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Phosphorus in Potatoes:
Uptake and Utilization

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William B. Evans

has been accepted towards fulfillment
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Ph.D. degree in Soil Fertility

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PHOSPHORUS IN POTATOES:
UPTAKE AND UTILIZATION

By

William B. Evans

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Crop and Soil Sciences

1994

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ABSTRACT

PHOSPHORUS IN POTATOES:
UPTAKE AND UTILIZATION

By

William B. Evans

Three sets of experiments were conducted: one to determine yield responses of potato to fertilizer phosphorus (P) in three Michigan soils, another to evaluate relative responses of potato to applied and indigenous (truly indigenous and residual applied) P in McBride sandy loam, and a third to determine P uptake kinetics in several potato cultivars grown in solution culture. Results from the first experiments support the hypothesis that potatoes are more responsive to fertilizer P in the McBride soil than in a Capac loam or Martisco muck. Data from the second set of experiments reveal that potatoes grown in McBride sandy loam soils with over 400 kg available $P \cdot ha^{-1}$ show positive growth and yield responses to applied P. Plant height, leaf number, tuber number and tuber yield per plant were all increased by banding 50 kg $P \cdot ha^{-1}$ into McBride soils with 200 to 900 kg available $P \cdot ha^{-1}$. The influence of applied P on growth and yield diminished to none as soil test P levels approached 900 $kg \cdot ha^{-1}$. Applying 100 to 200 kg $P \cdot ha^{-1}$ had no greater effect on growth and yield than did applying 50 kg $P \cdot ha^{-1}$. Data from the third set of experiments indicate that all of the six potato cultivars tested had similar phosphorus uptake rates per unit of root at a given initial

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solution P concentration. However, the rate of P uptake was higher at higher initial solution P concentrations. Uptake rates were similar to those reported elsewhere for other crops, indicating that the rate of P uptake per unit of root is not the limiting factor in potato's apparent inability to utilize soil P as efficiently as do other crops. The changes in P uptake rate with changing solution P concentrations appear to follow two slopes. The steeper of the two occurred at solution P concentrations between 1 μM and 2.7 μM, the highest concentration tested. The presence of two slopes may indicate biphasic uptake and the presence of a dual uptake mechanism.

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Thank you Dr. Warncke for serving as my Advisor and for your friendship. Thanks also to the other members of my guidance committee: Drs. Smucker, Chase, Ellis, and Widders. Thanks also to Dr. Hansen for replacing Dr. Widders on the committee during his sabbatical leave. I must also recognize Drs. Davenport and Hammerschmidt in Botany and Plant Pathology for helping with the field and greenhouse work.

My work was greatly simplified though the work of several technicians, staff members and their crews: Cal Bricker, Dallas Hyde, Brian Graff, Ron Gnagey, Dick Crawford, Jerri Wardwell, Dick Kitchen, and John Dahl. Thanks also to the growers who allowed me to collect data on their property.

My friends and family were very important during this work. Every year I gain a deeper appreciation for the strength and wisdom my parents, Barbara and Gordon Evans, possess. My brothers and sisters, Lindsey, John, Leslie and

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Sarah, have been unwavering in their encouragement. Tom Fernandez, Mike and Amy McLean, and myself worked through our preliminary examinations with friendship, food and commitment to a common goal. I could not have finished this work without the help of fellow students Joe Strzalka, Deliana Siregar, Mike VanMiddlesworth, Bob Battel, Anne Ng, and Autumn Deer.

Finally, thanks also to Fiona Crocker for her love and her smile.

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CHAPTER 1

REVIEW OF LITERATURE

Introduction

Potatoes are one of the most universally grown crops in the world, with production from the tropics to the countries along the arctic circle. The crop's value in human nutrition, versatility in cooking and keeping quality have given potatoes this prominence in world agriculture. Michigan produced almost 2.5 billion kg on 18,400 ha in 1991 (Espie, 1992), making it the 8th largest potato producing state in the United States (Chase, personal communication). Although many soil and climatic conditions favor excellent potato production in Michigan, environmental and cultural factors can limit potato yields. Potatoes require more field management than most agronomic crops and tubers cannot be stored as long as many other staple crops can. This review will focus on one field management problem in potatoes: phosphorus (P) fertility. The review begins with an overview of potato production, leading to a discussion of soil P chemistry and important relations between soil chemistry and potato growth and yield. The review concludes with a discussion of P relations in and near the plant.

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Potato Production

Potatoes (*Solanum tuberosum* L.) are annual plants, grown solely for their edible swollen underground stems or tubers. Potatoes require 20 to 28 C days and 10 to 20 C nights for 90 to 130 days for optimal growth and yield in Michigan, depending on variety. Tillage consists of a plow-plant program with any secondary tillage done before planting. At planting, a complete fertilizer is banded 5 cm below and 5 cm to the side of the row (Vitosh, 1990). Potatoes are grown from whole tubers or ones cut into seed piece sizes between 50 and 75 g. Buds on the tubers, referred to as "eyes", sprout soon after planting 2 to 8 cm below the soil surface. The crop is hilled when plants are 25 to 30 c, tall by disks or sweeps which make a wide and flattened hill over the row. Harvest is 90 to 130 days after planting (DAP), depending on cultivar and growing conditions. Management practices during the growing season are selected to promote steady growth, maximizing yields and producing tubers with qualities suitable for their intended use. In 1991, the Michigan fall crop received averages of 164 kg $N \cdot ha^{-1}$, 71 kg $P \cdot ha^{-1}$ and 138 kg $K \cdot ha^{-1}$ (Espie, 1992), as well as supplemental water, and several fungicide and insecticide applications. After harvest, the tubers are either sold immediately or are held in storage for later sale. Markets for Michigan potatoes include "table stock", potato chip production, frozen processing, canning and seed.

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The nutrient requirements of potato are high. In 1991, N, P and K applications per hectare of the Michigan potato crop exceeded those applied to field corn (another highly fertilized crop) by 18, 131, and 139% for the three elements, respectively (Espie, 1992). Potato crops grown by Vitosh (1990) removed averages of less than 7 kg $P \cdot ha^{-1}$ and 336 kg $K \cdot ha^{-1}$ (Vitosh, 1990), compared to an average 1991 Michigan application of 72 kg $P \cdot ha^{-1}$ and 117 kg $K \cdot ha^{-1}$ (Espie, 1992). The removal of P from the soil appears to be much less efficient than that of K, presenting a significant management problem.

Regardless of how efficiently N, P and K are taken up, each is quite important in plant nutrition. Nitrogen is a major constituent of proteins and genetic material in the plant. Its effects on potatoes include yield enhancement, altering size distribution and decreasing the specific gravity (dry matter) of tubers (Vitosh, 1990). Cell membranes and many energy related compounds contain P. Phosphorus has not been shown to influence tuber specific gravity (Vitosh, 1990). Potassium helps regulate photosynthesis and gas exchange in the leaves and is important in cellular water relations. It is applied to increase potato yields but may decrease tuber specific gravity in certain situations (Vitosh, 1990).

The general ontogeny and morphology of the potato plant are very different than those of most crops. This is

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apparent from the plant's start as a sprout on a seed piece through its harvest and utilization. Seed tuber selection is very important in determining final yield. The seed tuber supplies nutrients to the sprouting buds for early growth. Generally, larger seed pieces (50 g) produce higher yields than smaller ones (<40 g) (e.g. Bremner and Taha, 1966 and Toosey, 1960). Larger seed tubers produce more vigorous stems and greater numbers of stolons available for tuber set (Svensson, 1966). From each seed piece, one or several sprouts emerge, with a greater number of sprouts resulting in higher yields (Toosey, 1960). Benepal (1967a) found sprout growth and emergence unaffected by P fertilization. Tubers are generally initiated before flowering. Tubers set earlier are more likely to size and contribute to marketable yield. The developing tubers rely on the shoots and roots for almost all of their nutrients.

Phosphorus is recycled (Pursglove and Sanders, 1981) within the potato plant and is transported from roots to green shoots and then back down to the developing tubers. Senescence of the above-ground shoots begins soon after flowering and fruit set. The fruit are 1 to 4 cm green berries, similar to small, hard tomatoes. During senescence, carbohydrates and other nutrients continue to move into tubers. Nutrient partitioning as well as the amounts of nutrients available influence tuber yield.

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Soil Phosphorus Relations

The P status of plants is determined primarily by the amounts available to the plant. Soil chemistry and physics control the amounts of external P available to the plant (e.g. the soil and any applied materials).

Available P is determined by the amounts held in each soil P pool: unavailable, labile, and solution. Unavailable P is tightly held as mineral or precipitated P, and occluded P that is dissolved only very slowly into solution. Labile P is a combination of solution P and weakly bound P that can move into solution and become available to the plant quickly (Foth and Ellis, 1988). Solution P, the only P which is immediately available for plant uptake, is ionic P which occurs in the liquid phase of the soil. Availability of P depends on soil parent material, fertilizer inputs, pH, elemental interactions, clay content, organic matter, and soil moisture. Plants generally take up the HPO_4^{-2} and $H_2PO_4^-$ ionic species from the soil solution (Foth and Ellis, 1988). The ratios of the various soluble orthophosphate species in solution is determined by solution pH. As pH decreases, H^+ ions attach to P ions, resulting in a succession of prominent species from PO_4^{-3} through H_3PO_4, the latter of which does not normally occur at pHs found in soil systems. Because soil pH is a reflection of elemental and mineral species in the soil, its influence on P avai

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availability is also through elemental interactions between P and other ions.

Calcium's role in pH control is an important factor in soil P relations. Because of calcium's prominence in all but highly weathered soils, very little P remains free in solution. Ca-phosphates usually are the dominant P precipitates formed at high pH, and Al and Fe precipitates dominate at low pH (Barber, 1984). Al and Fe-phosphates tend to be less available for uptake than Ca-phosphates. Most temperate agricultural soils contain Ca, Fe, and Al phosphates. Barber (1984) noted that Ca, Fe and Al-phosphates precipitates are most likely to form when soil solution P concentrations exceed 160 μM. Liming of sandy soils can cause reduced P availability due to Ca-phosphate precipitation (Payton, et al., 1989).

Ca and liming can alter uptake by, concentration in (Barber, 1984) and utilization of P by plants. Payton, et al. (1989) noted that the effectiveness of P fertilizer on improving potato yield depends on soil pH. They suggest that liming reduced available P levels in sandy soils due to Ca-phosphate precipitation. Ivanov and Solyarova (1973) found that liming decreased the average bond strength of soil held P without changing the total quantity of adsorbed P. Laughlin, et al. (1974), working with a pH 4.8 Alaskan Cryothod soil, found there were increases in Kennebec potato yield and foliar P concentration from both P and lime

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application but not an interaction between the two. In addition, liming did not change tuber P concentrations in their studies. Rue, et al. (1981) studied this interaction using two P carriers and also found no interaction between P and liming. Contradictory research by Franklin (1970) showed that polyvalent cations, such as Ca, improve P absorption by plants and may do this by neutralizing charges in root pores, allowing passage of P. Franklin speculated that this same process may block P movement into plants with small root pores. Although the idea of ionic movement through open root pores has been replaced by theories involving active transport across membranes such as those described by Marschner (1986), the inhibition of P transport by Ca cannot be ruled out.

Westermann (1992) has confirmed a relationship between Ca and P uptake in potatoes. In greenhouse experiments using sudan grass and potato, liming at rates of 6, 29, 75, or 126 g $CaO \cdot kg^{-1}$ soil decreased the effectiveness of Ca-phosphate fertilizers applied at 25 or 75 mg $P \cdot kg^{-1}$. At either P rate, increasing the liming rate decreased dry matter and P accumulation.

In soils with little exchangeable Ca, Al and Fe-phosphates are the dominant P binding ions. This is important in the studies reported in succeeding chapters because Fe and Al can control indigenous P availability in moderately weathered soils such as those found in Michigan.

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Fe appears especially important in the McBride sandy loam (Yerokun, 1987) that was used in the studies reported here. Iron and Al-phosphates are also important products of fertilizer reactions in slightly acidic soils (pH 5.5 to 7.0) (Barber, 1984 and Foth and Ellis, 1988). In temperate, moderately weathered soils, Fe interacts with P but has little influence on pH. Al also readily precipitates with indigenous and applied P (Foth and Ellis, 1988). When P concentrations in the soil solution are less than 160 μM near applied P, the P is likely to be adsorbed on Fe and Al oxides/hydroxides rather than be precipitated in discrete mineral forms. The Fe oxides which can form are among the first sites of adsorption for fertilizer P (Barber, 1984). When solution P concentrations exceed 160 μM, as they often do near fertilizer granules, Ca, Fe and Al precipitates form. At pH 5.5 to 7.0, complex Fe and Al-phosphates are likely to be the main precipitated species (Foth and Ellis, 1988). In these soils, the precipitated forms may not control solution P as much as adsorbed P will. On low pH, highly weathered soils, Al and Fe precipitates predominate. Lindsay and Stephenson (1959), studying monocalcium phosphate reactions in an acidic sandy loam, found that monocalcium P fertilizer applications can cause temporary increases in soil solution Fe and Al concentrations by dissolving the two metals into solution. Then, as the pH of the solution around the fertilizer granules increases, phosp

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phosphorus precipitates form with Al, Fe and Mn, lowering the concentrations of all four elements in solution. Using solution cultures to study snap bean roots, Ragland and Coleman (1962) found that Al (1.0×10^{-4} M) increased uptake of P from solution when P concentrations were at or below 0.25 mM. Greater Al concentrations caused precipitation of Al-phosphates, reducing effective P concentrations and thus uptake.

The relationship between Zn and P has been widely studied because P applications can induce Zn deficiency symptoms (Foth and Ellis, 1988). Zinc phosphates occur and supply some available Zn and P in soils, but it is more likely that P controls Zn availability than the reverse (Lindsay, 1979). Boawn and Leggett (1964) showed that Zn and P interfere with each other's uptake. They grew Russet Burbank potato plants and found Zn deficiency symptoms in leaves and stems with an internal P:Zn concentration ratio greater than 400. Kingston and Jones (1980) showed that banding of P resulted in higher P and Zn concentration in leaves than broadcasting did and that the Zn concentration trends reversed themselves late in the season. Loneragan, et al. (1979) found that Zn deficiency develops in plants with moderate Zn status when P is applied. They concluded that increased growth and in some instances increased internal [P] may reduce Zn absorption by plant roots.

Other nutrients known to precipitate with P in soil solutions are Mn (Lindsay and Stephenson, 1959) and Mg (Lindsay, 1979). Potassium and Na-phosphates are too soluble to form and supply P in soils (Lindsay, 1979). Borates and molybdates, being anionic species that occur at low concentrations, do not significantly influence soil P chemistry. N and K are not as important in soil P chemistry as they are in fertilizer P chemistry and plant responses to P.

The chemistry of soil P can be modified by soil texture and structure. These two soil properties influence P chemistry by their effects on the water and nutrient holding capacity in soil.

Soil texture, especially clay content, controls nutrient holding and supplying ability in soils. Much of the P that is held on particle surfaces is adsorbed weakly and can become available for uptake by plants. Sands and silts found in coarse soils have very little anion and cation exchange capacity which limits their ability to supply nutrients to plants. Sandy and organic soils have little adsorbed P (Foth and Ellis, 1988). Phosphates can bind to exterior oxide and hydroxide coatings on clay particles of soils high in clay (Foth and Ellis, 1988).

Farmers raise potatoes (*Solanum tuberosum* L.) in sandy soils that have lower nutrient holding capacity than high clay soils. This does not necessarily mean that potatoes grown on clay soils will produce higher yields. On the contrary, Boyd and Dermott (1967) found less applied fertilizer is required for growing potatoes on a sandy soil than on clay soil. Although the soil texture had some role in yield alteration, they attributed the greater plant growth to better drainage and a deeper hardpan layer in sandy soil than in clay soil.

The findings of Boyd and Dermott (1967) lead to the question of how soil structure regulates P availability. Much of the water in well aggregated soils is available for uptake by plants. Plants growing with adequate water supplies are likely to be more efficient at nutrient uptake than those suffering from water stress. Olsen, et al. (1962) noted that as soil moisture decreases, P uptake rate by plant roots decreases. Holliday and Draycott (1968) found if the surface soil had a tendency to dry out, deep (15 cm) incorporation of liquid fertilizer produced higher potato yields and leaf area indexes (LAIs) than shallow (5 cm) incorporation. Structured soils also tend to have higher organic matter content than most unstructured soils. Soil organic matter contains nutrients from its parent material. As fresh organic matter (plant residue) is broken down, significant quantities of P can be released into the soil solution. This P can be an important source for agronomic plants (Foth and Ellis, 1988).

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Movement of P through soil and around roots is regulated by P availability and fixation, soil moisture, and plant uptake. Chemical precipitation keeps P concentrations in soil solutions below 0.258 μM (Foth and Ellis, 1988). The concentration of P in solution for most U.S. soils is much lower, averaging less than 0.0016 μM (Barber, 1984). P concentration is highly dependent on soil parent material and the movement of water into and around clay particles. At practical concentrations created during the weathering of soil parent material, P does not remain a free ion in soil solution as nitrate often does. Instead, most P in soil solution quickly reacts to form amorphous metal precipitates (Lindsay, 1979), as discussed earlier. The Fe and Al coatings on clays, as well as calcium carbonate on calcareous soils, provide a buffer for P supply in the soil solution (Foth and Ellis, 1988). Root uptake of P is highly dependent on the ability of the soil to maintain a constant supply of P in solution (Nye, 1966).

The P in solution can be taken up only if it comes in contact with root absorbing surfaces. In the soil solution, N comes into contact with the root surface by root interception, mass flow or diffusion. Potassium also comes into contact with roots through all of these processes. Phosphorus, on the other hand, reacts so quickly to other ions that mass flow does not move P through soil to any great extent. Potassium and P concentrations in solution

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are low enough that root interception and mass flow do not provide the plant with enough of these nutrients for proper growth. Instead, diffusion is the primary pathway for K and P movement through soils to sites of uptake (Foth and Ellis, 1988). The lack of mobility in the soil solution, compared to that of N, is of less consequence for K uptake because K binds more weakly to cation exchange sites and occurs at much higher concentrations in soils than does P. These two factors allow desorption to quickly replenish depleted K in most soil solutions. The problem of binding is far greater for P, although plants are still able to get most of their required P. Indeed, Barber, et al. (1963) and Olsen, et al. (1962) have shown clearly that roots can get most of their P through diffusion. The diffusion of solution P is very slow, with $H_2PO_4^-$ diffusion averaging at 0.004 cm/day (Foth and Ellis, 1988) or less than 0.5 cm in a 100 day growing season. Diffusion rate increases as soil temperature increases (Grewal and Singh, 1976).

When fertilizer is added, much of the P quickly binds with the Fe and Al oxides/hydroxides of clay particles (Barber, 1984). On calcareous soils, Ca-phosphates can also be important in controlling solution P levels (Foth and Ellis, 1988). Barber (1984) described three distinct regions of activity around fertilizer P granules. At the center is the residual granule. Moving outward, one then finds a region dominated by P precipitating Al, Fe, and/or

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Ca from the soil, followed by a much larger zone where P is adsorbing to soil particles. Lindsay and Stephensen (1959) found that Al and Fe are dissolved into solution near granules of monocalcium phosphate, only to later precipitate, probably as Fe and Al-phosphates. The P concentrations in solution decreased over time. Much of the P that is adsorbed or precipitated is unavailable for uptake. To delay adsorption and precipitation, P is often applied in bands below and to the side of seeds or crops. This practice is especially beneficial on acid soils where adsorption and precipitation can be "considerable and rapid" (Foth and Ellis, 1988).

One important effect of maintaining high solution P levels is possible pollution of surface and ground waters with P. Extractable P levels in the plow layer of many agricultural soils have gone up considerably from indigenous levels. Ground water pollution by applied P is not a major problem yet. Diffusion of P is so slow and binding so rapid, that little downward movement of P has occurred. Ellis, et al. (1987) wrote that runoff from high P soils will be rich in P but tile drain water will be low due to adsorption of P by deep soil layers containing less P than surface layers. Taylor (1977) reported that on Michigan loams, P moved down only 15-30 cm, with a little moving 45 cm; on sandy loams, P moved down 60-75 cm, with some soils having movement greater than 100 cm through soil.

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Erosion of high P soil into streams may increase P concentrations in surface waters, leading to algal growth, eutrophication, and disruption of the ecosystem. Potato growers have applied P for years resulting in rising P levels in surface soils. Potato soils should be managed to limit erosion and the non-point source pollution it may cause. Ellis, et al. (1987) considered a 112 kg P·ha^{-1} Bray-Kurtz test to be threshold of environmental safety but went on to write that total farm P inputs tend to be low or of an unavailable or slowly available P type. They concluded that reducing these inputs is not of immediate importance in the P load reduction plans for the Great Lakes.

Plant Phosphorus Relations

Phosphorus movement into the plant is regulated by both soil and plant factors. The soil factors such as P supply and soil moisture were previously discussed. The plant factors include root surface area, root zone microflora, the metabolic needs of the plant, and the cellular physiology of the plant.

Phosphorus uptake is against a concentration gradient and active. The rate of uptake is influenced by the ability of the root to move P across cell membranes. Nye (1966) proposed that P uptake should increase as absorbing power increases until diffusion through the soil becomes limiting.

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Ullrich-Eberius, et al. (1984) proposed a membrane bound cotransport mechanism for P uptake in *Lemna gibba* and that this mechanism was dependent on both pH and internal P concentration.

The areas of soil from which crops remove P vary depending on root growth and morphology. For grasses and other crops with long, fine root systems, a small amount of available P throughout the soil provides an opportunity for optimal uptake and plant growth. Producers of these crops broadcast and incorporate P fertilizer. Other crops, because of their smaller, less fibrous root systems, respond better to banding or pelleting the fertilizer into areas of soil most likely to be explored by actively absorbing roots. Potatoes respond best to band applications of fertilizer (Pandy and Sinha, 1970; Vitosh, 1980). Different cultivars have different rooting patterns, however. This has been shown in wheat (Gardiner and Christensen, 1990) and potato (Sattelmacher, et al., 1990), among other species. When Sattelmacher, et al. (1990) evaluated potato responses to N fertilizer, they found that fertilizer N rate influenced root growth in potato cvs. Astrid and Bodenkraft. The two cultivars tested also differed in overall rooting pattern, N acquiring ability and in their growth responses to N treatment. Whether or not fertilizer P significantly alters potato rooting patterns remains to be determined. Sommer (1936) concluded that increasing P concentrations in sol

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solution did not increase root growth of several species, including tomato in the Solanaceae family.

Banding fertilizer can effect root growth. Roots can be more abundant in and around fertilizer bands than in other regions within agricultural soils (Miller and Vij, 1962). The authors correlated greater volumes and surface areas of sugarbeet roots in fertilizer bands with greater P uptake. This does not mean that P increased root growth. On the contrary, root growth caused by the additions of ammonium sulfate to the band accounted for up to 87 percent of the variability in P absorption. The authors also found that ammonium sulfate additions increased shoot P concentration in sugar beet tops.

The majority of plant P uptake occurs through unsuberized roots, although suberized roots also take up some P. Emmond (1968) reported (without presenting specific data) that young potato plants get most of their P from fertilizer bands and that older plants get most of their P from soil P. This implies that early season P uptake is by roots near the fertilizer band. As the season progresses and younger, unsuberized roots are growing further to the side and below the fertilizer band, more P is taken up from other soil sources than from the fertilizer band.

For species with root hairs, their quality and health can influence nutrient uptake (Barber, 1984). Fumigation can improve root hair health and increase P uptake by

potatoes (Gardiner and Christensen, 1990). Caradus (1979) found root hair length can be selected for in clover (*Trifolium repens* L.). The author's selection program resulted in increases of up to 11% in the volume of soil explored per foot (30 cm) of root.

Root hairs are not the only way plants can greatly increase the effective surface area of their roots. The roots of certain families of plants (Pinaceae and Solanaceae, among others) can form symbiotic relationships with mycorrhizal fungi which provide P for the host plant while providing C for the invading fungus. On low P soils, fungal hyphae can significantly increase effective root system size and provide significant quantities of P for the plant. Mycorrhizae have been shown to double P uptake rates by tomato roots (Cress, et al., 1979). P is absorbed into the hyphae of mycorrhizae as $H_2PO_4^-$, then transferred into root cortical cells by cytoplasmic streaming (Barber, 1984). Uptake of P by mycorrhizal mycelia is more important for unfertilized crops than for fertilized crops (Foth and Ellis, 1988).

Once taken up, plants move P to where it is needed, sometimes moving it several times during growth and development, and use it for many vital functions. Phosphorus occurs in both DNA and RNA (Marschner, 1986). Phosphorus is also part of many important energy transfer compounds including ATP and ADP; NAD, NADP and NADPH; and

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the rubisco group of enzymes (Salisbury and Ross, 1978). Phosphorus occurs at the hydrophilic end of bipolar phospholipids that make up cell and organelle membranes. Many aspects of respiration and C fixation, such as starch synthesis and carbohydrate transport, are influenced by inorganic P concentrations in plant cells (Marschner, 1986).

Phosphorus uptake from fertilizer continues through harvest but much of the P in new organs is retranslocated from other organs. Pursglove and Sanders (1981) reported that potato roots stopped accumulating P 54 DAP. During their work, P accumulation in leaves increased until 65 days after planting (DAP), then declined. In tubers the rate of P accumulation continued to increase through harvest. They found only four or five percent of fertilizer P is recovered by the crop and suggested P immobility and low root density were the causes.

Most P taken up is eventually transported into the tubers. Soltanpour (1969) reported that 81 to 86% of all P taken up was in the tubers at harvest. The idea that most P is retranslocated during growth is supported by the work of McCollum (1978), which showed that P translocation to tubers exceeds P uptake in the tuberization stage.

The translocation of P within a plant can be influenced by P source and placement, as well as plant ontogeny. Pursglove and Sanders (1981) found that potato (cv. Pentland Javelin) plants given 87 kg P$\cdot$ha^{-1} from triple superphosphate and 109 kg $K \cdot ha^{-1}$ from KCl had lower shoot P contents than those given equal amounts of P and K from potassium KH_2PO_4. In a separate paper, Pursglove (1981) reported that the ratio of internal plant P derived from fertilizer to that from other sources varied among plant organs in potato (cv. Pentland Javelin). The ratio of newly absorbed P to recycled P in the plants studied also varied over time. Pursglove's work "confirmed the great mobility of P within the potato plant". In concluding remarks, the author speculated that shallow banding of P would result in most fertilizer P being taken up early in the growing season; deep P banding would cause uptake to be delayed until later in the season.

Crop yield depends on the ability of a crop to capture C through photosynthesis and allocate that C to its harvested structures. Phosphorus, because of its importance in energy compounds, plays a role in determining both a plant's ability to fix C and how that C will be partitioned. Phosphorus can increase dry matter (carbon) accumulation in potato (Westermann, 1992). Pursglove and Sanders (1981) monitored dry weight accumulation in potato plants (cv. Pentland Javelin) receiving fertilizer P. They reported that prior to the appearance of shoots above the soil, potato plants lose P and dry matter, with net dry matter accumulation (especially in shoots) beginning 46 DAP. The seed piece, which was included in these calculations, lost dry matter through 66 DAP. Loss of plant dry matter, mainly from the seed piece and its presprouted stems, was attributed to respiration and leakage. Loss of P was due to leakage alone. Roots accumulated dry matter only through 54 DAP. Tuber initiation began between 46 and 54 DAP. Plant P content increased until the final sampling at 90 DAP. Dry matter content began to decline about 66 DAP. McCollum reported that P and dry matter accumulation tend to parallel each other during potato growth (McCollum, 1978), although Pursglove and Sanders (1981) and Vitosh (1979) showed slight differences.

Because of its role in dry matter production, P can strongly influence tuber yield and quality. An extensive review by Allen and Scott (1980) is a good primer on potato growth and tuber production. They concluded that all management practices should be geared toward maximizing light interception because this, rather than leaf area index, net assimilation ratio, or light incidence (if each is taken alone), is most strongly correlated with total and tuber dry matter production. Bremner and Radley (1966) indirectly support this hypothesis by reporting that leaf area duration (the time when LAI is equal to or greater than 3.0) had greatest influence on yields.

Shoot growth is very important in determining potato yield. Stem height (Benepal, 1967a,b) and leaf number (Benepal, 1967b) can be increased by superphosphate

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fertilization on soils low (31 kg $P \cdot ha^{-1}$ available) in P. McCollum (1978) postulated that maintaining P supply to the shoots, which the author claimed can be done with very modest applications, may be very important in maintaining tuber growth. McCollum concluded that the critical P level in a southern U.S. Portsmouth fine sandy loam soil is greater than or equal to 66 kg $P \cdot ha^{-1}$, but less than or equal to 110 kg $P \cdot ha^{-1}$. Marsh, et al. (1987,1989) found that increasing P concentration from 0.2 to 1.3 mM in microculture agar media increased shoot dry weight and node number but decreased percent dry weight. They also studied the influence of Mn on growth and responses to P, finding that the effects of P were more pronounced at medium (1.0 mM) or high (2.0 mM) Mn concentrations than at low (0.5 mM) Mn concentrations. Tukaki and Mahler (1990) found that vegetative weight increased in tissue culture plantlets as media P concentrations reached 40 to 45 μg P/ml. Leaf area of field grown tobacco has also been increased with P applications of up to 269 kg $P \cdot ha^{-1}$ (Crafts-Brandner, et al. 1990). Sommer (1936), working with six species, found increasing P supply decreased root:shoot ratio. Similar results were found by Cogliatti and Clarkson (1983), who reported that P stress in solution culture decreased leaf area, shoot and root dry weight, and increased root:shoot ratio of potatoes. These effects became exceptionally appare

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apparent after five days in zero P conditions. The P stress also caused more C export from the shoot to the roots.

Despite increasing levels of soil P in all potato growing regions potato yields can still be increased with P fertilizer (Dubetz and Bole (1975); Kingston and Jones (1980); Pandey and Sinha (1970); Singh, et al. (1968); and Vitosh (1979). Benepal (1967b) found P fertilizer (34 kg $P \cdot ha^{-1}$) hastened tuber weight gain. In another paper, Benepal (1967a) suggested that increases in yield caused by P fertilizer resulted from increased C assimilation. McCollum (1978) reported that on low P soil (< 38 kg available $P \cdot ha^{-1}$) without P additions, shoots continue to accumulate dry matter after plants with access to more soil and/or fertilizer P have begun to lose shoot dry matter. In the plants receiving fertilizer P and or growing on soils with more than 66 kg $P \cdot ha^{-1}$ available, the dry weight of tubers increased after no further increases in total plant dry weight occurred. The author concluded that this indicated dry matter accumulation in the tubers was likely from translocation of previously assimilated materials. Singh, et al. (1968) found increased potato yields with applications of up to 112 $kg \cdot ha^{-1}$ P fertilizer on soil with 19 kg available $P \cdot ha^{-1}$. Vitosh (1979), in Michigan, found that P fertilizer application increased tuber yield (mainly A and Jumbo grades), but not leaf weight, root weight, tuber number, and dry matter accumulation per plant. Widdowson, et al. (1974) found yields of dry matter and tubers were lower when potatoes were fertilized with manure alone than with fertilizer alone or fertilizer with manure. Pursglove and Sanders (1981) reported that neither foliar P sprays nor soaking seed tubers in a solution equivalent to 2.6 kg $P \cdot ha^{-1}$ increased tuber yields or plant dry matter accumulation in cv. Pentland Javelin. However, they did find that P from seed tubers can be as important to yield as that from fertilizer.

How potatoes respond to fertilizer P depends on amount of P applied and amount available. Benepal (1967b) found that potatoes responded to superphosphate fertilizer (37 kg $P \cdot ha^{-1}$) on low P soils (30.9 kg available P $kg \cdot ha^{-1}$), but not on soil with 109 kg available $P \cdot ha^{-1}$. Dean, et al. (1947), using radiotracer techniques, showed quantitatively that as P status of the soil improves, the percent of P in potato plants that comes from applied fertilizer decreases. Mombiela, et al. (1981) related yield to P in the soil and from fertilizer with the following equation:

$$y = A[1-\exp(-c(bT + X))],$$

where:

y = predicted tuber yield
A = maximum tuber yield attainable
exp = exponent of
c = efficiency of P sources (soil and fertilizer)
T = soil P test level
X = amount of P fertilizer applied
b = constant relating total effective P in the soil and fertilizer to the soil test P value.

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Payton, et al. (1989) used this equation to help correlate potato yields with P fertilizer rates and soil test P levels on an Ellzey fine sand in Florida over several seasons. They found that the Mehlich I P test was inadequate at predicting the availability of residual soil P over several seasons. The authors stated that the extractant may have overestimated the availability of certain Ca-phosphate fractions for plant uptake.

Sommer (1936) concluded that lower P concentration in solution cultures results in faster maturity in several species. In potatoes this might shorten leaf area duration and possibly reduce yield.

Klein, et al. (1980) evaluated the influence of P fertilizer on tuber nutritional quality and chemistry. They found P application (56 or 112 kg $P \cdot ha^{-1}$) decreased phospholipid content of tubers and increased ascorbic acid concentration. Application of 56 kg $P \cdot ha^{-1}$, P caused increased total tuber N, protein N, and non-protein N concentration. The influence of P on specific gravity, a measure of starch and sugar content of tubers, is only partially understood. Dubetz and Bole (1975), Hukkeri (1968), and Vitosh (1979) found no change in specific gravity from P application.

Uptake Kinetics

Phosphorus uptake studies are based on the premises of active uptake and Michaelis-Menton enzyme kinetics. These kinetics relate the amount of carrier capacity to the amount of available substrate, in this case P. The terminology used to describe the kinetics of uptake includes I_{max}, the maximum rate of influx (net uptake) per unit of root (from V_{max}, the maximum rate of an enzymatic reaction); K_m, the external concentration at which uptake rate is one half of maximum; and C_{min}, the minimum external concentration at which net uptake is positive. Marschner (1986) related uptake rate, v, to ionic concentration, C_S, as:

$$v=(V_{max} \cdot C_S)/(K_m + C_S).$$

By determining K_m and V_{max}, the rate of uptake can be predicted for any given concentration. The parameters K_m and V_{max} can be determined by monitoring uptake in solution culture.

The methods used to study uptake vary, each having its own strong and weak points. Most methods involve some form of solution culture. In steady state methods, the amount of the nutrient being studied is held constant and uptake calculated based on additions made to the solution. Steady state methods allow long term monitoring of one plant at a single concentration. In depletion studies, the nutrient is not replaced and periodic sampling allows monitoring of uptake rate. This method allows one to monitor uptake rate at different nutrient levels in one plant. Radiotracers may be used because they allow monitoring of the fates of nutrients within the plant. Flowing culture in which the roots are bathed constantly or periodically with a stream of solution are also used. This method is preferred by some researchers because periodic bathing of plant roots with flowing solutions are less likely to create hypoxia in the root zone than static, aerated solutions.

It is likely that as root growth proceeds changes in P uptake patterns over time are similar among most species. This is because as plant roots grow and mature they almost all follow a similar developmental pattern: cell division, elongation and differentiation, and suberization. Although the patterns of uptake are probably similar among genotypes, the specific uptake rates and patterns vary considerably. Root hair growth, root exudates, and root respiration can all influence nutrient uptake rate (Marschner, 1986). In corn, Olsen et al. (1962) showed diffusion of P to the root surface can account for most P taken up. Root growth must continue, however, since they found that a constant uptake at the root surface is possible for only a short period (less than 2 days) and that decreasing uptake over time is more likely at any one root surface than is constant uptake. At the first stages of uptake at a given location the P concentration in soil solution would permit infinitely high P uptake. As plants remove P from this region a zone depleted of available P develops and P uptake rates decline to zero. Fertilization creates artificially strong gradient to the root surface and thus can increase the total amount of P encountered by roots. Lewis and Quirk (1965) presented the following equation for calculating P diffusion to roots:

$$\delta C/\delta T = [\delta/(r\cdot\delta r)]\cdot[rD(\delta c/\delta r)],$$

where:

$C = C_{(r,t)}$ = P concentration at any time t over distance r from the root's center
D = diffusion coefficient
r = root radius.

The authors related the diffusion coefficient curvilinearly to fertilizer P additions as:

$$D = KP^2$$

where:

D = diffusion coefficient, measured in the soil
K = a constant
P = concentration of added P in micrograms P per gram of soil.

The optimal, adequate, and toxic soil solution P concentrations differ among species (Asher and Loneragan, 1967; Sommer, 1936). Asher and Loneragan (1967) showed that many species take up sufficient P from solutions considered to have low P levels if the solution flows around the roots in a manner which provides the roots with continuously replenished P supplies. Barber (1984) showed that some plants absorb P down to 0.2 μM soil solution. Since U.S. soils average 1.7 μM P in solution (Barber,1984) this probably means that plants can take up some P at most solution concentrations they encounter. Cogliatti and Clarkson (1983) found P uptake by roots of unstressed potato sprouts ranged from 288 to 320 μM P$\cdot$g total dry weight$^{-1}\cdot$day^{-1} with K_m = approximately 21.6 μM P. The V_{max} for another group of rooted sprouts was approximately 209 μM$\cdot$g root dry weight$^{-1}\cdot$day^{-1}, increasing if the plants were subject to P stress. In 1954, Hill et al. reported that growth of Green Mountain potatoes was no greater in solutions containing 2400 μM P than in those containing 640 μM. Using micropropagated Russet Burbank, Tukaki and Mahler (1990) found optimal growth could be attained with media P concentrations of 480 μM, even though leaf P levels were higher when media concentrations exceeded that level. Neither total tuber weight nor tuber number was increased if media P concentrations exceeded 322 μM.

To more concretely define possible influences in P uptake kinetics among potato cultivars one must investigate studies of nutrient uptake in potatoes as well as other species. In solution, Sattelmacher, et al. (1990) have shown differences in N uptake rate per unit of root surface area between two potato cultivars. The cultivar Astrid, known to have a larger root system and greater total uptake of N than the cultivar Bodenkraft, had lower uptake rate per unit of root area. The authors claim the difference in root system size may be very important in acquisition of P and other relatively immobile soil nutrients. Asher and Loneragan (1967) found wide differences in plant growth among pasture species grown in solution culture. When the solutions contained 0.2 μM P, all tested species grew to at least 50% of maximum dry weight attained by plants in their trials. The minimum P concentration needed for maximum growth also varied widely among species, ranging from a low of 0.1 μM for silver grass (*Vulpia* (*Festuca*) *myuros*(L.) Gmel.) to more than 24 μM for barrel medic (*Medicago tribuloides* Desr.) and flatweed (*Hypochoeris glabra* L.). Houghland (1947) reported that optimal potato growth (cv. Green Mountain) required solutions containing 48 μM. This number appears quite low but is thirty times the mean level found in U.S. soils, 1.6 μM P(Barber, 1984). Other nutrients, including K (Wild, et al., 1974), are also taken up at different rates in different species.

The differences in uptake rates and minimum requirements found among species have been attributed in part to root system size (Sommer, 1936), root hairs (Itoh and Barber, 1983) and relative growth rate (Asher and Loneragan, 1967). Some recent uptake and nutrient use studies contain data which more closely define the role of these factors in nutrient uptake. Nielsen and Schjorring (1983) suggested breeders could select barley (*Hordeum vulgare*) cultivars for lower C_{min} or K_m, or for higher I_{max} or length of root per gram of root dry matter. Differences in P uptake rate have also been found among corn inbreds (Clark and Brown, 1973). Teo, et al. (1992), however, found no differences in P uptake kinetics among three rice cultivars. The differences in P uptake rates between two corn inbreds were attributed to possible differences in rhizosphere pH changes by the roots or to different levels of root phosphatase activities (Clark and Brown, 1973). The findings of Iwama, et al. (1979) indicate that large differences in potato root systems exist between cultivars and that these differences impact shoot growth and tuber yield. They reported that maximum root dry weights were attained near flowering, before shoot dry weights reached their maxima. The strong correlation between root dry weights and tuber yield was explained more as a function of total plant size, including shoots, than solely based on the influence of root system size.

Summary

Researchers understand the general flow of P into and through potato plants but few of the regulatory points controlling the process. Agricultural soils supply P from their parent minerals, organic matter and applied fertilizer. Phosphate ions in solution remain available until they are taken up by plants or other soil-dwelling organisms, or until they react with soil cations, organic matter, or clay surfaces. Soil cations may be bound to soil solids or free in solution. Phosphate ions are available for uptake when they come in contact with roots through a combination of root growth and diffusion of the P ions through the soil solution. The ions are taken up by roots through an active process. The speed of the uptake process is determined by various requirements of the plant components, plant capabilities for uptake and ion availability. The uptake process closely follows the rules of Michaelis-Menten enzyme kinetics. Once in the plant, P is incorporated mainly into energy related compounds and membrane systems. Because of its important roles in these systems, P status of plants has a strong impact on photosynthesis, growth and yield. Potatoes are sensitive to low P even in soils with high soil-test P levels. Causes of this sensitivity might include a small root system, the crop's rapid growth rate, inefficient uptake, or insufficient P utilization within the plant. The studies reported in the following chapters were designed to confirm potato responses to applied and indigenous P and to determine differences in uptake rates and P utilization among several potato cultivars.

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CHAPTER 2

INFLUENCES OF BANDED PHOSPHORUS FERTILIZER ON POTATO YIELDS AND QUALITY DURING FIELD EXPERIMENTS, 1989 AND 1990

Introduction

Michigan ranks 8th among the fifty states in potato acreage and production (Chase, personal communication). The main growing region of Michigan is in the West Central lower peninsula, around Montcalm County. The soils of the region are generally stony sandy loams which have naturally porous structures and allow good drainage, two factors important for potato production. The second largest area of production is in the east central region of Bay County. In addition, potatoes are grown in sandy soils around the state as well as in organic sands and muck soils.

Most Michigan potato growers band a complete fertilizer 5 cm to the side of and slightly below the tuber seed pieces at planting. Banding is preferred to broadcast application because banding concentrates nitrogen, phosphorus and potassium in a small region of the soil, providing the potato plant with concentrated, readily available nutrients. The placement of nitrogen and P is particularly important for early growth. It has been shown that plant roots are more concentrated in and around fertilizer bands than in the general soil profile (Miller and Vij, 1962). Fertilizer is a very important source of P to the growing potato plant, providing as much as 62% of the crop's P needs (Nelson, et al., 1947). The main advantage of P fertilizer application appears to be in providing P early in the season. Later, as the root system develops and provides access to a larger volume of soil, potatoes acquire a greater percentage of their P from native soil P (Emmond, 1968).

Throughout the world, researchers have found tuber yield increases with P fertilizer applications even when soil P test levels appear high (Ohms, et al., 1977; Rhue, et, al., 1981). At high soil P levels, other agronomic crops, such as wheat and corn, do not benefit from P applications (Foth and Ellis, 1988). The reasons potato plants seem more dependent on fertilizer P than other crops may include: their small root system; limited ability of potato roots to acquire P from the soil; inefficient partitioning of P within the potato plant; as well as physical and chemical differences between soils used to produce grains and those used for potato production.

One of the common soil series in the West Central Michigan potato growing region, McBride sandy loam (Coarse-loamy, mixed, Eutric Glossoboralf), may be significantly limited in its ability to supply P to potato plants. Michigan researchers have reported yield increases due to applied P in McBride sandy loam testing very high (over 400 $kg \cdot ha^{-1}$) in extractable P (Vitosh, 1979). The inability of a high P McBride soil to supply adequate P for potato growth may be caused by soil management practices, the soil's low pH, and micronutrient interactions which can limit P concentrations in the soil solution. Potatoes growing in other Michigan soils are reportedly less responsive to applied P than those growing in soils in the McBride and closely allied series. Using previous observations as a guide, field studies were established to determine if potato yield responses to applied P fertilizer differ in a McBride soil from those in two other Central Michigan soils, a Capac loam and a Martisco muck.

In addition to evaluating potato responses in three Michigan soil series, the studies were also designed to determine: if cultivars differ in their response to P fertilizer; if P fertilizer influences tuber quality; and if aldicarb, a previously labeled soil applied insecticide, influences how potatoes respond to P.

Materials and Methods

1989

In 1989, the responses of two potato cultivars, Atlantic and Russet Burbank, to banded P fertilizer were evaluated in three soils: a McBride sandy loam (Coarse-loamy, mixed, Eutric Glossoboralf) at the Michigan State University Montcalm Potato Research Farm near Entrican, Michigan; a Capac loam (fine-loamy, mixed, mesic Udollic Ochraqualf) at the Michigan State University's campus Soils Research Farm; and a Martisco muck (fine-silty carbonatic mesic Histic Humaquaept) at a cooperator's farm in southern Clinton County.

Cut and suberized seed pieces, 50 to 75 g each, were planted 10 cm deep by hand or with a plate type planter, in rows 0.9 m apart, 15.3 m long. Atlantic pieces were set 25 cm apart in the row; Russet Burbank pieces 30 cm apart. Initial Bray-Kurtz P-1 soil test P levels were 529, 102, and 357 kg $P \cdot ha^{-1}$ in the McBride, Capac and Martisco soils, respectively. Fertilizer, including urea (49 kg $N \cdot ha^{-1}$), potassium chloride (35.2 kg $K \cdot ha^{-1}$), and one of eight triple super phosphate treatments (0, 11, 22, 33, 44, 55, 65, and 76 kg $P \cdot ha^{-1}$) was banded 2 cm below and 5 cm to the side of the seed pieces at planting. Prior to planting in the Capac soil, ammonium nitrate (130 kg $N \cdot ha^{-1}$) and potassium (92 kg $K \cdot ha^{-1}$) were disked into the soil. Aldicarb, a previously labeled systemic pesticide which controls many potato pests including Colorado potato beetles and nematodes, was applied at labeled rates to one half of the McBride and Capac plots to evaluate its effect on yield and quality, as well as interactions between it and P treatments. Planting dates were 17 May, 8 June and 24 May in the McBride, Capac and Martisco soils, respectively. Standard grower practices of irrigation and pest management were used during the growing season. The plants were hilled prior to flowering. Petioles from the youngest fully expanded leaves were collected on 11 July (55 days after planting (DAP)), 26 July

(48 DAP) and 13 July (50 DAP) in the McBride, Capac and Martisco soils, respectively for later elemental analysis. Tubers were harvested on 20 September (126 DAP), 18 October (132 DAP), and 26 September (127 DAP) at Entrican, East Lansing, and Clinton County, respectively. Tubers were sorted into four sizes: oversize (greater than 280 g, or 10 cm diameter for Russet Burbank and Atlantic, respectively), A's (110 to 280 g, or 6.3 to 10 cm), B's (less than 110 g, or 6.3 cm), and culls (tubers with significant external blemishes, knobs, and/or other defects. Yield and tuber numbers within each grade were recorded. Specific gravities of A grade tubers were determined by the weight in water/weight in air method.

Petiole analysis for P was conducted using a dry ash procedure. Oven-dried tissues (60 C for 24 h) were ground to pass through a 40 mesh screen. One-half gram of tissue was ashed in a muffle furnace for 5 h at 500 C. The ash was digested in 3 N nitric acid + 1000 ppm LiCl for 1 h. The samples were filtered through Whatmann No. 2 filter paper and stored at 2 C for later analysis. Phosphorus was determined colorimetrically using the ascorbic acid-molybdate method (Murphy and Riley, 1962).

1990

The response of potato cultivar Russet Norkotah to banded P fertilizer was evaluated at the same three locations as in 1989. The influence of aldicarb was not evaluated as the product was voluntarily removed from the market by its manufacturer. Phorate (0,0-diethyl s-[(ethylthio)- methyl]phosphorodi-thioate), a soil applied insecticide was used at planting for general insect control. Initial soil test P levels were 480, 102 and 357 kg $P \cdot ha^{-1}$ in the McBride, Capac and Martisco soils, respectively. Phosphorus was applied in a band 5 cm below and 5 cm to the side of the seed pieces at a rate of 0, 50, 100, 150, or 200 kg $P \cdot ha^{-1}$. Planting dates were 15 May, 23 May, and 25 May in the McBride, Capac and Martisco soils, respectively. All plots received nitrogen (18 kg $N \cdot ha^{-1}$) and potassium (28.4 kg $K \cdot ha^{-1}$) along with the appropriate P treatment. Plots were hilled when plant growth reached approximately 25 cm. Petiole samples from the youngest, fully expanded leaves (usually leaf 4) were collected in early July at all locations, with harvest occurring on 11 September (119 DAP), 27 September (127 DAP), and 26 September (124 DAP) at the three sites, respectively. Tubers were graded and their specific gravities and P content determined as in 1989. Petioles from East Lansing were analyzed for complete macro- and micronutrient concentration using plasma emission spectroscopy (ARL DCP Spectra Span VB Model SSVB/DCP, Be

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Beckman Instr., Fullerton, CA). Cores from tubers were dried at 60 C, ground to a fine powder in a mortar and pestle, dry ashed at 500 C for 6 h, and analyzed colorimetrically (Brinkman colorimeter model PC800, Brinkman Instruments, Westbury, NY, or Lachat QuickChem System IV, Lachat Instruments, Milwaukee, WI) for P content using the ascorbic acid-molybdate method (Murphy and Riley, 1962).

The experimental design used both years was a randomized complete block with four replications. All data were analyzed using the GLM procedure of SAS (SAS Institute, 1988).

Results

1989

Tuber yields and numbers were minimally influenced by P treatment (Table 2.1). In the McBride soil, the Russet Burbank plots receiving aldicarb were misplanted and these plots were not harvested. Without aldicarb, Russet Burbank showed no responses to P application. The yield of cull tubers of Russet Burbank appears statistically larger in the 175 $kg \cdot ha^{-1}$ treatment, but this is likely an anomaly because the number of tubers graded as culls was small in each plot and had a large coefficient of variation. There were no statistically significant yield responses to P application within the two aldicarb treatments in Atlantic. However,

Table 2.1. Effects of banded P fertilizer on tuber yield and numbers of tubers, within cultivar and aldicarb treatment, in McBride sandy loam, 1989.

Table 2.1. Effects of banded P fertilizer on tuber yield and numbers of tubers, within cultivar and aldicarb treatment, in McBride sandy loam, 1989.

Cultivar /aldicarb	P rate ($kg \cdot ha^{-1}$)	Tuber yield ($Mg \cdot ha^{-1}$) Total	<5cm	5-8cm	>8cm	Tuber number/ha (X1000) Total	<5cm	5-8cm	>8cm
Atlantic /Yes	0	35a	6a	28a	1a	340a	110a	230a	3a
	25	36a	8a	27a	0a	390a	160a	220a	0a
	50	39a	6a	30a	1a	380a	120a	240a	4a
	75	41a	5a	33a	0a	350a	90a	250a	0a
	100	39a	8a	29a	2a	380a	150a	220a	4a
	125	36a	7a	27a	1a	340a	130a	190a	3a
	150	43a	6a	34a	1a	380a	110a	260a	1a
	175	43a	6a	34a	1a	360a	110a	250a	3a
	p =	0.43	0.28	0.27	0.74	0.77	0.06	0.58	0.73
/No	0	33a	8a	25a	0a	370a	160a	210a	0a
	25	38a	8a	30a	1a	410a	160a	250a	1a
	50	33a	9a	23a	0a	400a	190a	210a	0a
	75	34a	9a	25a	0a	400a	180a	220a	0a
	100	37a	7a	28a	1a	400a	170a	220a	2a
	125	31a	8a	23a	0a	370a	170a	210a	0a
	150	32a	10a	21a	1a	390a	200a	190a	3a
	175	35a	7a	29a	0a	390a	140a	250a	0a
	p =	0.22	0.55	0.07	0.49	0.88	0.61	0.37	0.48

Table 3.1. (Cont'd).

Table 2.1. (cont'd).

Cultivar /aldicarb	P rate ($kg \cdot ha^{-1}$)	Tuber yield ($Mg \cdot ha^{-1}$) Total	<110g	110-280g	>280g	Tuber number/ha (X1000) Total	<110g	110-280g	>280g
Russet	0	31a[v]	18a	13a	0a	330a	240a	80a	0a
Burbank	25	29a	15a	13a	1a	300a	210a	90a	2a
/No	50	31a	17a	13a	0a	330a	240a	90a	0a
	75	27a	14a	13a	0a	290a	200a	90a	0a
	100	28a	16a	10a	1a	310a	230a	70a	1a
	125	32a	17a	14a	1a	330a	230a	90a	2a
	150	28a	16a	10a	1a	290a	220a	70a	1a
	175	31a	16a	11a	1a	310a	220a	70a	4a
	p =	0.72	0.80	0.92	0.21	0.57	0.91	0.83	0.23

[z,y]Diameter used to grade Atlantic, mass to grade Russet Burbank.
[x]Total yield and number of tubers include cull tubers not included in size categories.
[v]Means followed by different letters are significantly different, within columns, at $p = 0.05$ level, as determined by LSD.

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where aldicarb was applied total and marketable yields trended higher with P applications. Aldicarb increased yields and tuber number of Atlantic (Table 2.2). Yields and numbers of small tubers decreased, while those of larger tubers increased. The pesticide also increased the yields of cull grade tubers, accounting for 27% of the yield increase.

On the Capac loam in 1989, both aldicarb and P treatments were evaluated for the two cultivars. No consistent statistically significant differences in yield, tuber number, or tuber quality occurred among P treatments within aldicarb treatments and cultivars (Tables 2.3 and 2.4). Aldicarb did not consistently alter tuber yield or numbers in either cultivar (Tables 2.5 and 2.6). The insecticide reduced tuber P concentration in both cultivars.

On the Martisco muck, flooding damaged many plots, leaving two replications of Russet Burbank and three replications of Atlantic for harvest and evaluation. Analysis of the data from these replications showed no statistically significant differences in yield or tuber quality among P treatments within cultivars (Tables 2.7 and 2.8).

Table 2.2. Effects of aldicarb treatment on tuber yield and numbers of tubers[z], within cv. Atlantic and across P fertilizer rates, in McBride sandy loam,

Table 2.2. Effects of aldicarb treatment on tuber yield and numbers of tubers[z], within cv. Atlantic and across P fertilizer rates, in McBride sandy loam, 1989.

	Tuber yield ($Mg \cdot ha^{-1}$)				Tuber number/ha (X1000)			
Aldicarb	Total	<5cm	5-8cm	>8cm	Total	<5cm	5-8cm	>8cm
Yes	39a[y]	7b	30a	1a	380b	120b	230a	2a
No	34b	8a	26b	1a	390a	170a	220a	1a
p =	0.0004	0.0005	0.0004	0.24	0.04	0.0001	0.24	0.11

[z]Total yield and number of tubers include cull tubers not included in size categories.
[y]Means followed by different letters are significantly different, within columns, at p = 0.05 level as determined by LSD.

Table 2.3. Effects of banded P fertilizer rate on tuber yield and numbers of tubers[x]*, within cultivar and aldicarb treatment,* in Capac loam, 1989.

Table 2.3. Effects of banded P fertilizer rate on tuber yield and numbers of tubers[x], within cultivar and aldicarb treatment, in Capac loam, 1989.

Cultivar /aldicarb	P rate ($kg \cdot ha^{-1}$)	Tuber yield ($Mg \cdot ha^{-1}$) Total	<5cm	5-8cm	>8cm	Tuber number/ha (X1000) Total	<5cm	5-8cm	>8cm
Atlantic /Yes	0	35a	14bc	19a	2a	301abc	180abc	115a	6a
	25	37a	16abc	20a	1a	343ab	220ab	121a	2a
	50	31a	12c	17a	1a	258cd	160cd	97a	2a
	75	31a	13c	17a	1a	282abcd	180abc	100a	2a
	100	33a	13bc	18a	1a	234d	120d	108a	1a
	125	36a	13c	20a	2a	289bcd	170bcd	112a	4a
	150	40a	17a	19a	2a	347a	220a	114a	6a
	175	31a	16ab	13a	1a	321abc	230a	84a	3a
	p =	0.10	0.04	0.50	0.84	0.03	0.01	0.46	0.85
/No	0	34a	13a	18a	1a	265a	170a	82a	4a
	25	33a	13a	18a	0a	282a	180a	100a	0a
	50	36a	14a	20a	1a	299a	170a	114a	1a
	75	38a	15a	20a	1a	308a	190a	113a	3a
	100	35a	13a	20a	2a	285a	160a	115a	5a
	125	35a	14a	19a	1a	304a	190a	112a	2a
	150	35a	16a	16a	1a	330a	220a	99a	3a
	175	37a	14a	20a	1a	308a	190a	113a	4a
	p =	0.88	0.94	0.86	0.54	0.79	0.84	0.68	0.45

Table 2.3. (cont'd).

Table 2.3. (cont'd).

Cultivar /aldicarb	P rate ($kg \cdot ha^{-1}$)	Tuber yield ($Mg \cdot ha^{-1}$) Total	<110g	110-280g	>280g	Tuber number/ha (X1000) Total	<110g	110-280g	>280g
Russet	0	48a	2a	35a	10a	276a	41a	201a	30a
Burbank	25	41a	2a	28a	10a	289a	46a	203a	28a
/Yes	50	41a	2a	30a	7a	195a	37a	124a	21a
	75	43a	2a	31a	7a	266a	39a	197a	21a
	100	45a	1a	29a	14a	266a	23a	197a	39a
	125	36a	1a	24a	10a	245a	38a	177a	29a
	150	41a	3a	32a	6a	304a	71a	214a	16a
	175	46a	2a	26a	16a	268a	38a	174a	45a
	p =	0.55	0.29	0.82	0.12	0.83	0.42	0.77	0.17
/No	0	50a	2a	32a	16a	292a	42a	205a	43a
	25	48a	2a	30a	15a	283a	44a	185a	48a
	50	47a	2a	26a	16a	278a	54a	161a	48a
	75	50a	2a	34a	12a	316a	47a	227a	34a
	100	50a	2a	32a	13a	317a	54a	207a	47a
	125	45a	1a	29a	14a	246a	30a	172a	40a
	150	43a	2a	29a	11a	251a	47a	171a	29a
	175	41a	2a	26a	13a	236a	40a	154a	38a
	p =	0.83	0.91	0.58	0.69	0.50	0.80	0.26	0.36

[z,y]Diameter used to grade Atlantic, mass to grade Russet Burbank.
[x]Total yield and number of tubers include cull tubers not included in size categories.
[v]Means followed by different letters are significantly different, within columns, at p = 0.05 level as determined by LSD.

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Table 2.4. Effects of banded P fertilizer rate on percentage of Grade A tubers[z], mean tuber weight, specific gravity, and tuber P concentration, within cultivar and aldicarb treatment, in Capac loam, 1989.

Cultivar /aldicarb	P rate ($kg \cdot ha^{-1}$)	Percent Grade A (%)	Mean Tuber wt. (g)	Specific Gravity (g/cm^{-3})	Tuber [P] (ppm)
Atlantic	0	53a[y]	118a	1.076a	2830a
/Yes	25	54a	108a	1.074a	2830a
	50	55a	120a	1.076a	2820a
	75	54a	110a	1.071a	2980a
	100	54a	166a	1.073a	2940a
	125	56a	126a	1.079a	2960a
	150	50a	114a	1.074a	2950a
	175	42a	98a	1.072a	3170a
	p =	0.46	0.13	0.72	0.57
/No	0	55a	129a	1.073a	3210a
	25	57a	118a	1.074a	3240a
	50	54a	123a	1.075a	3440a
	75	53a	122a	1.075a	3140a
	100	56a	123a	1.077a	3480a
	125	55a	117a	1.070a	3300a
	150	47a	104a	1.078a	3340a
	175	54a	119a	1.072a	3440a
	p =	0.88	0.46	0.47	0.83

Table 2.4. (cont'd).

Cultivar /aldicarb	P rate ($kg \cdot ha^{-1}$)	Percent Grade A (%)	Mean Tuber wt. (g)	Specific Gravity (g/cm^{-3})	Tuber [P] (ppm)
Russet Burbank /Yes	0	74a	241a	1.076a	2830a
	25	66a	151a	1.077a	2900a
	50	73a	240a	1.076a	2820a
	75	73a	146a	1.079a	2660a
	100	64a	174a	1.076a	3010a
	125	68a	156a	1.079a	2920a
	150	77a	140a	1.076a	2820a
	175	58a	172a	1.078a	2870a
	p =	0.50	0.43	0.67	0.19
/No	0	65a	171abc	1.077a	2930a
	25	63a	171abc	1.076a	2970a
	50	55a	172ab	1.079a	2850a
	75	69a	157bc	1.077a	3300a
	100	67a	157c	1.073a	3060a
	125	64a	185a	1.075a	2990a
	150	69a	170abc	1.075a	3020a
	175	63a	172bc	1.074a	3100a
	p =	0.31	0.0233	0.46	0.35

[z]Size used to grade Atlantic, mass to grade Russet Burbank.
[y]Means followed by different letters are significantly different, within columns, at p = 0.05 level as determined by LSD.

Table 2.5. Effects of aldicarb treatment on tuber yield and numbers of tubers[z,y],

Table 2.5. Effects of aldicarb treatment on tuber yield and numbers of tubers[z][y], within cultivars and across P fertilizer rates, in Capac loam, 1989.

Cultivar /aldicarb	Tuber yield ($Mg \cdot ha^{-1}$) Total	<5cm/ <110g	5-8cm/ 110-280g	>8cm/ >280g	Tuber number/ha (X1000) Total	<5cm/ <110g	5-8cm/ 110-280g	>8cm/ >280g
Atlantic								
/Yes	34a	14a	18a	1a	298a	190a	105a	3a
/No	35a	14a	19a	1a	297a	180a	106a	3a
p =	0.32	0.96	0.32	0.52	0.80	0.91	0.98	0.58
Russet Burbank								
/Yes	43a	2a	30a	10b	266a	42a	189a	29b
/No	47a	2a	29a	14a	279a	45a	186a	41a
p =	0.06	0.64	0.91	0.004	0.57	0.61	0.86	0.002

[z]Diameter used to grade Atlantic, mass to grade Russet Burbank.
[y]Total yield and number of tubers include cull tubers not included in size categories.
[x]Means followed by different letters are significantly different, within columns, at $p = 0.05$ level as determined by LSD.

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Table 2.6. Effects of aldicarb treatment on percentage of Grade A tubers[z], mean tuber weight, specific gravity, and tuber P concentration, within cultivars and across P fertilizer rates, in Capac loam, 1989.

Cultivar /aldicarb	Percent Grade A (%)	Mean Tuber wt. (g)	Specific Gravity (g/cm^{-3})	Tuber [P] (ppm)
Atlantic				
/Yes	52a[y]	118a	1.074a	2930b
/No	54a	119a	1.074a	3330a
p =	0.49	0.97	0.97	0.0001
Russet Burbank				
/Yes	69a	179a	1.077a	2850b
/No	64a	169a	1.076a	3030a
p =	0.12	0.48	0.12	0.0012

[z]Diameter used to grade Atlantic, mass to grade Russet Burbank.

[y]Means followed by different letters are significantly different, within columns, at p = 0.05 level as determined by LSD.

Table 2.7. Effects of banded P fertilizer treatments on tuber yield and numbers of tubers[zy], within cultivars, in Martisco muck, 1989.

Table 2.7. Effects of banded P fertilizer treatments on tuber yield and numbers of tubers[z][y], within cultivars, in Martisco muck, 1989.

Cultivar	P rate ($kg \cdot ha^{-1}$)	Tuber yield ($Mg \cdot ha^{-1}$) Total	<5cm/ <110g	5-8cm/ 110-280g	>8cm/ >280g	Tuber number/ha (X1000) Total	<5cm/ <110g	5-8cm/ 110-280g	>8cm/ >280g
Atlantic	0	48a[x]	4a	32a	8a	338a	95a	201a	19a
	25	35a	4a	23a	3a	314a	95a	181a	9a
	50	53a	6a	31a	9a	429a	161a	207a	25a
	75	53a	5a	39a	6a	446a	123a	284a	17a
	100	34a	4a	20a	9a	268a	87a	144a	25a
	125	59a	5a	41a	10a	424a	109a	267a	30a
	150	49a	5a	29a	12a	348a	110a	192a	30a
	175	47a	4a	32a	8a	397a	97a	262a	23a
	p =	0.56	0.25	0.29	0.90	0.40	0.18	0.32	0.89
Russet Burbank	0	29a	13a	10a	0a	283a	192a	61a	0a
	25	24a	15a	8a	0a	288a	228a	49a	0a
	50	29a	15a	11a	1a	306a	222a	66a	2a
	75	28a	11a	11a	0a	243a	150a	66a	0a
	100	26a	18a	8a	0a	308a	251a	51a	0a
	125	33a	16a	13a	1a	294a	201a	80a	4a
	150	26a	14a	9a	0a	256a	179a	59a	0a
	175	38a	19a	16a	0a	386a	274a	101a	0a
	p =	0.75	0.28	0.77	0.58	0.41	0.36	0.73	0.58

[z]Diameter used to grade Atlantic, mass to grade Russet Burbank.
[y]Total yield and number of tubers include cull tubers.
[x]Means followed by different letters are significantly different, within columns, at p = 0.05 level as determined by LSD.

Table 2.8. Effects of banded P fertilizer treatments on percentage of Grade A[z] tubers and mean tuber weight within cultivars and across aldicarb treatments, on Martisco muck, 1989.

Cultivar	P Fertilizer ($kg \cdot ha^{-1}$)	Percent A grade tubers (%)	Average tuber size (kg)
Atlantic	0	68a[y]	139a
	25	65a	109a
	50	59a	122a
	75	74a	118a
	100	59a	127a
	125	71a	138a
	150	63a	139a
	175	68a	121a
	p =	0.70	0.37
Russet Burbank	0	32a	100a
	25	32a	85a
	50	37a	98a
	75	38a	113a
	100	29a	90a
	125	40a	111a
	150	33a	102a
	175	43a	98a
	p =	0.91	0.87

[z]Diameter used to grade Atlantic, mass to grade Russet Burbank.

[y]Means followed by different letters are significantly different, within columns, at p = 0.05 level as determined by LSD.

1990

On the McBride sandy loam at Entrican, P significantly influenced yield (Tables 2.9 and 2.10). Applying P resulted in greater total yield and higher tuber P concentrations. Total number of tubers, mean tuber size, tuber specific gravity, as well as yield and numbers of all but the jumbo grade tubers tended to be higher with increasing P fertilizer applications, but the increases were not statistically significant. Higher P fertilizer rates had little effect on percentage of A sized tubers or on percentage of jumbo tubers with hollow heart. No statistically significant differences were seen in the jumbo and cull grades at least in part because the number of these tubers harvested from an individual plot was much smaller than the total number of tubers. Small differences between replications could have masked any treatment differences. Despite the increase in tuber P concentrations, petiole P concentrations trended lower with increased P applications.

At East Lansing, yields and tuber number trended higher (but not significantly) as P fertilizer rate increased from 50 to 200 $kg \cdot ha^{-1}$ (Table 2.11). Tuber weight, specific gravity and percentage of grade A tubers were not influenced by P treatment (Table 2.12). Petiole and leaf blade P

Table 2.9. Effects of banded P fertilizer treatments on tuber yield and numbers of tubers[z] of Russet Norkotah potatoes grown in McBride sandy loam, 1990.

Table 2.9. Effects of banded P fertilizer treatments on tuber yield and numbers of tubers[z] of Russet Norkotah potatoes grown in McBride sandy loam, 1990.

	Tuber yield ($Mg \cdot ha^{-1}$)				Tuber number/ha (X1000)			
P rate ($kg \cdot ha^{-1}$)	Total	<5cm/ <110g	5-8cm/ 110-280g	>8cm/ >280g	Total	<5cm/ <110g	5-8cm/ 110-280g	>8cm/ >280g
0	30c[y]	10a	22a	2a	275a	132a	134a	2a
50	38bc	12a	23a	3a	302a	154a	137a	3a
100	39ab	11a	25a	3a	311a	150a	151a	3a
150	43a	12a	27a	4a	331a	161a	156a	4a
200	39ab	11a	24a	3a	309a	152a	143a	3a
p =	0.02	0.35	0.10	0.48	0.06	0.32	0.16	0.48

[z]Total yield and number of tubers include cull tubers not included in size categories.

[y]Means followed by different letters are significantly different, within columns, at p = 0.05 level as determined by LSD.

Table 2.10. Effects of banded P fertilizer treatments on percentage of

Table 2.10. Effects of banded P fertilizer treatments on percentage of grade A tubers, mean tuber weight, specific gravity, and tuber P concentration of Russet Norkotah potatoes grown on McBride sandy loam, 1990.

P rate ($kg \cdot ha^{-1}$)	Percent Grade A (%)	Mean Tuber wt. (g)	Specific Gravity (g/cm^{-3})	Hollow tubers[z] (%)	Tuber [P] (%)	Petiole [P] (%)
0	64a[Y]	124a	1.063a	14	0.48c	0.55a
50	62a	125a	1.065a	7	0.52b	0.53a
100	63a	126a	1.066a	10	0.51b	0.49a
150	62a	130a	1.065a	6	0.56a	0.47a
200	62a	128a	1.066a	11	0.57a	0.46a
p =	0.89	0.35	0.83	n.d.[x]	0.0001	0.65

[z]Hollow tubers among those >280 g; too few large tubers available for statistical analysis.
[Y]Means followed by different letters are significantly different, within columns, at $p = 0.05$ level as determined by LSD.
[x]Not determined.

Table 3.11. Effects of banded P fertilizer treatments on tuber yield and numbers[z] of

Table 2.11. Effects of banded P fertilizer treatments on tuber yield and numbers[z] of Russet Norkotah potatoes grown in Capac loam, 1990.

P rate	Tuber yield ($Mg \cdot ha^{-1}$)				Tuber number/ha (X1000)			
($kg \cdot ha^{-1}$)	Total	<110g	110-280g	>280g	Total	<110g	110-280g	>280g
0	30a[y]	10a	17a	2a	232a	126a	97a	7a
50	30a	11a	14a	2a	212a	107a	98a	5a
100	33a	11a	18a	3a	254a	143a	101a	8a
150	32a	12a	17a	3a	256a	147a	101a	7a
200	35a	11a	19a	4a	260a	144a	104a	11a
p =	0.21	0.70	0.92	0.16	0.36	0.45	0.92	0.17

[z]Total yield and number of tubers include cull tubers not included in size categories.

[y]Means followed by different letters are significantly different, within columns, at $p = 0.05$ level as determined by LSD.

Table 2.12. Effects of banded P fertilizer treatments on percentage of

Table 2.12. Effects of banded P fertilizer treatments on percentage of grade A tubers, mean tuber weight, specific gravity, and tissue P concentration of Russet Norkotah potatoes grown in Capac loam, 1990.

P rate ($kg \cdot ha^{-1}$)	Percent Grade A (%)	Mean Tuber wt. (g)	Specific Gravity (g/cm^{-3})	Petiole [P] (ppm)	Tip Leaflet [P] (ppm)
0	58a[z]	130a	1.076a	5020a	5380a
50	56a	150a	1.074a	4010b	4780b
100	55a	130a	1.074a	3930b	4840b
150	55a	120a	1.076a	4130b	4760b
200	55a	130a	1.076a	4240b	5080ab
p =	0.90	0.60	0.43	0.03	0.04

[z]Means followed by different letters are significantly different, within columns, at p = 0.05 level as determined by LSD.

levels were highest in plots receiving no P (Table 2.12). The first 50 kg of applied P increased petiole Zn and Cu concentrations whereas larger applications lowered them (Table 2.13). The concentrations of other nutrients in the petioles were not influenced by P treatment.

On the Martisco muck in Clinton County, tuber yields and numbers were not significantly changed by P fertilizer rate (Table 2.14). Mean tuber size declined with increasing P application (Table 2.15). Tuber specific gravity and percent A grade tubers were not significantly affected by P treatment (Table 2.15). Petiole P concentration, while not significantly different among treatments, trended higher with P application (Table 2.15).

Discussion

The results of these experiments illustrate the complexity of potato responses to P applications. Of the six experiments, only two (on the McBride sandy loam and the Capac loam in 1990) produced results supporting the need for continued P applications when soil test P levels are high. In only one of these two instances (on the McBride sandy loam) did P fertilization significantly increase yield. In no instance did P application affect specific gravity, tuber size, or percentage of grade A tubers produced.

Based on these facts, the general conclusion can be made that a small (approximately 50 kg $P \cdot ha^{-1}$) application of P

Table 2.13. Effects of banded P fertilizer treatments on nutrient concentrations in petioles of Russet Norkotah potatoes grown in Capac loam, 1990.

P rate ($kg \cdot ha^{-1}$)	Nutrient Concentration (ppm)					
	Al	Zn	Fe	B	Mn	Cu
0	83a[z]	36bc	62a	21a	88a	9a
50	101a	54a	64a	20a	119a	10a
100	97a	43ab	61a	20a	119a	7b
150	87a	27c	58a	22a	105a	6b
200	100a	29bc	65a	19a	116a	7b
p =	0.44	0.01	0.56	0.47	0.31	0.002
	Mg	Ca	Mo	K	P	
0	8,220a	8,780a	9.6a	73,020a	2,580a	
50	7,020a	8,960a	9.9a	74,240a	2,110b	
100	7,950a	7,220a	10.3a	66,210a	2,030b	
150	7,570a	9,430a	10.0a	67,880a	2,100b	
200	7,020a	8,670a	9.4a	67,940a	2,240b	
p =	0.48	0.56	0.42	0.20	0.02	

[z]Means followed by different letters are significantly different, within columns, at p = 0.05 level as determined by LSD.

Table 2.14. Effects of banded P fertilizer treatments on tuber yield and number of Russet Norkotah potatoes grown in Martisco muck, 1990.

P rate	Tuber yield ($Mg \cdot ha^{-1}$)				Tuber number/ha (X1000)			
($kg \cdot ha^{-1}$)	Total	<5cm	5-8cm	>8cm	Total	<5cm	5-8cm	>8cm
0	39a[Y]	4a	30a	5a	302a	85a	200a	14a
50	40a	4a	33a	4a	335a	92a	229a	10a
100	36a	4a	28a	4a	305a	95a	194a	11a
150	45a	4a	28a	2a	318a	106a	207a	6a
200	44a	4a	29a	2a	334a	106a	217a	7a
p =	0.22	0.21	0.24	0.09	0.44	0.25	0.33	0.12

[Z]Total yield and number of tubers include cull tubers not included in size categories.
[Y]Means followed by different letters are significantly different, within columns, at p = 0.05 level as determined by LSD.

Table 2.15. Effects of banded P fertilizer treatments on percentage of Grade A tubers, mean tuber weight, specific gravity, and tuber and petiole P concentration of Russet Norkotah potatoes grown on Martisco muck, 1990.

P rate ($kg \cdot ha^{-1}$)	Percent Grade A (%)	Mean Tuber wt. (g)	Specific Gravity (g/cm^{-3})	Petiole [P] (ppm)
0	76a[z]	129a	1.065a	4330a
50	81a	123ab	1.065a	4930a
100	77a	120ab	1.065a	4550a
150	80a	113b	1.064a	5230a
200	80a	110b	1.064a	5180a
p =	0.44	0.05	0.88	0.35

[z]Means followed by different letters are significantly different, within columns, at $p = 0.05$ level as determined by LSD.

fertilizer provides some insurance that a grower's potato yields will approach the maximum attainable on their site.

The results of these studies are similar to the findings of many other researchers. Vitosh (1979,1980) and Vitosh, et al. (1968) reported that P application increased yields in some years in some potato cultivars grown in the McBride sandy loam. In 1968, they reported an insignificant trend toward higher yields of Russet Burbank in one of two studies. In 1979, Vitosh found that P applications increased potato yields, mainly in the A and jumbo grades. In 1980, Vitosh reported that yields and tuber specific gravity of Russet Burbank potatoes were unchanged by fertilizer P applications of more than 55 kg $P_2O_5 \cdot ha^{-1}$ of P. Those results were similar to the total and A grade increases found in the 1990 research on the McBride soil using Russet Norkotah reported here.

The responses to P fertilizer reported here are more likely related to soil factors than to other environmental factors. All sites are within 120 km of each other and have very similar weather and precipitation patterns within a given growing season. In a Capac loam, at the East Lansing site, no yield differences were imparted by P rates in either year. Yields in both the McBride sandy loam and the Martisco muck were higher as P application rate increased.

The pH (5.9) of the McBride sandy loam at Entrican probably plays an important role in determining P availability. Soil solution P levels are buffered mainly by interactions of clays and reactions with soil Ca, Fe and Al. Extractable P levels have reached over 400 $kg \cdot ha^{-1}$ Bray-Kurtz P1 in the McBride sandy loam tested, but the P may not be as readily available to plants as the soil test would indicate. Yerokun and Christenson (1989) have shown that predictions based on common soil tests over-estimate the amount of P that plants will remove from the McBride sandy loam. Yerokun (1987) had earlier reported that the P in a Montcalm sandy loam, synonymous with McBride sandy loam, was influenced by adsorption as Fe-phosphates or incorporation into strengite, $FePO_4 \cdot 2H_2O$, especially in unlimed plots. The unlimed plots would have less Ca to bind with P and greater Al and Fe concentrations in solution than limed plots, allowing more reaction with Fe and/or Al. Other data indicate that Al-phosphates may be very important in controlling P in the McBride soil. Juo (1966) reported that synthesized colloidal Al- and Fe-phosphates were equally available to sand-grown sudan grass. After studying P fractionation in several acid Michigan soils (not including McBride), the author concluded that inorganic P is primarily incorporated into Ca-phsophates in the sand fraction of these soils. Over time, this inorganic P may precipitate as Al- and Fe-phosphates. Considering native and fixed inorganic P sources, Juo concluded that Al-phosphates were more available to plants in these acid soils than Fe-phosphates. The continued responses of potato to P fertilizer applications is probably due to this dominance of Fe- and Al-phosphates, as opposed to more easily solubilized organic or Ca forms in the McBride soil.

Other soil properties may further limit P availability in the McBride sandy loam. The soil structure of the McBride soil may have been weakened through years of potato and grain production, possibly limiting oxygen availability in the soil. Saini (1976) has shown subsoil oxygen diffusion rate to be the single most influential soil physical property effecting potato yields. Reduced solution oxygen concentrations can reduce uptake rate and total P uptake in pines (Topa and Cheeseman, 1992). Low oxygen diffusion rates may be a significant cause of the yield responses to P found at the Clinton County site in the Martisco muck. Oxygen diffusion rate is reduced when soil structure is weakened by tillage or other operations. Tillage and other operations which disturb the soil are more frequent in potato and vegetable production than in grain production. This may result in poorer soil structure, greater soil compaction and lower oxygen diffusion rates in potato producing fields than in grain fields. Compaction, as described by bulk density of the soil, did not correlate well with potato yields in Saini's (1976) work. Burpee (1989) evaluated the influence of several tillage practices on potato growth and yield. The author reported similar yields in plots subject to deep zone type tillage or conventional tillage. Conventional tillage did result in greater areas of potential aeration stress from greater compaction than did zone tillage. Strzalka (1990), working with onions and carrots, has shown compaction can significantly reduced yields in muck soils. Saini's potato research was conducted in clay loams.

Phosphorus appears to influence potato tuber yield indirectly, by impacting overall plant growth and health. Many researchers have provided evidence which indicates shoot (vine) vigor is the most important plant factor influencing potato yields. First, Bremner and Radley (1966) claimed that the number of days that leaf area index (LAI), the ratio of leaf area per unit of ground, exceeded 3.0 was the single most important shoot factor influencing yield. Bremner and Taha (1966) suggested that the maintenance of LAI was more important in yield determination if it was due to leaf growth rather than maintenance of existing leaf area. This implies that steady crop growth is very important in determining yield. Westermann and Kleinkopf (1985) have shown potato yields are correlated with the number of days between the date on which total shoot P concentration reaches 2.2 $g \cdot kg^{-1}$ and that on which tuber set occurs. It has also been shown that limited P availability can reduce leaf area (Cogliatti and Clarkson, 1983), leaf number (Benepal, 1967), and plant height (Benepal, 1967) in potato plants and decrease root to shoot ratio (R:S) in other species (Chapin, 1982). Benepal (1967) found strong, although indirect, correlations between plant height and tuber yields in cv. Patna Red grown in sandy loam soil. The yield increases reported resulted mainly from an increase in tuber size rather than number. Benepal found greater leaf numbers and plant heights throughout the growing season in plants receiving P than in those not receiving P. The author also suggested that increasing P supply may improve assimilation rate. Vitosh (1979) reported P fertilizer applications increased shoot weight in potatoes grown at Entrican. Improved shoot vigor through P applications would allow production of more carbohydrate and production of larger tubers. An increase in shoot growth could also explain the observed decrease in petiole P concentration in 1990 in the Capac loam. Increased shoot growth without a similar increase in P uptake would result in lower shoot P concentration even though content (concentration X dry weight) might be higher.

Researchers may reduce the need for P fertilizer in potato production by improving fertilizer use efficiency. Root growth and soil moisture may play important roles in controlling fertilizer use efficiency. Just as excessive soil moisture can limit P uptake (by limiting oxygen diffusion to the roots), so can too little soil moisture. Phosphorus moves to the root by diffusing through the soil solution. If soil moisture levels are low enough to limit root growth or diffusion, they are likely low enough to limit P uptake. Diffusion may be the limiting step in P uptake and may be especially important in sandy soils with relatively little ability to resupply solution P removed by plant roots (Olsen, et al., 1962). This may be an important issue in the McBride sandy loam which has lower clay and silt contents, and thus lower water holding capacity, than the Capac loam at the East Lansing site. It may have less importance in explaining the P response in the Martisco muck soil in Clinton County. Pursglove (1981) linked P uptake to root growth and soil moisture conditions. The author found that uptake of fertilizer P varied during the growing season. Pursglove surmised that decreasing soil moisture during summer months and continuing root growth into soil below fertilizer bands may reduce fertilizer P uptake later in the season.

Conclusions

These Michigan field experiments suggest that P fertilization can sometimes increase potato yields even at high soil P test level. The application of fertilizer P did not affect tuber size or specific gravity. Positive responses to applied P are more likely in the McBride sandy loam than in the Capac loam or Martisco muck. The increased yields are likely due to improved health and vigor of the foliage and root systems, which make more carbohydrate available for tuber production. Any further research needs to focus on soil P chemistry and interactions between potato roots and the soil.

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CHAPTER 3

RESPONSES OF POTATO TO FERTILIZER AND AVAILABLE SOIL PHOSPHORUS

Introduction

The Michigan State University Extension Service recommends phosphorus applications to potato soils testing up to 650 kg extractable $P \cdot ha^{-1}$ (Christenson, et al., 1992). Vitosh (1979) has reported that fertilizer phosphorus can increase yields of Russet Burbank potatoes growing in a Michigan McBride sandy loam (coarse-loamy, mixed Eutric Glossoboralf) with a Bray-Kurtz P1 (B-K P1) extractable phosphorus level of greater than 400 kg $P \cdot ha^{-1}$. Data presented in the previous chapter indicated that yields of potato cultivar Russet Norkotah can also be increased by banding phosphorus fertilizer in high-phosphorus McBride soil. Yields, however, were not increased for potatoes growing in a Martisco muck (fine-silty carbonatic mesic Histic Humaquaept) or a Capac loam (fine-loamy, mixed, mesic Udollic Ochraqualf), with 357 and 102 kg B-K P1 extractable $P \cdot ha^{-1}$, respectively. Potatoes are known to be especially responsive to fertilizer phosphorus while many other crops only respond to fertilizer phosphorus when B-K P1 extractable phosphorus levels are below 100 kg $P \cdot ha^{-1}$. Sweet corn yields have been increased with band application of phosphorus to soils testing up to 38 kg B-K P1 extractable $P \cdot ha^{-1}$ (Peck and MacDonald, 1989). In their work, Peck and MacDonald demonstrated that both current season banded phosphorus and residual fertilizer phosphorus were effective in increasing sweet corn seedling size and harvested ear weight. They also reported that even with current season applications, plants growing in soil with higher residual phosphorus level had greater weights than those grown in soil with lower residual P levels.

Two experiments were conducted to evaluate potato responses to banded and available soil phosphorus (truly indigenous plus residual fertilizer P which is B-K P1 extractable)) in McBride sandy loam. The first was a field experiment conducted during two consecutive seasons. The second was a greenhouse experiment. The objective of the field experiment was to determine relative tuber yield responses by potato (cv. Russet Norkotah) to available and banded phosphorus in a McBride sandy loam. The objective of the greenhouse experiment was to determine relative growth responses in corn and potato to combined previous season's residual fertilizer and available phosphorus levels in a McBride sandy loam.

Materials and Methods

Field Experiment

For the field experiments, five blends of two McBride sandy loams were created to get a range of available phosphorus levels. The soils were collected prior to each growing season from the Michigan State University Montcalm Research Farm in Entrican, Michigan and a commercial potato farm, west of Stanton, approximately 6.5 km from the Research Farm. The M.S.U. site was cropped to alfalfa in 1989 and 1990, and the commercial farm was planted to corn in 1989 and potatoes in 1990. Initial soil test data are shown in Table 3.1. The soils were proportionally blended for five minutes in an electric-powered concrete mixer (Model 907, J.B. Foote Foundry Co., Fredericktown, OH) to form five soils with evenly spaced amounts of Bray-Kurtz P1 extractable phosphorus (available phosphorus).

Five rates of triple superphosphate fertilizer were superimposed on these five soils, resulting in a 5 X 5 factorial arrangement of treatments. The experiments had six replications in a randomized complete block design during both seasons.

Each plot in the field experiments consisted of one potato plant growing within a 30 cm length of 25 cm diameter black polyethylene, corrugated, unperforated drainage tile. Initially, 15 cm of one soil blend was placed in a tile section which had been set in a 30 cm trench in Capac loam at the M.S.U. Soils Research Farm in East Lansing. Granular nitrogen, potassium, and phosphorus, according to treatment, were placed in a ring approximately 10 cm in diameter. Rates of P were 0, 25, 50, 75, and 100 kg $P\cdot ha^{-1}$. Five centimeters of soil were placed above the fertilizer, a

Table 3.1. Initial soil test results for 1990 and 1991 field available and fertilizer phosphorus experiments.

Soil Property	Location			
	1990		1991	
	Entrican	Stanton	Entrican	Stanton
Sand(%)	75	75	76	76
Silt(%)	13	14	12	11
Clay(%)	12	11	12	13
pH	5.2	5.2	5.6	6.0
CEC(meq/100g)	4	4	5	6
P($kg \cdot ha^{-1}$)	241	778	271	867
K($kg \cdot ha^{-1}$)	122	395	109	373
Ca($kg \cdot ha^{-1}$)	897	734	838	838
Mg($kg \cdot ha^{-1}$)	154	224	122	200
Zn(ppm)	n.d.[z]	n.d.	1	3
Mn (ppm)	n.d.	n.d.	20	43

[z]Not determined.

whole 50 to 65 g seed tuber (cv. Russet Norkotah) was set on the center of the soil. The tile was then filled with soil and watered well.

During 1990, the plants exhibited symptoms of early die (*Verticillium dahliae*) seemingly in proportion to the amount of low phosphorus, Montcalm Research Farm soil in which they were growing. Tests revealed this soil had active *Verticillium dahliae* and had likely caused the plant symptoms. In 1991, the soils were fumigated before planting. A 20 cm layer of each soil was placed on polyethylene sheets for fumigation with sodium methyldithiocarbamate at labeled rates. The soils were covered for 7 days and then allowed to aerate for 7 more days before being blended as in 1990.

Plot preparation and planting methods used in 1991 were similar to those in 1990. After trenches were dug in the Capac soil, a 3-5 cm layer of gravel (<1 cm mean diameter) was spread in the bottom of each trench to promote drainage from the tile and to reduce root proliferation and bunching at the interface between the soil within the tile and that at the bottom of the trench. Prior to planting, seed tubers were sorted to uniform size to reduce variability within each replication. The tiles were then filled and planted on 2 and 3 June. Phosphorus fertilizer treatments were identical to those used in 1990, as was fertilizer blending and placement. The newly planted seed were hand watered within 24 h of planting. Plants received periodic hand watering, one nitrogen side dressing (1.5 g N/plant) and two potassium side dressings (0.7 g K/plant each). Recommended insect and disease control programs were utilized during the growing season.

During the 1990 season, plant height and a visual disease rating were recorded once. In 1991, sprout emergence, plant height, leaf number, and presence of flowers were recorded on 28 June, 5 July and 12 July. From these data growth rates, leaf emergence rates and relative maturity (based on when plants flowered) were determined for this portion of the growing season. At harvest both years, after complete senescence of the haulms, tubers were graded, counted and weighed. Tuber specific gravities (using only tubers greater than 110 g) were determined by the weight in water/weight in air method. To determine tuber phosphorus concentration, two cores, one longitudinal and one latitudinal, were taken from several larger tubers. Using a razor blade, the skin (periderm) and less than 0.25 cm of cortical tissue were removed from the ends of each core. The cores were then rinsed in deionized water and dried for 24 to 48 h at 60 C. The dried cores were ground to a powder with a mortar and pestle and analyzed for phosphorus using the methods outlined in the previous chapter.

1991 Corn and Potato Greenhouse Experiment

The greenhouse experiment was conducted in the spring of 1991. Batches of the 25 soil blends (5 blends X 5 banded application rates) used during the 1990 field tile experiment were fumigated in 80 l Rubbermaid Roughneck trash cans with sodium methyldithiocarbamate at labeled rates. The fumigated soils were then allowed to air in these containers for two weeks. Soil test data from the aired soils, sampled prior to planting the greenhouse experiment, appear in Table 3.2. Each experimental unit was a single potato plant or 3 corn plants in a 4 l polyethylene standard nursery pot. Soil was placed in the pots lined with cotton cheese cloth. Each pot was planted with either six corn seeds (cv. Great Lakes 29) or one whole or cut potato (cv. Russet Norkotah) seed piece (40 to 60 g). Potatoes were planted 22 February 1991, corn on 7 March. After emergence, the corn was thinned to three plants per pot. Potato plants were trimmed to a single sprout per pot. All plants received water-soluble nitrogen and potassium (as ammonium nitrate and potassium nitrate) during growth. No fertilizer phosphorus was applied pre- or post-planting. Harvest was 23 April 1991, 60 DAP (days after planting) for potato, 47 DAP for corn. Leaf number, corn ligule number, stem height, and fresh weights were recorded. Leaf area was determined using a Licor LI-3100 leaf area meter (Licor Instruments, Lincoln, NE). Shoot tissues were dried at 60 C for 24 h,

Table 3.2. Bray-Kurtz P1 extractable phosphorus in twenty five soils recovered from the 1990 field available/fertilizer phosphorus experiment for use in the 1991 greenhouse corn/potato experiment, 11 Feb., 1993.

Original fertilizer phosphorus (kg P·ha^{-1})	Original Preseason B-K P1 available soil P level (kg P·ha^{-1})				
	241	399	526	669	778
0	234	370	520	649	719
25	278	418	554	673	782
50	325	457	628	673	760
75	370	538	628	717	826
100	418	570	673	837	896

ground and analyzed for phosphorus using the methods described in the previous chapter.

Selected root data were collected after gently removing soil from the root system of the potato plants by hand screening with a 0.25 cm screen. Potato tuber number, weight and stolon numbers were recorded. Dry weights of roots from both crops were determined for roots collected from the corner treatments of the 5 X 5 arrangement (i.e. the 11, 15, 51 and 55 treatments). Final Bray-Kurtz P1 soil phosphorus levels were also determined using the methods described in the previous chapter.

All data were analyzed using MSTAT, MSTAT-C (MSTAT Development Team, 1991) or PC-SAS (SAS Institute Inc., 1988).

Results

1990 Field Experiment

Band applications of phosphorus significantly increased tuber yields, as averaged across the five available soil phosphorus levels (Table 3.3). Application of phosphorus influenced tuber number and yield in the 241 and 526 kg available P soils only (Table 3.4). In the 399 kg P soil, yields trended higher with greater P applications but this trend was not statistically significant. In the 669 and 778 kg P soils, with less early die disease than the three lower P soils, banded phosphorus rate had no detectable influence

Table 3.3. Effect of fertilizer phosphorus applications in McBride sandy loam averaged across five available soil phosphorus levels on potato yield, 1990.

Fertilizer rate ($kg\ P \cdot ha^{-1}$)	Yield (g/plant)		Percent large (>110g) yield	Tuber number per plant	
	Total	>110g	(% of total)	Total	>110g
0	660c[z]	430c	53a	7.6a	2.2a
25	730bc	480bc	63a	7.2a	2.5a
50	830ab	580ab	66a	8.2a	3.1a
75	860a	600ab	65a	7.8a	3.3a
100	900a	640a	66a	8.7a	3.2a
p =	0.0001	0.005	0.14	0.39	0.007

[z]Mean separation within columns by LSD at $P < 0.05$.

Table 3.4. Effect of fertilizer phosphorus applications in McBride sandy loam within available phosphorus levels on potato yield, 1990.

Soil available phosphorus (kg P/ha)	Fertilizer rate ($kg \cdot ha^{-1}$)	Yield (g/plant)		Large (>110g) yield	Tuber number /plant	
		Total	>110g	(% of total)	Total	>110g
241	0	310b[z]	120b	32a	4.5b	0.5b
	56	500ab	290ab	61a	5.5b	1.5a
	112	580a	370a	63a	5.7b	2.2a
	168	640a	420a	64a	6.0b	2.2a
	224	620a	310ab	45a	9.7a	2.0a
	p =	0.02	0.048	0.05	0.0002	0.004
399	0	380a	180a	37a	6.0a	1.0a
	56	600a	410a	67a	6.3a	2.2a
	112	640a	390a	55a	7.5a	2.5a
	168	590a	340a	47a	6.7a	1.3a
	224	710a	450a	55a	9.2a	2.7a
	p =	0.13	0.42	0.59	0.14	0.22
526	0	630c	400b	59a	7.3a	2.5ab
	56	720bc	360b	44a	7.7a	2.0b
	112	900ab	670a	74a	10.2a	3.8a
	168	790abc	440ab	56a	8.0a	2.5ab
	224	1000a	690a	69a	9.5a	3.8a
	p =	0.03	0.048	0.22	0.27	0.048

Table 3.4 (cont'd).

Soil available phosphorus (kg P/ha)	Fertilizer rate ($kg \cdot ha^{-1}$)	Yield (g/plant) Total	Yield (g/plant) >110g	Large (>110g) yield (% of total)	Tuber number /plant Total	Tuber number /plant >110g
669	0	860a	530a	60a	11.0a	2.5a
	56	750a	540a	73a	7.3a	3.2a
	112	940a	660a	66a	9.7a	3.3a
	168	950a	760a	80a	8.2a	4.2a
	224	970a	740a	76a	8.0a	3.8a
	p =	0.36	0.43	0.43	0.70	0.12
778	0	1120a	920a	76a	9.2a	4.5a
	56	1090a	790a	70a	9.2a	3.8a
	112	1080a	790a	74a	7.8a	3.5a
	168	1360a	1050a	76a	10.3a	4.8a
	224	1200a	960a	84a	7.3a	3.8a
	p =	0.38	0.43	0.53	0.34	0.53

[z]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns and soil extractable phosphorus levels.

on total and large tuber number (Table 3.4). The yields and tuber numbers produced in these soils were higher than in the lower phosphorus, disease infested soils but these differences cannot be attributed to available soil phosphorus levels alone because these levels were completely confounded with disease incidence. In the 241 and 526 kg $P \cdot ha^{-1}$ soils, increasing banded phosphorus rates increased total and large (>110g/tuber) tuber yield and number. In these soils, banded phosphorus increased tuber number more than tuber size. Percent large tubers did not significantly increase. Across available soil phosphorus levels, plants had higher tuber P concentrations and appeared healthier in plots with higher P application rates (Table 3.5). Within the 241, 699 and 778 kg soils, banded phosphorus application significantly increased tuber phosphorus concentration (Table 3.6).

1991 Field Experiment

Both available soil and banded phosphorus influenced potato growth and yield in 1991. Each source of phosphorus influenced yield more than tuber number. For many yield parameters the analysis of variance showed that the two phosphorus sources interacted to affect yield and other measured plant growth parameters. The influence of banded phosphorus on total tuber yield was greater in the 271 and

Table 3.5. Effect of fertilizer phosphorus applications averaged across five available soil phosphorus levels on potato plant and tuber quality, 1990.

Fertilizer rate (kg $P \cdot ha^{-1}$)	Mean tuber weight (g/tuber)	Tuber phosphorus concentration (ppm)	Tuber specific gravity ($g \cdot cm^{-3}$)	Number of stems 7-14-90	Plant health 7-14-90[z]
0	93a[y]	4020c	1.075a	4.0a	3.6c
25	108a	4310b	1.074a	4.4a	4.9ab
50	107a	4450b	1.075a	3.9a	5.2ab
75	114a	4740a	1.073a	4.4a	4.5b
100	116a	4760a	1.073a	4.6a	5.4a
p =	0.17	0.0001	0.42	0.19	0.0001

[z]Visual rating of shoot vigor and disease symptoms; 1 = dead shoots, 8 = vigorous with no disease symptoms.

[y]Means followed by different letters are significantly different (by LSD) at $p < 0.05$ level, within columns.

Table 3.6. Effect of fertilizer phosphorus applications in McBride sandy loam within available phosphorus levels on potato plant and tuber characteristics, 1990.

Soil available phosphorus (kg P/ha)	Fertilizer rate ($kg \cdot ha^{-1}$)	Mean tuber weight (g)	Tuber phosphorus conc. (ppm)	Tuber specific gravity ($g \cdot cm^{-3}$)	No. of stems 7-14	Plant health 7-14[z]
241	0	72b[y]	3810c	1.077a	3.7ab	2.2c
	56	111a	4190bc	1.073a	3.8ab	4.1a
	112	102a	4380b	1.073a	2.8b	4.0ab
	168	107a	4720ab	1.074a	4.8a	2.8bc
	224	70b	5130a	1.072a	4.7a	4.0a
	p =	0.016	0.0002	0.44	0.022	0.020
399	0	63a	4260a	1.078a	3.2a	1.5a
	56	98a	4630a	1.074a	3.8a	3.3a
	112	90a	5050a	1.077a	3.7a	4.2a
	168	106a	5120a	1.072a	3.8a	4.5a
	224	80a	4820a	1.074a	5.2a	4.9a
	p =	0.62	0.28	0.62	0.07	0.09
526	0	89a	4230a	1.070a	3.7a	2.8b
	56	93a	4411a	1.075a	5.0a	5.0a
	112	96a	4230a	1.078a	5.0a	5.4a
	168	98a	5000a	1.070a	4.3a	3.3b
	224	111a	4410a	1.072a	4.7a	5.0a
	p =	0.49	0.058	0.32	0.40	0.002

Table 3.6 (cont'd).

Soil available phosphorus (kg P/ha)	Fertilizer rate ($kg \cdot ha^{-1}$)	Mean tuber weight (g)	Tuber phosphorus conc. (ppm)	Tuber specific gravity ($g \cdot cm^{-3}$)	No. of stems 7-14	Plant health 7-14[z]
669	0	117a	4220b	1.075a	4.8a	4.5a
	56	109a	4170b	1.074a	4.5a	5.0a
	112	101a	4440ab	1.075a	4.7a	5.7a
	168	124a	4560ab	1.075a	4.2a	4.5a
	224	137a	4940a	1.071a	5.0a	5.0a
	p =	0.64	0.007	0.69	0.78	0.73
778	0	122a	3610b	1.078a	4.7a	5.8a
	56	129a	4160ab	1.074a	4.7a	6.6a
	112	142a	4160ab	1.073a	3.5a	6.1a
	168	136a	4320a	1.075a	4.7a	6.5a
	224	179a	4490a	1.075a	3.3a	6.7a
	p =	0.15	0.037	0.34	0.054	0.54

[z]Visual rating of shoot vigor and disease symptoms; 1 = dead shoots, 8 = vigorous with no disease symptoms.

[y]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns and available soil P levels.

421 kg P·ha^{-1} soils than in the 575, 707 and 867 kg P·ha^{-1} soils (Figure 3.1). Large (>110g) tuber yield was also increased more by fertilizer P in the 271 and 421 kg P·ha^{-1} than in the three higher P soils (Figure 3.2). Total and large tuber yields of plants growing in each of the five blends benefitted most from the first 25 kg P·ha^{-1} increment of fertilizer phosphorus. Each additional 25 kg·ha^{-1} increment of phosphorus had less impact on yield than the previous one. Total and large tuber number were not significantly affected by available soil P (Table 3.7), but were increased by fertilizer P (Table 3.8). Tuber phosphorus concentration was raised more by increasing fertilizer phosphorus than by growing the plants in soils with higher available P concentrations (Tables 3.9 and 3.10). Specific gravity of the tubers was unaffected by fertilizer phosphorus but was strongly depressed by some aspect of the high phosphorus soil (Tables 3.9 and 3.10), most likely potassium (see discussion).

Shoot growth was influenced much more by fertilizer phosphorus than by available soil phosphorus. Plant height, leaf number, and growth rate were unaffected by available soil phosphorus levels (Table 3.11), but were affected by fertilizer phosphorus rate (Table 3.12). Fertilizer P increased stem growth rate more in the lower phosphorus soils than in the high phosphorus soils (Figure 3.3).

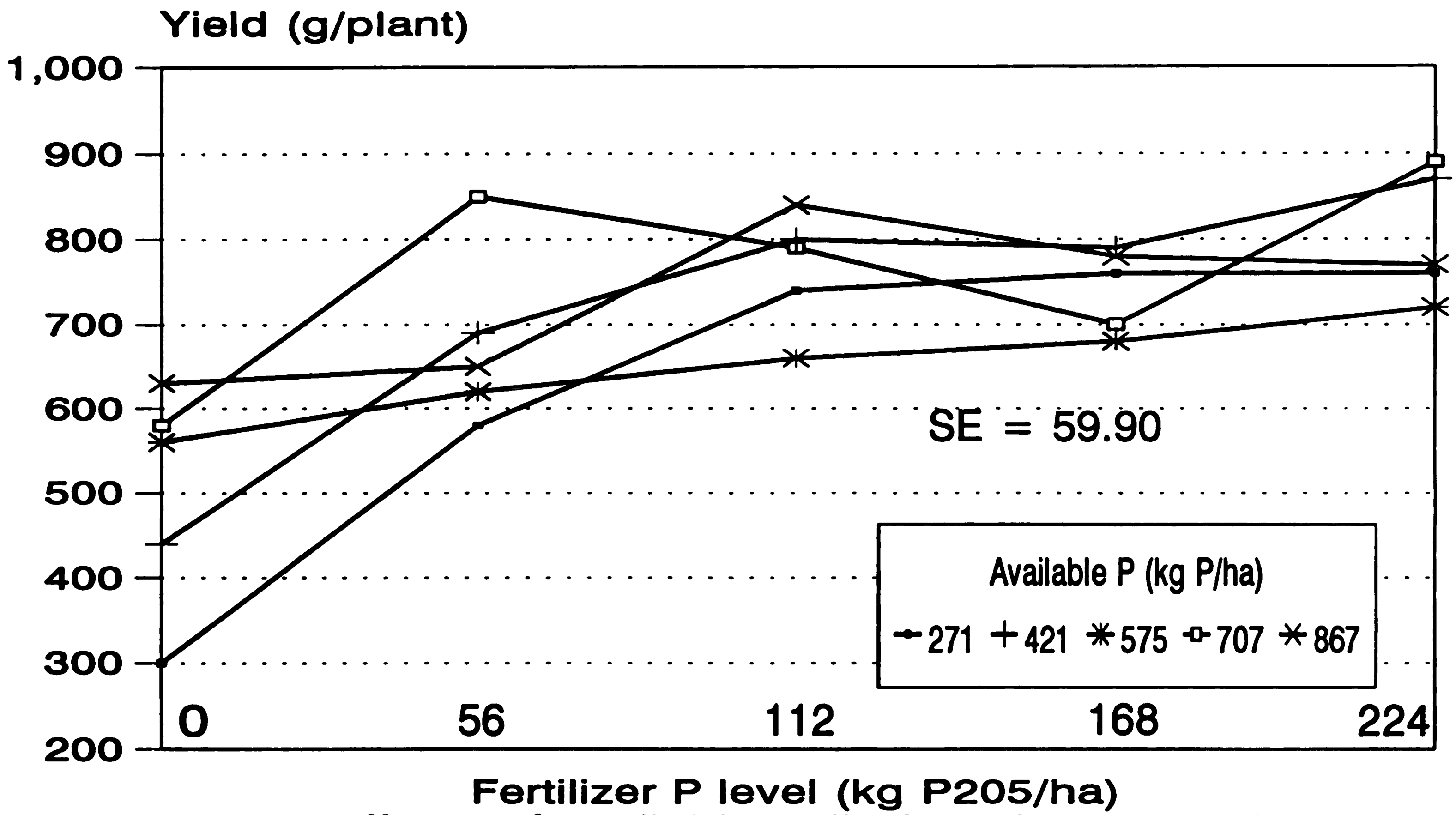

Figure 3.1 Effects of available soil phosphorus levels and fertilizer phosphorus applications on total tuber yield, 1991.

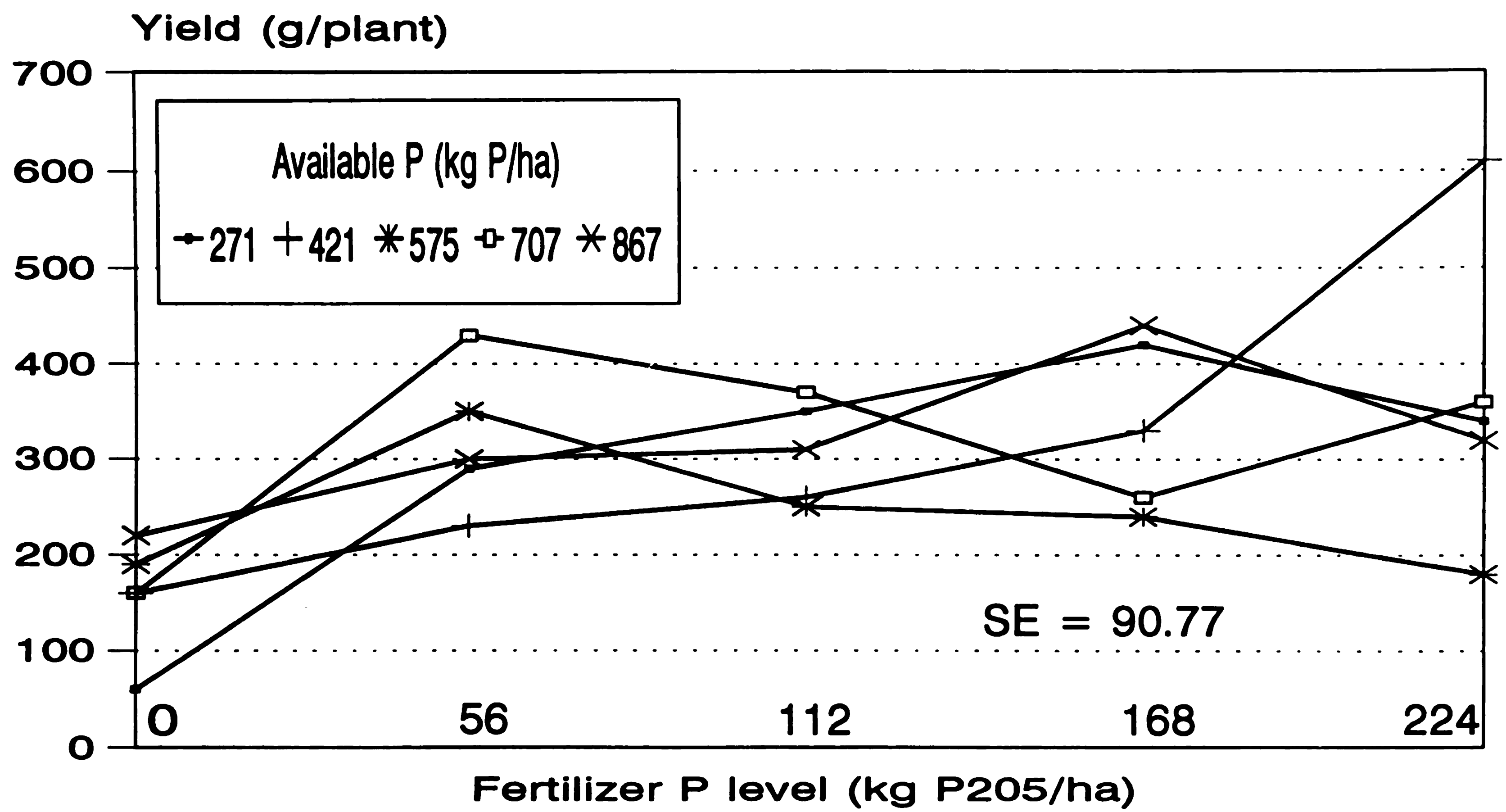

Figure 3.2. Effects of available soil phosphorus levels and fertilizer phosphorus applications on large (>110g) tuber yield, 1991.

Table 3.7. Effect of available soil phosphorus level averaged across five fertilizer phosphorus application rates on potato tuber number and percent of yield in large tubers, 1991.

Soil available phosphorus ($kg\ P \cdot ha^{-1}$)	Tuber number per plant		Large (>110g) yield (% of total)
	Total	>110 g	
271	7.0a[z]	1.8a	48a
421	7.9a	2.0a	50a
575	8.1a	1.6a	42a
707	6.8a	2.2a	55a
867	8.6a	2.0a	49a
p =	0.18	0.32	0.55

[z]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns.

Table 3.8. Effect of fertilizer phosphorus applications averaged across five available soil phosphorus levels in McBride sandy loam on potato yield, tuber number, and percent large tubers, 1991.

Fertilizer rate (kg P·ha^{-1})	Tuber number per plant		Large (>100g) yield (% of total)
	Total	>110g	
0	6.3c[z]	1.1b	35b
25	7.1bc	2.2a	56a
50	8.0abc	2.1a	50a
75	8.1ab	2.1a	54a
100	9.0a	2.2a	48ab
p=	0.02	0.002	0.03

[z]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns.

Table 3.9. Effect of available soil phosphorus level averaged across five fertilizer phosphorus application rates on potato tuber quality, 1991.

Soil available phosphorus ($kg\ P \cdot ha^{-1}$)	Mean tuber weight (g/tuber)	Tuber phosphorus concentration (ppm)	Tuber specific gravity ($g \cdot cm^{-3}$)
271	103b[z]	3370a	1.071a
421	103b	3230a	1.070ab
575	92b	3450a	1.069b
707	130a	3500a	1.068bc
867	101b	3600a	1.066c
p=	0.04	0.07	0.001

[z]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns.

Table 3.10. Effect of fertilizer phosphorus applications, averaged across five available soil phosphorus levels, on potato tuber quality, 1991.

Fertilizer rate ($kg\ P \cdot ha^{-1}$)	Mean tuber weight (g/tuber)	Tuber phosphorus concentration (ppm)	Tuber specific gravity ($g \cdot cm^{-3}$)
0	91a[z]	3070c	1.070a
25	113a	3330bc	1.068a
50	113a	3470ab	1.069a
75	109a	3690a	1.069a
100	102a	3590a	1.068a
p =	0.34	0.0001	0.37

[z]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns.

Table 3.11. Effect of available soil phosphorus level averaged across five fertilizer phosphorus application rates on leaves per potato plant, leaf emergence and plant height, 1991.

Soil available phosphorus ($kg P \cdot ha^{-1}$)	Number of leaves		Leaf emergence (leaves/day)[z]	Plant height (cm)		
	7-5	7-12		6-28	7-5	7-12
271	33a[y]	62a	4.1a	11.2a	24.3a	41.7b
421	36a	67a	4.5a	12.1a	25.6a	44.5a
575	30a	64a	4.9a	9.9a	22.3a	39.6b
707	34a	69a	4.9a	12.4a	25.8a	43.9a
867	33a	65a	4.5a	11.5a	24.6a	42.7ab
p =	0.32	0.63	0.21	0.15	0.14	0.03

[z]7-5 through 7-12.
[y]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns.

Table 3.12. Effect of fertilizer phosphorus applications averaged across five available soil phosphorus levels on leaves per potato plant, leaf emergence and plant height (cm), 1991.

Fertilizer rate (kg P·ha^{-1})	Number of leaves		Leaf emergence (leaves/ day)[z]	Plant height (cm)		
	7-5	7-12		6-28	7-5	7-12
0	30a[Y]	56b	3.7b	10.9a	23.7a	38.6c
25	32a	62ab	4.4ab	10.2a	22.4a	40.9bc
50	35a	69a	4.8a	12.1a	25.8a	44.7a
75	35a	71a	5.1a	12.2a	25.5a	44.5a
100	33a	69a	5.0a	11.6a	25.1a	43.7ab
p =	0.29	0.01	0.003	0.29	0.11	0.001

[z]7-5 through 7-12.

[Y]Means followed by different letters are significantly different (by LSD) at $p < 0.05$ level, within columns.

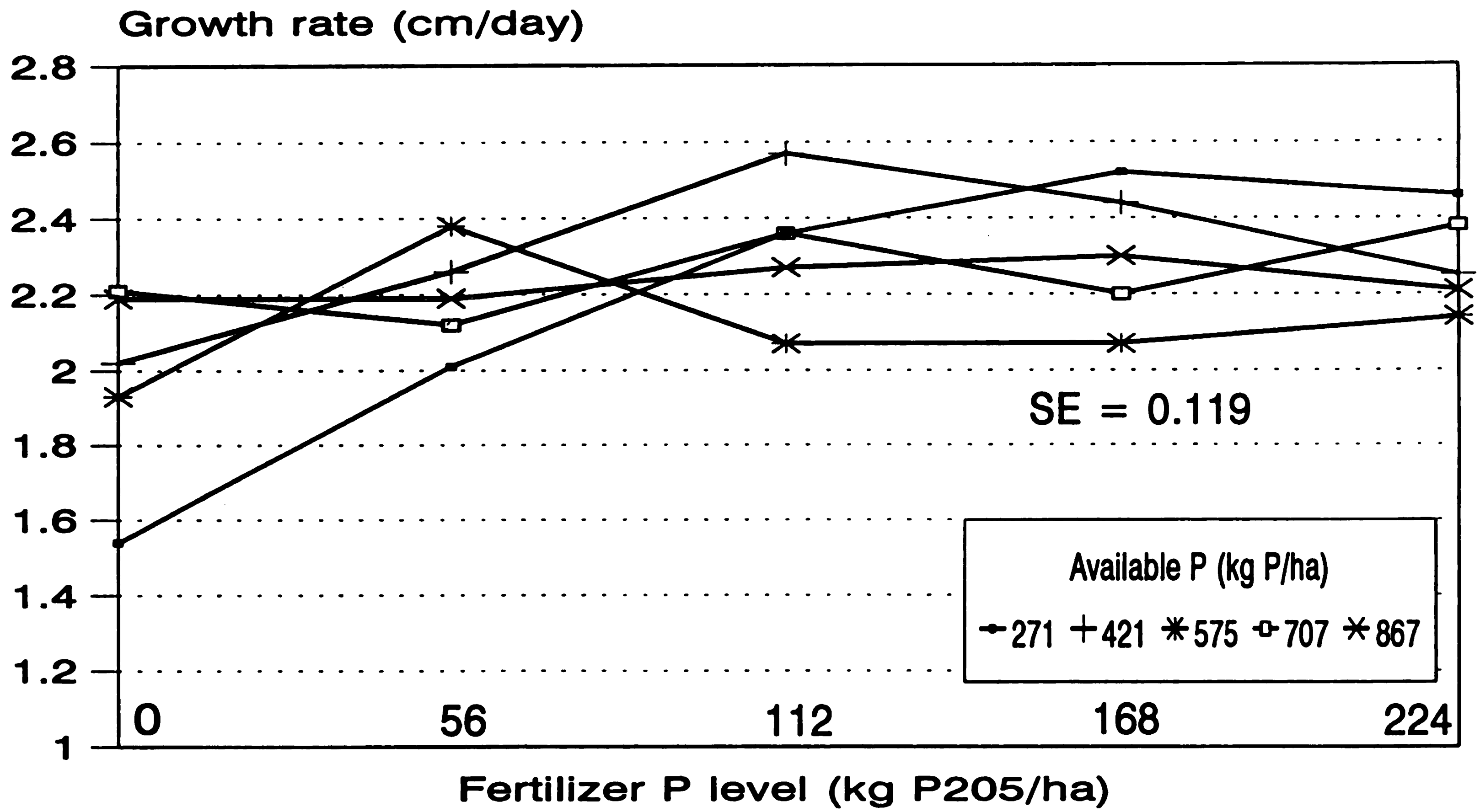

Figure 3.3. Effects of available soil phosphorus levels and fertilizer phosphorus applications on stem growth rate, 28 June through 12 July, 1991.

1991 Corn and Potato Greenhouse Experiment

Potato shoot growth responses to available soil and residual fertilizer phosphorus were less dramatic than expected; those of corn more dramatic. Some potato root and underground tuber-related responses were significant and pose some interesting questions. Corn root growth responses were not determined.

Potato

Based on the significance of the interaction term of the analysis of variance, fresh weights of potato leaves (Figure 3.4), stems (Figure 3.5) and whole shoots (Figure 3.6) were affected by both previous season's available soil P and residual fertilizer P. Most of the weights varied greatly within main effects and it is unlikely that any real changes in potato leaf or stem fresh weight can be attributed to either P source. When combined to get total shoot fresh weight it appears that residual fertilizer P increased fresh weight more in the 271 kg $P \cdot ha^{-1}$ soil than in any other soil (Figure 3.6). Potato dry weight at 60 DAP was unaffected by treatment (Tables 3.13 and 3.14). The interaction of available soil P and residual fertilizer P appears significant in determining leaf dry weight but again the dry weights follow no discernible pattern (Figure 3.7). Percent dry weight in the potato shoots was significantly

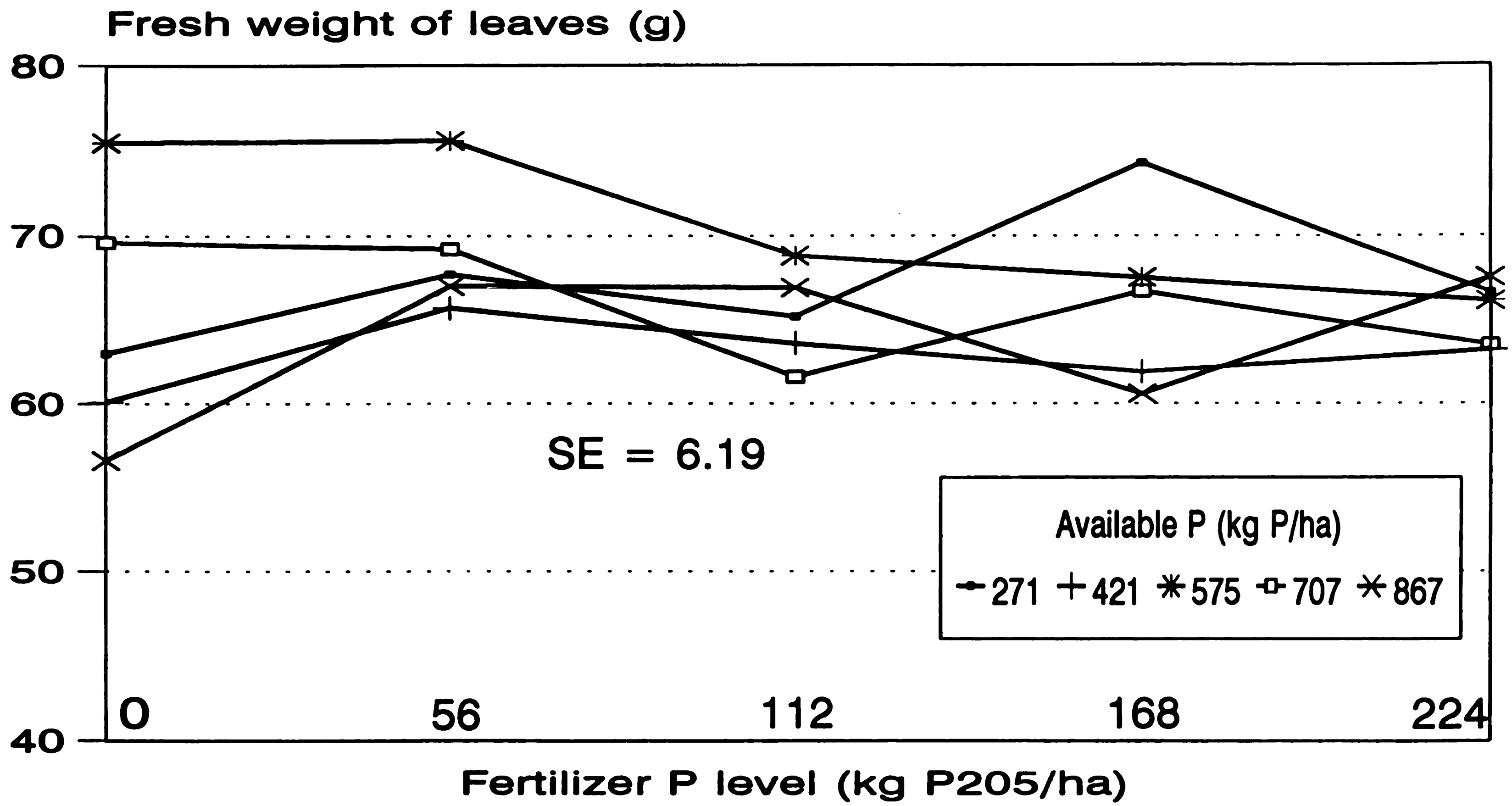

Figure 3.4. Effects of available soil phosphorus levels and residual fertilizer phosphorus on leaf fresh weight of greenhouse-grown potato plants grown in McBride sandy loam, 1991.

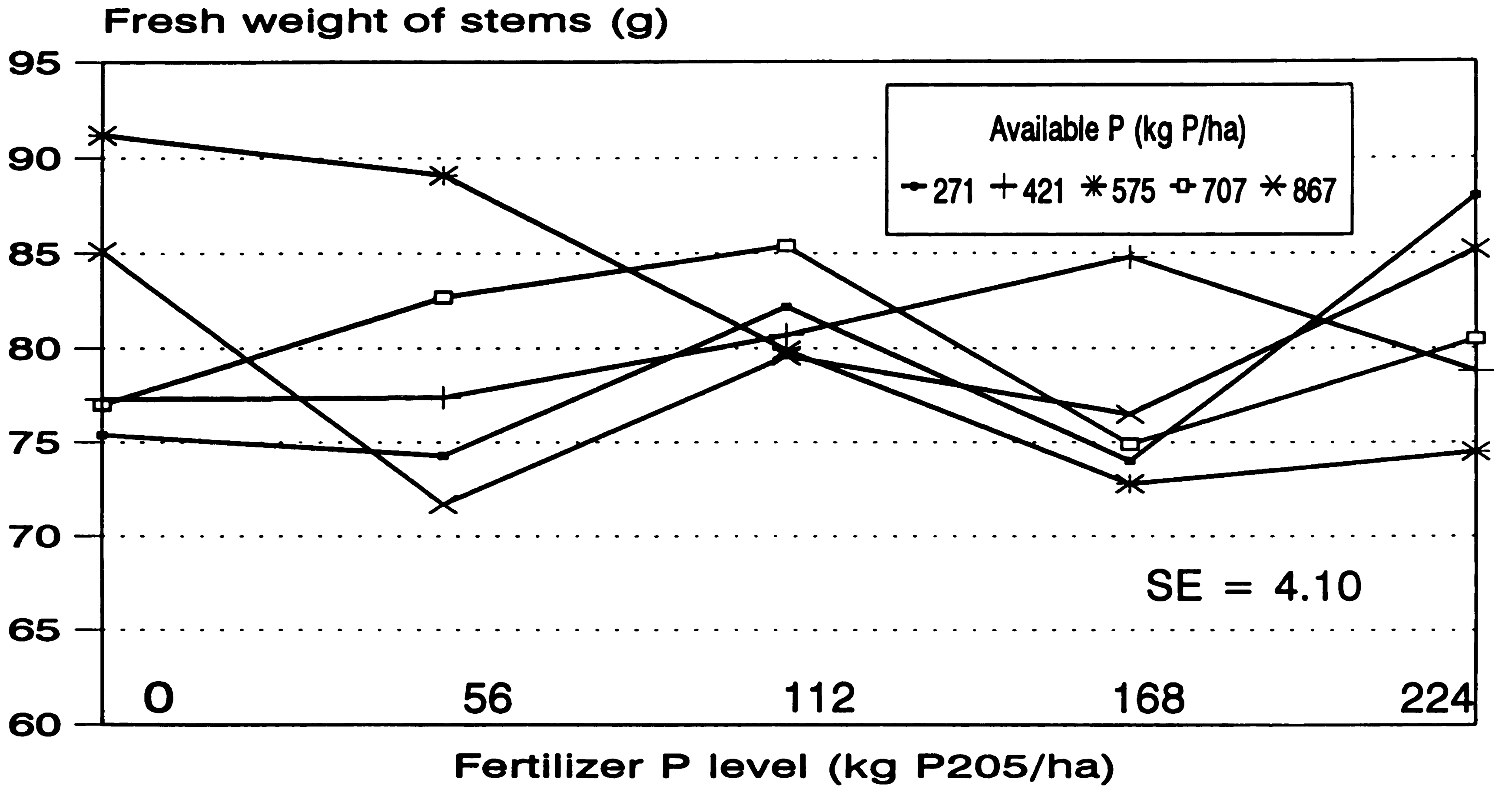

Figure 3.5. Effects of available soil phosphorus levels and residual fertilizer phosphorus on stem fresh weight of greenhouse-grown potato plants grown in McBride sandy loam, 1991.

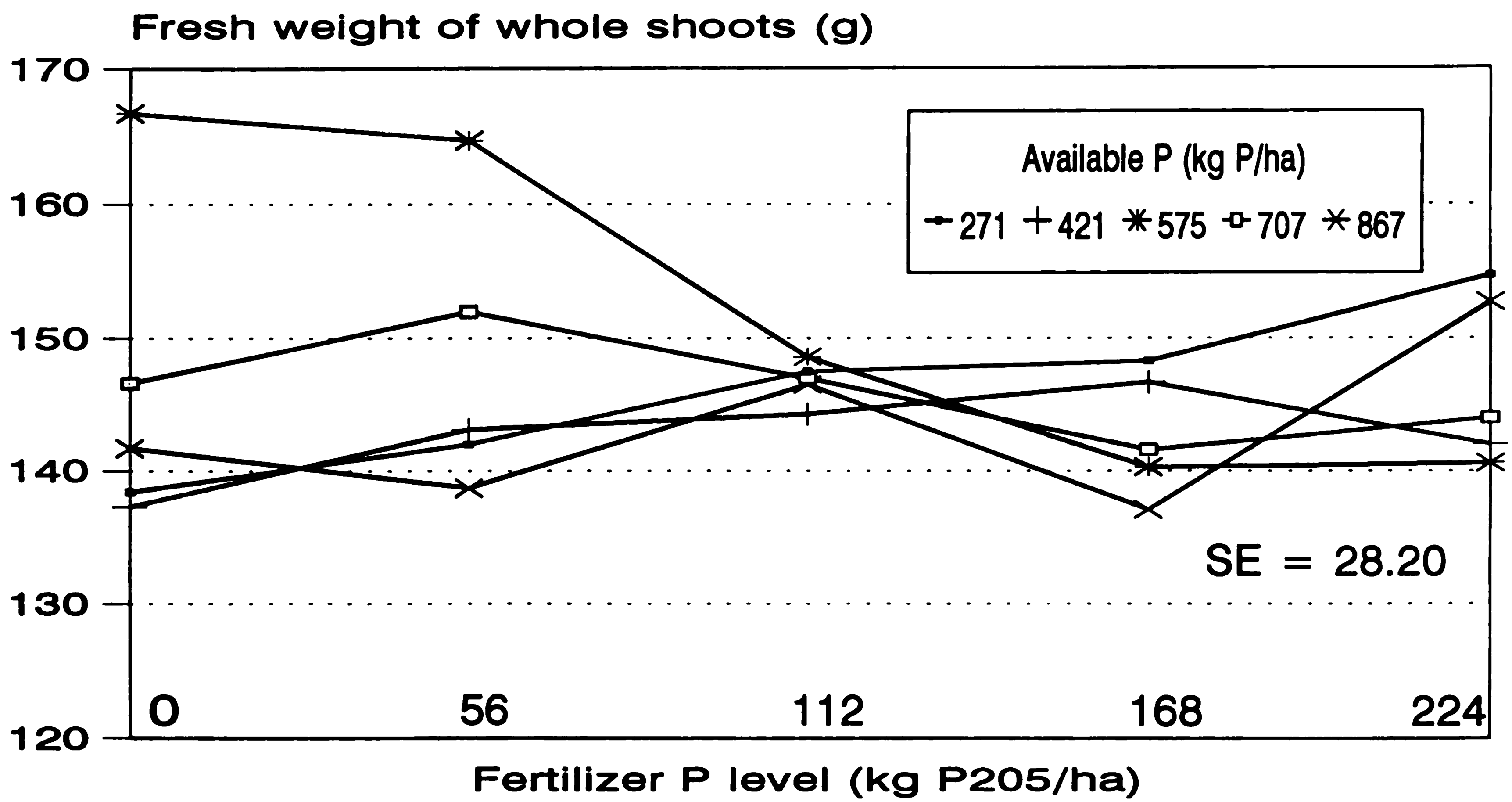

Figure 3.6. Effects of available soil phosphorus levels and residual fertilizer phosphorus on whole shoot fresh weight of greenhouse-grown potato plants grown in McBride sandy loam, 1991.

Table 3.13. Effect of available soil phosphorus averaged over five levels of residual fertilizer phosphorus on dry matter and plant height at harvest production of individual greenhouse-grown potato plants in McBride sandy loam, 1991.

Soil available phosphorus ($kg\ P \cdot ha^{-1}$)	Dry weight (g/plant)		Shoot percent dry wt. (%)	Plant height (cm)
	Stem	Shoot		
241	9.0a[z]	18.4a	12.6b	7.2a
399	9.2a	18.4a	13.0a	7.2a
526	8.9a	18.5a	12.1c	6.8a
669	9.7a	18.9a	13.0ab	8.0a
778	9.1a	18.2a	12.7ab	8.2a
p =	0.16	0.62	0.0004	0.053

[z]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns.

Table 3.14. Effect of residual fertilizer phosphorus averaged over five levels of available soil phosphorus on dry matter production and height at harvest of individual greenhouse-grown potato plants in McBride sandy loam, 1991.

Original fertilizer rate ($kg\ P \cdot ha^{-1}$)	Dry weight (g/plant)		Shoot percent dry wt. (%)	Plant height (cm)
	Stem	Shoot		
0	9.1a[z]	18.3a	12.6a	7.7a
25	9.2a	18.6a	12.6a	7.7a
50	9.2a	18.4a	12.6a	8.1a
75	9.0a	18.5a	13.0a	6.8a
100	9.3a	18.5a	12.6a	7.1a
p=	0.90	0.93	0.29	0.17

[z]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns.

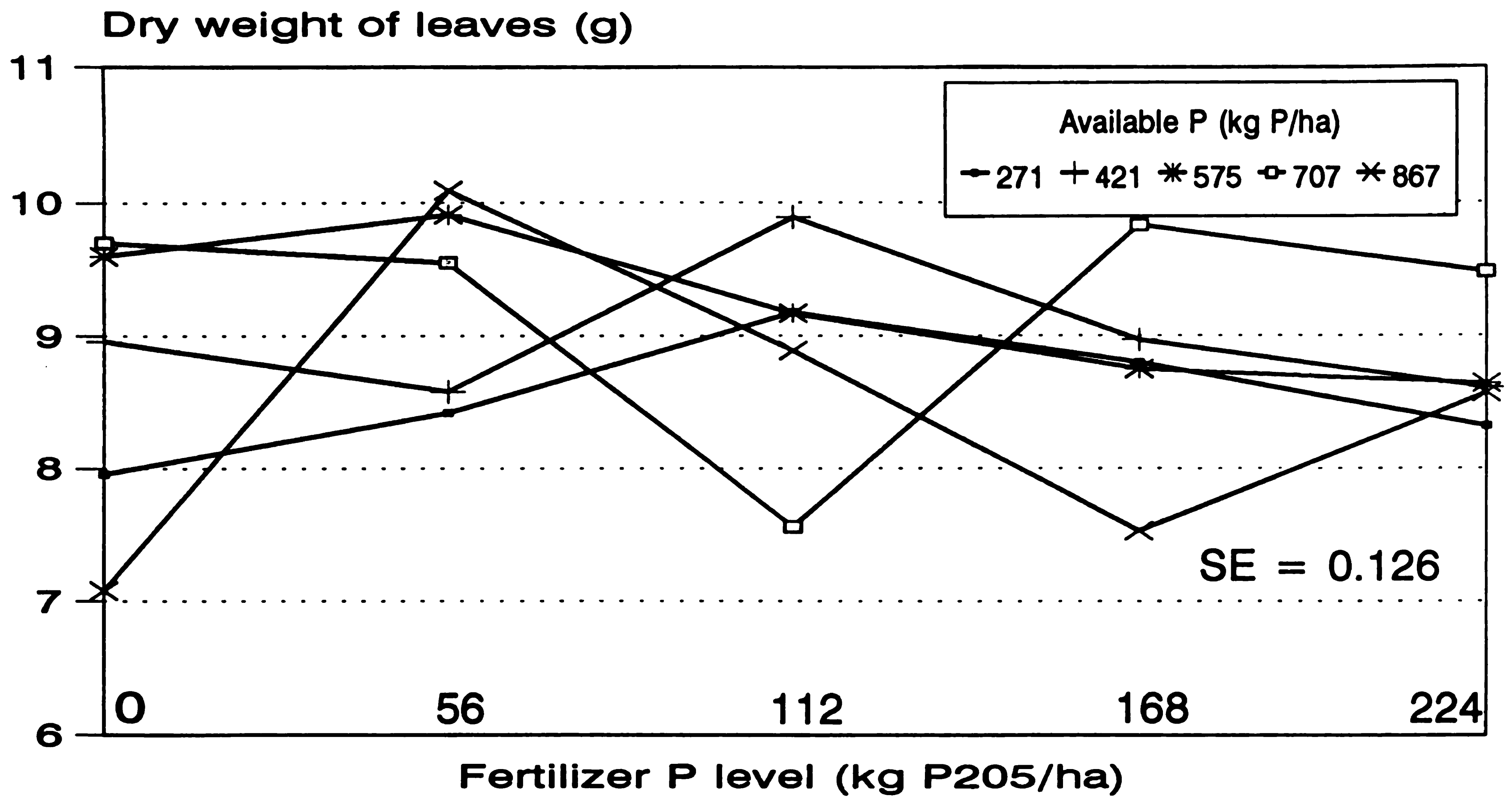

Figure 3.7. Effects of available soil phosphorus levels and residual fertilizer phosphorus on leaf dry weight of greenhouse-grown potato plants grown in McBride sandy loam, 1991.

different among available soil P levels but also followed no discernible trend (Table 3.13). Residual fertilizer P did not affect percent dry weight in the shoots. Potato plant height was unaffected by either P source (Tables 3.13 and 3.14).

Tuber number at the time of harvest was lower with higher levels of available soil P or residual fertilizer phosphorus (Tables 3.15 and 3.16). Data from two replications indicate that potato tuber and rhizome development were influenced by both available soil and residual fertilizer phosphorus (Tables 3.15 and 3.16). Higher residual fertilizer phosphorus levels reduced or delayed tuber initiation and increased rhizome and rhizome tip production. Residual fertilizer phosphorus also delayed or reduced tuber production.

Corn

Corn fresh weights were influenced more by the treatments than were potato fresh weights. Residual fertilizer phosphorus influenced fresh weight production less than available soil phosphorus. Fresh weights of corn leaves (Figure 3.8), stems (Figure 3.9) and whole shoots (Figure 3.10) were influenced by both previous season's available soil P level and residual fertilizer P. The yield of each shoot component was lowest when grown in the 271 kg

Table 3.15. Effect of available soil phosphorus averaged across five levels of residual fertilizer phosphorus on tuber and rhizome characteristics of greenhouse-grown potato plants in McBride sandy loam, 1991[z].

Original available phosphorus (kg $P \cdot ha^{-1}$)	Number of tubers	Number of rhizomes	Number of tubers + rhizome tips	Tuber fresh weight (g)	Tubers, rhizomes, recovered roots fresh weight (g)
241	3.2a[y]	5.6bc	10.2ab	17.7a	42.2a
399	2.7ab	4.6c	7.7b	19.0a	36.1a
526	3.4a	5.7abc	11.8a	20.5a	38.1a
669	2.8ab	6.4ab	12.3a	18.9a	35.5a
778	2.2a	7.1a	14.2a	21.4a	46.3a
p =	0.048	0.024	0.035	0.93	0.11

[z]Data are means of two replications, except for number of tubers which are of 5 replications.
[y]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns.

Table 3.16. Effect of residual fertilizer phosphorus averaged across five levels of available soil phosphorus on tuber and rhizome characteristics of greenhouse-grown potato plants in McBride sandy loam, 1991[z].

Original fertilizer rate ($kg\ P \cdot ha^{-1}$)	Number of tubers	Number of rhizomes	Number of tubers + rhizome tips	Tuber fresh weight (g)	Tubers, rhizomes, recovered roots fresh weight (g)
0	3.9a[y]	6.3a	15.3a	20.8ab	46.4a
25	3.1ab	6.6a	9.8b	16.3b	33.2b
50	2.3c	5.1a	7.8b	29.4a	44.5a
75	2.6bc	5.5a	11.5ab	15.1b	33.9b
100	2.3c	5.9a	11.8ab	16.7b	40.2ab
p=	0.0003	0.26	0.013	0.030	0.019

[z]Data are means of two replications, except for number of tubers which are of 5 replications.

[y]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns.

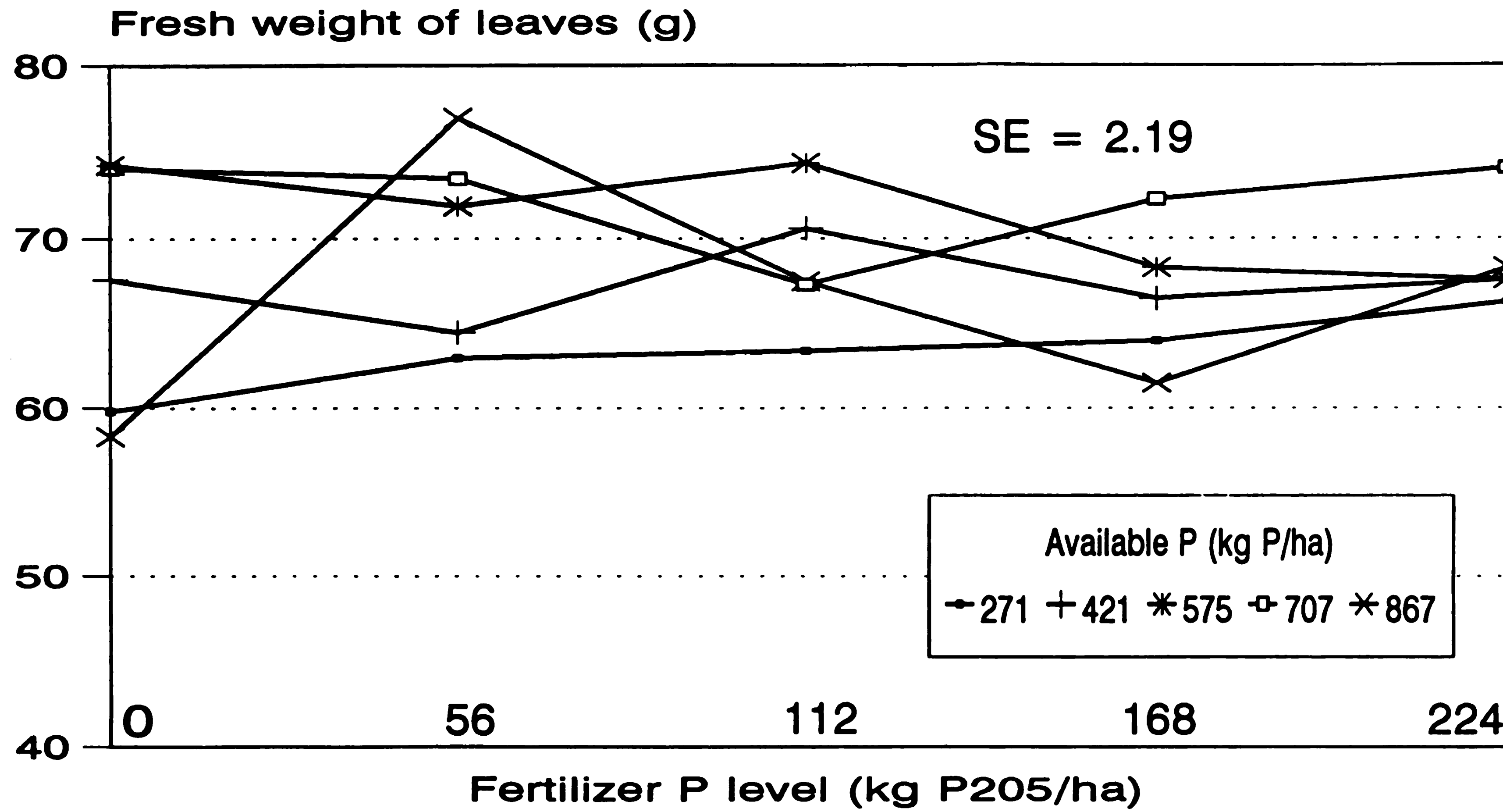

Figure 3.8. Effects of available soil phosphorus levels and residual fertilizer phosphorus on leaf fresh weight of greenhouse-grown corn plants grown in McBride sandy loam, 1991.

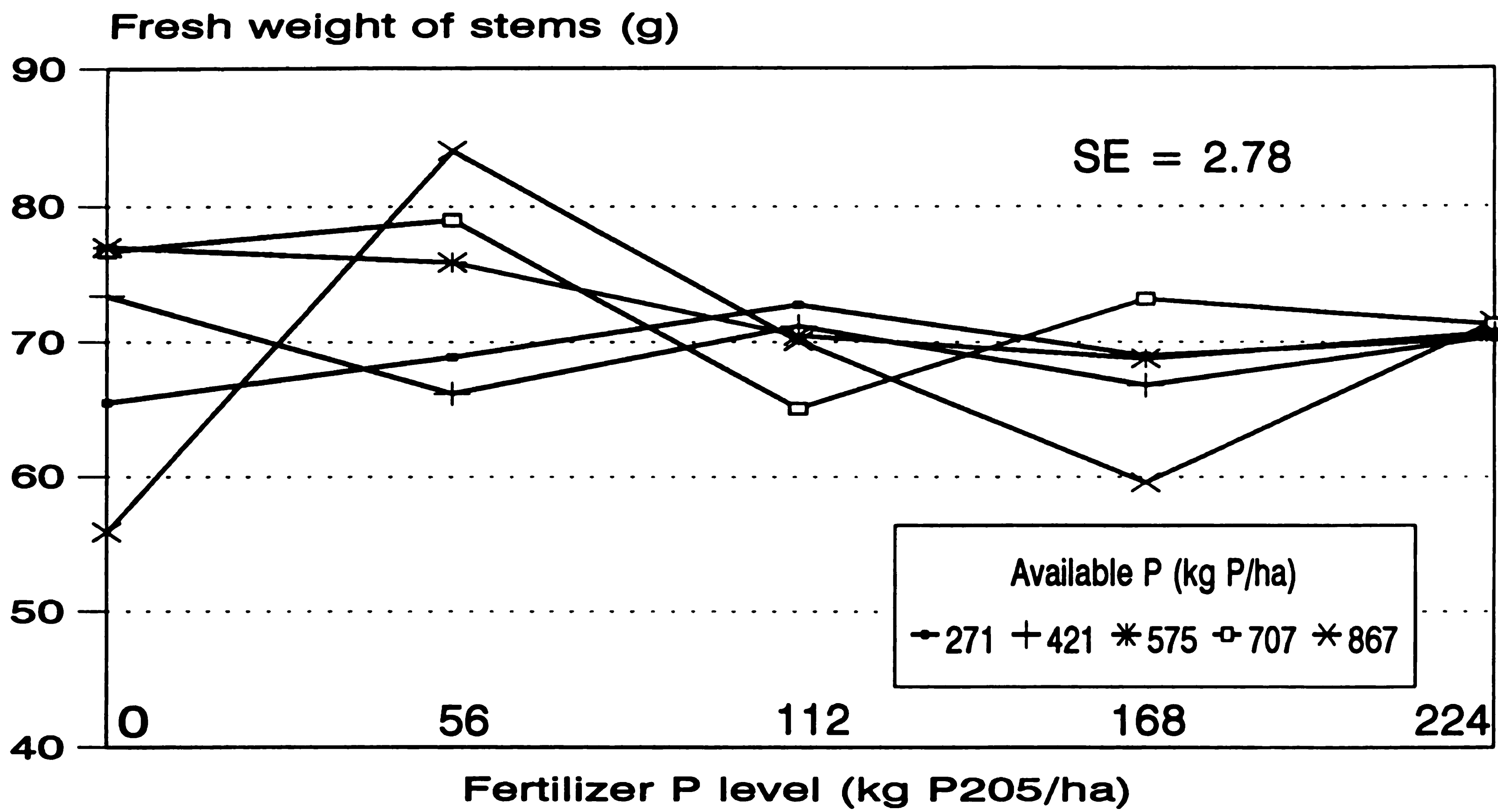

Figure 3.9. Effects of available soil phosphorus levels and residual fertilizer phosphorus on stem fresh weight of greenhouse-grown corn plants grown in McBride sandy loam, 1991.

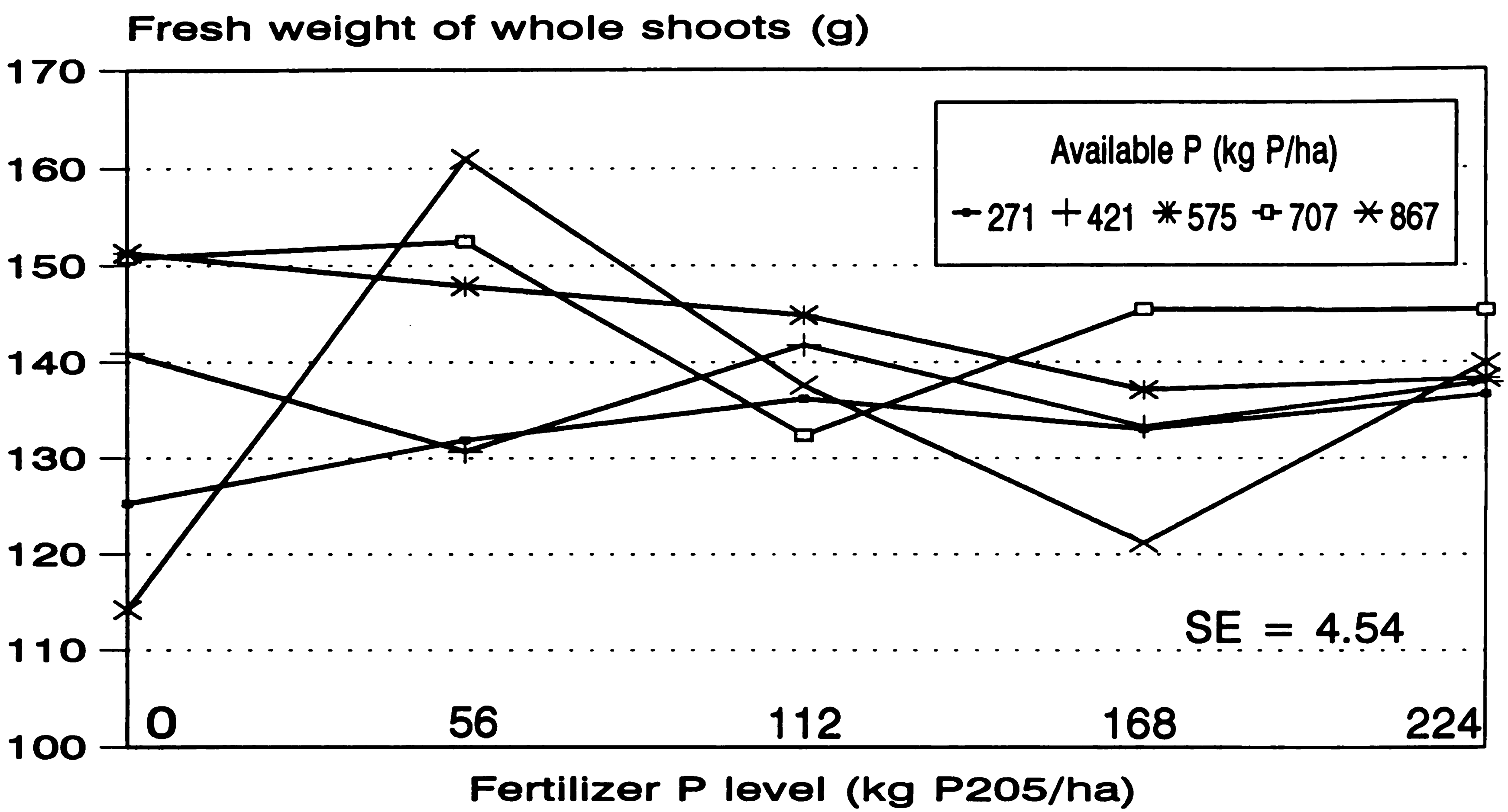

Figure 3.10. Effects of available soil phosphorus levels and residual fertilizer phosphorus on whole shoot fresh weight of greenhouse-grown corn plants grown in McBride sandy loam, 1991.

$P \cdot ha^{-1}$ soil and was increased slightly by the presence of residual fertilizer P. In the four higher available P soils, yields were influenced less consistently by residual fertilizer P and follow no discernable pattern.

Measured shoot physical characteristics, including corn stem height to the top-most ligule, number of visible ligules, and number of leaves were unaffected by treatment (Tables 3.17 and 3.18). Data from the four extreme treatments show that leaf area, specific leaf weight (g/cm^2) and mean leaf size were unaffected by either phosphorus source (data not shown).

Corn shoot dry weight characteristics were influenced much more by interactions of the available soil and residual fertilizer phosphorus than was potato shoot dry weight, for which there were no significant interactions. Leaf (Figure 3.11), stem (Figure 3.12), and total shoot (Figure 3.13) dry weight, as well as percent dry matter in the shoots (Figure 3.14) were greatest in the intermediate treatments.

Discussion

These experiments have shown that fertilizer applications influence potato growth and yield on high phosphorus McBride sandy loam. It has also been shown that early season corn growth can be influenced by residual

Table 3.17. Effect of available soil phosphorus averaged over five levels of residual fertilizer phosphorus on shoot characteristics of greenhouse-grown corn plants in McBride sandy loam, 1991[z].

Soil available phosphorus (kg $P \cdot ha^{-1}$)	Number of visible ligules	Number of leaves	Stem height[y] (cm)
241	18.9a[x]	30.0a	92.2a
399	18.8a	29.8a	88.6a
526	19.1a	30.3a	91.2a
669	19.0a	30.4a	87.1a
778	19.0a	30.3a	90.4a
p =	0.95	0.20	0.17

[z]Data are means from totals of three plants grown in each pot.
[y]Heights measured to youngest visible ligules.
[x]Means followed by different letters are significantly different (by LSD) at $p < 0.05$ level, within columns.

Table 3.18. Effect of residual fertilizer phosphorus averaged over five levels of available soil phosphorus on shoot characteristics of greenhouse -grown corn plants in McBride sandy loam, 1991[z].

Original fertilizer rate ($kg\ P \cdot ha^{-1}$)	Number of visible ligules	Number of leaves	Stem height[Y] (cm)
0	18.8a[x]	30.0a	90.7a
25	19.3a	30.3a	92.1a
50	19.3a	30.3a	87.8a
75	18.6a	30.0a	88.5a
100	19.0a	30.3a	90.7a
p =	0.09	0.67	0.23

[z]Data are means from totals of three plants grown in each pot.
[Y]Heights measured to youngest visible ligules.
[x]Means followed by different letters are significantly different, by LSD, at $p < 0.05$ level, within columns.

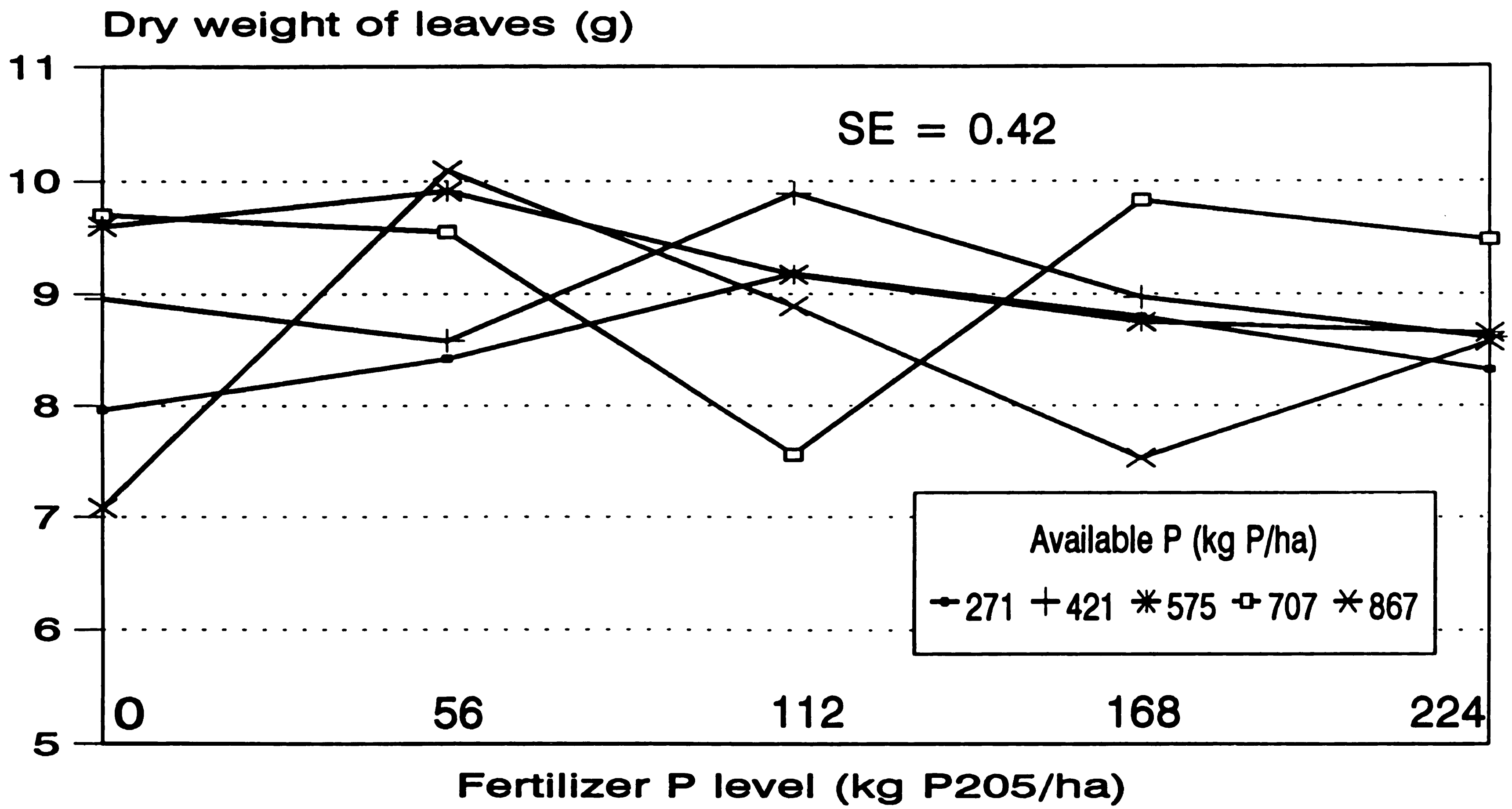

Figure 3.11. Effects of available soil phosphorus levels and residual fertilizer phosphorus on leaf dry weight of greenhouse-grown corn plants grown in McBride sandy loam, 1991.

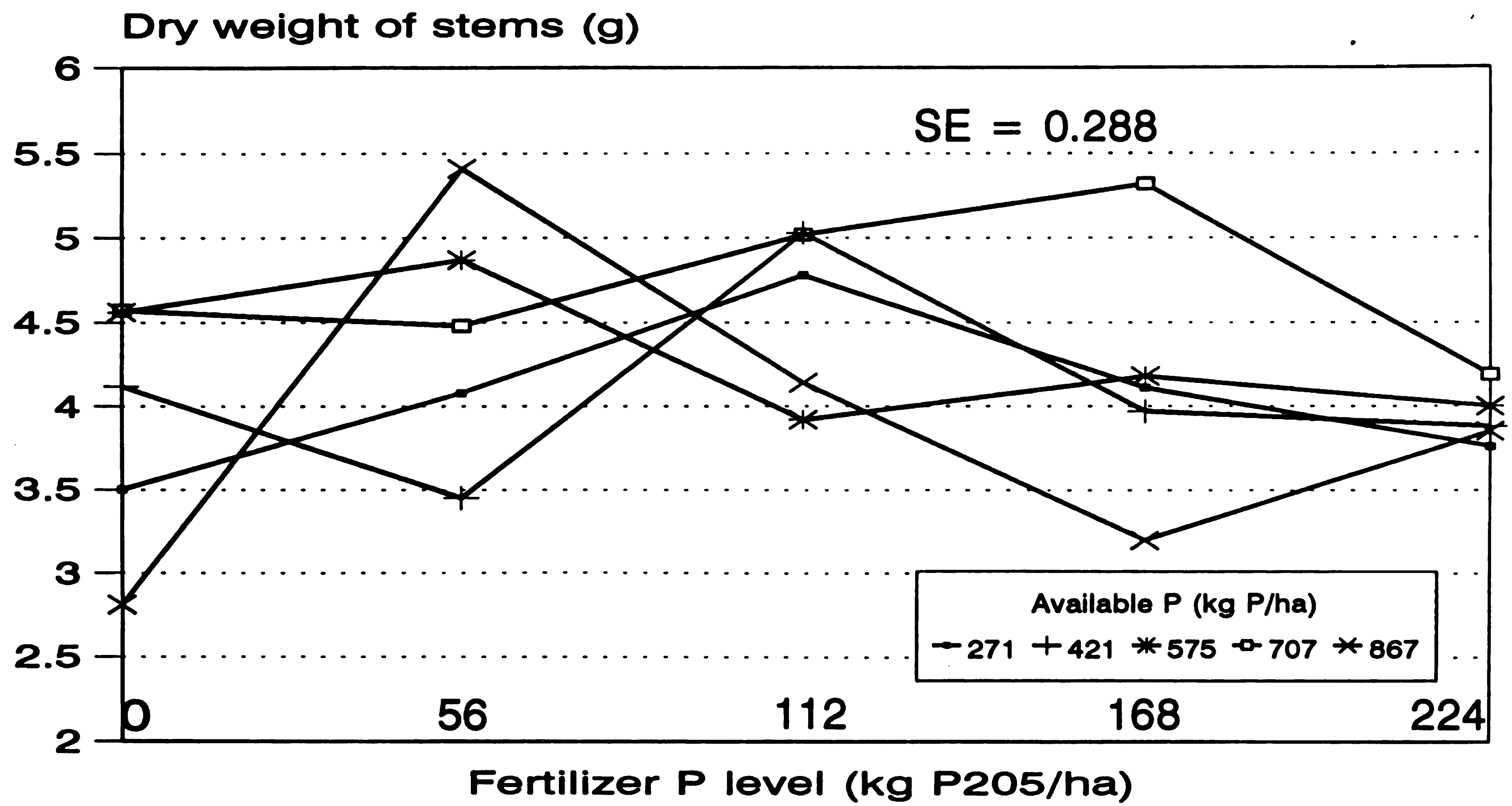

Figure 3.12. Effects of available soil phosphorus levels and residual fertilizer phosphorus on stem dry weight of greenhouse-grown corn plants grown in McBride sandy loam, 1991.

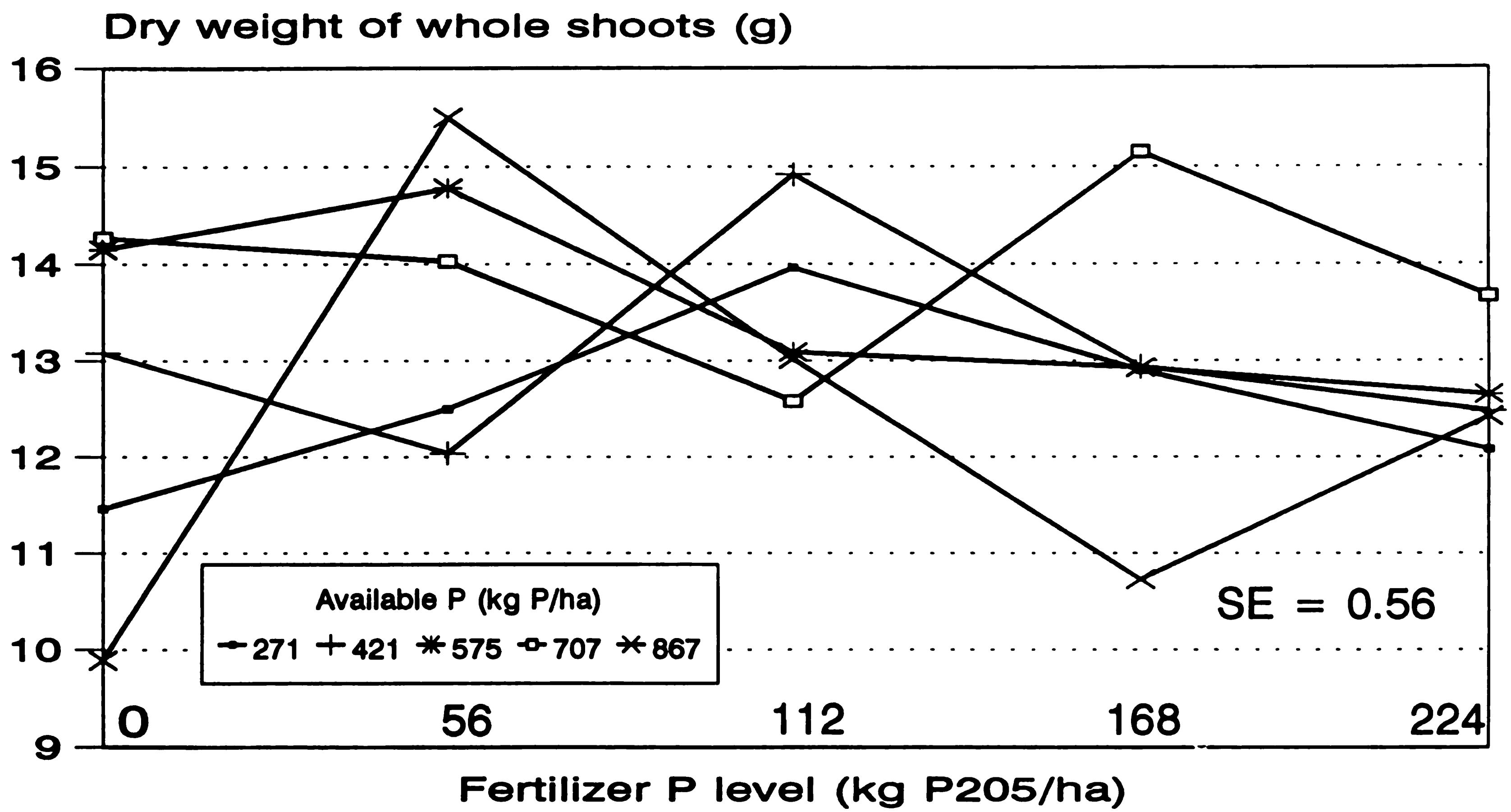

Figure 3.13. Effects of available soil phosphorus levels and residual fertilizer phosphorus on whole shoot dry weight of greenhouse-grown corn plants grown in McBride sandy loam, 1991.

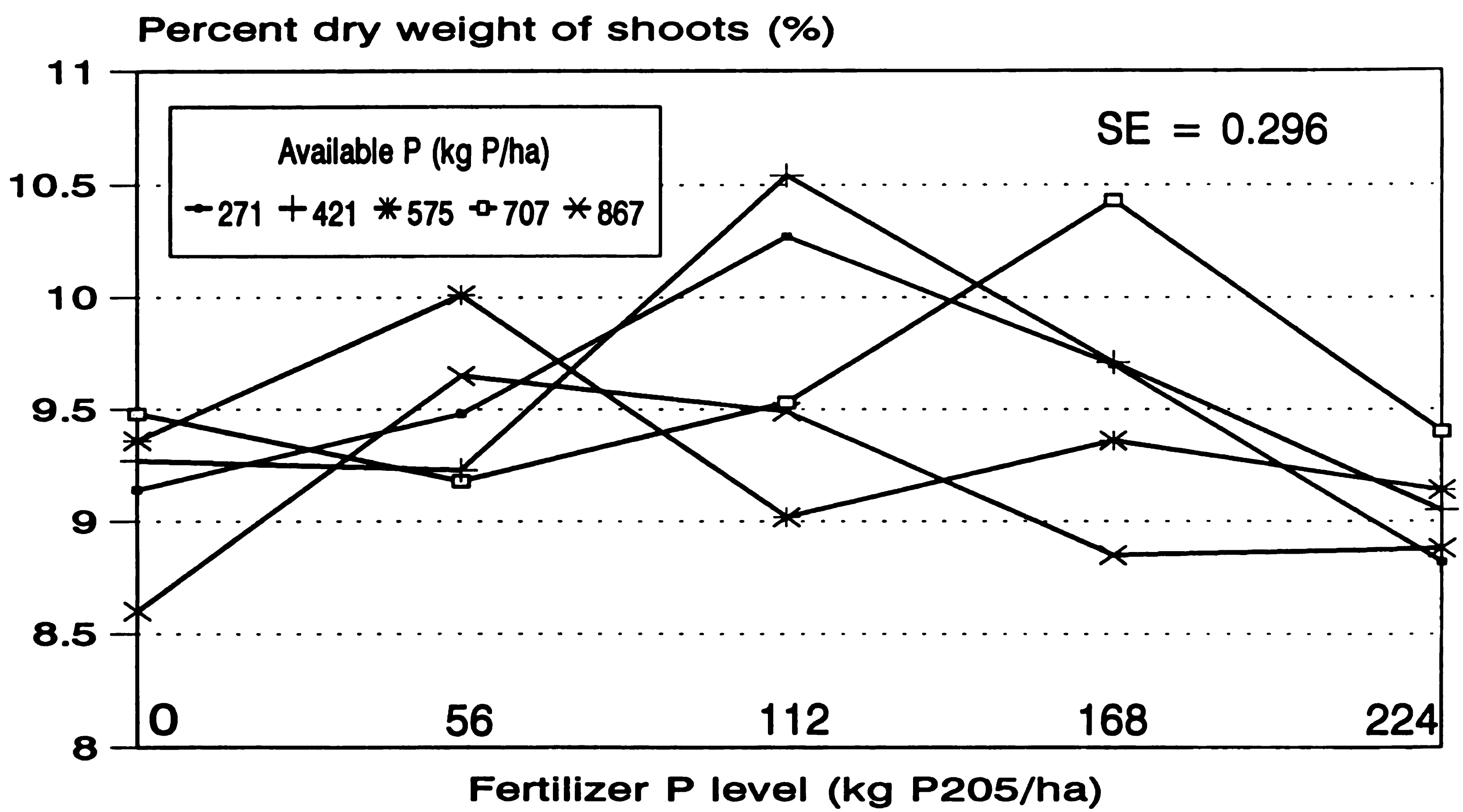

Figure 3.14. Effects of available soil phosphorus levels and residual fertilizer phosphorus on percent dry weight in shoots of greenhouse-grown corn plants grown in McBride sandy loam, 1991.

fertilizer phosphorus on soils with 271 kg available P·ha^{-1}. These results support the need for continued P fertilization of potatoes in McBride sandy loam. They also support the need for research into the phosphorus uptake efficiency in potato as well as investigations of potato root growth patterns. Before discussing these points, two other findings, which interfered with complete interpretation of the data, need to be addressed.

In the 1990 field experiment, the responses to available soil phosphorus could not be determined because of verticillium wilt in the plots with the lower phosphorus soils. Plants growing in the lower P soil with the high disease pressure produced reasonable yields with > 50 kg P·ha^{-1} banded phosphorus applications. The foliage of those plants receiving no banded phosphorus became severely necrotic by mid-season (Malcolmson scale = 2, from Cruickshank, et al., 1982), whereas the foliage of plants receiving applications of 50 kg P·ha^{-1} or more banded phosphorus was only slightly damaged (Malcolmson scale = 7, 8 = no visible disease symptoms or signs). Davis, et al. (1990) have reported similar effects of phosphorus fertilizer on disease development. In their work, Russet Burbank plants receiving band application of 120 or 240 kg P·ha^{-1} had lower rates of infection when inoculated with *Verticillium dahliae* than those not receiving fertilizer phosphorus. It is inferred from these results that even if no yield responses are found from fertilizer phosphorus in soils testing high in available phosphorus, continued band application of phosphorus may provide a measure of plant protection and thus more stable yields over time.

During 1991, the apparent negative influence of available soil phosphorus on tuber specific gravity may have been an artifact caused by a higher extractable potassium concentration in the higher phosphorus soil used. In 1990, available soil phosphorus did not influence specific gravity. In neither season did banded phosphorus influence specific gravity levels. This leaves something in the 1991 soils as the cause of the specific gravity changes observed in 1991. The idea that potassium may have influenced tuber specific gravity in the 1991 experiment has strong support in the literature. Neither Ohms, et al. (1977), in Idaho, nor Vitosh (1979), growing potatoes in the McBride sandy loam soil in Michigan, found changes in tuber specific gravity due to phosphorus fertilizer application. Dubetz and Bole (1975) have shown clearly that of nitrogen, phosphorus and potassium, only applications of potassium, as muriate of potash, influenced tuber specific gravity. In their lysimeter work, in a soil with 336 ppm (8.6 mM) exchangeable K and 12 ppm (387μM) B-K P1 phosphorus, an application of 372 kg $K \cdot ha^{-1}$ produced Netted Gem (i.e. Russet Burbank) tubers with specific gravities averaging 1.093 versus 1.099 for those not receiving any potassium.

They found no differences in yields or tuber size due to potassium, supporting the conclusion that differences in yield parameters found in the present work are not likely due to difference in soil potassium. As for corn responses to potassium in the greenhouse experiment, these are likely of little importance also. Peck and MacDonald (1989) have shown that sweet corn responds much more to residual fertilizer phosphorus than to residual potassium.

Yield increases due to banded phosphorus application were clear and profound in each year of the field experiment. Banded phosphorus strongly influenced total tuber yield and number when averaged across all available soil phosphorus levels. Neither available soil nor banded phosphorus had a significant influence on yield and average size of tubers weighing <110 g (data not shown). Yields and numbers of tubers reaching more than 110 g in weight were significantly increased by banding phosphorus, although the percentage of large tubers was not significantly improved by phosphorus application. Within each available soil phosphorus level one sees some influences of banded phosphorus on total and large tuber yield. One also sees differences in tuber numbers within the lower two available soil phosphorus levels. Combining the 1990 and 1991 data reinforces the conclusion that banded phosphorus applications continue to be important for maximum potato growth and yield in McBride sandy loams with extractable phosphorus contents of over 400 kg $P \cdot ha^{-1}$.

The research of McCollum (1978) produced results quite similar to those presented here. In McCollum's work, phosphorus fertilizer was applied at one of three rates to potatoes growing in soils whose phosphorus levels were artificially changed. Three years prior to the experiment, phosphorus was applied at three rates to a fine sandy loam, creating three soil phosphorus levels. As in the experiments discussed here, McCollum reported greater yield increases from higher fertilizer P rates than from higher soil P levels.

In 1991, plants growing in the fumigated soils were not influenced by disease and the effects of both available soil and banded phosphorus were determined. The available soil phosphorus interacted with the banded phosphorus, as expected, to cause the observed differences in yields. Only banded phosphorus appeared to influence tuber phosphorus concentrations, implying that current season's banded phosphorus may be more plant available than B-K 1 available soil phosphorus in the McBride soil. This idea is supported by the general concepts of soil phosphorus chemistry and several field experiments reported in the literature. Many field experiments have indicated that most phosphorus accumulated by potatoes, especially early in the season, is taken up from fertilizer rather than available soil sources (e.g. Grunes, et al., 1958). For phosphorus to be taken up, it must be in solution in ionic form, as either $H_2PO_4^-$ or HPO_4^-. In the McBride soil, banded phosphorus will be solubilized into solution and much of it will be influenced by reactions with iron, forming iron phosphates and strengite (Yerokun, 1987), which are only slowly soluble (Lindsay, 1979). Extensive work by Juo (1966) indicated that the available phosphorus in many Michigan soils is influenced strongly by aluminum phosphates. The author reported that fertilizer phosphorus was first incorporated into calcium phosphates in the sand fraction of several acid soils from Michigan. These fractions later react to form aluminum and iron phosphates which then control the soil solution phosphorus. In soils, any phosphorus that remains in solution moves very slowly through the soil solution, diffusing less than 0.01cm/day (Foth and Ellis, 1988). Thus a band of phosphorus fertilizer should provide a relatively large (2 or 3 cm/day versus the diffusion distance of <0.1 cm/day) area of concentrated $H_2PO_4^-$ in the soil solution for developing roots. Roots growing outside the band will find far lower $H_2PO_4^-$ concentrations which will not be replenished quickly. For some species (e.g. grasses), the size and efficiency of root systems can make up for the limited amount of phosphorus in solution. For potatoes this does not appear to be the case because of a relatively small root system which appears unable to adequately utilize the relatively low $H_2PO_4^-$ concentrations throughout the soil.

The responses of corn and other grain crops to phosphorus has been thought to be less extreme than those of potato and many vegetable crops. Data from the 1991 field and greenhouse studies show that early shoot growth of both corn and potato was affected more by banded phosphorus than by available soil phosphorus. In the 1991 field experiment, plants receiving 50 kg $P \cdot ha^{-1}$ or more banded phosphorus, had more leaves and were taller at flowering (12 July) than those receiving less banded phosphorus (Tables 3.11 and 3.12). In the greenhouse experiment, effects of residual fertilizer and available soil phosphorus were less pronounced. No significant effects on potato shoot growth were observed (Tables 3.15 and 3.16). The middle treatments of residual fertilizer (25, 50, and 75 kg $P \cdot ha^{-1}$) and available soil phosphorus (421, 575, and 707 kg $P \cdot ha^{-1}$) produced corn plants with larger dry weights than the lowest or highest phosphorus treatments (Figure 3.13). Clark and Brown (1973) found that dry matter production by corn plants growing in solution culture was higher in plants growing in 1 or 4 ppm P solutions than in solutions with lower phosphorus concentrations. Dry matter production was not significantly different in the 4 ppm solution or the 1 ppm solution. Caldwell (1960) found that corn took up between 2 and 66% of its phosphorus from fertilizer, depending on the sources and ratios of nitrogen and phosphorus used. Nelson, et al. (1947), working with three soils of the same series but at four locations, found the percent of plant phosphorus derived from current season fertilizer was greater in corn than in potato at the first of three sampling dates. During two subsequent samplings, corn was found to take up a lower percentage of its phosphorus from fertilizer than potato did. In potato, the percentage of plant phosphorus taken up from fertilizer declined slightly over the three sampling dates while that of corn declined markedly from over 50 % at 30 DAP to around 20 % at 103 DAP. The corn began the season absorbing more of its phosphorus from fertilizer than did any other crop (cotton and tobacco were also evaluated) and finished the season with the lowest percent phosphorus from fertilizer. This point is important in discussion of the 1991 greenhouse experiment because Nelson, et al. found no difference in corn grain yields among phosphorus treatments. Early growth of potato and final tuber yield were both improved by phosphorus fertilizer in their work. It is likely that our greenhouse results mirror their findings, with corn exhibiting early responses to residual fertilizer phosphorus which probably would not have changed final yield as the corn roots grew and gained access to greater amounts of available soil phosphorus. As for potatoes in the greenhouse experiment, it is likely that the increased early growth of the plants growing in soil blends with greater amounts of available soil and residual fertilizer phosphorus would have continued throughout the season resulting in higher tuber yields than those of plants without access to residual fertilizer phosphorus.

The question to ask next is whether or not root system growth and size are the only characteristics controlling the ability of each crop to efficiently take up available soil phosphorus. Potatoes have a smaller root system than corn. If potatoes are as efficient at phosphorus uptake as corn, the potato plant cannot take up the same amount of phosphorus per root system because of size limitations. Corn plants grown in solutions by Jungk, et al. (1990) had higher phosphorus uptake rates per unit length of root than soybeans grown in similar solutions. This implies either (1) corn plants need more phosphorus per length of root than soybeans; (2) they are more prone to luxury consumption, or (3) they are simply more efficient at acquiring available phosphorus than are soybean roots are. In the greenhouse experiment reported here, growth of young corn plants was increased more by residual fertilizer phosphorus than was growth of young potato plants. This seems to support the idea that corn plants may be more efficient than potatoes at acquiring and using available soil solution phosphorus. Sharma, et al. (1968), after studying phosphorus/zinc interactions, reported that tomatoes were much more responsive to fertilizer phosphorus than corn. In both tomatoes and corn, phosphorus applications increased shoot growth much more than root growth. They also reported the two crops were much more responsive to fertilizer phosphorus when zinc was also applied, raising the possibility that interactions of phosphorus with soil micronutrients such as aluminum and iron, prevalent in the McBride soil, may significantly influence potato responses to fertilizer phosphorus.

Each soil has a unique phosphorus supplying and buffering system. Almost all natural soils are low in plant available phosphorus. When crops are put under cultivation, their responses to phosphorus vary greatly from one soil to another. The critical level of soil test extractable phosphorus has been one way to categorize the value of fertilizer phosphorus for crop production in specific soils. Grewal and Singh (1976) reported strong correlations between soil available phosphorus and potato yield responses to fertilizer phosphorus. The soils they used were loamy sands and sandy loams in India, with Olsen's extractable (available) phosphorus concentrations of up to 48 kg $P \cdot ha^{-1}$. They determined the critical available phosphorus level averaged over all tested soils was under 30 kg $P \cdot ha^{-1}$. But yields increased even when the available phosphorus exceeded the recommended critical level. Field studies reported in the previous chapter had similar results, with banded phosphorus causing tuber yield increases in soils thought not to require phosphorus applications for production of most crops. The yield increases reported by Grewal and Singh (described by a quadratic equation) began to diminish as available P increased but did not approach zero as soil available P reached 48 $kg \cdot ha^{-1}$. The authors claimed, however, that no economical yield increases could be expected in soils testing above the critical P level of 30 $kg\ P \cdot ha^{-1}$. The critical level of available phosphorus in the McBride sandy loam appears to fall somewhere between 200 and 900 $kg\ P \cdot ha^{-1}$, perhaps in the 300 to 500 $kg\ P \cdot ha^{-1}$ range, based on the total yield data from the 1991 field experiment.

Dean, et al. (1947) evaluated responses of crops to phosphorus fertilizer in light of available soil phosphorus. They found that the percentage of phosphorus derived from fertilizer in potato plants varied with application rate and method, as well as with soil phosphorus content. The percentage of phosphorus derived from fertilizer was greater in tubers than in leaves. Unfortunately, the three soils the researchers used were very different from one another and the data probably should only be discussed within each soil. As one might expect, ryegrass, a crop thought to have a great ability to explore the soil for nutrients, exhibited great differences in the percentage of phosphorus derived from fertilizer among the Evesboro sand, Caribou silt-loam, and Davidson clay loam tested. Ryegrass took up adequate phosphorus in the phosphorus-rich silt loam. Giroux, et al. (1984) reported a strong correlation between soil-test available phosphorus (extracted with 0.03N NH_4F + 0.1N HCl) and potato yields from plants growing in 24 different soils with available phosphorus levels from 44 to 1000 kg $P \cdot ha^{-1}$. With this many soils, they clearly showed a strong correlation which can be discussed despite the differences in other soil factors among the soils. The authors found one soil with 71 kg $P \cdot ha^{-1}$ available phosphorus that produced 90 % of the top yields and one testing at 279 kg $P \cdot ha^{-1}$ available phosphorus that only produced 60 % of the highest yield. Their main conclusion was as much as 25 kg $P \cdot ha^{-1}$ fertilizer phosphorus should be applied to soils testing up to 400 kg $P \cdot ha^{-1}$ available phosphorus.

Conclusions

Results of the three experiments reported here support the need for continued phosphorus applications to McBride sandy loam containing up to 600 kg extractable $P \cdot ha^{-1}$. In both years of the field studies tuber yields were increased by applications of phosphorus. In 1990, total yield was increased by phosphorus applications in the 241 and 526 $kg \cdot ha^{-1}$ soils. In 1991, across all available soil phosphorus levels, applications of phosphorus increased total and marketable yields and, for the period studied, increased shoot vigor. Data from the greenhouse experiment indicate that early growth of the potato and corn crops are influenced by phosphorus applications during a preceding season. This implies conversion of fertilizer phosphorus to the less soluble phosphorus fractions which make up much of what the Bray-Kurtz P1 soil test indicates is available for plants. The studies did not answer questions about potato root system size and phosphorus uptake kinetics. These questions must be answered before a complete solution to the problem of potato phosphorus fertilization can be answered.

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CHAPTER 4

PHOSPHORUS UPTAKE BY SIX POTATO CULTIVARS

Introduction

Uptake of phosphorus by plant roots is controlled by plant needs, availability of phosphorus (P) and the ability of roots to access available P. Potato yields can be increased by applying phosphorus even if soil test P levels are above a level at which P fertilizer is not recommended for many crops (Foth and Ellis, 1988). In Michigan, potatoes are often grown on sandy, acidic soils. The plants respond to fertilizer P on these soils even when soil tests indicate more than 300 kg $P \cdot ha^{-1}$ is available (Vitosh, 1979). Either these soil tests are not accurately measuring available P or potato plants are less able to acquire available soil P than are many other crops.

Most soils contain between 200 to 5000 ppm total phosphorus, with the average concentration being 600 ppm (Lindsay, 1979). These values are lower than those for nitrogen and potassium, but higher than for most secondary and micronutrients. In soil solution, phosphorus concentrations range from less than 0.32μM to 258μM (Foth and Ellis, 1988), 1.61μM being the most frequently reported concentration in U.S. soils (Barber, 1984). Plants take up most of their phosphorus as $H_2PO_4^-$ (Marschner, 1986), the predominate ionic form in most soils where pH is under 7

(Foth and Ellis, 1988). Because most Michigan soils used to grow potatoes have pHs below 7, solution phosphorus is likely to be in a form suitable for uptake. The amount of P in solution can be limited in these soils, however, because of their unique chemistry. Metal oxides and hydroxides, either free in solution or adsorbed to clay surfaces, can adsorb and release P as solution P levels change. In soils with pHs below 5.5, which include some Michigan potato soils, iron and aluminum can precipitate with P more than at higher pHs. Precipitated P is less easily brought back into solution than P that is simply adsorbed to iron and aluminum oxides and hydroxides (Ellis, personal communication).

In addition to the soil factors adversely influencing P availability, plant related factors limit the ability of potatoes to acquire P. Potatoes may require larger amounts of phosphorus fertilizer than that which may be required by other crops. As an example, Foth and Ellis (1988) list fertilizer recommendations of no more than 44 kg $P \cdot ha^{-1}$ for several agronomic crops. However, the authors list 85 kg $P \cdot ha^{-1}$ as the top recommended amount for potatoes. The Michigan State University Cooperative Extension Service recommends up to 39 kg $P \cdot ha^{-1}$ be applied to potato crops (Christenson, 1992). Even 8.7 kg are recommended to be applied to potato soils testing 600 kg $P \cdot ha^{-1}$ (Vitosh, 1990), despite the crop removing less than 30 kg $P \cdot ha^{-1}$ in reported field trials (McCollum, 1978). The potato plant's need for phosphorus fertilizer at high soil test phosphorus levels and its low phosphorus removal relative to soil test levels may indicate an insufficient uptake rate, inefficient allocation of phosphorus within the plant, and/or an inability of the potato plant's root system to adequately explore the soil for phosphorus.

Most phosphorus moves to the root by diffusion, rather than by mass flow or root interception (Barber, et al., 1963). This means the size of the root system (both in length and surface area) is very important in phosphorus uptake. Uptake of phosphorus results in rapid depletion of phosphorus from the soil around plant roots (e.g. Bhat and Nye, 1973, in *Brassica rapa*), implying that root extension throughout the season is important. Root to shoot ratio (R:S) can indicate the relative efficiency of a plant's root system. A smaller ratio implies greater efficiency in shoot dry matter production per unit of root. In solution culture, Cogliatti and Clarkson (1983) reported R:S ratios (dry weight basis) in potatoes of 0.23 to 0.38, with the ratio increasing (due to less shoot growth) with prolonged exposure to zero phosphorus solutions. This implies that plant development was altered by the presence or absence of P. For comparison, Maizlich (1980) reported corn (*Zea mays* L.) R:S ratios in flowing culture of 0.33 to 1.47, depending on N rate and time of sampling. The ratio generally declined over time and with increasing nitrogen concentration in solution. The lower ratios found in potato may indicate greater efficiency of P uptake and/or utilization than in corn.

Phosphorus uptake rates may differ among potato cultivars. Differences in phosphorus uptake rates within species have been reported in corn (Baligar and Barber, 1979) and barley (Nielsen and Schjorring, 1983), among others. In other species, authors have reported similar nutrient uptake kinetics among cultivars. Teo, et al. (1992) reported no differences in phosphorus uptake kinetics (K_m, C_{min}, and I_{max}) among three rice cultivars. Gardiner and Christensen (1990) found no differences in phosphorus uptake rate between two wheat cultivars they tested. Based on the diverse morphology among cultivars, it is likely that there are differences in R:S ratio, phosphorus uptake rate and phosphorus utilization efficiency among potato cultivars.

Knowing Michigan potatoes are grown in soils which may be unable to maintain adequate solution P concentrations and that potatoes are more responsive to fertilizer phosphorus than are other crops, experiments were designed to investigate phosphorus uptake rates in potatoes grown at P concentrations likely to be encountered under field conditions. The objective of these experiments was to determine phosphorus uptake rates in several potato

cultivars at several initial solution phosphorus concentrations.

Materials and Methods

Preliminary Experiment with cv. Russet Burbank

On 27 July 1989, thirty stem-tip cuttings were taken from field-grown Russet Burbank potato plants, trimmed to 8 cm and 4 or 5 leaves, and placed in aerated 1/10 strength modified Hoagland's solution (based on Hoagland and Arnon, 1950) (Table 4.1) for rooting in the Michigan State University Plant and Soil Sciences Greenhouses. The nutrient sources were as described by Hoagland and Arnon, except iron was supplied with Sequestrene 138Fe, sodium ferric ethylenediamine di-(o-hydroxyphenylacetate). Greenhouse light levels averaged 800 $\mu mol \cdot m^{-2} \cdot sec^{-1}$. On 14 August, the cuttings were moved to a controlled environment chamber with a mean light level of 173 $\mu mol \cdot m^{-2} sec^{-1}$ and 16 h days. Temperatures were 24 C days and 15 C nights. Each of twenty selected cuttings were placed into 1800 ml of one of the following solutions: 100, 50, 25 or 12.5 μM P in 1/10 modified Hoagland's solution (1/10 MH). This resulted in five replications and four treatments in a randomized complete block design. Solution volumes were maintained by periodic additions of like solution. On 17 August, the solutions were sampled. Twenty milliliter samples of the culture solutions were drawn at 800 h, and every four hours

Table 4.1. Nutrient concentrations and sources used in 1/10 strength Hoagland's[z] nutrient solution for potato phosphorus uptake studies.

Nutrient	Concentration (μM)	Sources
Nitrogen	1500	$Ca(NO_3)_2 \cdot 4H_2O$ and KNO_3
Phosphorus	100	KH_2PO_4
Potassium	600	KH_2PO_4 and KNO_3
Calcium	500	$Ca(NO_3)_2 \cdot 4H_2O$
Magnesium	200	$MgSO_4 \cdot 7H_2O$
Sulfur	200	$MgSO_4 \cdot 7H_2O$ and $ZnSO_4 \cdot 7H_2O$
Iron	2.5	Sequestrene 138
Manganese	0.91	$MnCl_2 \cdot 4H_2O$
Zinc	0.076	$ZnSO_4 \cdot 7H_2O$
Copper	0.031	$CuSO_4 \cdot 5H_2O$
Boron	4.64	H_3BO_3
Molybdenum	0.01	$H_2MoO_4 \cdot H_2O$

[z]Based on Hoagland and Arnon, 1959.

until 2000 h. Solution samples were stored at 3 C until analyzed for phosphorus content by the molybdate method, using a Lachat QuickChem System IV (Lachat Instruments, Milwaukee, WI) or a Brinkman PC800 (Brinkman Instruments Co., Westbury, NY) colorimeter. On 21 August, a second series of samples was drawn for analysis of solution P concentration. Again, four 20 ml samples were drawn, four hours apart, from each pot. After the fourth sample was drawn, the experiment was terminated and the plants harvested. Shoot and root fresh weights were recorded. Roots were stored at 3 C in a 10% methanol solution until their root lengths were determined using the methods of Tennent (1975). Dry weights of the roots and shoots were determined after drying at 60 C for 24 to 48 h. Root phosphorus concentrations were determined from dried samples. Tissue samples (0.25 g) were ashed at 500 C in a muffle furnace. Ashed samples were digested for 1 h in 3N nitric acid with 1000 ppm lithium from lithium chloride. Digested samples were filtered through Whatmann #2 filter paper and stored in polyethylene vials at 3 C until [P] determination by the molybdate method as described in the previous chapter.

Cultivar Comparison Experiment

The potato cultivars Atlantic, Sebago, Onaway, Russet Burbank, Lemhi Russet, and Norland were grown in the

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Michigan State University Plant and Soil Sciences Greenhouse to determine phosphorus uptake kinetics in aerated solution culture. The selected cultivars represent a wide range of maturities and tuber characteristics (Chase, et al., 1990). Atlantic, Sebago and Onaway produce round white tubers, used for fresh market and producing potato chips. Onaway matures early; Sebago matures late. Atlantic has mid- to late-season maturity. Norland produces red tubers used for fresh market and matures early. Lemhi Russet and Russet Burbank produce long, russetted, white-fleshed tubers used as fresh baking potatoes. Atlantic and Russet Burbank tubers have a high specific gravity making them ideal for processing into an array of frozen products.

Single-eye tuber cores, averaging 10 g each, from each cultivar were set 5 cm deep in pots of acid-washed silica sand for production of rooted shoots. The cores were allowed to sprout in a greenhouse under natural day length and 28 C days and 20 C nights. The sand was watered during shoot production with modified 1/5 strength Hoagland's nutrient solution (1/5 MH), using Sequestrene 138Fe as the iron source (twice the concentrations reported in Table 4.1). When the shoots were 12 to 16 cm tall, individual shoots were pulled from the sand, their roots rinsed in deionized water, and placed in pots containing aerated 1/5 MH. Solution volumes were maintained at 1200 ml -/+ 200 ml through periodic additions of fresh nutrient solution.

After two weeks of growth in solution, the plants were acclimated to their assigned treatment phosphorus levels by replacing the common solution with 1/5 MH containing 1.94, 5.5, 11.3, 22.6, 45.2, or 87.1 μmol $P \cdot L^{-1}$ as KH_2PO_4. At 800 h of the following day, these solutions were replaced with fresh solution of like phosphorus concentration for the uptake study. Solution samples (20 ml) were drawn at 800 h, and every three hours until 1700 h.

At 1700 h, final solution volumes and the fresh weights of whole plants, leaves, and roots were recorded. Leaf areas, including petioles, were determined using a LiCor 3100 Leaf Area Meter (LiCor Inc., Lincoln, Nebraska). Root tissues were rinsed in deionized water and stored in 10 % methanol at 2 C for later length determination using the method of Tennent (1975). Plant tissues were dried for 24 to 48 h at 60 C and their dry weights recorded. Tissue samples (0.25 g) were ashed at 500 C in a muffle furnace. Ashed samples were digested for 1 h in 3N nitric acid with 1000 ppm lithium from lithium chloride. Digested samples were filtered through Whatmann #2 filter paper and stored in polyethylene vials at 3 C until [P] determination colorimetrically by the molybdate method using a Lachat QuickChem System IV (Lachat Instruments, Milwaukee, WI) or a Brinkman PC800 (Brinkman Instruments Co., Westbury, NY) colorimeter.

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All data for Atlantic, Sebago, and Onaway are means of five replications. Norland, Russet Burbank, and Lemhi Russet were tested with three replications. Analyses of variance and regression statistics were calculated using PC-SAS (SAS Institute, 1988).

Results

Preliminary Experiment with Russet Burbank

The solution pH was as much as 0.15 units higher in those solutions with the highest phosphorus concentrations (Table 4.2). Roots were longer and root internal phosphorus concentrations lower in plants growing in solutions containing less phosphorus (Table 4.3). Plants grown in the lower phosphorus solutions also had less dry matter per length of root. Total root dry weight was highest in the plants growing in either 25 or 50 μM phosphorus solutions. Shoot dry weight, total dry weight, and leaf number were not different among treatments (Table 4.4).

Phosphorus uptake rate per length of root was lower in solutions with lower initial phosphorus concentrations (Table 4.2). The relation of initial solution phosphorus concentration to uptake was best described by the equation:

$$\text{P uptake } (\mu\text{mol}\cdot\text{m}^{-1}\cdot\text{h}^{-1}) = 0.567 + 0.0155(\log_n(\text{Initial solution}[\text{P}])),\ R^2 = 0.646.$$

Table 4.2. Phosphorus uptake rate by Russet Burbank potatoes in solution culture, August, 1989.

Initial solution [P] (μM)	Solution pH	Phosphorus uptake rate ($\mu mol \cdot m^{-1} h^{-1}$)
100	7.65a[z]	0.103a
50	7.65a	0.095a
25	7.60ab	0.043b
12.5	7.50b	0.005c

[z]Means followed by different letters are significantly different by LSD, within columns ($p < 0.05$).

Table 4.3. Root characteristics of Russet Burbank potato plants grown in solution cultures with different phosphorus concentrations, August, 1989.

	Plant Characteristic				
Initial Solution [P], μM	Root length (cm)	Root DW (g)	Root DW: shoot DW	Root [P] ($mg \cdot kg^{-1}$)	Specific root mass ($g\ DW \cdot m^{-1}$)
100	3334b[z]	0.229b	0.102a	2183a	0.069a
50	4694ab	0.283ab	0.118a	1471b	0.063a
25	5619a	0.351a	0.135a	1412b	0.063a
12.5	5478a	0.236b	0.122a	1428b	0.043b

[z]Means followed by different letters are significantly different by LSD, within columns ($p < 0.05$).

Table 4.4. Shoot and whole plant characteristics of Russet Burbank potato plants grown in solution cultures with different phosphorus concentrations, August, 1989.

	Plant Characteristic		
Initial Solution [P], ppm	Shoot DW (g)	Leaf Number	Total DW (g)
100	2.29a[z]	12.8a	2.51a
50	2.39a	10.6a	2.67a
25	2.65a	11.4a	3.00a
12.5	1.85a	9.8a	2.08a

[z]Means followed by different letters are significantly different, by LSD, within columns ($P < 0.05$).

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The model R^2 is improved by stepwise addition of a term relating total dry weight of the plants to P uptake. With this term included, the equation becomes:

$$\text{P uptake } (\mu\text{mol}\cdot\text{m}^{-1}\cdot\text{h}^{-1}) = -\ 0.0871 + 0.0143(\log_n(\text{Init Solution[P]})) + 0.0080(\text{Total DW}),\ R^2 = 0.794,$$

where ln (Init solution [P]) is the natural log of the initial P concentration (μM) in solution and DW is the total plant dry weight (grams).

Cultivar Comparison Experiment

Phosphorus uptake rates were dependent on initial solution phosphorus concentration (Table 4.5). Within each solution concentration, the rate of phosphorus uptake for the six cultivars tested was within one order of magnitude, although uptake by Onaway was consistently lower than by the other cultivars. The uptake data has been described graphically in Figure 4.1. In each cultivar, P uptake was higher in solutions with higher initial P solution. Uptake rate did not change linearly over the range of concentrations tested. The difference in uptake rate between any two concentrations was less among the higher concentrations tested than among the lower concentrations tested.

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Table 4.5. Phosphorus uptake by six potato cultivars in solution culture.

Cultivar	Initial solution phosphorus concentration (μM)					
	1.93	5.48	10.97	22.58	45.16	87.10
	Uptake ($\mu mol \cdot m^{-1} \cdot h^{-1}$)					
Atlantic	0.003	0.015	0.046	0.066	0.010	0.121
Sebago	0.009	0.009	0.026	0.047	0.092	0.136
Onaway	0.003	0.004	0.021	0.015	0.031	0.097
Norland	0.008	0.016	0.025	0.072	0.155	0.244
Rus. Burbank	0.017	0.034	0.062	0.083	0.182	0.240
Lemhi Russet	0.012	0.022	0.044	0.073	0.260	0.307

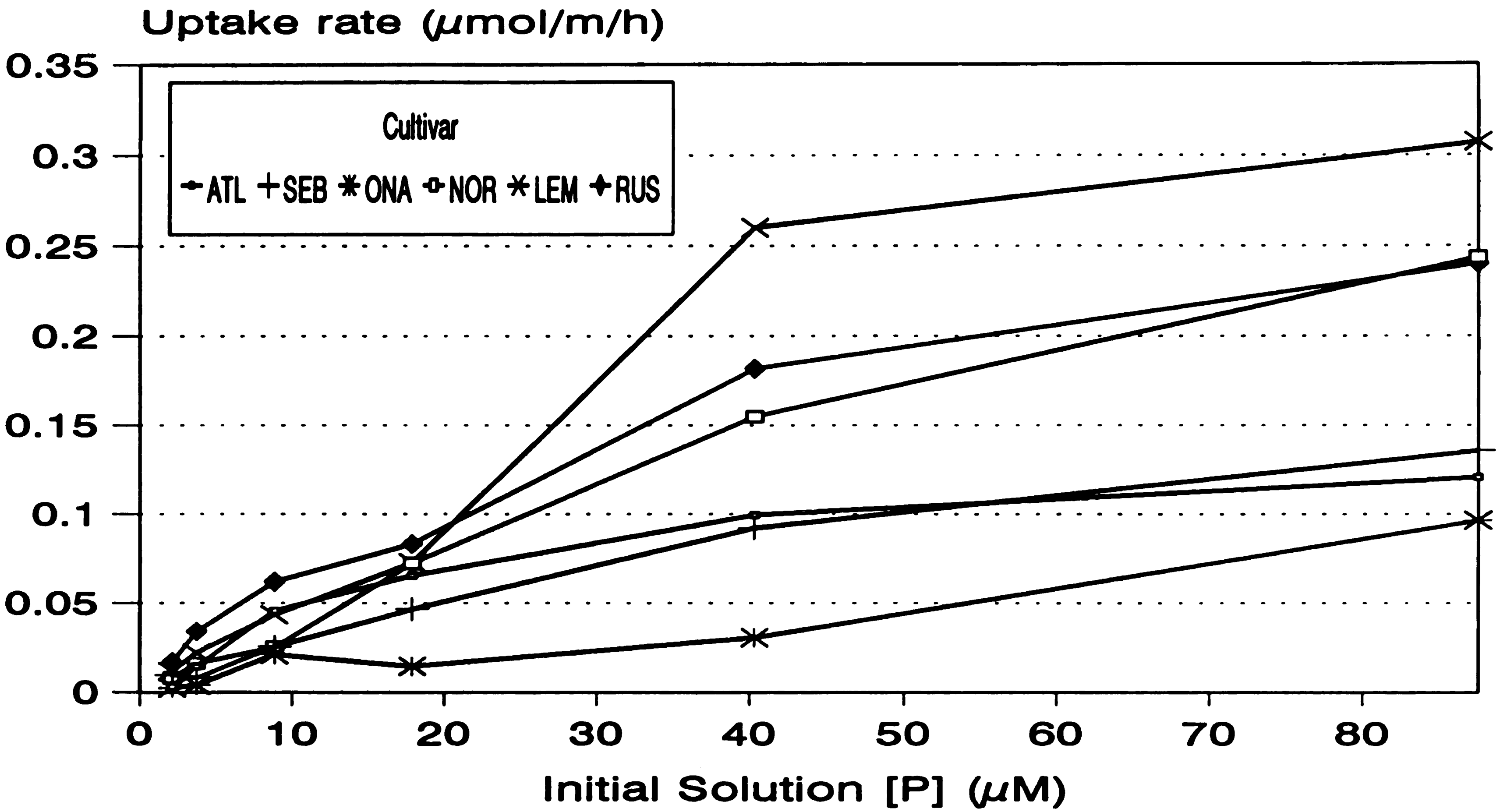

Figure 4.1 Phosphorus uptake by six potato cultivars in solution culture.

Lineweaver and Burk (1934) developed a way to linearize enzyme kinetic data, a method which is applicable to nutrient uptake data as well. The Lineweaver-Burk plot, as the method has come to be known, shows the inverse of substrate concentration plotted versus the inverse of product production. In phosphorus uptake experiments, the substrate is solution phosphorus and the product is P removal from solution per unit of root. For the cultivar comparison experiment, it is assumed that all P no longer in solution is taken up by plant roots. Lineweaver-Burk plots are most useful when a single product is produced by a single enzyme. In other situations, the plots can be nonlinear. Competition, temperature, and enzyme type can all cause nonlinearity. Lineweaver-Burk plots also show the maximum rate of reaction (V_{max}) as the inverse of the y-intercept. The substrate concentration at which the reaction is at 1/2 V_{max}, designated K_m, is found by taking the negative of the inverse of the x-intercept. In uptake experiments V_{max} is often written as I_{max} denoting influx of substrate rather than velocity of enzymatic activity. The K_m is useful for comparing the relative affinity of an enzyme for a substrate. In terms of uptake, K_m can indicate the relative affinity of membrane bound carriers for the ion being taken up. A lower K_m indicates more affinity for the ion. A higher I_{max} can indicate relatively large amounts of active carrier present in the roots.

When data for all treatments were plotted using the Lineweaver-Burk method a distinctly nonlinear pattern resulted (data not shown). The nonlinear pattern is more clearly illustrated in a plot of the natural log of initial P concentration versus P uptake (Figure. 4.2). For all cultivars, except Atlantic the curves appear to have two distinct regions, one for the three or four lowest concentrations and another for the three highest concentrations. This implies that the uptake kinetics of P in these potato cultivars are characterized by something other than a single, linear uptake mechanism easily described by Lineweaver-Burk plots. Plots of all data resulted in negative K_m and I_{max} values. If data from only the three greatest concentrations were used, the plots were much closer to linear (Figures. 4.3-4.8). K_m and I_{max} values calculated from these plots were also positive for most cultivars (Table 4.6). These K_m and I_{max} values are high compared to those previously reported for Russet Burbank potato (Cogliatti and Clarkson, 1983).

The minimum solution P concentration needed for uptake was calculated from the regression of all concentrations versus P uptake (Table 4.6). They are slightly above the lowest concentrations employed in the experiment and were subject to large error. The inability to clearly define C_{min} occurred with all cultivars. A partial explanation may

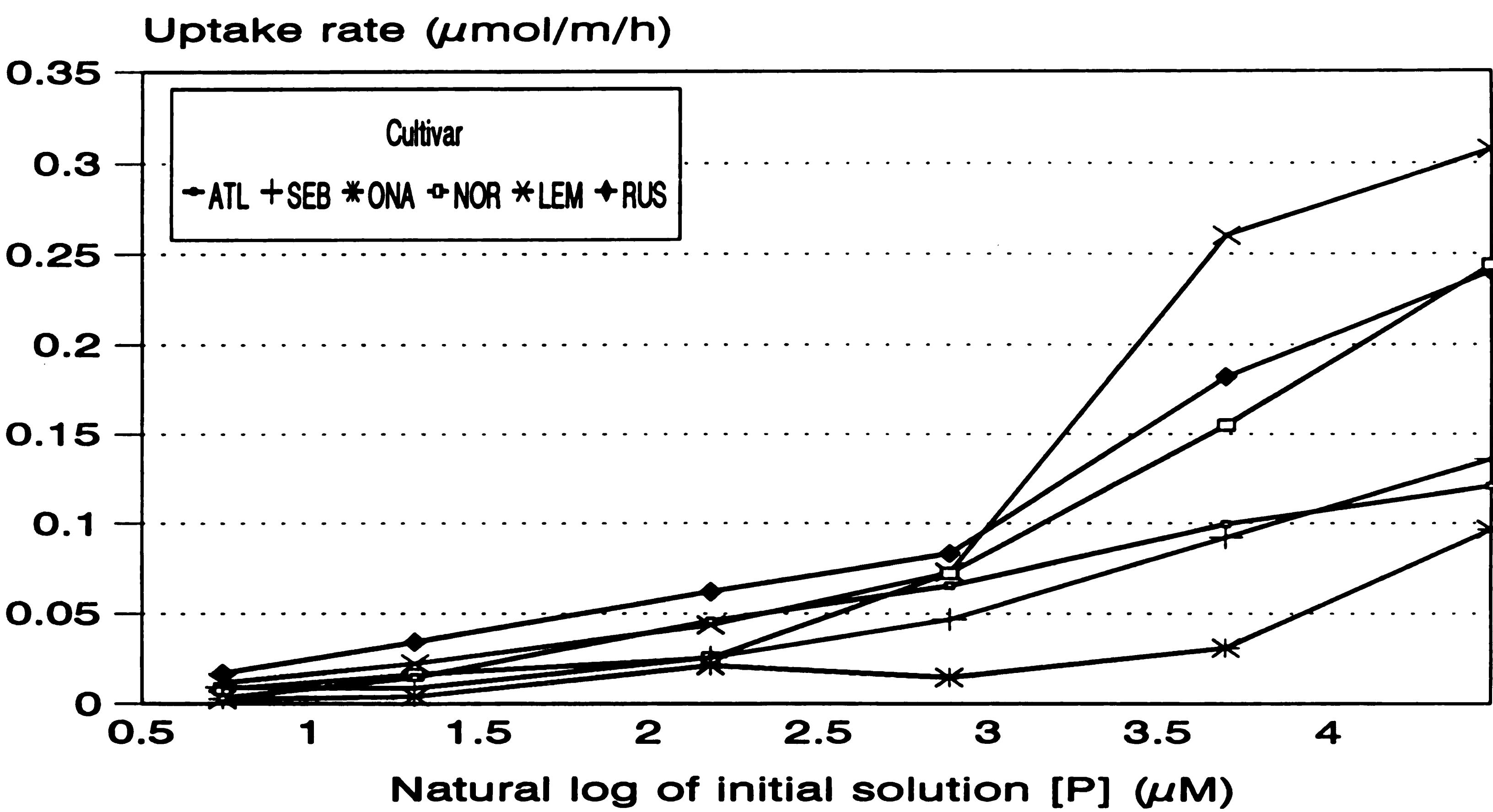

Figure 4.2. Phosphorus uptake by six potato cultivars in solution culture.

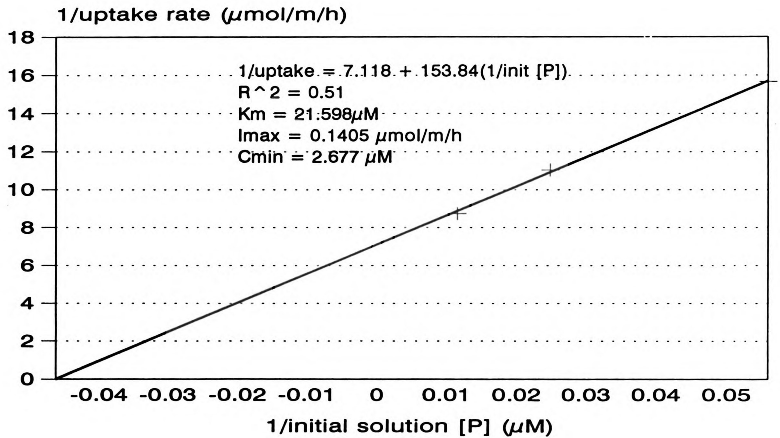

Figure 4.3. Phosphorus uptake by cv. Atlantic.

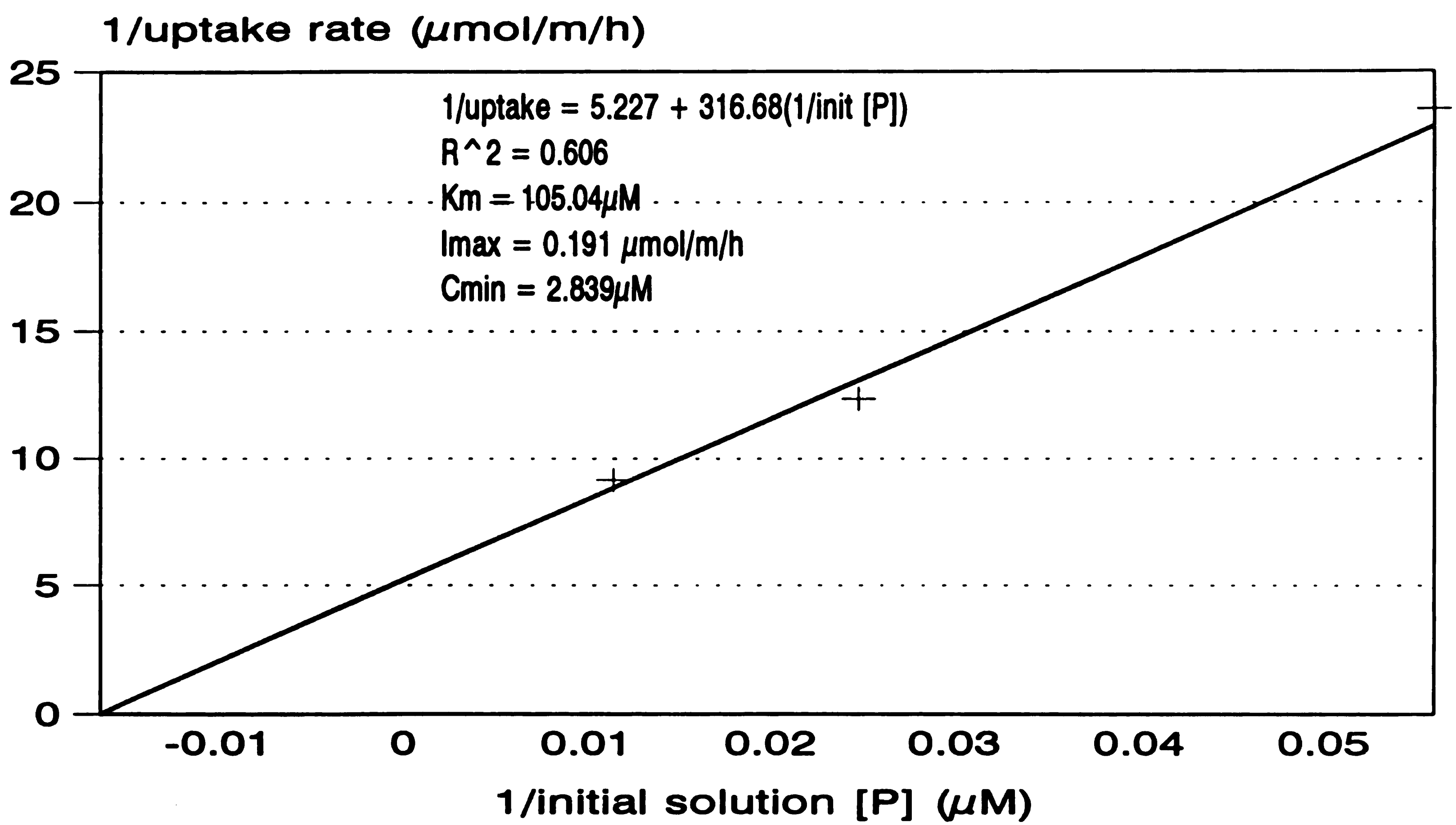

Figure 4.4. Phosphorus uptake by cv. Sebago.

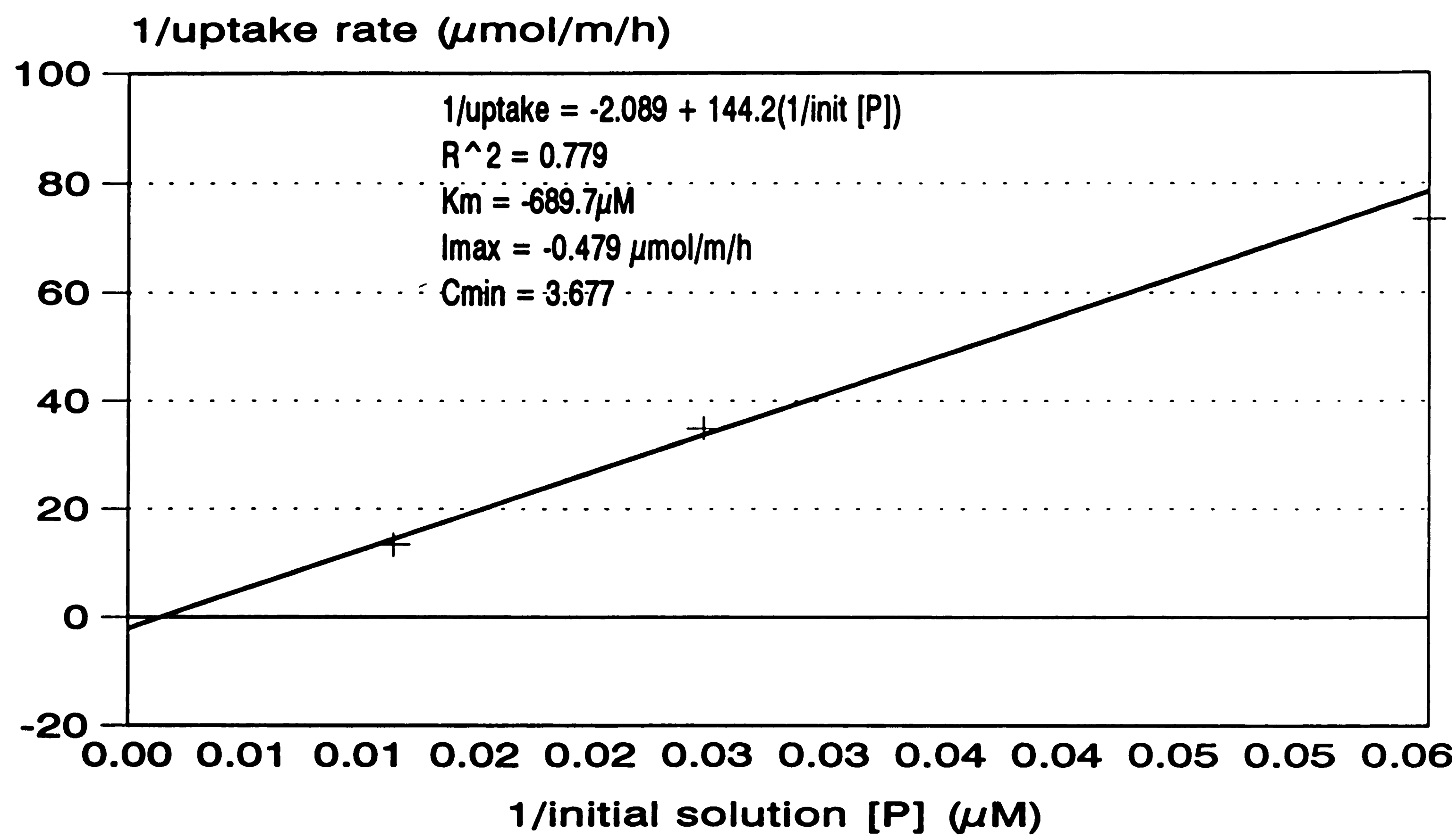

Figure 4.5. Phosphorus uptake by cv. Onaway.

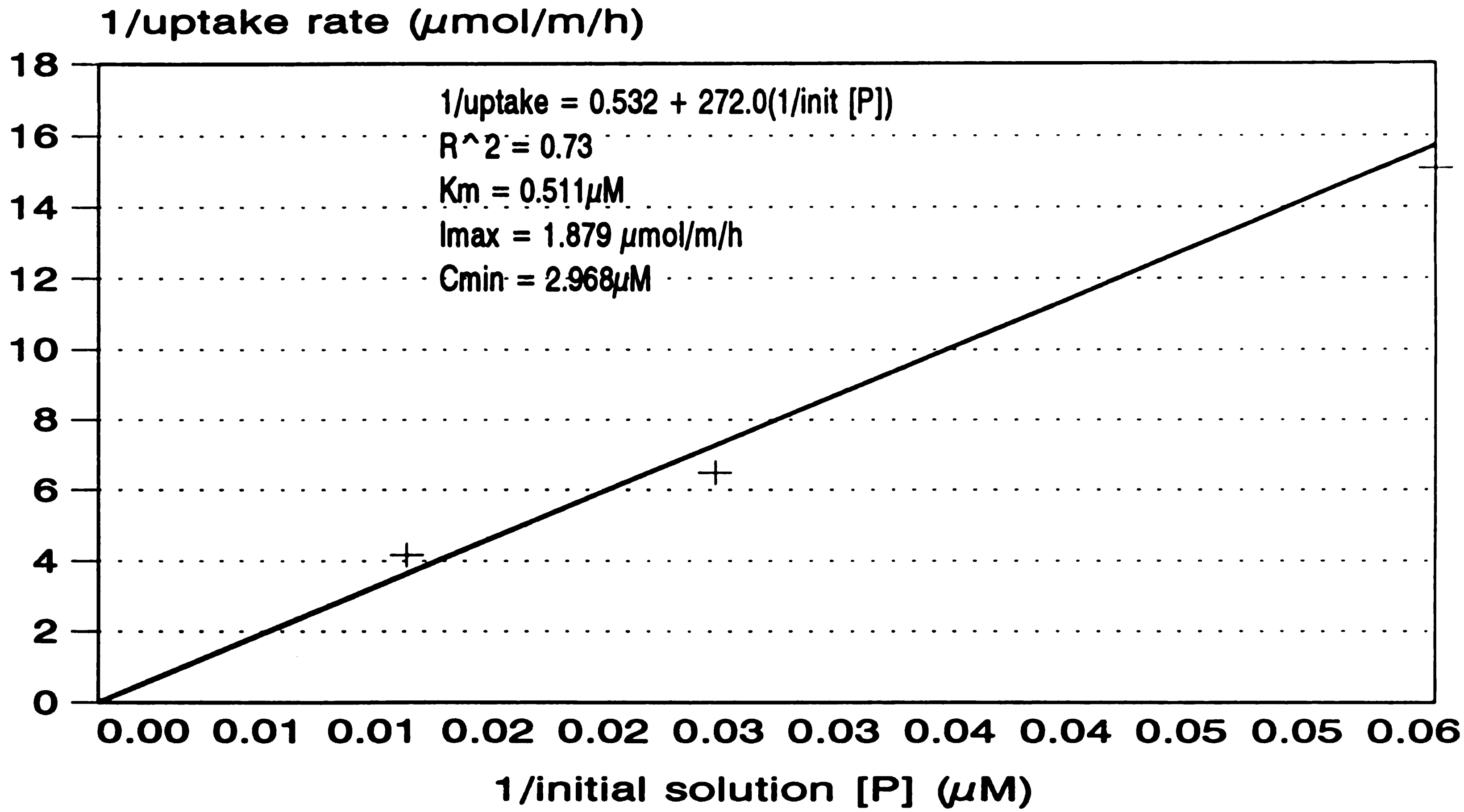

Figure 4.6. Phosphorus uptake by cv. Norland.

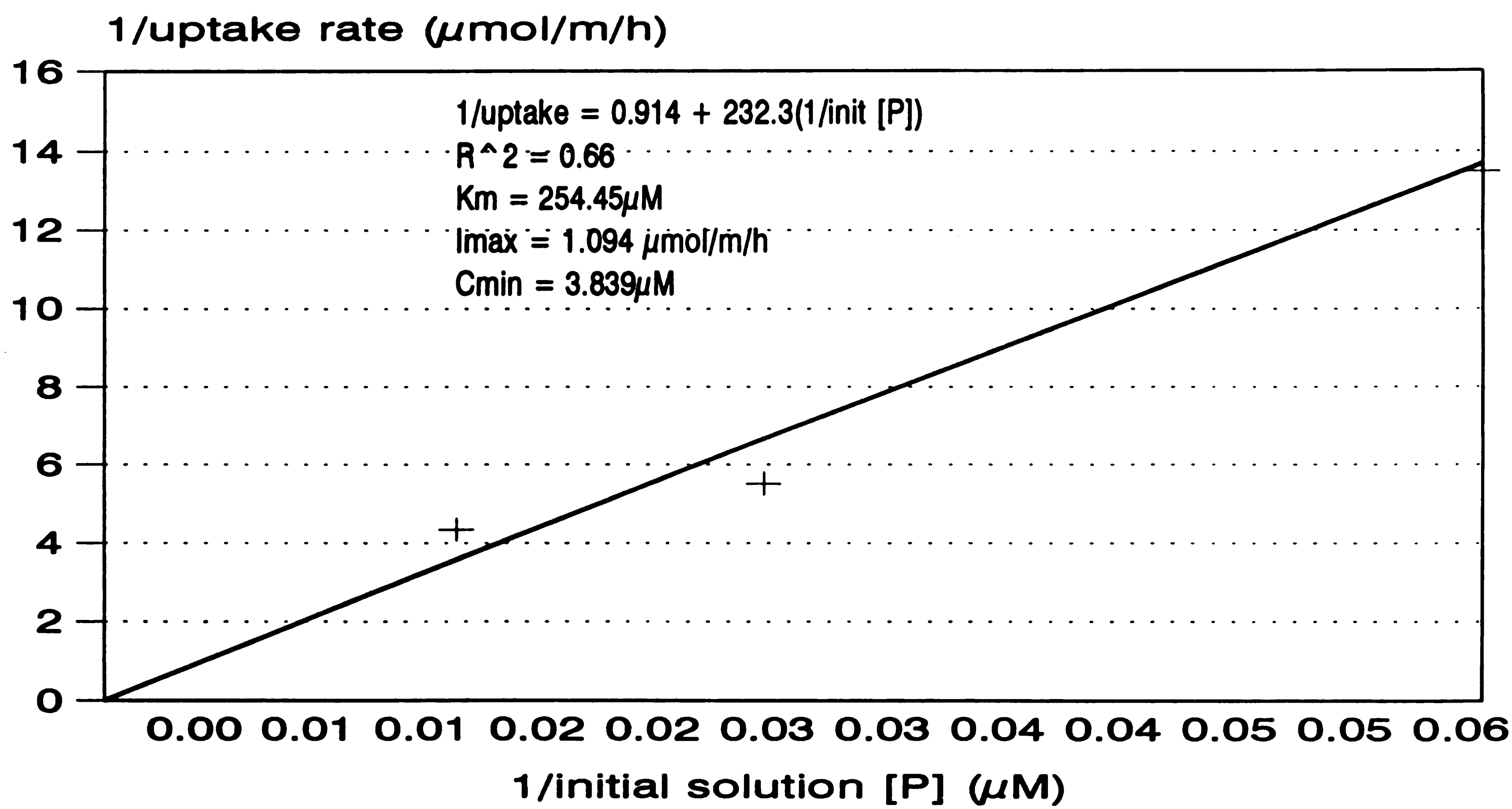

Figure 4.7. Phosphorus uptake by cv. Russet Burbank.

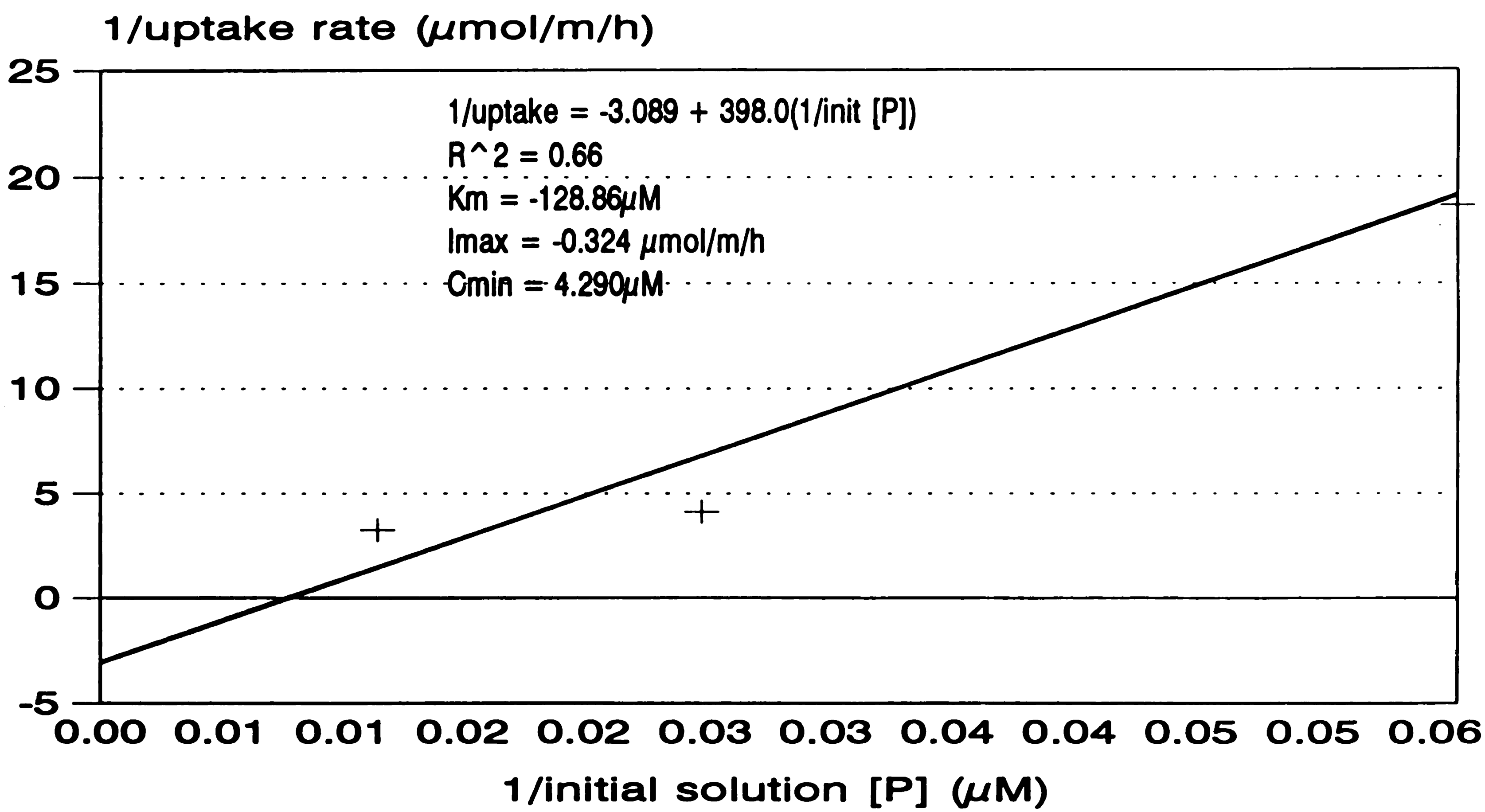

Figure 4.8. Phosphorus uptake by cv. Lemhi Russet.

Table 4.6. Minimum solution phosphorus concentration needed for phosphorus uptake (C_{min}), maximum phosphorus uptake rate (I_{max}), and solution [P] at which uptake is predicted to be 1/2 I_{max} (K_m) for six potato cultivars in aerated solution culture.

Cultivar	C_{min} (μM)	I_{max} ($\mu mol \cdot m^{-1} \cdot h^{-1}$)	K_m (μM)
Atlantic	2.677	0.141	21.60
Sebago	2.839	0.191	105.04
Onaway	3.677	-[z]	-
Norland	2.968	1.879	511.00
Russet Burbank	3.839	1.094	254.45
Lemhi Russet	4.290	-	-

[z]Unable to calculate due to skewed data.

be errors resulting from phosphorus uptake by microorganisms (as suggested by Cogliatti and Clarkson, 1983). More ambiguity was added to the data because the lowest concentrations measured were at the detection limits for the colorimeter system employed for analyses, adding more ambiguity to the calculated C_{min} values. As a result, the values for I_{max} are much more reliable than those for C_{min}.

Of the six cultivars tested, the strongest correlations between initial solution phosphorus concentration and uptake rate occurred with Norland, Russet Burbank, and Lemhi Russet (Table 4.7), resulting in R^2 of 0.94, 0.86 and 0.82, respectively.

When one tries to correlate uptake rate with more than just the initial solution P concentration, the findings become even more complex. The relative influences of initial solution phosphorus concentration and several physical parameters of the plants were evaluated using a stepwise regression procedure. In five of the six cultivars tested, regression equations including initial and/or the natural or $\log_{10}$ of the initial solution phosphorus concentration and plant physical characteristics were better predictors of uptake rate than were those containing initial solution phosphorus concentration alone (Tables 4.7 and 4.8). For Sebago, the addition of plant physical characteristics to the regression models did not significantly improve the R^2. Based on R^2 values, the

Table 4.7. Regression equations relating phosphorus uptake rate ($\mu mol \cdot m^{-1} \cdot h^{-1}$) to initial phosphorus concentration (μM) in aerated solution culture.

Cultivar	Regression equation
Atlantic	Y = 0.0216 + 0.00139(Initial [P]), R^2 = 0.646
Sebago	Y = 0.0106 + 0.00170(Initial [P]), R^2 = 0.740
Onaway	Y = -0.00028 + 0.00102(Initial [P]), R^2 = 0.535
Norland	Y = 0.01137 + 0.00286(Initial [P]), R^2 = 0.941
Russet Burbank	Y = 0.03059 + 0.00267(Initial [P]), R^2 = 0.857
Lemhi Russet	Y = 0.01612 + 0.0038(Initial [P]), R^2 = 0.821

Table 4.8. Regression equations relating phosphorus uptake rate by potato roots to initial solution phosphorus concentration and plant characteristics.

Cultivar	Best equation
Atlantic	Y = - 0.013 + 0.077(Log$_{10}$ initital solution [P]^{z}) - 0.0097(Shoot dry weight^{y}), R^2 = 0.847
Sebago	Y = 0.0106 + 0.0017(Initial solution [P]), R^2 = 0.734
Onaway	Y = 0.0516 + 0.000000715(Initial solution [P]^2) + 0.0168(Ln initial solution [P]^{x}) - 0.142(Root length:leaf area^{w}) - 0.000083(leaf area^{v}), R^2 = 0.806
Norland	Y = 0.085 + 0.0034(Initial [P]) - 0.000014(Initial [P]^2) + 0.0528(Log$_{10}$ initial solution [P]) - 0.304(Root length:leaf area) - 0.000405(Leaf area), R^2 = 0.994
Russet	Y = 0.0521 + 0.00543(Initial solution [P] - 0.0000306(Initial solution [P]^2 - 0.24468(Root length:shoot DW^{u}), R^2 = 0.936
Lemhi	Y = 0.0567 + 0.0158(Initial solution [P]) - 0.00010(Initial solution [P]^2) - 0.173(Log$_{10}$ initial solution [P]), R^2 = 0.914

^{z}Log$_{10}$, µM.
^{y}Grams.
^{x}Natural log.
^{w}Meters/cm^2.
^{v}Cm^2.
^{u}Meters:dry weight, in grams.

phosphorus uptake rate for any one cultivar was best described by a set of terms unique for that cultivar. Five of the six equations in Table 4.8 contains at least one term related to initial solution phosphorus concentration (Log_n of the initial concentration, etc.) and one related to plant characteristics. According to the six regression models, leaf area, shoot dry weight, the ratio of root length to leaf area, and the ratio of root length to shoot dry weight were significant factors related to P uptake in at least one of the cultivars tested. As an example, predicted P uptake by Atlantic was best described by a regression equation including the $\log_{10}$ of initial solution phosphorus concentration and the dry weight of the shoot (Table 4.8). The highest R^2 were found for Norland, Russet Burbank, and Lemhi Russet. The mean value of several plant physical characteristics for each cultivar tested appear in Table 4.9.

Discussion

It is unlikely that low phosphorus uptake rate per unit length of root is the reason potatoes require large supplies of phosphorus fertilizer. Uptake of phosphorus in solution culture averaged more than 70 $nmol \cdot m^{-1}h^{-1}$ in the cultivars studied. This is a rate comparable to those found in other crops (Itoh and Barber, 1983, and Teo, et al. 1992). The I_{max} for each potato cultivar was also higher than those

Table 4.9. Physical characteristics of tested cultivars at termination of 1991 phosphorus uptake study.

Cultivar	Plant Characteristic: Leaf area (cm^2)	Root length (m)	Mean root diameter (cm)	Root length: leaf area[z]	Root length: shoot dry weight[y]
Atlantic	214	26.09	0.102	12.4	0.16
Sebago	245	33.69	0.095	13.1	0.17
Onaway	355	126.45	0.055	34.4	0.26
Norland	134	37.33	0.077	27.6	0.25
Russet Burbank	138	19.48	0.103	13.7	0.19
Lemhi Russet	154	19.79	0.107	13.2	0.16

[z]Meters per cm^2.
[y]Meters per g.

reported by Itoh and Barber (1983) for wheat, carrot and onion, and in the case of Onaway, Norland and Lemhi Russet, greater than that of tomato (Table 4.10).

The plots of phosphorus uptake rate versus the natural log of solution phosphorus concentration may indicate the presence of a two carrier system of phosphorus uptake in potatoes. A similar dual mechanism has been proposed for mineral uptake by plants (Marschner, 1986). In this model, one carrier moves phosphorus across root cell membranes when soil solution phosphorus levels are low. A second carrier, either on the cell or vacuolar membrane, joins in the uptake process if soil solution phosphorus concentrations increase to a certain level. Plots of uptake rate versus the natural log of the soil solution phosphorus levels for plants thought to have a two carrier uptake mechanism will have a region of low slope and a region of much greater slope. The plot in Figure 4.2 shows this pattern and would seem to indicate the presence of a dual mechanism of P uptake in these potato cultivars. The slope increases when the initial solution culture P concentration exceeds 11 μM ($\log_n$ = 2.8.

All six cultivars exhibited similar rates of phosphorus uptake at a given solution phosphorus concentration. This indicates phosphorus uptake rate may not be worthy of breeders' attention when developing new cultivars. Similar

Table 4.10. Maximum phosphorus uptake rate (I_{max}) from solution culture by roots of several species (Itoh and Barber, 1983).

Crop	I_{max} ($\mu mol \cdot m^{-2} \cdot h^{-1}$)
Wheat	40
Tomato	120
Carrot	50
Onion	61

results have been found for nitrogen utilization by potatoes (Kleinkopf, et al., 1981). They found no differences in total nitrogen removal among field grown potato crops. However, the six lines they tested (including Lemhi Russet and Russet Burbank) did have different nitrogen use efficiencies (NUE), i.e. the amount of nitrogen taken up relative to amount available. The authors recommend that information on NUE be used to formulate specific fertilizer recommendations for each cultivar and growing area. It is possible that field data using several phosphorus fertilizer rates would result in similar recommendations. It is also possible that the six lines tested by Kleinkopf, et al. had different root systems and there sizes and morphologies influenced NUE.

Potato breeders should investigate root characteristics as they develop cultivars. Total root length, mean root diameter and total root surface area may play roles in phosphorus nutrition of potatoes. The results presented here cannot be used to draw any firm conclusions because the root systems were either produced in the artificial environment of liquid solution, as in the preliminary experiment, or were torn during transfer from sand to solution culture, as in the cultivar comparison study. These handling techniques in the cultivar comparison study prevented quantification of true root to shoot ratios, total root dry weight production, and complete root length.

Taking these facts into account, some inferences can be discussed. The calculated root:shoot ratio of the Onaway plants used was almost twice that of the five other cultivars. Norland also had a relatively large root:shoot ratio. There were also differences among cultivars in the ratio of root length to leaf area (Table 4.9). Onaway and Norland had more root length per square centimeter of leaf area than the other four cultivars tested. Onaway had a lower rate of P uptake per unit of root length at each concentration than the other cultivars did. This is likely because the larger root system was able to supply the shoot with the same total amount of P as the root systems of the other cultivars using a lower rate of uptake per unit of length. Norland also had fairly large root:shoot ratio and root length:leaf area but had relatively strong uptake rates at the high concentrations. The large root:shoot ratio and root length:leaf area ratio were as much due to small shoot size as anything else. The root lengths of Norland were greater than those of all cultivars tested except those of Onaway, which had root systems three or four times the length of those in the other five cultivars. The relatively strong uptake rates in Norland may imply greater P demand per unit of shoot, an inefficiency of partitioning and utilization of P, and/or luxury P consumption. Which ever of these is the case, if any are, the difference in uptake rate between Norland and the four cultivars with similar root system size were not greater than one order of magnitude. Thus it is likely that they are inconsequential. It may also imply a lack of controls on P uptake rate in Norland.

True differences in root system development among potato cultivars have been shown. *In sito* observations during 1993 have shown that root growth differs among potato cultivars in McBride sandy loam in Michigan (Warncke and Evans, 1993). Root growth of four cultivars was recorded using minirhizotrons. The four cultivars had different root counts per 1 cm^2 frame at most of the measured depths in the soil. Russet Norkotah consistently had lower total root counts than the other cultivars evaluated, implying that its root system was significantly smaller than those of other cultivars. Onaway, which in the cultivar comparison experiment had relatively large root systems, produced intermediate sized root counts in the minirhizotron experiment.

Researchers involved in all aspects of potato production should focus some of their future efforts on potato root systems for at least two reasons. First, phosphorus uptake rate per unit of root does not appear to be limiting the potato plant's ability to acquire phosphorus. Secondly, root system size may vary greatly among cultivars. It can be inferred from these two facts that physical factors related to the roots, such as size, diameter, and turnover, may influence potato productivity. Iwama, et al. (1981) reported significant positive correlations between potato root length and tuber yield. They showed that these correlations varied among different genetic crosses, as did the absolute ratios of root dry weight to yield. The authors found that the correlation of root dry weight to tuber yield early in the growing season, through flowering, was negative, but became positive as the plants neared maturity. They predicted that higher yielding clones could be obtained through crosses with late maturing lines than through crosses with early maturing lines because the later maturing lines have larger root systems.

Researchers should continue improving cultural practices to further guarantee adequate phosphorus supplies to the plant. Cultural practices that provide the plant with adequate soil moisture and nitrogen supplies throughout the growing season may also reduce the crop's dependence on applied phosphorus. Potatoes are very sensitive to soil moisture (Singh, et al., 1968) and nitrogen (Benepal,1967), both of which may influence phosphorus uptake (Olsen, et al., 1962; and Grunes, 1959; and Dubetz and Bole, 1975). Grunes, et al. (1962) reviewed research on the effects of nitrogen on phosphorus availability to and utilization by plants. Some of the work cited included nitrogen effects on root and shoot growth, on efficiency uptake of fertilizer P, and on plant metabolism. Olsen, et al. (1962) stated that soil solution P concentrations are higher at higher (-0.9 MPa) soil moisture tensions but that P uptake by corn roots is greater at lower tensions (-0.033 MPa).

Through results of these experiments on phosphorus uptake by potato cultivars using six initial solution phosphorus concentrations, one concludes that uptake rate is strongly correlated with solution phosphorus concentration and may be altered by changes in plant physical characteristics. The six potato cultivars studied did not exhibit extreme differences in P uptake rate within each P concentration tested. The minimum solution phosphorus concentration required for net uptake by potatoes was not clearly defined by these studies, although it is likely below 0.003mM P, a conclusion supported by the early work of Houghland (1947). The maximum influx rate appears to be less than 1.9 μmol $P \cdot m^{-1} \cdot h^{-1}$ for all cultivars tested.

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