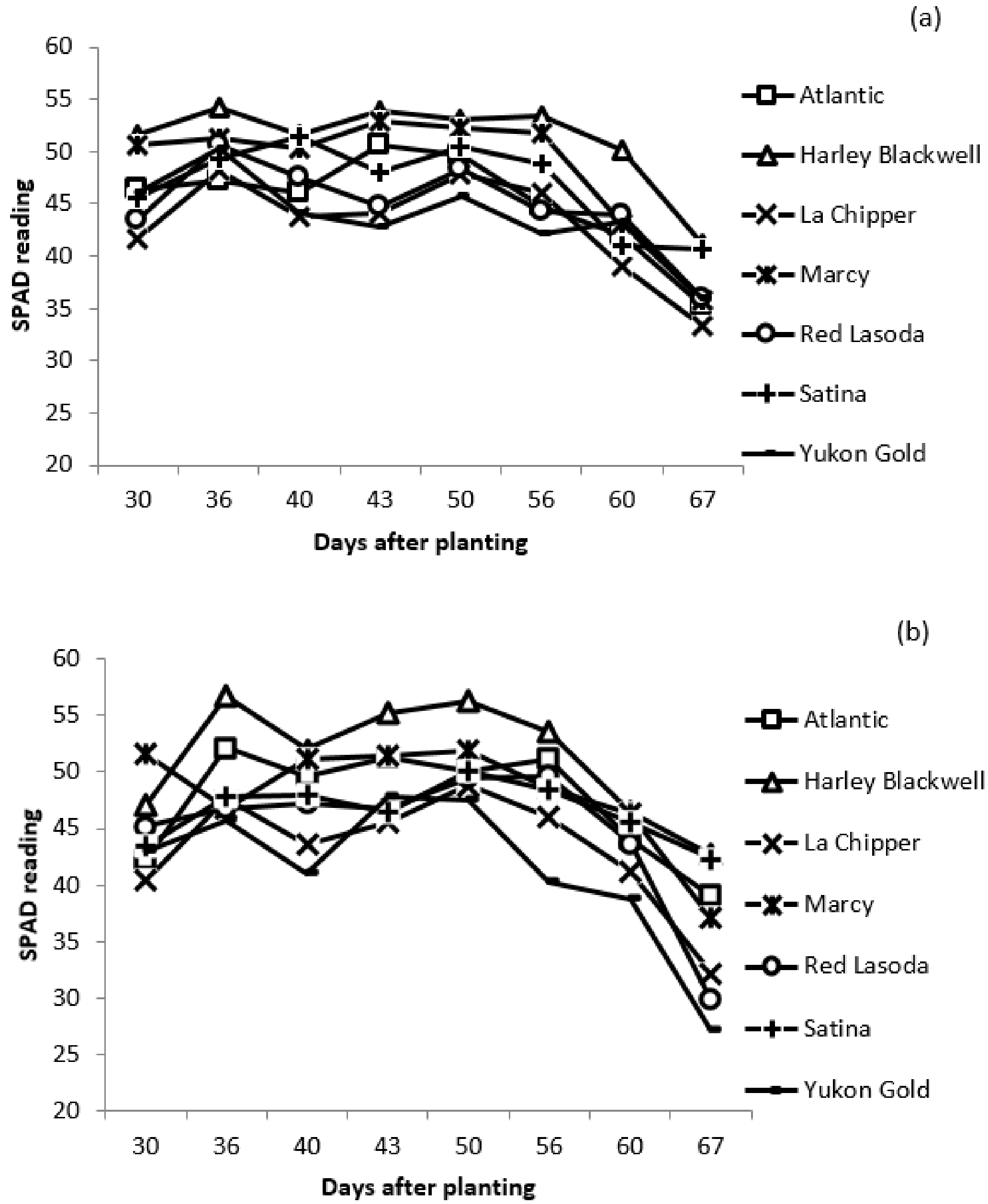

Figure 2-7. SPAD readings of cultivars with (a) 59 kg/ha P and (b) without P fertilization in a pot experiment conducted at Hastings, FL.

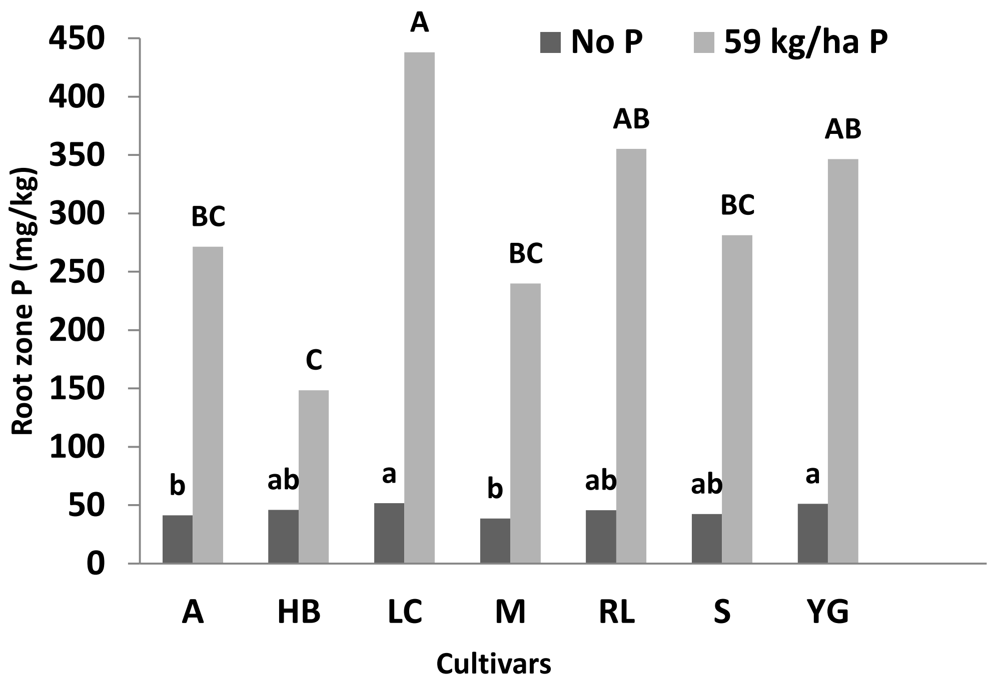

Figure 2-8. P concentration in root zone soil at the end of 84 days of potato plant growth with no-P or 59 kg/ha P application in a pot experiment in Hastings, FL. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina', and YG-'Yukon Gold'. Means followed by similar letters are not significantly different at $P \leq 0.05$.

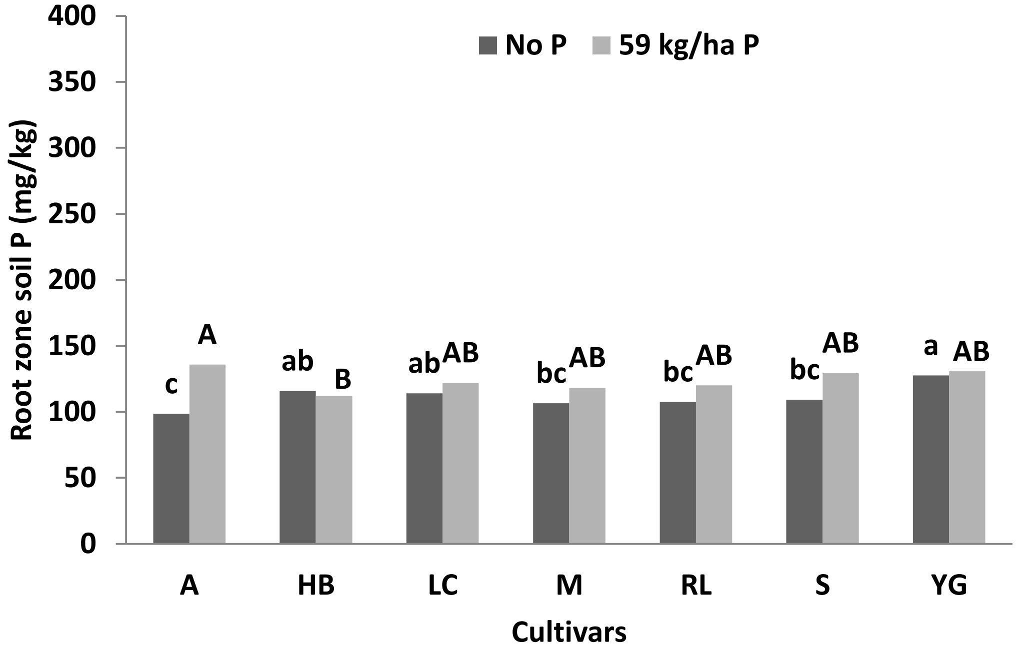

Figure 2-9. P concentration in root zone soil at the end of 84 days of potato plant growth with no-P or 59 kg/ha P application on a pot experiment in Gainesville, FL. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina', and YG-'Yukon Gold'. Means followed by similar letters are not significantly different at $P \leq 0.05$.

Table 2-1. ANOVA table for Shoot biomass of the pot experiment in Hastings, FL, 2012

Source	DF	F ratio	P value
Cultivars	6	4.7058	0.0023**
P	1	9.7026	0.0044**
Cultivars*P	6	1.0495	0.4171
Replicates	2	0.1981	0.8215

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 2-2. ANOVA table for tuber fresh weight in a pot experiment in Gainesville, FL, 2013

Source	DF	F ratio	P value
Cultivars	6	1.0828	0.3827
P	1	4.3195	0.0422**
Cultivars*P	6	1.0755	0.3879
Replicates	6	0.2514	0.9568

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 2-3. ANOVA table for shoot P concentration (%) in a pot experiment in Hastings, FL, 2012

Source	DF	F ratio	P value
Cultivars	6	2.0592	0.0934*
P	1	13.9796	0.0009**
Cultivars*P	6	1.7667	0.1454
Replicates	2	1.0970	0.3388

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 2-4. ANOVA table for shoot Phosphorus use efficiency (PUE) in a pot experiment in Hastings, FL, 2012.

Source	DF	F ratio	P value
Cultivars	6	11.442	<.0001***
P	1	1.5350	0.2264
Cultivars*P	6	0.7138	0.6418
Replicates	2	0.3935	0.6787

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 2-5. ANOVA table for Tuber P concentration (%) in a pot experiment at Gainesville, FL, 2013.

Source	DF	F ratio	P value
Cultivars	6	1.3853	0.2363
P	1	16.5846	0.0001***
Cultivars*P	6	1.1195	0.3626
Replicates	6	1.2267	0.3063

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 2-6. ANOVA table for Tuber Phosphorus use efficiency (PUE) of the pot experiment at Gainesville

Source	DF	F ratio	P value
Cultivars	6	1.2446	0.2976
P	1	0.0930	0.7616
Cultivars*P	6	0.5979	0.7307
Replicates	6	0.9334	0.4783

Table 2-7. ANOVA table for photosynthetic rates in a pot experiment at Hastings, FL, 2012.

Source	DF	F ratio	P value
Cultivars	6	14.7710	<.0001***
P	1	0.3035	0.5840
Replicates	7	0.0464	0.9999
Cultivars*P	6	6.9601	<.0001***
Time	2	72.1449	<.0001***
Cultivars*Time	12	2.5284	0.0054**
P*Time	2	11.4318	0.3898
Cultivars*P*Time	12	2.8780	0.0017**

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 2-8. Photosynthetic rates (CO_2 μmol $m^{-2}s^{-1}$) for seven potato cultivars grown in a sandy soil without P addition (-P) or with 59 kg/ha P addition in a pot experiment in Hastings, FL, 2012.

Cultivars	36 DAP		48 DAP		64 DAP	
	-P	P	-P	P	-P	P
A	6.62^{abcde}	7.54^{abc}	9.13^{abc}	10.27^{abc}	7.87^{bc}	10.63^{a}
HB	4.2^{def}	5.00^{bcdef}	12.10^{ab}	4.96^{bc}	8.80^{abc}	7.24^{bc}
LC	7.14^{abcd}	7.88^{ab}	10.15^{abc}	14.96^{a}	8.43^{abc}	8.87^{ab}
M	3.41^{f}	3.78^{ef}	12.10^{ab}	9.86^{abc}	6.34^{abc}	6.56^{bc}
RL	4.53^{cdef}	9.12^{a}	10.42^{abc}	10.34^{abc}	8.01^{abc}	8.80^{abc}
S	4.08^{def}	10.18^{a}	9.41^{abc}	3.84^{c}	6.87^{bc}	6.03^{c}
YG	5.62^{bcdef}	7.93^{ab}	15.16^{a}	9.83^{abc}	9.04^{ab}	8.23^{abc}

Comparison was made within time of measurement. Means followed by similar letters are not significantly different at P≤0.05.

Table 2-9. ANOVA table for photosynthetic rates in a pot experiment at Gainesville, FL, 2013.

Source	DF	F ratio	P value
Cultivars	6	3.1745	0.0138**
P	1	0.8273	0.3694
Replicates	3	0.9885	0.4094
Cultivars*P	6	1.9819	0.0954*
PTime	1	6.6993	0.0137**
Cultivars*Time	6	1.3562	0.2576
P*Time	1	0.7572	0.3898
Cultivars*P*Time	6	1.5699	0.1832

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 2-10. Photosynthetic rates (CO_2 µmol $m^{-2}s^{-1}$) for seven potato cultivars grown in a sandy soil without P addition (-P) or with 59 kg/ha P addition in a pot experiment in Gainesville, FL, 2013.

Cultivars	36 DAP		48 DAP	
	-P	P	-P	P
Atlantic	18.16^{ab}	17.73^{ab}	15.82^{abcde}	17.39^{abc}
Harley Blackwell	15.21^{ab}	16.80^{ab}	17.50^{abc}	8.41^{def}
La Chipper	13.96^{ab}	16.84^{ab}	8.14^{ef}	11.47^{cdef}
Marcy	18.99^{a}	16.56^{ab}	21.76^{a}	16.74^{abc}
Red LaSoda	15.25^{ab}	17.38^{ab}	13.58^{cdef}	7.53^{f}
Satina	17.09^{ab}	12.59^{b}	16.37^{abcd}	12.96^{bcdef}
Yukon Gold	17.22^{ab}	17.23^{ab}	12.48^{bcdef}	19.90^{ab}

Comparison was made within time of measurement. Means followed by similar letters are not significantly different at P≤0.05.

Table 2-11. ANOVA table for SPAD reading

Source	DF	F ratio	P value
Cultivars	6	5.7711	<.0001***
P	1	0.0118	0.9136
Cultivars*P	6	0.2921	0.9394

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 2-12. ANOVA table for P concentration in root zone soil in a pot experiment in Hastings, FL, 2012.

Source	DF	F ratio	P value
Cultivars	6	3.4880	0.3490
P	1	239.0724	<.0001***
Cultivars*P	6	2.9238	0.0258**
Replicates	2	0.5110	0.6058

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 2-13. ANOVA table for P concentration in root zone soil in a pot experiment in Gainesville, FL, 2013.

Source	DF	F ratio	P value
Cultivars	6	1.1512	0.3490
P	1	20.4049	<.0001***
Cultivars*P	6	4.1072	0.0023**
Replicates	6	1.0251	0.4219

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

CHAPTER 3
FIELD EXPERIMENT

Introduction

Potato (*Solanum tuberosum* L.) is one of the major winter/spring crops in Florida, mostly grown in St. Johns, Putnam and Flagler counties. A typical yield range for Florida chip potato production is from 275 to 400 cwt/acre (Zotarelli et al., 2013). Yield increases as the production moves into northern counties. Parrish is the main potato production area in southwest Florida and located in Manatee County, which annual impact of agriculture to economy is about $500 million. The field we carried our experiment was regularly applied with P fertilizer; the accumulation of P in the soil is quite high (110-120ppm). Even with this high soil P concentration, grower still regularly apply P fertilizer, and potato do response to the P application. Most of the P in soil were fixed as plant unavailable forms. The cultivars with outstanding P mobilizing ability to dissolve the fixed P in the soil into plant available form could greatly reduce the P fertilizer requirement. Several plant mechanisms were reported to increase soil P solubility, the most common one is to change the rhizosphere pH to optimum range for insoluble P change into soluble P forms (Bertin et al., 2003). Organic acids, citrate and malate, may be the most effective root exudates on P mobilization (Chen et al., 2006; Duffner et al., 2012; Gietl, 1992; Gyaneshwar et al., 1998; Kochuan, 1995; Martinoia and Rentsch, 1994; Schulze et al., 2002).

Phosphorus is one of the macronutrients for plant. The deficiency of P could cause yield reduction, anthocyanins accumulation, root shoot ratio and specific leaf weight (SLW) enhancement (Hammond et al., 2003; Hegney and McPharlin, 1999; Hegney et al., 2000; Uhde-Stone et al., 2003). In this study, a field experiment was conducted to understand seven potato cultivars responses to P limitation on SLW, bulking, shoot biomass accumulation, tissue P concentration, and tuber size. The objective of this study was to evaluate the cultivar P efficiency by comparing the physiological and morphological response between P and non-P treated plots.

Materials and Methods

Tuber Planting and Nutrient Management

This experiment was conducted at Jones Potato Farm, a private farm for commercial production of potatoes at Parrish, Florida in Manatee County. Seven potato cultivars most commonly grown in Florida were used: ‘Atlantic,’ ‘Harley Blackwell,’ ‘La Chipper,’ ‘Marcy,’ ‘Satina,’ ‘Red LaSoda,’ and ‘Yukon gold’. Certified seeds were obtained from Seed Pro Inc, Crystal, ME. Seed pieces (approximately 85g) were planted at 8 inch spacing in seepage irrigated sandy soil field in Jones potato farm at Parrish, FL. Treatments included: no P, which received N-P-K fertilizers at 80-0-150 and P which received 80-120-150 lbs/ac, respectively as pre-plant applications using ammonium nitrate, ammonium sulfate, triple super phosphate, and muriate of potash, respectively. Both treatments were applied with 100-0-100 and 50-0-30 fertilizers at emergence and layby, respectively. A randomized complete block design was adapted with five replications and each plot size was 80 ft long for both P and no P amended plots. At 3 weeks after planting (WAP), emergence rate was determined by visual estimation.

Specific Leaf Weight Measurement

Leaf area (cm^2) was measured with an electronic planimeter LiCor-3000 (Li-Cor, Inc., Lincoln, NE), than oven dried at 70℃ till constant weight. Leaf specific mass was calculated from leaf dry mass (mg) divided by leaf area (cm^2). Measurements were taken at 5, 8, and 12 weeks after planting (WAP).

Shoot and Tuber Biomass Measurement

Shoot biomass was measured at 5, 8, and 12 WAP. Tuber biomass was measured at 8, 12, and 15 WAP. At harvest (15 WAP), potatoes were graded into four sizes, and following are the correlation to USDA standard grade; XL (A3-A4) >3.5 inch, L (A2) =2.8-3.5 inch, M (A1-A2) =1.8-2.8 inch, S (B-C) <1.8 inch.

Plant Tissue P Content Analysis

The oven-dried plant shoots were ground to pass a 40 mesh stainless steel sieve, and dry ashed (Kalra, 1998). Ground tissue sample was weighed (300 ± 50 mg) into porcelain crucibles and placed in a Thermolyne Muffle Furnace-53600 (Cole-Parmer North America,Vernon Hills, IL). The temperature was increased at 10°C/min till 250°C, which was maintained for 30 min, and then increased to 550°C for 6 hours. The ash was cooled and dissolved with 2.25 mL 6N HCl, 15 min later filtered through No.41 filter paper, and diluted to 50 mL with de-ionized water. P concentration was analyzed by Automated Discrete Analyzer (AQ2, SEAL Analytical, Hanau, Germany) based on US EPA Method 365.1 (U.S. environmental Protection Agency, 1993). Phosphorus use efficiency was calculated as following:

$$PUE = \frac{\text{tissue dry matter (g)}}{\text{P (mg)}}$$

Soil extraction and P analysis

Root zone soil was collected by shaking off the soil from the roots at 5 and 8 WAP. Soil samples were air dried and 2±0.2 g soil sample extracted with 20 mL of

Mehlich 3 extractant (Mehlich, 1984). The suspension was shaken for 5 min, filtered, and P concentration was analyzed by AQ2 (SEAL Analytical, Hanau, Germany).

Statistical Analysis

All data were transformed to follow a normal distribution values and subjected to analysis of variance using Statistical Analysis software SAS (Institute Inc., Cary, N.C.). Student's t was used for evaluation of significance between the two means.

Results

This field experiment was conducted in two plots with or without P application. Because these two plots were identical with the history of planting, and the soil test showed that P concentration was the same between two plots before planting. The soil P concentration background of the 2 plots were the same with F test and P value as 0.2540 and 0.6490, respectively. 59 kg/ha phosphate application in P plot should increase soil P concentration by 60 ppm. Only the interaction of P*time and cultivar*P*time significantly influenced rhizosphere P concentration during the growth period, no significantly difference was found in rhizosphere soil P concentrations for all treatments at all time (Table 3-1).

The Emergence Rate

The emergence rate at 3 WAP was influenced by cultivar and P application (Table 3-2). Only 'Atlantic' and 'Marcy' showed greater emergence rate in P treatment as compared to non-P treatment (Figure 3-1). In both P and non-P treatments, 'Satina' showed the greater or equal emergence rate than other cultivars.

Specific Leaf Weight

Specific leaf weight was affected by measuring time for all of the cultivars, and the interaction between time*P was significant for most of the cultivars (Table 3-3).

Phosphate application only affected SLW in ‘Marcy’. For relative SLW, no difference was found at 8 WAP, while ‘Marcy’ was significantly greater than other cultivars at 5 WAP, and ‘La Chipper’ and ‘Marcy’ were significant or equal than the other cultivars at 12 WAP (Table 3-3).Cultivar, time, and the interaction between cultivar and time showed significant impact on relative SLW (Table 3-4). ‘Atlantic’ and ‘Satina’ showed lower or equal relative SLW than the other cultivars at 12 WAP (Table 3-5). We were able to find a negative linear correlation between shoot P concentration and SLW at 8 and 12 WAP (Figure 3-2).

The Shoot Growth

The shoot growth rate was greater with P application than that without P application, especially between 8 to 12 WAP (Figure 3-3). Most of the cultivars, except ‘Satina’ and ‘Yukon Gold’, shoot growth leveled off after 8 WAP without P application. Either P or P*time have significant impact on shoot biomass for all the cultivars, except for ‘La Chipper’ and ‘Yukon Gold’ (Table 3-6). Most of the cultivars showed greater shoot biomass between P and no P treatment at 12 WAP (Table 3-7). Relative shoot biomass was influenced by cultivar, time, and interaction between cultivar and time (Table 3-8). ‘Satina’ and ‘Yukon Gold’ showed greater or equal relative shoot biomass at both 5 and 12 WAP as compared to the other cultivars (Table 3-9).

Tuber Yield and Size

Potato started bulking between 6 to 8 WAP, and the samples were taken at 8, 12 and 15 WAP. The bulking rate was slower at non P treatment between 12 to 15 WAP (Figure 3-4). Tuber biomass of ‘Harley Blackwell,’ ‘Marcy,’ and ‘Red LaSoda’ was affected by the interaction between P application and time of measuring (Table 3-10). Phosphorus treated ‘Atlantic,’ ‘Harley Blackwell,’ and ‘Red LaSoda’ showed greater tuber yield as compared to non P treated at 15 WAP (Table 3-11). Relative tuber biomass was significantly influenced by time of measuring (Table 3-12). ‘Satina’ showed greater or equal tuber biomass than other cultivars at all the time of measuring (Table 3-13).

Tuber size was compared between P and no P treatments for a given cultivar. No difference was found in all of the tested cultivars in any size, except ‘Yukon Gold’ had more S size tubers with P than without P application (Table 3-14).

Phosphorus Concentration, Accumulation, and Use Efficiency

Shoot P concentration was increasing between 5 to 8 WAP, and decreasing between 8 to 12 WAP (Figure 3-5). Only time of measurement had the influence on shoot P concentration (Table 3-15). No difference was found between P treatments for all of the tested cultivars regarding shoot P concentration (Table 3-16). Relative shoot P concentration was not affected by cultivar effect (Table 3-17), that no difference in relative shoot P concentration was found for all of the cultivars at all time (Table 3-18).

Tuber P concentration was decreasing from 8 to 12 WAP, and was increasing from 12 to 15 WAP (Figure 3-6). Most of the cultivars tuber P concentration was greater with P application as compared to non-P treatment, except for ‘La Chipper,’ ‘Red LaSoda,’ and ‘Satina’ (Table 3-19).

‘Atlantic’ and ‘Yukon Gold’ showed greater tuber P concentration with P application than without at 15 WAP (Table 3-20). Cultivar, time of measurement, and the interaction between cultivar and time of measurement were significantly affecting relative tuber P concentration (Table 3-21). ‘Satina’ and ‘Marcy’ showed greater or equal relative tuber P concentration at 12 and 15 WAP as compared to the other cultivars (Table 3-22).

Phosphorus accumulation in plant was only affected by time of measurement (Table 3-23). No significant difference was found between P treatments for all cultivars (Table 3-24). However, cultivar did show significant influence on relative P accumulation (Table 3-25). ‘Satina’ and ‘Yukon Gold’ showed greater or equal relative P accumulation as compared to other cultivars at 8 and 15 WAP.

Tuber PUE was influenced by P application for ‘La Chipper,’ ‘Red LaSoda,’ and ‘Yukon Gold’, and these three cultivars showed greater tuber PUE without P application than with P application at 15 WAP (Table 3-26, 3-27). Relative tuber PUE was influenced by cultivar, time, and the interaction between cultivar and time (Table 3-28). Opposite to tuber P concentration, ‘Yukon Gold’ showed significantly greater PUE and relative PUE at 15 WAP as compared to other cultivars, while ‘Satina’ showed lower or equal relative PUE than the other cultivars at all time (Table 3-29).

Discussion

This field experiment was conducted in two plots with or without P application. Because these two plots were identical with the history of planting, and the soil test showed that P concentration was the same between two plots before planting. Phosphorus treated plot was considered as standard, and the difference between P and non-P treated plot is what we are focusing in this study.

In literature, reduced wheat tiller emergence rate was reported under Phosphorus deficiency (Rodriguez et al., 1998). Because potato was planted from seed pieces, which contain nutrients to support the emergence, that external P status had less influence than cultivar itself on emergence rate.

Increasing SLW could be triggered by P deficiency, and it’s been report on many plant species (Gutiérrez-boem and Thomas, 1998; Radin and Eidenbock, 1984;

Hanada, 1995; Gutiérrez-boem and Thomas, 1999).Usually SLW is considered to reflect carbon accumulation in the leaf, but it is not the major factor to inhibit leaf expansion. Leaf expansion is also sensitive to P and water stress (Schlesinger and Chabot, 1977; Sobrado and Medina, 1980; Field and Monney, 1986; Witowski and Lamont, 1999). Plant P status could regulate the water status by altering stomatal conductance and density, and it is negative related to SLW in many plant species (Gutiérrez-Boem and Thomas, 1998; Gutiérrez-boem and Thomas, 1999; Radin and Eidenbock, 1984). In the early season of our study, plant may not sense the P stress yet or the seedling is so small that water was sufficient to maintain leaf cell turgor pressure at all time. At the end of season, P stress may diminished the potato's ability to defense the diseases and pests (Huber, 1980), which caused the damage of leaf and reduced the dry mass. Therefore, only at the mid-season may all seven cultivars showed the greater or equal SLW with P application than without P application. 'Satina' SLW was either affected by P supply nor by the interaction between P and time. Also, 'Satina' relative SLW was less or equal to the other cultivars at 12 WAP suggesting that this cultivar may have the ability to maintain turgor under wider range of water deficit or have better P acquisition ability in no P application plot to maintain the stomatal conductance.

Potato started bulking in between 5 to 8 WAP. In this period, tuber was the main sink for the plant (Moorby, 1968), and shoot growth rate increased to support the demand of the sink. But in P deficiency condition, root shoot ratio usually increased, that shoot growth rate been reduced to support root growth (Cakmak, 2002; Fernandes and Soratto, 2011). Also, shoot P concentration decreased between 8 to 12 WAP, which was overlap to the period bulking started. And the trend of shoot P concentration was opposite to tuber P concentration. Indicated that translocation of P from shoot to tuber occurred during 8 to 12 WAP. This result was agreed with Moorby (1968) that tuber is a stronger P sink for potato.

Among seven cultivars, ‘Satina’ and ‘Yukon Gold’ showed similar shoot and tuber production with or without P application. Either these two cultivars have better P acquisition ability or have better P utilization ability to keep as high production as with P application treatment. Though ‘Yukon Gold’ showed similar productivity between P and non P, its low yield has it become undesirable. Though ‘Yukon Gold’ did not showed great productivity, this cultivar showed significant enhancement in PUE on non P treatment compare to P treatment is interested to us. Previous research found that PUE could be manipulated by genes expression under P deficiency condition (Hammond et al., 2003; Lopez-Bucio et al., 2000; Vance et al., 2003). The genes expression of ‘Yukon Gold’ in P deficiency could be study to further understand the mechanisms of increasing potato PUE. We did not find greater tuber PUE in ‘Satina’ than the other cultivars without P application at the end of the season but the relative P accumulation was high, suggested that the greater tuber yield may due to better P acquisition ability instead of P utilization ability. The cultivars with outstanding P mobilizing ability to dissolve the fixed P in the soil into plant available form is desired for Florida region.

Potato tuber size is an important component to determine market price. Generally, size M (1.8 to 2.8 inches) tuber has the better price. For yellow and red potato, M grade price is more than double as compared to L and XL grade. We were not able to find any size portion change between P and no P treatment for the seven tested cultivars. Suggesting that tuber size is not affected by P availability.

Summary

Among seven cultivars, ‘Satina’ always showed greater or equal relative value in biomass, tissue P concentration, and P accumulation than other cultivars. Therefore, ‘Satina’ was considered P efficient cultivars in this experiment. Suggesting ‘Satina’ was better in maintaining its growth and P content without P application than the other cultivars. With all the measurements we make on these seven potato cultivars, SLW seems to reveal the cultivar P efficiency. Specific leaf weight is relatively easy to measure, and it is less destructive than other measurements. It could be an index for evaluating potato P efficiency in the future study.

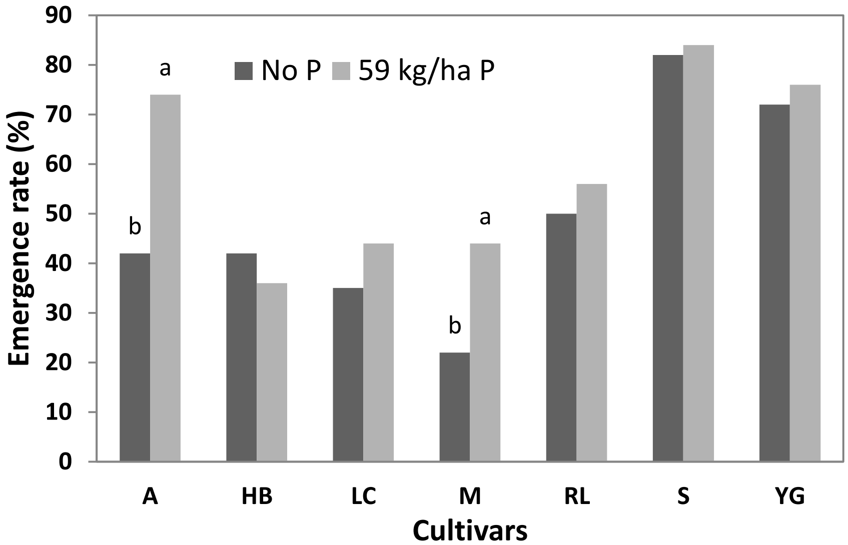

Figure 3-1. Emergence rate at 3 weeks after planting. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina,' and YG-'Yukon Gold'. Comparison was made within the cultivar. Means followed by similar letters are not significantly different at P≤0.1.

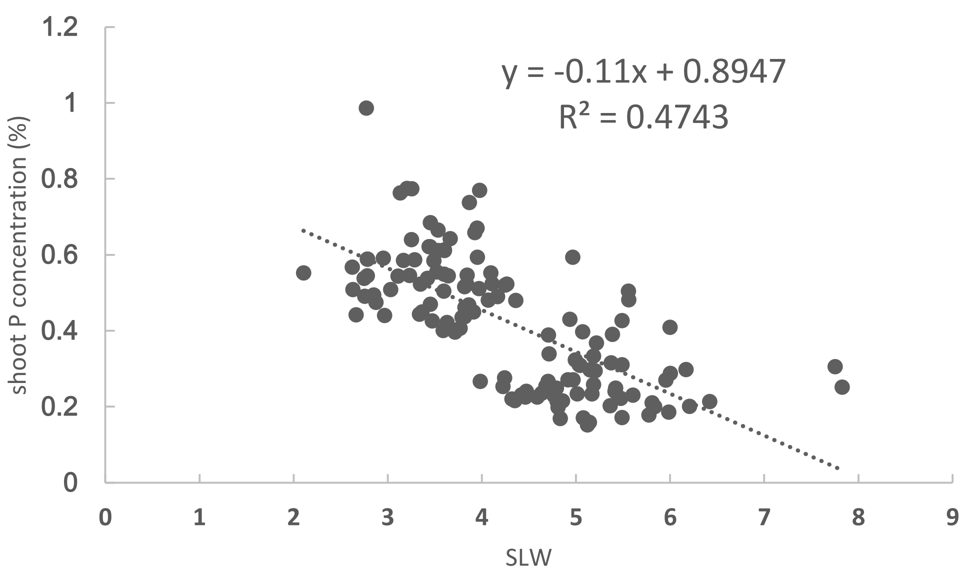

Figure 3-2. Linear regression of specific leaf weight (SLW) to shoot P concentration at 8 and 12 WAP.

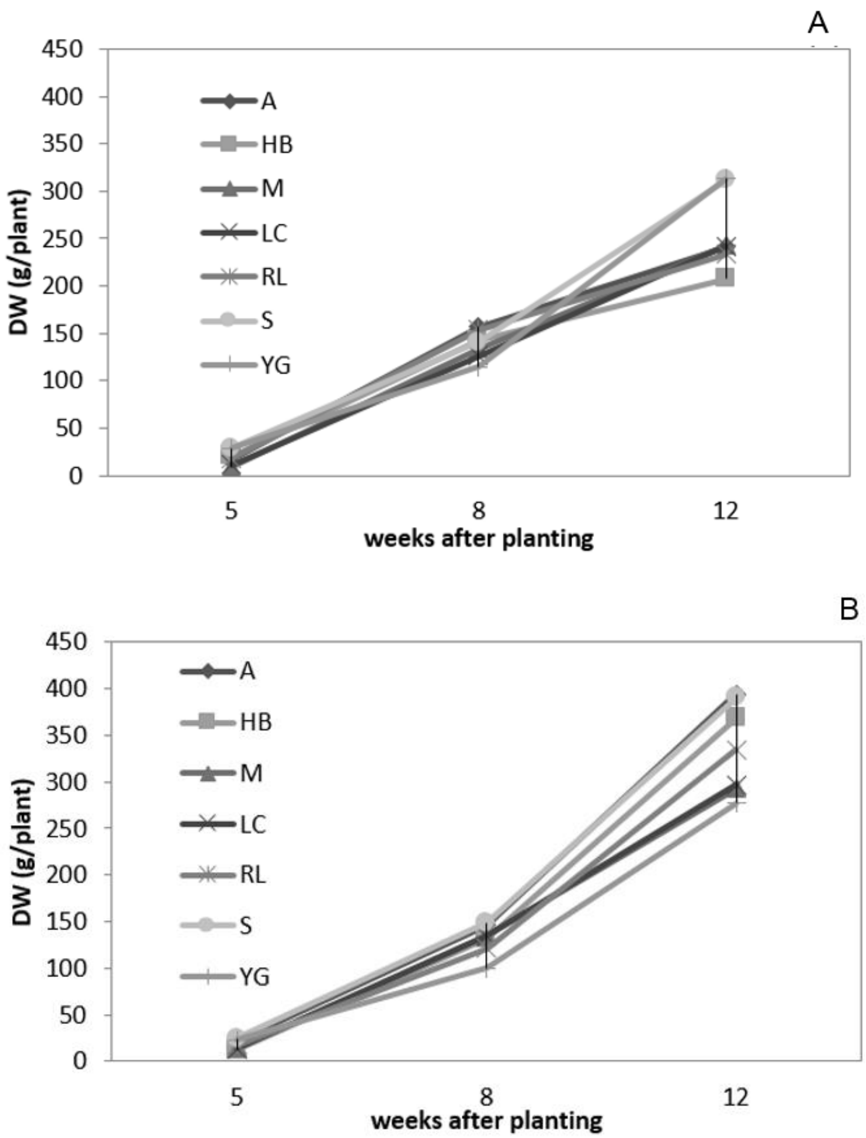

Figure 3-3. Shoot biomass for A) all cultivars without P and B) with 59 kg/ha P application at 5, 8, and 12 weeks after planting. A-‘Atlantic’, HB-‘Harley Blackwell’, LC-‘La chipper’, M-‘Marcy’, RL-‘Red LaSoda’, S-‘Satina,’ and YG-‘Yukon Gold’.

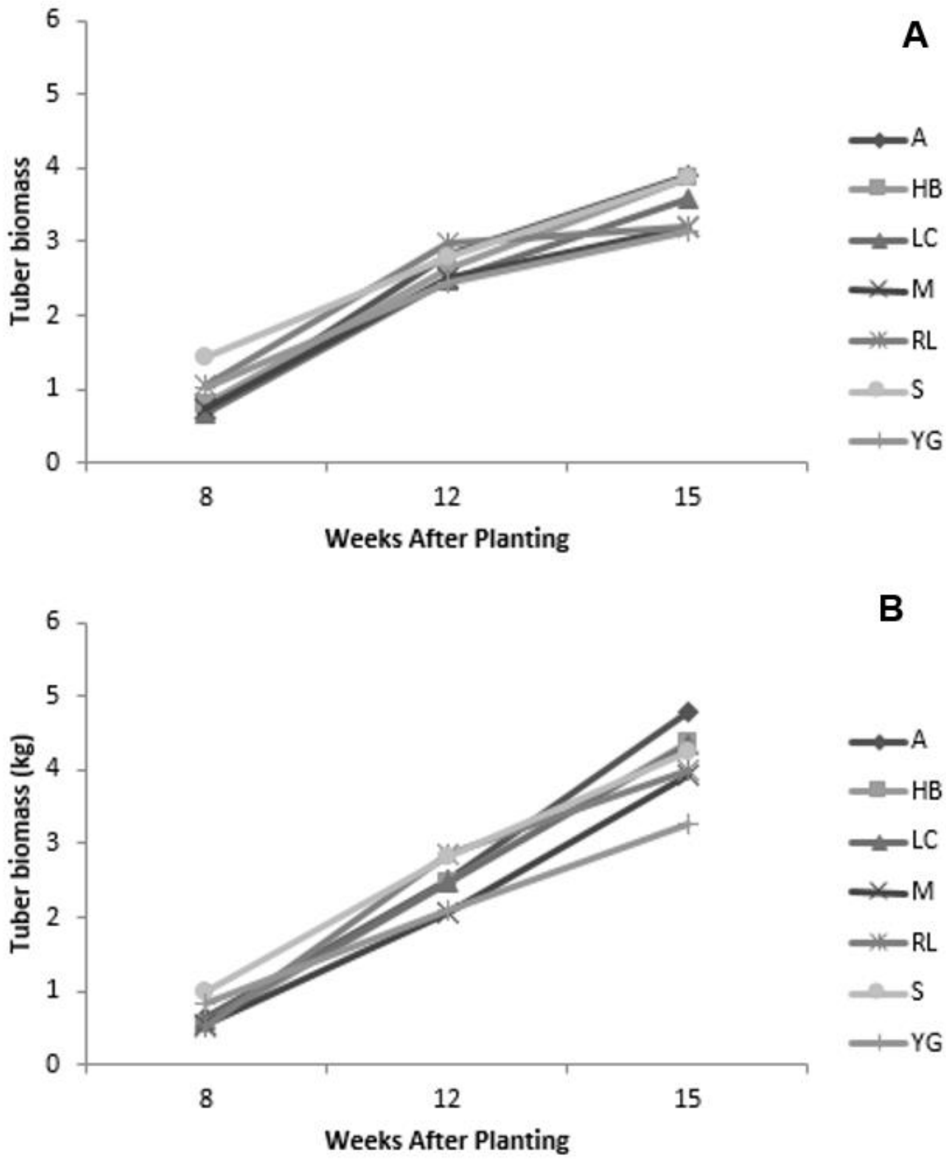

Figure 3-4. Tuber biomass at 8, 12, and 15 weeks after planting A) without P and B) with 59 kg/ha P application. A-‘Atlantic’, HB-‘Harley Blackwell’, LC-‘La chipper’, M-‘Marcy’, RL-‘Red LaSoda’, S-‘Satina,’ and YG-‘Yukon Gold’.

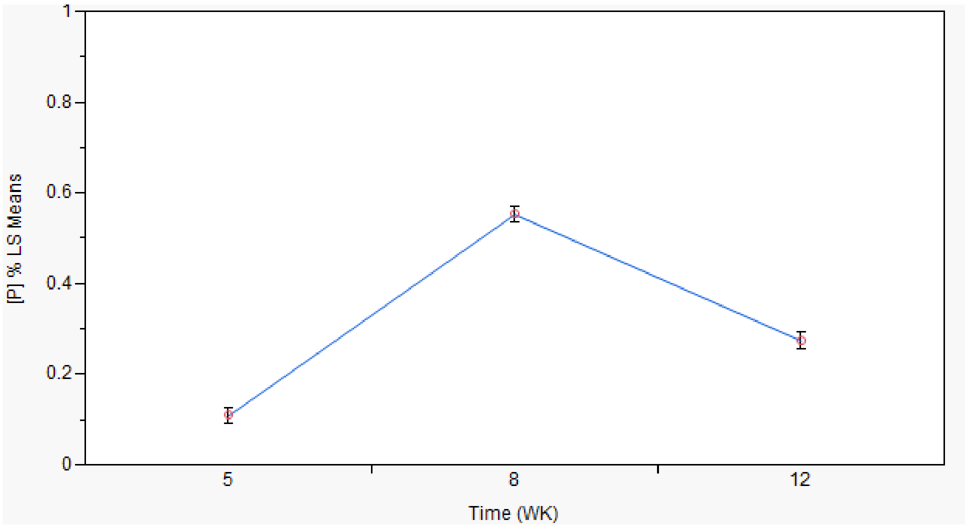

Figure 3-5. Shoot P concentration least square means at 8, 12, and 15 weeks after planting.

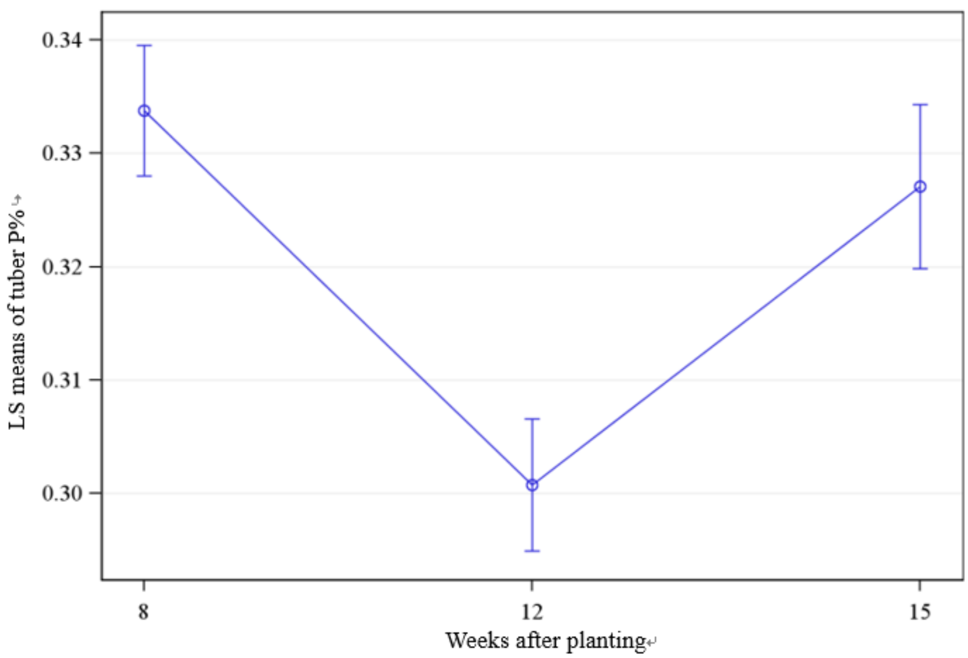

Figure 3-6. Tuber P concentration least square means at 8, 12 and 15 weeks after planting.

Table 3-1. ANOVA table for rhizosphere soil P concentration

Source	DF	F ratio	P value
Cultivar	6	0.77	0.5986
P	1	0.97	0.3285
Cultivar*P	6	0.07	0.9987
Time	2	1.57	0.2149
Cultivar*Time	12	0.21	0.9720
P*Time	2	6.26	0.0153*
Cultivar*P*Time	12	4.78	0.0005**

Time= Time of measurement. P= P application. *, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-2. ANOVA table for emergence rate

Source	DF	F ratio	P value
Cultivar	6	12.4097	<.0001*
P	1	5.9330	0.0183**
Cultivar*P	6	1.4551	0.2120

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-3. Specific leaf weight

Cultivars	5 WAP		8 WAP		12 WAP	
	-P	P	-P	P	-P	P
A	4.555^{ab}	4.372^{ab}	3.928^{a}	3.445^{ab}	4.915 ^{a}	5.796^{a}
HB	4.371^{ab}	5.144^{ab}	4.371^{a}	3.385^{ab}	4.688 ^{a}	4.258^{a}
LC	4.52^{ab}	4.334^{ab}	4.52^{a}	3.417^{ab}	5.46 ^{a}	5.002^{a}
M	5.554^{a}	4.056^{b}	5.554^{a}	3.584^{ab}	5.344 ^{a}	5.209^{a}
RL	4.286^{ab}	4.29^{ab}	4.286^{ab}	2.7^{b}	4.821 ^{a}	5.236^{a}
S	3.886^{b}	3.87^{b}	3.886^{ab}	3.203^{ab}	4.907 ^{a}	5.807^{a}
YG	4.421^{ab}	5.021^{ab}	4.421^{ab}	3.36 ^{ab}	5.038 ^{a}	5.21^{a}

Comparison was made within time of measurement. Means followed by similar letters are not significantly different at P≤0.05. A-‘Atlantic’, HB-‘Harley Blackwell’, LC-‘La chipper’, M-‘Marcy’, RL-‘Red LaSoda’, S-‘Satina,’ and YG-‘Yukon Gold’.

Table 3-4. ANOVA table for relative specific leaf weight

Source	DF	F ratio	P value
Cultivar	6	4.12	0.0012**
Time	2	18.4	<0.0001***
Cultivar*Time	12	3.37	0.0005**

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-5. Relative specific leaf weight

Cultivars	5 WAP	8 WAP	12 WAP
Atlantic	1.041 ^{b}	1.139	0.847 ^{c}
Harley Blackwell	0.849 ^{b}	1.131	0.878 ^{bc}
La Chipper	1.040 ^{b}	1.139	1.090 ^{a}
Marcy	1.360 ^{a}	1.068	1.024 ^{ab}
Red LaSoda	0.991 ^{b}	1.172	0.918 ^{bc}
Satina	1.001 ^{b}	1.115	0.844 ^{c}
Yukon Gold	0.880 ^{b}	1.099	0.966 ^{abc}

Comparison was made within time of measurement. Means followed by similar letters are not significantly different at P≤0.1.

Table 3-6. ANOVA table for cultivar shoot biomass

Cultivars	P		Time		P*Time	
	F ratio	P value	F ratio	P value	F ratio	P value
A	9.11	0.0174**	253.46	<0.0001***	17.79	0.0001**
HB	18.89	0.0004**	736.02	<0.0001***	47.57	<0.0001***
LC	2.08	0.1868	277.06	<0.0001***	2.31	0.1328
M	5.55	0.0274**	364.44	<0.0001***	0.41	0.6681
RL	1.04	0.3179	335.06	<0.0001***	4.74	0.0189**
S	1.64	0.2389	626.77	<0.0001***	2.8	0.0926*
YG	2.54	0.1238	368.67	<0.0001***	0.22	0.806

A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina,' and YG-'Yukon Gold'. Time= Time of measurement. P= P application. *, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-7. Shoot biomass

Cultivars	5 WAP		8 WAP		12 WAP	
	-P	P	-P	P	-P	P
A	2.80	3.67	26.13	24.43	36.46 ^{b}	61.24 ^{a}
HB	3.33 ^{a}	2.03 ^{b}	23.70	21.97	31.59 ^{b}	57.43 ^{a}
LC	1.87	2.30	22.23	22.47	37.87 ^{b}	47.91 ^{a}
M	1.52 ^{b}	2.44 ^{a}	21.03	22.43	40.77	44.41
RL	3.05	2.94	25.57	22.40	40.94 ^{b}	52.97 ^{a}
S	4.73	4.04	23.43	24.73	43.94 ^{b}	52.28 ^{a}
YG	4.79	3.78	19.13	16.93	40.53	40.07

Comparison was made within cultivar at the time of measurement. Means followed by similar letters are not significantly different at P≤0.05. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina,' and YG-'Yukon Gold'.

Table 3-8. ANOVA table for relative shoot biomass

Source	DF	F ratio	P value
Cultivar	6	3.88	0.0061*
Time	2	16.55	<0.0001***
Cultivar*Time	12	4.63	<0.0001***

Time= Time of measurement. P= P application. *, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-9. Relative shoot biomass

Cultivars	5 WAP	8 WAP	12 WAP
Atlantic	0.745^{b}	1.067	0.481^{d}
Harley Blackwell	1.629^{a}	1.076	0.551^{cd}
La Chipper	0.737^{b}	0.959	0.735^{bc}
Marcy	0.603^{b}	0.918	0.841^{ab}
Red LaSoda	1.021^{ab}	1.136	0.771^{bc}
Satina	1.142^{ab}	0.943	0.859^{ab}
Yukon Gold	1.237^{ab}	1.127	1.027^{a}

Comparison was made within time of measurement. Means followed by similar letters are not significantly different at $P \leq 0.1$.

Table 3-10. ANOVA table for cultivar tuber biomass

	P		Time		P*Time	
Cultivars	F ratio	P value	F ratio	P value	F ratio	P value
A	0.08	0.7853	133.32	<0.0001***	2.28	0.1347
HB	0.34	0.5626	303.09	<0.0001***	3.83	0.0359**
LC	0.27	0.6205	225.03	<0.0001***	2.21	0.1419
M	0.07	0.8035	205.87	<0.0001***	2.96	0.082*
RL	0.04	0.8416	259.24	<0.0001***	12.07	0.0006**
S	0.09	0.7703	75.5	<0.0001***	2.42	0.1206
YG	0.66	0.4392	70.13	<0.0001***	0.78	0.4744

A-‘Atlantic’, HB-‘Harley Blackwell’, LC-‘La chipper’, M-‘Marcy’, RL-‘Red LaSoda’, S-‘Satina,’ and YG-‘Yukon Gold’. Time= Time of measurement. P= P application. *, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-11. Tuber biomass (kg/ha)

Cultivars	8 WAP		12 WAP		15 WAP	
	-P	P	-P	P	-P	P
A	4837.0	4226.5	19027.9	16892.6	26306.1[b]	32165.0[a]
HB	5275.8[a]	3585.3[b]	17628.6	16697.5	26061.9[b]	29479.6[a]
LC	4553.8	4029.1	16739.2	16678.7	24109.0	29296.5
M	4907.9	3568.6	15374.9	14267.2	22918.9	26550.2
RL	7095.7[a]	4125.0[b]	19691.2	19400.6	21484.7[b]	26855.3[a]
S	9702.3	6619.5	18898.7	18910.8	25939.9	28625.2
YG	6771.0	5504.9	16410.9	14050.9	21240.6	22033.9

Comparison was made within the cultivar at the time of measurement. Means followed by similar letters are not significantly different at $P \leq 0.1$. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina,' and YG-'Yukon Gold'.

Table 3-12. ANOVA table for relative tuber biomass

Source	DF	F ratio	P value
Cultivar	6	0.57	0.7470
Time	2	28.04	<.0001***
Cultivar*Time	12	1.23	0.2859

Time= Time of measurement. P= P application.*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-13. Relative tuber biomass at 8, 12 and 15 weeks after planting

Cultivars	5 WAP	8 WAP	12 WAP
Atlantic	1.109 [b]	1.111	0.669[bc]
Harley Blackwell	1.454[ab]	1.049	0.782 [b]
La Chipper	1.066 [b]	0.984	0.604 [bc]
Marcy	1.354 [ab]	1.074	0.745 [bc]
Red LaSoda	1.691 [a]	1.012	0.547 [c]
Satina	1.446 [ab]	0.987	1.044 [a]
Yukon Gold	1.217 [b]	1.154	0.788 [ab]

Comparison was made within time of measurement. Means followed by similar letters are not significantly different at $P \leq 0.1$.

Table 3-14. ANOVA table for tuber size by cultivar and treatment

Cultivars	XL		L		M		S	
	F ratio	P	F ratio	P	F ratio	P	F ratio	P
A	1.175	0.3393	0.0019	0.9672	0.5901	0.4852	0.2342	0.6538
HB	1.0292	0.3677	0.6799	0.456	0.008	0.9332	0.0013	0.9725
LC	0.0367	0.8574	0.4154	0.5544	0.1614	0.7084	0.0073	0.936
M	3.2054	0.1479	0.001	0.9765	1.9607	0.2395	0.083	0.7876
RL	0.5208	0.5104	0.4409	0.543	0.663	0.4612	0.4746	0.5287
S	0.0001	0.9943	0.3324	0.5951	0.8069	0.4198	0.0059	0.9424
YG	1.2415	0.3276	4.1716	0.1106	0.1225	0.744	6.6892	0.0609*

XL: >3.5 inches, L: 2.8 to 3.5 inches, M: 1.8 to 2.8 inches, S: <1.8 inches. P is P value. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina,' and YG-'Yukon Gold'. * Significant at 0.10.

Table 3-15. ANOVA table for shoot P concentration

Cultivars	P		Time		P*Time	
	F ratio	P value	F ratio	P value	F ratio	P value
A	0.2	0.6686	233.77	<0.0001***	1.01	0.3856
HB	0.71	0.4251	560.74	<0.0001***	8.38	0.0035**
LC	0.19	0.666	96.77	<0.0001***	0.01	0.9858
M	0.1	0.7554	161.04	<0.0001***	0.16	0.8531
RL	1.23	0.2987	152.31	<0.0001***	1.99	0.1698
S	0.04	0.8503	106.16	<0.0001***	1.92	0.17
YG	2.55	0.1487	112.07	<0.0001***	0.54	0.5927

A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina,' and YG-'Yukon Gold'. Time= Time of measurement. P= P application. *, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-16. Shoot P concentration

Cultivars	8 WAP		12 WAP		15 WAP	
	-P	P	-P	P	-P	P
A	0.093	0.088	0.479	0.466	0.261	0.311
HB	0.097[b]	0.114[a]	0.475	0.574	0.252	0.221
LC	0.118	0.122	0.568	0.593	0.299	0.295
M	0.112	0.116	0.597	0.633	0.335	0.327
RL	0.123	0.103	0.485	0.538	0.274	0.333
S	0.095	0.102	0.622	0.504	0.225	0.256
YG	0.109	0.125	0.535	0.661	0.237	0.254

Comparison was made within the cultivar at the time of measurement. Means followed by similar letters are not significantly different at $P \leq 0.1$. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina,' and YG-'Yukon Gold'.

Table 3-17. ANOVA table for relative shoot P concentration

Source	DF	F ratio	P value
Cultivar	6	1.06	0.4067
Time	2	1.25	0.2955
Cultivar*Time	12	2.92	0.0033**

Time= Time of measurement. P= P application.*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-18. Relative shoot P concentration

Cultivars	5 WAP	8 WAP	12 WAP
Atlantic	0.953	0.979	1.138
Harley Blackwell	1.168	1.194	0.861
La Chipper	1.030	1.033	0.986
Marcy	1.008	1.049	0.938
Red LaSoda	0.869	1.115	1.133
Satina	1.075	0.857	1.210
Yukon Gold	1.125	1.199	1.063

Table 3-19. ANOVA table for cultivar P concentration in tuber

Cultivars	P		Time		P*Time	
	F ratio	P value	F ratio	P value	F ratio	P value
A	7.33	0.0136**	17.09	<0.0001***	2.79	0.0857*
HB	3.55	0.0735*	10.72	0.0006**	1.06	0.3654
LC	0.46	0.5183	21.02	<0.0001***	0.91	0.4283
M	4.05	0.0577*	11.08	0.0006**	1.44	0.2608
RL	2.25	0.1491	11.15	0.0006**	2.47	0.11
S	0.62	0.4563	2.39	0.1311	1.79	0.2067
YG	4.23	0.0786*	3.24	0.0765*	3.56	0.0623*

A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina,' and YG-'Yukon Gold'. Time= Time of measurement. P= P application. *, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-20. Tuber P concentration

Cultivars	8 WAP		12 WAP		15 WAP	
	-P	P	-P	P	-P	P
A	0.109	0.106	0.074	0.088	0.102^{b}	0.138^{a}
HB	0.101^{b}	0.121^{a}	0.082	0.082	0.093	0.111
LC	0.146	0.128	0.099	0.096	0.122	0.125
M	0.106	0.107	0.094	0.082	0.094	0.083
RL	0.123^{b}	0.143^{a}	0.111	0.105	0.105	0.114
S	0.092	0.096	0.105^{a}	0.089^{b}	0.112	0.106
YG	0.085^{b}	0.117^{a}	0.085	0.085	0.082^{b}	0.126^{a}

Comparison was made within the cultivar at the time of measurement. Means followed by similar letters are not significantly different at P≤0.1. A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina,' and YG-'Yukon Gold'.

Table 3-21. ANOVA table for relative tuber P concentration

Source	DF	F ratio	P value
Cultivar	6	6.77	0.0002**
Time	2	10.26	0.0002**
Cultivar*Time	12	3.55	0.0009**

Time= Time of measurement. P= P application. *, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-22. Relative tuber P concentration

Cultivars	5 WAP	8 WAP	12 WAP
Atlantic	1.014[ab]	0.837 [d]	0.740 [de]
Harley Blackwell	0.828 [cd]	0.986 [c]	0.871 [cd]
La Chipper	1.132 [a]	1.031 [bc]	0.949 [bc]
Marcy	0.986 [abc]	1.134 [ab]	1.140 [a]
Red LaSoda	0.855 [bcd]	1.055 [abc]	0.915 [bc]
Satina	0.951 [bc]	1.174 [a]	1.056 [ab]
Yukon Gold	0.721 [d]	1.005 [bc]	0.646 [e]

Comparison was made within time of measurement by student's t. Means followed by similar letters are not significantly different at P≤0.1.

Table 3-23. Phosphorus accumulation (mg/plant)

Cultivars	8 WAP		12 WAP	
	-P	P	-P	P
Atlantic	14.958[ab]	13.395[b]	14.906[b]	21.551[ab]
Harley Blackwell	13.849[b]	14.639[b]	14.994[b]	16.204[ab]
La Chipper	15.436[ab]	15.760[ab]	17.558[ab]	18.509[ab]
Marcy	14.891[ab]	15.996[ab]	19.501[ab]	15.623[b]
Red LaSoda	16.622[ab]	15.030[ab]	21.542[ab]	22.946[a]
Satina	18.721[a]	15.563[ab]	19.063[ab]	18.482[ab]
Yukon Gold	12.975[b]	13.926[b]	15.974[ab]	15.777[b]

Comparison was made within time of measurement by student's t. Means followed by similar letters are not significantly different at P≤0.1.

Table 3-24. ANOVA table for relative P accumulation

Source	DF	F ratio	P value
Cultivar	6	3.0568	0.0094*
Time	1	0.9533	0.3896
Cultivar*Time	6	3.1443	0.001**

Time= Time of measurement. P= P application. *, **, Significant at 0.10, and 0.05 probability level, respectively.

Table 3-25. Relative P accumulation

Cultivars	8 WAP	12 WAP
Atlantic	1.230	0.414 [c]
Harley Blackwell	0.889	0.784 [b]
La Chipper	0.944	0.781 [b]
Marcy	0.854	1.470 [a]
Red LaSoda	1.213	0.818 [b]
Satina	1.426	1.022 [ab]
Yukon Gold	0.827	0.959 [ab]

Comparison was made within time of measurement by student's t. Means followed by similar letters are not significantly different at P≤0.1.

Table 3-26. ANOVA table for tuber PUE

	P		Time		P*Time	
Cultivars	F ratio	P value	F ratio	P value	F ratio	P value
A	0.62	0.4417	8.61	0.002**	1.07	0.3633
HB	0.1	0.7589	6.27	0.0073**	0.96	0.3996
LC	3.57	0.0946*	5.37	0.0178**	1.42	0.2727
M	2.03	0.1691	2.42	0.1144	0.64	0.537
RL	3.39	0.0803*	8.25	0.0024**	2.35	0.1213
S	0.9	0.3711	2.23	0.1465	1.61	0.2374
YG	5.63	0.0499**	5.96	0.0165**	6.03	0.016**

A-'Atlantic', HB-'Harley Blackwell', LC-'La chipper', M-'Marcy', RL-'Red LaSoda', S-'Satina,' and YG-'Yukon Gold'. *, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-27. Tuber PUE

Cultivars	8 WAP		12 WAP		15 WAP	
	-P	P	-P	P	-P	P
Atlantic	0.0238	0.0201	0.1281[a]	0.0939[b]	0.1333	0.1198
Harley Blackwell	0.0262	0.0149	0.1088	0.1084	0.1328	0.1416
La Chipper	0.0157	0.0158	0.0864	0.0870	0.1043[a]	0.1269[b]
Marcy	0.0235	0.0172	0.0818	0.0859	0.1311	0.1500
Red LaSoda	0.0284	0.0142	0.0883	0.0920	0.1035[a]	0.1158[b]
Satina	0.0549	0.0343	0.0912	0.1087	0.1133	0.1231
Yukon Gold	0.0423[a]	0.0278[b]	0.0971[a]	0.0843[b]	0.1433[a]	0.0893[b]

Comparison was made within the cultivar at the time of measurement. Means followed by similar letters are not significantly different at P≤0.1.

Table 3-28. ANOVA table for relative tuber PUE

Source	DF	F ratio	P value
Cultivar	6	10.03	<.0001***
Time	2	3.58	0.0351**
Cultivar*Time	12	4.31	0.0001***

Time= Time of measurement. P= P application. *, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 3-29. Relative tuber PUE

Cultivars	8 WAP	12 WAP	15 WAP
Atlantic	0.996 cd	1.383 a	0.917 bc
Harley Blackwell	1.442 ab	0.964 b	0.817 bc
La Chipper	0.776 d	0.920 b	0.406 c
Marcy	1.001 cd	0.780 bc	0.647 c
Red LaSoda	1.314 abc	0.898 bc	1.557 b
Satina	1.129 bc	0.701 c	0.744 bc
Yukon Gold	1.645 a	0.942 b	3.182 a

Comparison was made within time of measurement by student’s t. Means followed by similar letters are not significantly different at $P \leq 0.1$.

CHAPTER 4
HYDROPONICS

Introduction

In Florida's primary potato production region, soil is usually rich in total P. However, P availability to plants continue to be restricted due to P fixation with Fe, Al in low pH, and Ca in high pH soils. In this study, hydroponics with different forms of P was used to evaluate P-uptake efficiency of three popular potato cultivars in Florida. Tricalcium phosphate (TCP) as insoluble P source with addition of calcium sulfate. The addition Ca to TCP solution decreased the P solubility and hence bioavailability. In the solution containing TCP and $CaSO_4$, Ca released from $CaSO_4$ precipitated most of P released from TCP, resulting in available P concentration of only 0.04 ppm as a result of dynamic equilibrium between TCP and $CaSO_4$ in water. In addition, when TCP is the only P source, depletion of solution Ca concentration prompts increased release of Ca from TCP, which in turn also release P. Therefore, a cultivar with greater Ca uptake can be a P efficient cultivar since Ca uptake promotes increased P release and its uptake. We hypothesized that P efficient potato cultivar would have greater root : : shoot ratio under low P or insoluble P condition. A cultivar that performs better in TCP solution is expected to depict P mobilization ability, therefore, is well adapted to Florida production conditions. To understand the mechanisms that enhance cultivars' P efficiency, 'Harley Blackwell', 'La Chipper' (P-efficient) and 'Red LaSoda' (P-responsive) were used to further evaluate P-mobilization in hydroponics.

Materials and methods

Precipitation of soluble P by Ca was evaluated by adding 0.3 g of TCP to 50 mL solutions each containing 5, 10, 30, or 40 mM Ca as $CaCl_2$ or 7 mM Ca as $CaSO_4$.

These solutions were shaken for 12 hr and P concentration was analyzed by Automated Discrete Analyzer (AQ2)(SEAL Analytical, Hanau, Germany).

Plant Materials and Growth Conditions

Certified seeds of ‘Harley Blackwell’, ‘La Chipper’ and ‘Red LaSoda’ obtained from USDA, Beltsvillle, Maryland were used in this experiment. Tubers were grown in Correa modified Hoagland solution with the following composition (mg L^{-1}): NO_3^--N, 160; NH_4^+-N, 12; K, 239; Ca, 152; Mg, 38.2; S, 40; Fe, 1.68; Cu, 0.24; Mo, 0.128 ; Mn, 1.25; Zn, 0.6; B, 0.8; Si, 10, pH adjusted to 6.5 (Correa et al., 2008). The seed pieces were removed after the seedling had 4-6 unfolded leaves. Two seedlings were grown in 1750 mL plastic containers filled with the above Hoagland solution. Oxygen was supplied by adding 100µL 3 % H_2O_2 twice a week. The treatments included: (i) 10 mg L^{-1} P as control, (ii) 1mg L^{-1} P (iii) 0.5 g Tricalcium Phosphate (TCP) + 4 g $CaSO_4$, i.e. with an initial P concentration of 0.035 mg L^{-1}. TCP was used as the P source to mimic low P availability condition in the soil, and to evaluate the potential effects of P efficient cultivars to mobilize P. The experiment was conducted using the above three cultivars with 6 replications in a completely randomized design. After 28 days, the seedlings were harvested and oven dried at 70°C for 72 hr. Shoot and roots were weighted separately, and shoot P concentration was determined by AQ2, as described below.

Plant Tissue P Content Analysis

The oven dried plant biomass was ground to pass a 40 mesh stainless steel sieve, weighed (0.3±0.05g) into porcelain crucibles, and placed in a Thermolyne Muffle Furnace (Barndtead, Dubuque, USA). The temperature was increased at 10°C/min till 250°C, which was maintained for 30 min, and then increased to 550°C for 6 hours. The ash was cooled to room temperature and 2.25 mL 6N HCl was added, 15 min later filtered through No.41 filter paper, and diluted to 50 mL with de-ionized water. P concentration was analyzed by AQ2 based on US EPA Method 365.1 (O'Del, 1993).

Statistical Analysis

All data were subjected to analysis of variance using Statistical Analysis software JMP version 10 (SAS Institute Inc.). Student's t test was used for evaluation of significance between the two means.

Results

The concentration of P decreased while that of Ca increased (Table 4-1). The P concentration in TCP solution without the addition of Ca was 1.286 ppm. Both $CaSO_4$ and TCP are sparlingly soluble in water, i.e. K_{sp} values are 2.07×10^{-33} and 2.4×10^{-5} mol^2L^{-2}, respectively. The solubility of $CaSO_4$ in water at room temperature is 0.21g/100 mL. Therefore, addition of 4 g $CaSO_4$ to 1750 mL nutrient solution is expected to maintain the solution super saturated with respect to $CaSO_4$ throughout 28 days of seedling growth experiment. The P concentration in this solution was 0.035ppm.

After 28 days in hydroponics, seedlings biomass decreased significantly in the low P and TCP solution compared to high P solution (Table 4-2). With high P supply, 'Red LaSoda' shoot biomass was 65.5% greater than 'La Chipper', and 34.4% greater than 'Harley Blackwell'. However, with low P supply, 'Red LaSoda' shoot biomass was 48.9 % and 33.4% less than 'La Chipper' and 'Harley Blackwell', respectively. When TCP was the only P source in the solution, 'Red LaSoda' and 'Harley Blackwell' had the greater biomass than 'La Chipper' (Figure 4-1).

Relative biomass was calculated as the ratio of biomass of the plants grown with low P or with TCP in relation to that of the plants grown with high P solution. This response parameter was only influenced by the interaction between cultivar and treatment (Table 4-3). ‘Harley Blackwell’ and ‘Red LaSoda’ showed similar RB under both low P and TCP treatments, while ‘La Chipper’ showed greater RB in low P as compared that in TCP treatment (Figure 4-2). Both TCP and low P treated plants showed significantly greater root : shoot ratio than that of the high P treatment for all three cultivars (Table 4-4). There was no significant difference between cultivars in low P and TCP treatments regarding root : shoot ratio (Figure 4-3).

Seedling P accumulation was significantly influenced by cultivar, treatment, and the interaction between cultivar and treatment (Table 4-5). High P treated seedling showed significantly greater P accumulation as compared to low P and TCP, and ‘Red LaSoda’ showed greater P accumulation than ‘La Chipper’ and ‘Harley Blackwell’ in high P treatment (Figure 4-4). In low P condition, ‘Red LaSoda’ had less P accumulated as compared to other cultivars, while in TCP treatment it also had the least P accumulation than the other cultivars.

Discussion

Nutrient solution containing 10 ppm P provided sufficient P to support potato-seedling growth for 28 days. Phosphate ions are negatively charged. Therefore, uptake of phosphate results in the roots to shed negatively charged hydroxyl or bicarbonate ions to maintain electrical balance, which will in turn, increase the solution pH. Increasing pH will reduce TCP solubility; hence decrease the concentration of the most plant available-P forms, i.e. $H_2PO_4^-$ and HPO_4^{2-} (Hinsinger, 2001; John, 1967). Since $CaSO_4$ was added to decrease P bioavailability, to obtain P from growth media, P-efficient genotypes/cultivars can develop an adaptive mechanism including producing more root to intercept with P or to uptake more Ca ions (Bais et al., 2006; Dakora and Phillips, 2002; Gerke et al., 2000; Hoffland, 1992). Increased root growth is usually accompany with P stress to acquire more P from soil for different crop species including rape, wheat, barley, and rice (Raghothama, 1999). Increasing root shoot ratio is considered an adaption to low-P condition, and the ratio may become an index for P uptake efficiency (Mariotto-Cezar et al., 2013; Schenk, 2004). In this study, both TCP and low P treated plants showed significantly greater root : shoot ratio than that of the high P treatment for all of the three tested cultivars. These results are in agreement with previous study that enhanced root growth or reduced shoot biomass are positively related to low-P condition (Aziz et al., 2006; Lynch and Brown, 2001; Yaseen and Malhi, 2009).

Decreasing plant biomass is common in response to P deficiency (Wissuwa, 2005). The proportion of biomass reduction in low P or relative insoluble P (TCP) solutions as compared to the biomass in high P solution (Relative biomass; RB) can be important for identification of P responsive and P mobilizing cultivars. P responsive cultivars could increase biosynthesis with increasing P supply; therefore, P responsive cultivars will have greater difference between high P and low P or TCP treatment, i.e. smaller RB at low P or TCP treatment than other cultivars. ‘Red LaSoda’ showed the greatest biomass in high P but the least in low P. Though ‘Red LaSoda’ root : shoot ratio increased significantly in low P treatment, that did not enhance the total biomass. Since in the low P condition, no matter how much root mass has been produced, 1 ppm P was all the cultivar can get. Therefore, the energy ‘Red LaSoda’ deposited into root growth at the low P condition did not pay back by the greater P uptake. Also, ‘Red LaSoda’ P accumulation in both of the low P and TCP treatments was significantly lower than the high P treatment. This result suggested ‘Red LaSoda’ should have greater P demand than the other cultivars, and the cultivar's P uptake ability was low in P limiting conditions. However, 'Red LaSoda' did perform well with sufficient P supply, indicated that it is a P responsive cultivar, and its low RB in both low P and TCP suggested that 'Red LaSoda' was not able to adapt in P deficient condition.

'La Chipper' showed great RB in the low P treatment, but low RB in TCP treatment. Indicates this cultivar has better ability to adapt to low P condition but not equipped with P mobilizing ability. Compared to other cultivars, 'Harley Blackwell' had greater or equal total biomass, root : shoot ratio, RB and P accumulation in the TCP treatment, which indicated 'Harley Blackwell' has better P mobilization ability. This cultivar was able to continuously mobilize the P from TCP in solution to support the growth. Plant response to P availability may differ at different growth stages. The result showed in this study could only represent 28 days old seedling stage of these three potato cultivars.

Potato is a high nutrition demanding crop compared to other major crops (Hopkins et al., 2010; Stark and Love, 2003). Florida soils are typically sandy soils with high concentration of Ca due to the continuous Ca fertilization, and/or irrigation with high Ca water (Sartain, 2008). Phosphorus fixation with Ca can greatly reduce the plant available P concentration in soil; hence most of Florida soils with high pH need P fertilization despite containing high concentrations of total P. In soils with high amount of fixed P, a cultivar with the outstanding P mobilization ability is preferred to utilize this P reserve without excess P application, which will probably increase the amount of precipitated P in the soil. Since 'Harley Blackwell' was able to maintain its growth and P accumulation in sparingly P solution, indicating that 'Harley Blackwell' was able to acquire P from fixed P form in Florida soil. ‘Harley Blackwell’ can be classified as a P efficient cultivar which may have a great potential to be used for P-efficient breeding in the future.

Conclusion

Increasing root : shoot ratio was observed on potato grown in low P and sparingly soluble P solution, but no significant difference was found between cultivars. ‘Harley Blackwell’ showed similar biomass in high and sparingly soluble P solution that indicating this cultivar has a potential of acquiring P in Ca rich soil, such as Florida soil. ‘Red LaSoda’ is considered a P responsive cultivar, as its low biomass in both low P and TCP solution, but high biomass in high P solution.

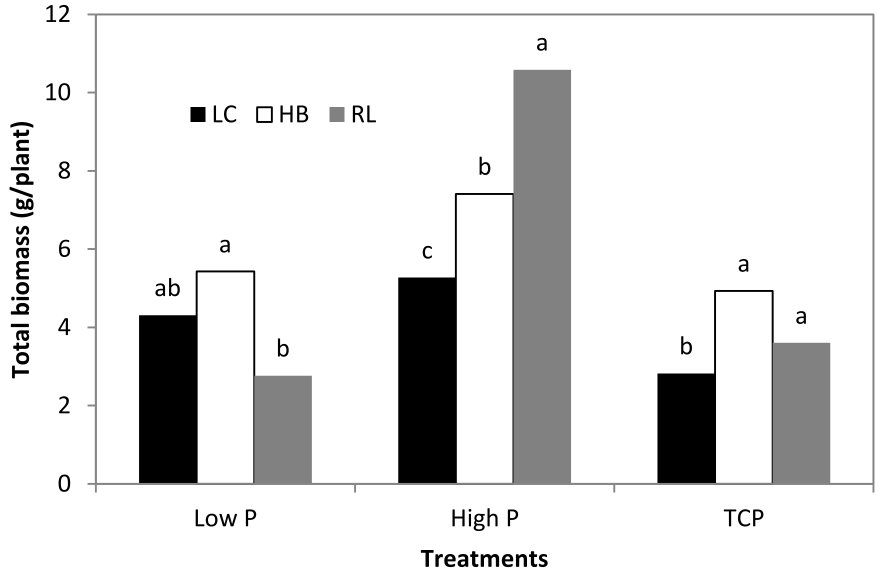

Figure 4-1. Total biomass of 28 days old three potato cultivars seedlings grown in modified Hoagland solution with different P concentrations Means followed by similar letters, within a P concentration, significantly different at $P \leq 0.1$. Low P-1ppm P, High P-10ppm P, TCP-Tricalcium phosphate. RL-'Red LaSoda', LC-'La Chipper', HB-'Harley Blackwell'.

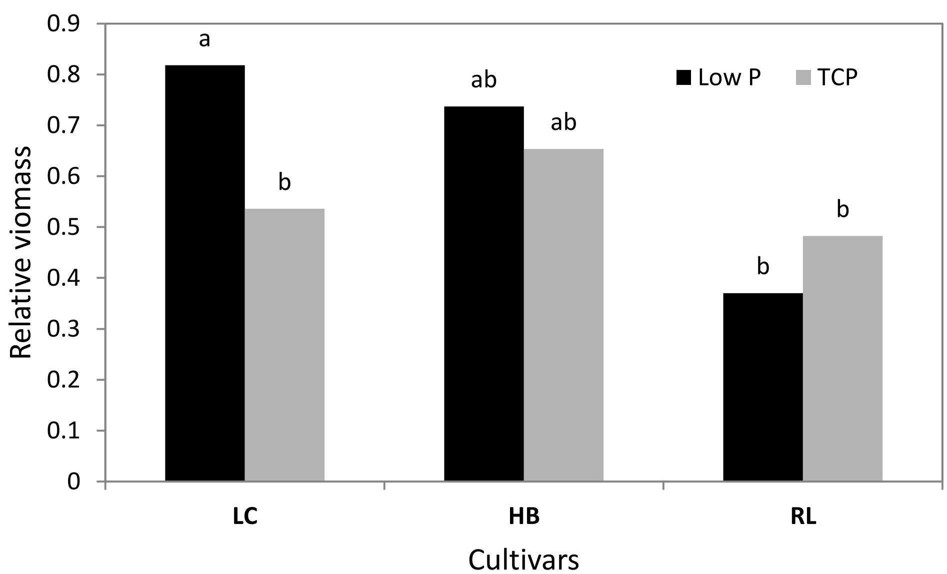

Figure 4-2. Relative biomass of 28 days old three potato cultivars seedlings grown in modified Hoagland solution with different P concentrations. Means followed by similar letters, within a P concentration, significantly different at $P \leq 0.05$. Low P-1ppm P, High P-10ppm P, TCP-Tricalcium phosphate. RL-'Red LaSoda', LC-'La Chipper', HB-'Harley Blackwell'.

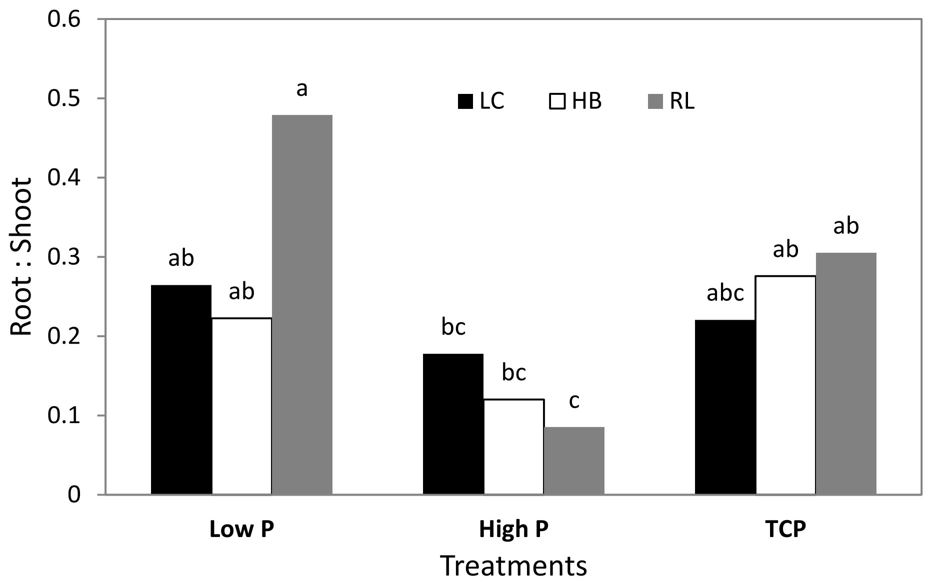

Figure 4-3. Root to shoot ratio of 28 days old three potato cultivars seedlings grown in modified Hoagland solution with different P concentrations. Means followed by similar letters, within a P concentration, significantly different at P ≤ 0.1. Low P-1ppm P, High P-10ppm P, TCP-Tricalcium phosphate. RL-‘Red LaSoda’, LC-‘La Chipper’, HB-‘Harley Blackwell’.

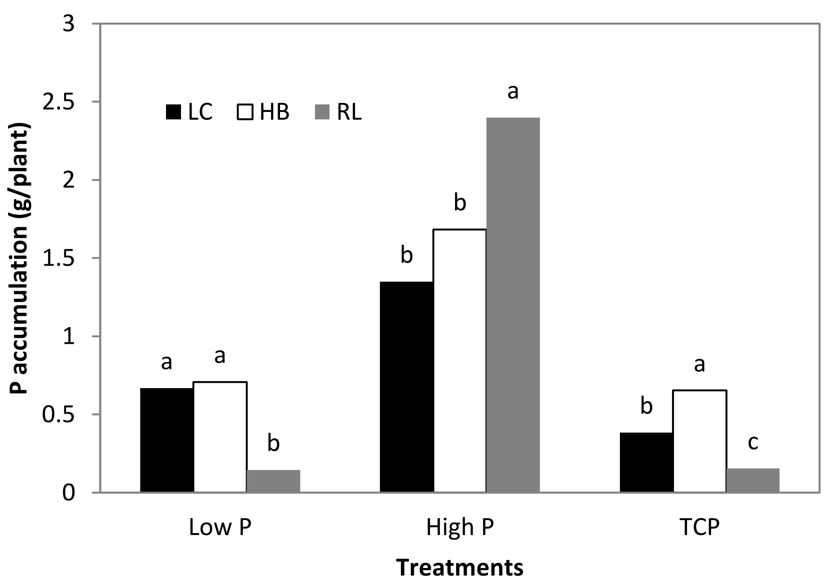

Figure 4-4. Phosphorus accumulation in 28 days old three potato cultivars seedlings grown in modified Hoagland solution with different P concentrations. Means followed by similar letters, within a P concentration, significantly different at P

≤ 0.1. Low P-1ppm P, High P-10ppm P, TCP-Tricalcium phosphate. RL-‘Red LaSoda’, LC-‘La Chipper’, HB-‘Harley Blackwell’.

Table 4-1. Concentration of P in 50 ml Hoagland solution with 0.3 g of tricalcium phosphate and addition of different amounts of CaCl2 or CaSO4 to attain different Ca concentrations 0 to 50 mM

Ca source	[Ca] (mM)	[P] (ppm)	SE
$CaCl_2$	0	1.286	0.027
$CaCl_2$	5	0.140	0.081
$CaCl_2$	10	0.149	0.026
$CaCl_2$	30	0.059	0.025
$CaCl_2$	40	0.049	0.019
$CaSO_4$	7	0.035	0.023
N=5			

Table 4-2. ANOVA table for total biomass

Source	DF	F ratio	P value
Cultivar	2	7.5963	0.0016**
Treatment	2	20.6973	<0.0001***
Cultivar*Treatment	4	4.1030	0.0072**

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 4-3. ANOVA table for relative biomass

Source	DF	F ratio	P value
Cultivar	2	0.9049	0.4169
Treatment	1	1.5348	0.2265
Cultivar*Treatment	2	3.3121	0.0523*

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 4-4. ANOVA table for root: shoot ratio

Source	DF	F ratio	P value
Cultivar	2	0.0324	0.9682
Treatment	2	3.9451	0.0275**
Cultivar*Treatment	4	1.1954	0.3281

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

Table 4-5. ANOVA table for P accumulation

Source	DF	F ratio	P value
Cultivar	2	3.1781	0.0542*
Treatment	2	124.0921	<0.0001***
Cultivar*Treatment	4	12.3948	<0.0001***

*, **, *** Significant at 0.10, 0.05, and 0.001 probability level, respectively.

CHAPTER 5
CONCLUSION

Phosphate is a limiting resource and it is also one of the essential nutrients to plant. Developing P efficient cultivars is an urgent task to protect world food security. Observation on the physiological and morphological responses of potato cultivars grown in Florida soil could help us identifying the P efficient cultivar that can maintain high yield without regularly P fertilizer application to reduce the production cost and the chance of eutrophication. Generally, Florida soil is rich in P, but the fixation effect is so strong that only the cultivar equipped with outstanding P mobilization ability could keep up the growth and yield as grown in P fertilized plot.

In the pot experiment conducted in Hastings and Gainesville, no evident showed that photosynthesis was reduced in the non P treated pot, but the differences between P and non-P treated shoot growth and tuber yield did varied. Since ‘Red LaSoda’ relatively poor production without P application, and great production with P application, it is considered a P responsive cultivar. While ‘Satina’ was considered as a P-efficient cultivar based on high productivity and PUE for both shoot and tuber in non P amended soil. Potato leaf greenness (SPAD) is not a representative index for potato P efficiency, but it could be used as an index for general cultivar evaluation.

The field experiment conducted in Parrish, FL. also showed that ‘Satina’ had greater or equal relative value in biomass, tissue P concentration, and P accumulation than the other cultivars. ‘Satina’ was further confirmed as a P efficient cultivars in this experiment. We also confirmed that tuber is the stronger P sink as compared to shoot, plant translocate most of the P into tuber when during tuber development. Specific leaf weight seems to reveal the cultivar P efficiency, and could be used as a less destructive way to evaluate P efficiency. Potato emergence rate and tuber size was not affected by external P status in this experiment.

In the hydroponics trial, increasing root : shoot ratio was observed on potato grown in low P and sparingly soluble P solution. ‘Harley Blackwell’ showed similar biomass in high and sparingly soluble P solution that indicating this cultivar has a potential of acquiring P in Ca rich soil, such as Florida soil. ‘Red LaSoda’ is considered a P responsive cultivar, as its low biomass in both low P and TCP solution, but high biomass in high P solution. This finding further is agreed with the previous field and pot experiment. Since ‘Red LaSoda’ did showed mass root production under P limited condition. The cause of its low productivity in P limited environment could be the lack of root exudes. Further study can focus on comparing ‘Red LaSoda’ and ‘Satina’ root exudates production under P deficiency condition.

LIST OF REFERENCES

Akhtar, M.S., Y. Oki, and T. Adachi. 2008. Genetic variability in phosphorus acquisition and utilization efficiency from sparingly soluble P-sources by Brassica cultivars under P-stress environment. J. Agron. Crop Sci. 194(5):380-392.

Al-Abbas, A.H. and S.A. Barber. 1964. A soil test for phosphorus based upon fractlonatlon of soil phosphorus: I. Correlation of soil phosphorus fractions with plant-available phosphorus. Soil Sci Soc Amer Proc. 28(2):218-221.

Alvarez-Sanchez, E., J. Etchevers, J. Ortiz, R. Nunez, V. Volke, L. Tijerina, and A. Martinez. 1999. Biomass production and phosphorus accumulation of potato as affected by phosphorus nutrition. J. Plant Nutr. 22(1):205-217.

Arunakumara, K.K.I.U., B.C. Walpola, and M. Yoon. 2013. Aluminum Toxicity and Tolerance Mechanism in Cereals and Legumes - A Review. J. Korean Soc. Appl. Biol. Chem. 56(1):1-9.

Aziz, T., M.A. Rahmatullah, M.A. Maqsood, I.A. Tahir, and C. MA. 2006. Phosphorus utilization by six Brassica cultivars (Brassica juncea L.) from tri-calcium phosphate; a relatively insoluble P compound. Pak. J. Bot. 38(5):1529-1538.

Bai, H., B. Murali, K. Barber, and C. Wolverton. 2013. Low Phosphate Alters Lateral Root Setpoint Angle and Gravitropism. Am. J. Bot. 100(1):175-182.

Bais, H.P., T.L. Weir, L.G. Perry, S. Gilroy, and J.M. Vivanco. 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. Annu.Rev.Plant Biol. 57:233-266.

Balemi, T. and K. Negisho. 2012. Management of soil phosphorus and plant adaptation mechanisms to phosphorus stress for sustainable crop production: a review. J. Plant Nutr. Soil Sci. 12(3):547-562.

Balemi, T. and M.K. Schenk. 2009. Genotypic variation of potato for phosphorus efficiency and quantification of phosphorus uptake with respect to root characteristics. J. Plant Nutr. Soil Sci. 172(5):669-677.

Bates, T. and J. Lynch. 2000. The efficiency of Arabidopsis thaliana (Brassicaceae) root hairs in phosphorus acquisition. Am. J. Bot. 87(7):964-970.

Beebe, S., M. Rojas-Pierce, X. Yan, M. Blair, F. Pedraza, F. Munoz, J. Tohme, and J. Lynch. 2006. Quantitative trait loci for root architecture traits correlated with phosphorus acquisition in common bean. Crop Sci. 46(1):413-423.

Bertin, C., X. Yang, and L. Weston. 2003. The role of root exudates and allelochemicals in the rhizosphere. Plant Soil. 256(1):67-83.

Bhat, K.K.S. and P.H. Nye. 1973. Diffusion of phosphate to plant roots in soil. I. Quantitative autoradiography of the depletion zone. Plant Soil. 38:161-175.

Bhattacharyya, P., S. Das, and T.K. Adhya. 2013. Root Exudates of Rice Cultivars Affect Rhizospheric Phosphorus Dynamics in Soils with Different Phosphorus Statuses. Commun. Soil Sci. Plant Anal. 44(10):1643-1658.

Bieleski, R.L. 1973. Phosphate Pools, Phosphate Transport, and Phosphate Availability. Annu. Rev. Plant Physiol. Plant Mol. Biol. 24:225-252.

Blair, G. and D. Godwin. 1991. Phosphorus efficiency in pasture species. VII. Relationships between yield and P uptake in two accessions of white clover. Crop and Pasture Sci. 42(7):1271-1283.

Bohm, W. and U. Kopke. 1977. Comparative root investigations with 2 profile wall methods. J. Agron. Crop Sci. 144(4):297-303.

Bonser, A., J. Lynch, and S. Snapp. 1996. Effect of phosphorus deficiency on growth angle of basal roots in Phaseolus vulgaris. New Phytol. 132(2):281-288.

Brooks, A., K.C. Woo, and S.C. Wong. 1988. Effects of phosphorus nutrition on the response of photosynthesis to CO_2 and O_2, activation of ribulose bisphosphate carboxylase and amounts of ribulose bisphosphate and 3-phosphoglycerate in spinach leaves. Photosynth. Res. 15(2):133-141.

Buckingham, D.A. and S.M. Jasinski. 2010. Phosphate rock sstatistics. Historical Statistics for Mineral and Material Commodities in the United States, Washington, DC: U.S 140.

Byerlee, D. 1996. Modern varieties, productivity, and sustainability: Recent experience and emerging challenges. World Dev. 24(4):697-718.

Cakmak, I., C. Hengeler, and H. Marschner. 1994. Partitioning of shoot and root dry matter and carbohydrates in bean plants suffering from phosphorus, potassium and magnesium deficiency. J. Exp. Bot. 45(9):1245-1250.

Cakmak, I. 2002. Plant nutrition research: Priorities to meet human needs for food in sustainable ways. Plant Soil. 247(1):3-24.

Campbell, C. and R. Sage. 2002. Interactions between atmospheric CO2 concentration and phosphorus nutrition on the formation of proteoid roots in white lupin (Lupinus albus L.). Plant Cell Environ. 25(8):1051-1059.

Carpenter, S.R. 2008. Phosphorus control is critical to mitigating eutrophication. Proc. Natl. Acad. Sci. U. S. A. 105(32):11039-11040.

Chen, J., L. Xu, Y. Cai, and J. Xu. 2009. Identification of QTLs for phosphorus utilization efficiency in maize (Zea mays L.) across P levels. Euphytica 167(2):245-252.

Chen, K. and F. Lenz. 1997. Responses of strawberry to doubled CO2 concentration and phosphorus deficiency .2. Gas exchange and water consumption. Gartenbauwissenschaft. 62(2):90-96.

Chen, Y.P., P.D. Rekha, A.B. Arun, F.T. Shen, W.-. Lai, and C.C. Young. 2006. Phosphate solubilizing bacteria from subtropical soil and their tricalcium phosphate solubilizing abilities. Appl. Soil Ecol. 34(1):33-41.

Chen, Z., Q. Cui, C. Liang, L. Sun, J. Tian, and H. Liao. 2011. Identification of differentially expressed proteins in soybean nodules under phosphorus deficiency through proteomic analysis. Proteomics. 11(24):4648-4659.

Ciereszko, I. and A. Barbachowska. 2000. Sucrose metabolism in leaves and roots of bean (Phaseolus vulgaris L.) during phosphate deficiency. J. Plant Physiol. 156(5-6):640-644.

Cisse, L. and T. Mrabet. 2004. World Phosphate Production: Overview and Prospects. Phosphorus Research Bulletin. 15:21-25.

Clarksib, D.T. and C.B. Scattergood. 1982. Growth and phosphate-transport in barley and tomato plants during the development of, and recovery from, phosphate-stress. J. Exp. Bot. 33(136):865-875.

Correa, R.M., J.E. Brasil Pereira Pinto, C.A. Brasil Pereira Pinto, V. Faquin, E.S. Reis, A.B. Monteiro, and W.E. Dyer. 2008. A comparison of potato seed tuber yields in beds, pots and hydroponic systems. Sci. Hortic. 116(1):17-20.

Czarnecki, O., J. Yang, D.J. Weston, G.A. Tuskan, and J. Chen. 2013. A dual role of strigolactones in phosphate acquisition and tilization in plants. Int. J. Mol. Sci. 14(4):7681-7701.

da Silva, A.A., I. Arn, C.V. Simoes de Lima, A.d.B. Schneider, and C.A. Delatorre. 2008. Differentiation in hydroponic solution of wheat genotypes in relation to tolerance to phosphorus starvation. Rev. Bras. Cienc. Solo. 32(5):1949-1958.

da Silva, E.C. and W.R. Maluf. 2012. Hydroponic technique for screening of tomato genotypes for phosphorus uptake efficiency. Hortic. Bras. 30(2):317-321.

Dakora, F. and D. Phillips. 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant Soil. 245(1):35-47.

Dakora, F. and D. Phillips. 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant Soil. 245(1):35-47.

Datta, S., C.M. Kim, M. Pernas, N.D. Pires, H. Proust, T. Tam, P. Vijayakumar, and L. Dolan. 2011. Root hairs: development, growth and evolution at the plant-soil interface. Plant Soil. 346(1-2):1-14.

de Campos, M.C.R., S.J. Pearse, R.S. Oliveira, and H. Lambers. 2013. Viminaria juncea does not vary its shoot phosphorus concentration and only marginally decreases its mycorrhizal colonization and cluster-root dry weight under a wide range of phosphorus supplies. Ann. Bot. 111(5):801-809.

De Roo, H.C. and P.E. Waggoner. 1961. Root development of potatoes. J. Agron. 53:15-17.

Dechassa, N., M. Schenk, N. Claassen, and B. Steingrobe. 2003. Phosphorus efficiency of cabbage (Brassica oleraceae L. var. capitata), carrot (Daucus carota L.), and potato (Solanum tuberosum L.). Plant Soil. 250(2):215-224.

Duffner, A., E. Hoffland, and E.J.M. Temminghoff. 2012. Bioavailability of zinc and phosphorus in calcareous soils as affected by citrate exudation. Plant Soil. 361(1-2):165-175.

Elloitt, K. and A. White. 1994. Effects of light, nitrogen, and phosphorus on red pine seedling growth and nutrient use efficiency. For. Sci. 40(1):47-58.

Eltrop, L. and H. Marschner. 1996. Growth and mineral nutrition of non-mycorrhizal and mycorrhizal Norway spruce (Picea abies) seedlings grown in semi-hydroponic sand culture .2. Carbon partitioning in plants supplied with ammonium or nitrate. New Phytol. 133(3):479-486.

Fernandes, A.M. and R.P. Soratto. 2011. Nutrition, dry matter accumulation and partitioning and phosphorus use efficiency of potato grown at different phosphorus levels in Nutrient solution. Revista Brasileira de Ciência do Solo. 36(5):1528-1537.

Field, C. and H. Mooney. 1986. The photosynthesis–nitrogen relationship in wild plants. Cambridge University Press, Cambridge.

Fleisher, D.H., Q. Wang, D.J. Timlin, J.-. Chun, and V.R. Reddy. 2013. Effects of carbon dioxide and phosphorus supply on potato dry matter allocation and canopy morphology. J. Plant Nutr. 36(4):566-586.

Foehse, D. and A. Jungk. 1983. Influence of phosphate and nitrate supply on root hair formation of rape, spinach and tomato plants. Plant and Soil 74:359-368.

Fohse, D., N. Claassen, and A. Jubgk. 1991. Phosphorus efficiency of plants .2. significance of root radius, root hairs and aation-anion balance for phosphorus influx in 7 plant-species. Plant Soil. 132(2):261-272.

Follmi, K. 1996. The phosphorus cycle, phosphogenesis and marine phosphate-rich deposits. Earth-Sci. Rev. 40(1-2):55-124.

Fox, T.R. and N.B. Comerford. 1990. Low-Molecular-Weight Organic-Acids in Selected Forest Soils of the Southeastern Usa. Soil Sci. Soc. Am. J. 54(4):1139-1144.

Fries, N. and B. Forsman. 1951. Quantitative determination of certain nucleic acid derivatives in pea root exudate. Physiol. Plantarum 4(2):410-420.

Gahoonia, T. and N. Nielsen. 1997. Variation in root hairs of barley cultivars doubled soil phosphorus uptake. Euphytica. 98(3):177-182.

Gahoonia, T. and N. Nielsen. 1998. Direct evidence on participation of root hairs in phosphorus (P-32) uptake from soil. Plant Soil. 198(2):147-152.

Gahoonia, T. and N. Nielsen. 2004. Root traits as tools for creating phosphorus efficient crop varieties. Plant Soil. 260(1-2):47-57.

Gao, N., Y. Su, J. Min, W. Shen, and W. Shi. 2010. Transgenic tomato overexpressing ath-miR399d has enhanced phosphorus accumulation through increased acid phosphatase and proton secretion as well as phosphate transporters. Plant Soil. 334(1-2):123-136.

Gardner, W.K., D.G. Parbery, D.A. Barber, and L. Swinden. 1983. The acquisition of phosphorus by lupinus-albus L .5. the diffusion of exudates away from roots - a computer-simulation. Plant Soil. 72(1):13-29.

Gerke, J., L. Beissner, and W. Romer. 2000. 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. J. Plant Nutr. Soil Sci. -Z. Pflanzenernahr. Bodenkd. 163(2):207-212.

Gietl, C. 1992. Malate-dehydrogenase isoenzymes - cellular locations and role in the flow of metabolites between the cytoplasm and cell organelles. Biochim. Biophys. Acta 1100(3):217-234.

Giletto, C.M. and H.E. Echeverria. 2013. Chlorophyll meter for the evaluation of potato N status. American Journal of Potato Research 90(4):313-323.

Gourley, C.J.P., D.L. Allan, and M.P. Russelle. 1993. Defining phosphorus efficiency in plants. Plant Soil. 155:289-292.

Gout, E., R. Bligny, R. Douce, A. Boisson, and C. Rivasseau. 2011. Early response of plant cell to carbon deprivation: in vivo P-31-NMR spectroscopy shows a quasi-instantaneous disruption on cytosolic sugars, phosphorylated intermediates of energy metabolism, phosphate partitioning, and intracellular pHs. New Phytol. 189(1):135-147.

Grewal, J.S. and S.N. Singh. 1976. Critical levels of available phosphorus for potato in alluvial soils. Indian J. Agric. Sci. 46(12):580-584.

Gutiérrez-Boem, F.H. and G.W. Thomas. 1998. Phosphorus nutrition affects wheat response to water deficit. Agron J. 90(2):166-171.

Gutiérrez-boem, F.H. and G.W. Thomas. 1999. Phosphorus nutrition and water deficits in field-grown soybeans. Plant and Soil 207(1):87-96.

Gyaneshwar, P., G. Kumar, and L. Parekh. 1998. Effect of buffering on the phosphate-solubilizing ability of microorganisms. World J. Microbiol. Biotechnol. 14(5):669-673.

Hammond, J.P., M.J. Bennett, H.C. Bowen, M.R.E. Broadley D.C., and May ST, Rahn C, Swarup R, Woolaway KE, White PJ. 2003. Changes in gene expression in arabidopsis shoots during phosphate starvation and the potential for developing smart plants. J. Plant Physiol. 132(578-596).

Harrison, A.F. 1987. Soil organic phosphorus: A review of world literature. CAB International, Wallingford, UK.

Heffer, P. 2009. Assessment of fertilizer use by crop at the global level. International Fertilizer Industry Association, Paris.

Hegney, M. and I. McPharlin. 1999. Broadcasting phosphate fertilisers produces higher yields of potatoes (Solanum tuberosum L.) than band-placement on coastal sands. Aust. J. Exp. Agric. 39(4):495-503.

Hegney, M., I. McPharlin, and R. Jeffery. 2000. Using soil testing and petiole analysis to determine phosphorus fertiliser requirements of potatoes (Solanum tuberosum L. cv. Delaware) in the Manjimup-Pemberton region of Western Australia. Aust. J. Exp. Agric. 40(1):107-117.

Hijmans, R. 2001. Global distribution of the potato crop. Am. J. Potato Res. 78(6):403-412.

Hinsinger, p. 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. Plant Soil. 237(2):173-195.

Hoch, W., E. Zeldin, and B. McCown. 2001. Physiological significance of anthocyanins during autumnal leaf senescence. Tree Physiol. 21(1):1-8.

Hoffland, E. 1992. Quantitative-evaluation of the role of organic-acid exudation in the mobilization of rock phosphate by rape. Plant Soil. 140(2):279-289.

Hoffland, E., G. Findenegg, and J. Nelemans. 1989. Solubilization of Rock Phosphate by Rape .2. Local Root Exudation of Organic-Acids as a Response to P-Starvation. Plant Soil. 113(2):161-165.

Hopkins, B.G., J.W. Ellsworth, T.R. Bowen, A.G. Cook, S.C. Stephens, V.D. Jolley, A.K. Shiffler, and D. Eggett. 2010. Phosphorus fertilizer timing for Russet Burbank potato grown in calcareous soil. J. Plant Nutr. 33(4):529-540.

Huber, D. M. 1980. The role of mineral nutrition in defense. Plant disease, an advanced treatise. 5:381-406.

Hurry, V., A. Strand, R. Furbank, and M. Stitt. 2000. The role of inorganic phosphate in the development of freezing tolerance and the acclimatization of photosynthesis to low temperature is revealed by the pho mutants of Arabidopsis thaliana. Plant J. 24(3):383-396.

Jacob, J. and D.W. Lawlor. 1991. Stomatal and mesophyll limitations of photosynthesis in phosphate deficient sunflower, maize and wheat plants. Journal of Experiment Botany 42:1003-1011.

Jain, A., V.K. Nagarajan, and K.G. Raghothama. 2012. Transcriptional regulation of phosphate acquisition by higher plants. Cell Mol. Life Sci. 69(19):3207-3224.

John, E.H. 1967. The Effect of pH on the uptake and accumulation of phosphate and sulfate ions by bean plants. Am. J. Bot. 54(5):560-564.

Johnson, J., D. Allan, and C. Vance. 1994. Phosphorus stress-induced proteoid roots show altered metabolism in Lupinus-Albus. Plant Physiol. 104(2):657-665.

Johnson, J., D. Allan, C. Vance, and G. Weiblen. 1996. Root carbon dioxide fixation by phosphorus-deficient Lupinus albus - Contribution to organic acid exudation by proteoid roots. Plant Physiol. 112(1):19-30.

Johnson, J., C. Vance, and D. Allan. 1996. Phosphorus deficiency in Lupinus albus - Altered lateral root development and enhanced expression of phosphoenolpyruvate carboxylase. Plant Physiol. 112(1):31-41.

Jungk, A. 1996. Dynamics of nutrient movement at the soil-root interface in Plant roots. The hidden half. Marcel Dekker, New York, USA.

Jungk, A. 2001. Root hairs and the acquisition of plant nutrients from soil. J. Plant Nutr. Soil Sci. -Z. Pflanzenernahr. Bodenkd. 164(2):121-129.

Kalra, Y.P. 1998. Handbook of reference methods for plant analysis . CRC Press, Florida.

Kania, A., N. Langlade, E. Martinoia, and G. Neumann. 2003. Phosphorus deficiency-induced modifications in citrate catabolism and in cytosolic pH as related to citrate exudation in cluster roots of white lupin. Plant Soil. 248(1-2):117-127.

Keerthisinghe, G., P. Hocking, P. Ryan, and E. Delhaize. 1998. Effect of phosphorus supply on the formation and function of proteoid roots of white lupin (Lupinus albus L.). Plant Cell Environ. 21(5):467-478.

Keyes, S.D., K.R. Daly, N.J. Gostling, D.L. Jones, P. Talboys, B.R. Pinzer, R. Boardman, I. Sinclair, A. Marchant, and T. Roose. 2013. High resolution synchrotron imaging of wheat root hairs growing in soil and image based modelling of phosphate uptake. New Phytol. 198(4):1023-1029.

Kikui, S., T. Sasaki, H. Osawa, H. Matsumoto, and Y. Yamamoto. 2007. Malate enhances recovery from aluminum-caused inhibition of root elongation in wheat. Plant Soil. 290(1-2):1-15.

Kim, H., W. Kim, M. Roh, C. Kang, J. Park, and K.A. Sudduth. 2013. Automated sensing of hydroponic macronutrients using a computer-controlled system with an array of ion-selective electrodes. Comput. Electron. Agric. 93:46-54.

Klug, B. and W.J. Horst. 2010. Oxalate exudation into the root-tip water free space confers protection from aluminum toxicity and allows aluminum accumulation in the symplast in buckwheat (Fagopyrum esculentum). New Phytol. 187(2):380-391.

Kochuan, L.V. 1995. Cellular mechanisms of aluminum toxicity and resistance in plants. Annu. Rev. Plant Physiol. Plant Mol. Biol. 46:237-260.

Krasilnikoff, G., T. Gahoonia, and N. Nielsen. 2003. Variation in phosphorus uptake efficiency by genotypes of cowpea (Vigna unguiculata) due to differences in root and root hair length and induced rhizosphere processes. Plant Soil. 251(1):83-91.

Kraus, M., A. Fusseder, and E. Beck. 1987. In situ-determination of the phosphate-gradient around a root by radioautography of frozen soil sections. Plant Soil. 97:407-418.

Kucey, R., H. Janzen, and M. Leggett. 1989. Microbially mediated increases in plant-available phosphorus. Adv. Agron. 42:199-228.

Lambers, H., J.C. Clements, and M.N. Nelson. 2013. How a phosphorus-acquisition strategy based on carboxylate exudation powers the success and agronomic potential of Lupines (Lupinus, Fabaceae). Am. J. Bot. 100(2):263-288.

Lee, R.B., R.G. Ratcliffe, and T.E. Southon. 1990. 31P NMR Measurements of the cytoplasmic and vacuolar Pi content of mature maize roots: relationships with phosphorus status and phosphate fluxes. J. Exp. Bot. 41(9):1063-1078.

Lee, R. and R. Ratcliffe. 1993. Nuclear-magnetic-resonance studies of the location and function of plant nutrients in-vivo. Plant Soil. 155:45-55.

Lei, M., Y. Liu, B. Zhang, Y. Zhao, X. Wang, Y. Zhou, K.G. Raghothama, and D. Liu. 2011. Genetic and genomic evidence that sucrose Is a global regulator of plant responses to phosphate starvation in Arabidopsis. Plant Physiol. 156(3):1116-1130.

Lewis, J.D., K.L. Griffin, R.B. Thomas, and B.R. Strain. 1994. Phosphorus supply affects the photosynthetic capacity of loblolly pine grown in elevated carbon dioxide. Tree Physiology 14(11):1229-1244.

Li, J., X. Liu, W. Zhou, J. Sun, Y. Tong, W. Liu, Z. Li, P. Wang, and S. Yao. 1995. Technique of wheat breeding for efficiently utilizing. Science in China Series B-Chemistry Life Sciences & Earth Sciences 38(11):1313-1320.

Li, X., J. Ma, and H. Matsumoto. 2000. Pattern of aluminum-induced secretion of organic acids differs between rye and wheat. Plant Physiol. 123(4):1537-1543.

Liang, C., M.A. Pineros, J. Tian, Z. Yao, L. Sun, J. Liu, J. Shaff, A. Coluccio, L.V. Kochian, and H. Liao. 2013. Low pH, aluminum, and phosphorus coordinately regulate malate exudation through GmALMT1 to improve soybean adaptation to acid soils. Plant Physiol. 161(3):1347-1361.

Liao, H., G. Rubio, X. Yan, A. Cao, K.M. Brown, and J.P. Lynch. 2001. Effect of phosphorus availability on basal root shallowness in common bean. Plant Soil. 232(1-2):69-79.

Liao, H., X. Yan, G. Rubio, S. Beebe, M. Blair, and J. Lynch. 20064. Genetic mapping of basal root gravitropism and phosphorus acquisition efficiency in common bean. Funct. Plant Biol. 31:959-970.

Lipton, D., R. Blanchar, and D. Blevins. 1987. Citrate, malate, and succinate concentration in exudates from P-sufficient and P-stressed Medicago-Sativa L seedlings. Plant Physiol. 85(2):315-317.

Liu, J., J.V. Magalhaes, J. Shaff, and L.V. Kochian. 2009. Aluminum-activated citrate and malate transporters from the MATE and ALMT families function independently to confer Arabidopsis aluminum tolerance. Plant J. 57(3):389-399.

Locascio, S. and R. Rhue. 1990. Phosphorus and micronutrient sources for potato. Am. Potato J. 67(4):217-226.

Lockhart, J.A. 1965. An analysis of irreversible plant cell elongation. J. Theor. Biol. 8(2):264-275.

Lopez-Bucio, J., M.F. Nieto-Jacobo, V. Ramırez-Rodrıguez, and L. Herrera-Estrella. 2000. Organic acid metabolism in plants: from adaptive physiology to transgenic varieties for cultivation in extreme soils. Plant Science. 160(1):1-13.

Luquet, D., B. Zhang, M. Dingkuhn, A. Dexet, and A. Clement-Vidal. 2005. Phenotypic plasticity of rice seedlings: Case of phosphorus deficiency. Plant. Prod. Sci. 8(2):145-151.

Lynch, J.P. and K.M. Brown. 2001. Topsoil foraging–an architectural adaptation of plants to low phosphorus availability. Plant Soil. 237(2):225-237.

Machado, C.T. and A.M.C. Furlani. 2004. Kinetics of phosphorus uptake and root morphology of local and improved varieties of maize. Scientia Agricola. 61:69-76.

Mardamootoo, T., K.F.N.K. Kwong, and C.C. Du Preez. 2013. Assessing environmental phosphorus status of soils in Mauritius following long-term phosphorus fertilization of sugarcane. Agric. Water Manage. 117:26-32.

Mariotto-Cezar, T.C., S.R. Machado Coelho, D. Christ, V. Schoeninger, and A.J. Bispo de Almeida. 2013. Nutritional and antinutritional factors during the storage process of common bean. J Food Agr Environ. 11(1):268-272.

Martinoia, E. and D. Rentsch. 1994. Malate compartmentation - responses to a complex metabolism. Annu. Rev. Plant Physiol. Plant Mol. Biol. 45:447-467.

Mccollum, R. 1978. Analysis of potato growth under differing P-regimes .2. time by P-status interactions for growth and leaf efficiency. Agron. J. 70(1):58-67.

McLaughlin, M.J., I.R. Fillery, and A.R. Till. 1992. Operation of the phosphorus, sulphur and nitrogen cycles. p. 67–116. In: R. Gifford and M. Barson (eds.). Australia's renewable sources: sustainability and global change.

Mimura, T. 1999. Regulation of phosphate transport and homeostasis in plant cells. p. 149-200. In: Anonymous International Review of Cytology. Academic Press.

Misra, R. and A. Gibbons. 1996. Growth and morphology of eucalypt seedling-roots, in relation to soil strength arising from compaction. Plant Soil. 182(1):1-11.

Miyasaka, S. and M. Habte. 2001. Plant mechanisms and mycorrhizal symbioses to increase phosphorus uptake efficiency. Commun. Soil Sci. Plant Anal. 32(7-8):1101-1147.

Moorby, J. 1968. The influence of carbohydrate and mineral nutrient supply on the growth of potato tubers. Ann. Bot. 32(1):57-68.

Muller, R., M. Morant, H. Jarmer, L. Nilsson, and T.H. Nielsen. 2007. Genome-wide analysis of the Arabidopsis leaf transcriptome reveals interaction of phosphate and sugar metabolism. Plant Physiol. 143(1):156-171.

Munoz-Arboleda, F., R.S. Mylavarapu, C.M. Hutchinson, and K.M. Portier. 2006. Root distribution under seepage-irrigated potatoes in northeast Florida. Am. J. Potato Res. 83(6):463-472.

Murphy, K., D. Lammer, S. Lyon, B. Carter, and S. Jones. 2005. Breeding for organic and low-input farming systems: An evolutionary-participatory breeding method for inbred cereal grains. Renew. Agr. Food Syst. 20(1):48-55.

Nakano, A., H. Ikeno, T. Kimura, H. Sakamoto, M. Dannoura, Y. Hirano, N. Makita, L. Finer, and M. Ohashi. 2012. Automated analysis of fine-root dynamics using a series of digital images. J. Plant Nutr. Soil Sci. 175(5):775-783.

Nelson, R. and L. Schweitzer. 1988. Evaluating soybean germplasm for specific leaf weight. Crop Sci. 28(4):647-649.

Neumann, G. and V. Romheld. 1999. Root excretion of carboxylic acids and protons in phosphorus-deficient plants. Plant Soil. 211(1):121-130.

Nielsen, K., T. Bouma, J. Lynch, and D. Eissenstat. 1998. Effects of phosphorus availability and vesicular-arbuscular mycorrhizas on the carbon budget of common bean (Phaseolus vulgaris). New Phytol. 139(4):647-656.

Nilsson, L., M. Lundmark, P.E. Jensen, and T.H. Nielsen. 2012. The Arabidopsis transcription factor PHR1 is essential for adaptation to high light and retaining functional photosynthesis during phosphate starvation. Physiol. Plantarum. 144(1):35-47.

Nilsson, L., R. Mueller, and T.H. Nielsen. 2007. Increased expression of the MYB-related transcription factor, PHR1, leads to enhanced phosphate uptake in Arabidopsis thaliana. Plant Cell Environ. 30(12):1499-1512.

Oburger, E., M. Dell'mour, S. Hann, G. Wieshammer, M. Puschenreiter, and W.W. Wenzel. 2013. Evaluation of a novel tool for sampling root exudates from soil-grown plants compared to conventional techniques. Environ. Exp. Bot. 87:235-247.

O'Del, J.W. 1993. Method 365.1 determination of phosphorus by semi-automated colorimetry. U.S. Environmental Protection Agency, Ohio.

Ohwaki, Y. and H. Hirata. 1992. Differences in carboxylic-acid exudation among p-starved leguminous crops in relation to carboxylic-acid contents in plant-tissues and phospholipid level in roots. Soil Sci. Plant Nutr. 38(2):235-243.

Owusubennoah, E. and A. Wild. 1979. Autoradiography of the depletion zone of phosphate around onion roots in the presence of vesicular-arbuscular Mycorrhiza. New Phytol. 82(1):133-140.

Paul, M. and T. Pellny. 2003. Carbon metabolite feedback regulation of leaf photosynthesis and development. J. Exp. Bot. 54(382):539-547.

Paul, M. and M. Stitt. 1993. Effects of nitrogen and phosphorus deficiencies an levels of carbohydrates, respiratory enzymes and metabolites in seedlings of tobacco and their response to exogenous sucrose. Plant Cell Environ. 16(9):1047-1057.

Pettigrew, W. 1999. Potassium deficiency increases specific leaf weights and leaf glucose levels in field-grown cotton. Agron. J. 91(6):962-968.

Plaxton, W.C. and H.T. Tran. 2011. Metabolic Adaptations of Phosphate-Starved Plants. Plant Physiol. 156(3):1006-1015.

Pratt, j.,Boisson,A.M.,Gout,E., Bligny,R.,Douce,R.,Aubert,S. 2009. Phosphate (Pi) starvation effect on the cytosolic Pi concentration and Pi exchanges across the tonoplast in plant cells: an in vivo 31P-nuclear magnetic resonance study using methylphosphonate as a Pi analog. Plant Physiol. 151(3):1646-1657.

Purnell, H. 1960. Studies of the family Proteaceae. I. Anatomy and morphology of the roots of some Victorian species. Aust. J. Bot. 8:38-50.

Pursglove, J.D. and F.E. Sanders. 1981. The growth and phosphorus economy of the early potato (Solanum tuberosum). Commun. Soil Sci. Plant Anal. 12(11):1105-1121. <http://www.tandfonline.com/doi/abs/10.1080/00103628109367222>.

Qiu, J. and D.W. Israel. 1994. Carbohydrate accumulation and utilization in soybean plants in response to altered phosphorus nutrition. Physiologia Plantarum. 90:722-728.

Radin, J.W. and M.P. Eidenbock. 1984. Hydraulic conductance as a factor limiting leaf expansion of phosphorus-deficient cotton plants. Plant Physiol. 75(2):372-377.

Raghothama, K. 1999. Phosphate acquisition. Annual review of plant biology. 50(1):665-693.

Rao, I.M. and N. Terry. 1995. Leaf phosphate status, photosynthesis, and carbon partitioning in sugar beet (IV. Changes with time following increased supply of phosphate to low-phosphate plants). Plant Physiol. 107(4):1313-1321.

Rausch,C., Bucher,M. 2002. Molecular mechanisms of phosphate transport in plants. Planta. 216(1):23-37.

Reich, P.B. and J. Oleksyn. 2009. Leaf phosphorus influences the photosynthesis–nitrogen relation: a cross-biome analysis of 314 species. Oecologia. 160(2):207-212.

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 Soil. 349(1-2):121-156.

Rodriguez, D., M.C. Pomar, and J. Goudriaan. 1998. Leaf primordia initiation, leaf emergence and tillering in wheat (Triticum aestivum L.) grown under low phosphorus conditions. Plant Soil. 202:149-157.

Rovira, A. 1969. Plant Root Exudates. Bot. Rev. 35(1):35-37.

Rubio, G., T. Walk, Z. Ge, X. Yan, H. Liao, and J. Lynch. 2001. Root gravitropism and below-ground competition among neighbouring plants: A modelling approach. Annals of Botany. 88(5):929-940.

Sain, S., D. Barnes, and D. Biesboer. 1994. Hydroponic and tissue-culture evaluation of Alfalfa (Medicago-Sativa L) subpopulations selected for phosphorus efficiency. Plant Sci. 99(1):17-26.

Sartain, J.B. 2008. Soil and tissue testing and interpretation for Florida turf grasses. The Institute of Food and Agricultural Sciences, Florida SL 181.

Sato, A., A. Oyanagi, and M. Wada. 1996. Effect of phosphorus content of the emergence of tillers in wheat cultivars. J. A. R. Q. 30:27-30.

Schachtman, D.P., R.J. Reid, and S.M. Ayling. 1998. Phosphorus uptake by plants: From soil to cell. Plant Physiol. 116(2):447-453.

Schenk, M.K. and S.A. Barber. 1979. Phosphate uptake by corn as affected by soil characteristics and root morphology. Soil Sci. Soc. Am. J. 43(5):880-883.

Schenk, M.K. 2006. Nutrient efficiency of vegetable crops. Acta Horticulturae 700:21-34.

Schenk, M. 2004. Nutrient efficiency of vegetable crops.

Schlesinger, W.H. and B.F. Chabot. 1977. The use of water and minerals by evergreen and deciduous shrubs in Okefenokee swamp. Bot. Gaz. 138(4):490-497. <http://www.jstor.org/stable/2473885>.

Schulze, J., M. Tesfaye, R. Litjens, B. Bucciarelli, G. Trepp, S. Miller, D. Samac, D. Allan, and C. Vance. 2002. Malate plays a central role in plant nutrition. Plant Soil. 247(1):133-139.

Sepehr, E., Z. Rengel, E. Fateh, and M.R. Sadaghiani. 2012. Differential capacity of wheat cultivars and white lupin to acquire phosphorus from rock phosphate, phytate and soluble phosphorus sources. J. Plant Nutr. 35(8):1180-1191.

Shane, M.W., E.T. Fedosejevs, and W.C. Plaxton. 2013. Reciprocal control of anaplerotic phosphoenolpyruvate carboxylase by in vivo monoubiquitination and phosphorylation in developing proteoid roots of phosphate-deficient Harsh Hakea. Plant Physiol. 161(4):1634-1644.

Sharpley, A.N. and P.J. Withers. 1994. The environmentally-sound management of agricultural phosphorus. Fert. Res. 39(2):133-146.

Shenoy, V. and G. Kalagudi. 2005. Enhancing plant phosphorus use efficiency for sustainable cropping. Biotechnol. Adv. 23(7-8):501-513.

Shin, H., H. Shin, G.R. Dewbre, and M.J. Harrison. 2004. Phosphate transport in Arabidopsis: Pht1;1 and Pht1;4 play a major role in phosphate acquisition from both low- and high-phosphate environments. The Plant Journal. 39(4):629-642.

Sinclair, T. and V. Vadez. 2002. Physiological traits for crop yield improvement in low N and P environments. Plant Soil. 245(1):1-15.

Singh, J.P. 1987. Role of phosphorous and potassium content of leaf in maximizing potato yield. J. Agric. Sci. 57:565–566.

Skene, K. 1998. Cluster roots: some ecological considerations. J. Ecol. 86(6):1060-1064.

Smit, A.L., P.S. Bindraban, J.J. Schröder, J.G. Conijn., and H.G. van der Meer. 2009. Phosphorus on agriculture: global resources, trends and developments. Nutrient Flow Task Group, Netherlands 282.

Sobrado, M.A. 2012. Leaf tissue water relations in tree species from contrasting habitats within the upper Rio Negro forests of the Amazon region. J. Trop. Ecol. 28:519-522.

Stark, J.C. and S.L. Love. 2003. Potato production systems. University of Idaho, Idaho.

Syers, J.K., Johnston A.E., Curtin, D. 2008. Efficiency of soil and fertilizer phosphorus: reconciling changing concepts of soil phosphorus behaviour with agronomic information. FAO, Rome 18.

Tardieu, F., C. Granier, and B. Muller. 2011. Water deficit and growth. Co-ordinating processes without an orchestrator? Curr. Opin. Plant Biol. 14(3):283-289.

Terry, N. and I.M. Rao. 1991. Nutrients and photosynthesis: iron and phosphorus as case studies. Cambridge, Cambridge, UK.

The World Bank. 2013. Phosphate rock. Index Mundi, 2013. <http://www.indexmundi.com/commodities/?commodity=rock-phosphate&months=120>.

Thomas, A., A.D. Tomos, J.L. Stoddard, H. Thomas, and C.J. Pollock. 1989. Cell expansion rate, temperature and turgor pressure in growing leaves of Lolium temulentum L. New Phytol. 112(1):1-5.

Ticconi, C. and S. Abel. 2004. Short on phosphate: plant surveillance and countermeasures. Trends Plant Sci. 9(11):548-555.

Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. Science. 292(5515):281-284.

Uhde-Stone, C., K.E. Zinn, M. Ramirez-Yanez, A. Li, C.P. Vance, and D.L. Allan. 2003. Nylon filter arrays reveal differential gene expression in proteoid roots of white lupin in response to phosphorous deficiency. Plant Physiol. 131:1064-1079.

Van Alphen, B.J. and J.J. Stoorvogel. 2000. A methodology for precision nitrogen fertilization in highinput farming systems. Precision Agric. 2(4):319–332.

Vance, C.P., C. Uhde-Stone, and D.L. Allan. 2003. Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol. 157(3):423-447.

Vanderzaag, D. and D. Horton. 1983. Potato production and utilization in world perspective with special reference to the tropics and sub-tropics. Potato Res. 26(4):323-362.

Vogt, K., D. Vogt, and J. Bloomfield. 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant Soil. 200(1):71-89.

Wang, B., J. Shen, C. Tang, and Z. Rengel. 2008. Root morphology, proton release, and carboxylate exudation in lupin in response to phosphorus deficiency. J. Plant Nutr. 31(3):557-570.

Wang, G., D. Zhou, Q. Yang, J. Jin, and X. Liu. 2005. Solubilization of rock phosphate in liquid culture by fungal isolates from rhizosphere soil. Pedosphere. 15(4):532-538.

Wang, J., J. Sun, J. Miao, J. Guo, Z. Shi, M. He, Y. Chen, X. Zhao, B. Li, F. Han, Y. Tong, and Z. Li. 2013. A phosphate starvation response regulator Ta-PHR1 is involved in phosphate signalling and increases grain yield in wheat. Ann. Bot. 111(6):1139-1153.

Wang, Y., H. Xu, J. Kou, L. Shi, C. Zhang, and F. Xu. 2013. Dual effects of transgenic Brassica napus overexpressing CS gene on tolerances to aluminum toxicity and phosphorus deficiency. Plant Soil. 362(1-2):231-246.

Ward, C.L., A. Kleinert, K.C. Scortecci, V.A. Benedito, and A.J. Valentine. 2011. Phosphorus-deficiency reduces aluminium toxicity by altering uptake and metabolism of root zone carbon dioxide. J. Plant Physiol. 168(5):459-465.

Warren, C.R. and M.A. Adams. 2002. Phosphorus affects growth and partitioning of nitrogen to Rubisco in Pinus pinaster. Tree Physiol. 22(1):11-19.

Watt, M. and J. Evans. 1999. Proteoid roots. Physiology and development. Plant Physiol. 121(2):317-323.

Weaver, J.E. 1926. Root development of field crops. McGraw-Hill Book Co, New York.

Winter, H. and S. Huber. 2000. Regulation of sucrose metabolism in higher plants: Localization and regulation of activity of key enzymes. Crit. Rev. Biochem. Mol. Biol. 35(4):253-289.

Wissuwa, M. 2005. Combining a modelling with a genetic approach in establishing associations between genetic and physiological effects in relation to phosphorus uptake. Plant Soil. 269(1-2):57-68.

Witowski, E.T.F. and B.B. Lamont. 1991. Leaf specif mass confounds leaf density and thickness. Oecologia. 88:486-493.

Xu, J., Y. Zhu, Q. Ge, Y. Li, J. Sun, Y. Zhang, and X. Liu. 2012. Comparative physiological responses of Solanum nigrum and Solanum torvum to cadmium stress. New Phytol. 196(1):125-138.

Xu, Y. and J.H. Crouch. 2008. Marker-assisted selection in plant breeding: From publications to practice. Crop Sci. 48(2):391-407.

Yan, X., H. Liao, S. Beebe, M. Blair, and J. Lynch. 2004. QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. Plant Soil 265(1-2):17-29.

Yaseen, M. and S.S. Malhi. 2009. Differential growth response of wheat genotypes to ammonium phosphate and rock phosphate phosphorus sources. J. Plant Nutr. 32(3):410-432.

Yu, L., J. Yan, S. Guo, and W. Zhu. 2012. Aluminum-induced secretion of organic acid by cowpea (Vigna unguiculata L.) roots. Sci. Hortic. 135:52-58.

Zeng, H., X. Feng, B. Wang, Y. Zhu, Q. Shen, and G. Xu. 2013. Citrate exudation induced by aluminum is independent of plasma membrane H+-ATPase activity and coupled with potassium efflux from cluster roots of phosphorus-deficient white lupin. Plant Soil. 366(1-2):389-400.

Zeng, X., W.S. Chow, L. Su, X. Peng, and C. Peng. 2010. Protective effect of supplemental anthocyanins on Arabidopsis leaves under high light. Physiol. 138(2):215-225.

Zhou, J., F. Jiao, Z. Wu, Y. Li, X. Wang, X. He, W. Zhong, and P. Wu. 2008. OsPHR2 is involved in phosphate-starvation signaling and excessive phosphate accumulation in shoots of plants. Plant Physiol. 146(4):1673-1686.

Zhu, J., S. Kaeppler, and J. Lynch. 2005. Mapping of QTL controlling root hair length in maize (Zea mays L.) under phosphorus deficiency. Plant Soil. 270(1-2):299-310.

Zhu, J. and J. Lynch. 2004. The contribution of lateral rooting to phosphorus acquisition efficiency in maize (Zea mays) seedlings. Funct. Plant Biol. 31(10):949-958.

Zhu, Y., S. Smith, A. Barritt, and F. Smith. 2001. Phosphorus (P) efficiencies and mycorrhizal responsiveness of old and modern wheat cultivars. Plant Soil 237(2):249-255.

Zhu, Y., F. Yan, C. Zorb, and S. Schubert. 2005. A link between citrate and proton release by proteoid roots of white lupin (Lupinus albus L.) grown under phosphorus-deficient conditions? Plant Cell Physiol. 46(6):892-901.

Zia-ul-Hassan and M. Arshad. 2010. Cotton growth under potassium deficiency stress is influenced by photosynthetic apparatus and root system. Pak. J. Bot. 42(2):917-925.

Zoghlami, L.B., W. Djebali, Z. Abbes, H. Hediji, M. Maucourt, A. Moing, R. Brouquisse, and W. Chaibi. 2011. Metabolite modifications in Solanum lycopersicum roots and leaves under cadmium stress. Afr. J. Biotechnol. 10(4):567-579.

Zotarelli, L., B.M. Santos, P.J. Dittmar, P.D. Roberts, and S.E. Webb. 2013. Potato production. In: S.M. Olson and E. Simonne (eds.). Vegetable production handbook for Florida. The Institute of Food and Agricultural Sciences.

BIOGRAPHICAL SKETCH

Wei Chieh Lee was born in Taiwan in 1987. She got her bachelor's degree in Plant Pathology from National Chung-Hsing University in 2009. Wei Chieh then got an intern position at Ohio State University Plant Pathology lab. She worked on Agrobacterium and E.coli component cell's preparation, Agrobacterium and E. coli transformation, DNA extraction from both plant tissue and fungi, PCR and sequencing, using fluorescence microscope, plasmid mini-prep, DNA electrophoresis and related greenhouse tasks. After a year of the lab work, Wei Chieh decided to pursue her master's degree in plant nutrition with Dr. Liu. After her master's program, she wants her career in agriculture to proceed.