

CONCERNS IN SOIL FERTILITY OF NUTRIENT BALANCE AND IMPROVED PERFORMANCE OF POTATOES¹

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Recent yield increases in potatoes have been achieved through improved fertility management of the macronutrients N, P, and K. However, the rapid rates of growth which potato plants undergo to attain these high yields may result in imbalances of other nutrients which may in turn have an adverse effect on tuber quality. As the Columbia Basin soils continue to be cropped, diminishing nutrient reserves increase the potential for nutrient imbalances. Future research in soil fertility should focus on nutrient interactions in the soil-plant system that not only affect nutrient availability in the soil, but also nutrient transport across the entire soil-plant system to the site of requirement within the plant. In this paper we present a brief review of the interactions in both the soil and the plant that may affect the nutrient balance in the tuber.

Soil factors

Soil nutrient availability to plants is governed by two basic factors, quantity and intensity. Quantity represents the amount of a nutrient that is held in ready reserve. Intensity is the immediate availability of a nutrient in the soil solution. A deficiency of a nutrient may be caused by an inadequate quantity of that nutrient in the soil. Conversely, the quantity of the nutrient may be adequate, but the intensity factor may be too low to meet the plant requirements.

Plant nutrients, whether applied as fertilizers or occurring naturally, are part of a dynamic soil system. Physical, chemical, and biological processes in the soil influence the behavior of elements in the soil. Physical processes move the nutrient. For example, the wind may blow the nutrient across the surface of the soil, or water flow may move plant nutrients into or below the plant root zone. Chemical and biological processes modify the chemical form, mobility, and plant availability of the nutrient. Microbial activity, for example, is responsible for transformations of N from urea to NH_4^+ and NO_3^- (see Table 1). Chemical transformations also affect the form of some nutrients. For example, a shift from alkaline to acid conditions results in the dissolution of CaCO_3 . Conversely, higher pH results in the conversion of boric acid to the borate anion (Table 1).

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The chemical form of the nutrient determines the ability of a nutrient to move within the soil, either vertically during leaching or laterally to an absorbing root surface. In general, cationic forms such as Ca^{+2} , Mg^{+2} , K^+ , and NH_4^+ are attracted to the negatively charged cation exchange surfaces of the soil and as a result exhibit limited movement in the soil. In contrast, anions such as Cl^- and NO_3^- are repulsed from the exchange surfaces and hence can travel rapidly through the soil with the movement of water. However, phosphorus is the obvious exception to this rule, since the H_2PO_4^- and HPO_4^{2-} anions may undergo specific adsorption on soil mineral surfaces or chemical precipitation with other elements in the soil solution, it is generally immobile in the soil. Neutral molecules, such as H_3BO_3 , may either be transported by water or undergo non-ionic interactions with the soil surfaces and move somewhat more slowly than anions. Nutrients immobilized within the microbial biomass are neither mobile in the soil nor immediately available to plants.

The form of the nutrient is also critical to the root absorption process. For example, among the nutrient forms of nitrogen, calcium, and boron found in soil as shown in Table 1, those most readily absorbed by potato roots are NO_3^- , Ca^{+2} , and H_3BO_3 .

There has been considerable discussion concerning the quantity of soil Ca^{+2} that is required to avoid the incidence of various internal disorders in potato. Researchers in Wisconsin (Tzeng et al., 1986) have found a negative correlation between the incidence of internal brown spot (IBS) and tuber Ca concentration. As the concentration of Ca in the tuber declined, the incidence of IBS increased. However, as Stevens (1987) indicated, the Wisconsin soils in these studies are quite different from central Washington soils, especially with respect to Ca content. Although the pH of some of our agricultural soils is declining, the base saturation is still quite high, indicating that the Ca supply of our soils appears to be adequate. However, additional investigations may be required to examine environmental or physiological factors that may influence the intensity factor of soils and the uptake and delivery rate of Ca and other phloem-immobile nutrients to the tuber.

Plant factors

It is conceivable that deficiencies may occur under conditions in which the quantity of a nutrient in the soil is considered adequate, yet the rate of transport to the tuber is not fast enough to meet the demands of a rapidly expanding tuber. In addition to the above-mentioned soil factors, numerous plant processes influence the rate of delivery of a nutrient to the site of requirement in the plant.

The initial process is the uptake or absorption of the nutrient by root cells. Nutrients vary greatly in their ability to pass through cell membranes in the uptake process. For example, K^+ is transported across membranes very readily and can be taken up in large amounts. At the other extreme, Ca^{+2} will pass through a biological membrane relatively slowly.

One consequence of this characteristic is that Ca^{+2} uptake primarily occurs in the region of the root very near the growing tip. It has been hypothesized that the length of root that is involved in calcium absorption decreases during periods of environmental stress. Thus, any stress which temporarily reduces root growth may contribute indirectly to a Ca^{+2} imbalance (Scaife and Clarkson, 1978).

The interaction among nutrients at the root surface can also influence the rate of nutrient uptake. Competition for sites of uptake among cations is an example of this type of interaction. It has been shown in potatoes (Davis, 1983) that, when ammonium (NH_4^+) is the sole N source, the uptake of the other cations Ca^{+2} , Mg^{++} , and K^+ is inhibited. Potassium has been shown to exhibit a similar effect on Ca and Mg uptake when supplied to barley plants (Forster and Mengel, 1969). Potassium is readily absorbed and is required in substantial quantities for the production of high quality potato tubers. Questions arise concerning the potential for inhibitory effects of high K fertilization on the uptake and physiological activity of Ca^{+2} and Mg^{+2} (Marschner, 1986).

Nutrients normally travel from one plant organ to another via xylem or phloem vessels. Xylem tissue at maturity consists of elongated, interconnected dead cells. Therefore, no membrane is present to impede or lend specificity to nutrient transport through these vessels. Thus, all nutrients readily move in the xylem. Xylem flow is determined by a water potential gradient created by evaporation from leaf surfaces. Upon entry into the xylem system, the nutrient travels passively along the transpiration stream toward transpiring surfaces. Most transpiration occurs from the more mature leaf surfaces. As leaves mature, cell division ceases, and the requirement for subsequent supplies of nutrients in these tissues declines. Most of the cell division occurs in shoot and root tips, fruits, and tubers which all have very low transpiration rates. Thus, xylem flow transports nutrients to tissues where they are only minimally required. There must be a retranslocation of the nutrients in order to reach the growing points with low transpiration rates. The phloem system is utilized for the delivery of nutrient elements and carbohydrates from mature leaves and stems to growing points. Unlike nutrient flow through xylem vessels, the transport of nutrients through the phloem is under metabolic control of functioning cell membranes. Since the ability of the nutrients to pass through cell membranes varies, their relative mobility within the phloem system also varies. Table 2 lists the relative immobility of Ca and B, one would expect that imbalances of these nutrients might occur in phloem-fed tissues. Indeed, bitter pit in apples, blossom-end rot in tomatoes (Shear, 1975), and internal brown spot in potato (Tseng et al., 1986) have been traced to Ca^{+2} deficiencies. Thus it appears that the low concentration of Ca (and perhaps other immobile nutrients) in the phloem may be a physiological constraint under certain conditions. Defining and predicting those conditions remain a challenge. If the phloem provides the sole pathway of transport of these nutrients to the tuber, then it would seem that to combat imbalances of these nutrients, tuber growth rates must not exceed the capacity of the phloem to supply these nutrients.

However, there is good evidence that Ca as well as other nutrients may reach the tuber by the xylem path as well. At night when transpiration drops to nearly zero, the pressure in xylem sap becomes positive. This is called root pressure. It has been observed at these times that tuber weight increases and growth occurs. Radio-labeled Sr (an element which behaves similarly to Ca) supplied to the xylem has also been shown to enter the tuber at night (Baker and Moorby, 1969). In addition, it has been suggested by researchers in Wisconsin (Kratzke and Palta, 1985) that Ca is also taken up by small roots directly on the tuber and on the stolon near the tuber (tuber and stolon roots) and supplied directly to the tuber by the xylem path. These researchers were able to increase tuber Ca concentrations three fold when Ca was supplied in the soil surrounding the tubers, but if the Ca was applied to the basal roots below the tuber zone, no increase in tuber Ca levels was obtained (Kratzke and Palta, 1986). Again, these studies were done on soils and climatic conditions quite different from those of this area. Nevertheless, it does point out the apparent necessity for Ca to be present in the soil near the tuber in order to increase tuber Ca levels. Furthermore, it has been shown by German researchers that Ca can be absorbed directly through the periderm of the tuber (Krause and Marschner, 1971). It is quite difficult to experimentally separate the last two Ca uptake pathways mentioned. However, for management purposes, there is no need to make a distinction as both suggest the same management approach: that is to increase Ca levels, or the level of any other similarly behaving nutrient, in the soil immediately adjacent to the tuber.

RESEARCH GOALS

With this background, several key questions emerge with respect to tuber nutrient balance. 1) What are the relative contributions of the xylem and phloem supply systems to tuber nutrient balance? 2) If Ca is supplied to the tuber through the xylem system, which of the xylem supply mechanisms described is dominant and what conditions may lead to Ca imbalance and how can we manage the system to alleviate the problem? 3) What is the character of the potato root system -- how extensive are stolon and tuber roots? 4) Since boron (B) is also immobile in the phloem, do these same conditions apply to its supply and balance in the tuber? These were the questions and background which led to a project proposal recently submitted to the Washington Potato Commission.

We felt the first step in developing answers to the questions posed above was to gain a better understanding of the potato root system. Regardless of the potential ability of stolon and tuber roots to supply the tuber, their effectiveness is directly proportional to the volume of soil with which they are in contact. Also, the growth and development of the root system as a whole needs better characterization to aid in the effectiveness of fertilizer placement and to improve crop modeling efforts conducted by others. To accomplish this goal, we have developed a method of sampling, intact, a quarter section of the potato root zone which is subsequently subdivided, measured, and characterized by root type and origin.

The next step is to assess the transport pathways of phloem-immobile nutrients in relation to the developing tuber. We have currently underway in the greenhouse a split-root experiment in which Ca, B, and manganese (Mn--intermediate in phloem mobility) are applied separately to the root zone containing the tubers and to the root zone below the tubers. By analysis of the various tissues, a measure of the effectiveness of the different roots to supply nutrients to the tubers can be assessed. We are also using the scanning electron microscope (SEM) and electron-induced X-ray analysis to trace the uptake and translocation of Sr from nodal roots to stolons and tubers.

With the results obtained from these experiments, we hope to establish the route by which phloem-immobile nutrients are transported to the tuber. We will know which roots are most effective in transporting various nutrients to the tuber. We will know where, physically, those roots will be present in the soil during the growing season. Armed with this knowledge, we should be able to suggest management strategies aimed at maintaining nutrient balance in tubers even under the rapid growth rates obtainable under high productivity.

SUMMARY

In the pursuit of maximum production, it becomes increasingly important, when conducting soil fertility research, to understand factors that affect the uptake from the soil, transport within the plant, and utilization of a nutrient inside the plant. When a fertilizer is applied, numerous soil and plant factors interact with the applied nutrient before it finally reaches its goal of utilization at the site of requirement within the plant. As diagrammed in Figure 1, the sequence of processes can become quite involved, even in this simplified view. Knowledge of the mode of transport of phloem-immobile nutrients to tubers is of critical importance in order that effective management strategies may be employed to attain nutrient balance for maximum production of quality tubers.

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Table 1.

**CHEMICAL FORMS OF SOME
PLANT NUTRIENTS IN SOIL**

CATION	NEUTRAL	ANION
NH_4^+	$\text{CO}(\text{NH}_2)_2$	NO_3^-
Ca^{++}	CaCO_3	
	H_2BO_3	H_4BO_4^-

Table 2.

**RELATIVE NUTRIENT MOBILITY
IN THE PHLOEM**

HIGH	MEDIUM	LOW
K	Fe	B
N	Mn	Ca
S	Zn	
P	Cu	
Mg	Mo	

Figure 1. Simplified flow chart for nutrient utilization in the soil-plant system.

