The Calcium KicK

Improving potato quality begins with supplemental application

BY JASON HARRIS, PUBLISHER, WITH JIwan PALTA

Recent studies show that potato tuber quality can be improved by increasing the calcium content of the tubers. Benefits from supplemental calcium application include reduced incidence of internal defects such as internal brown spot and hollow heart, according to Jiwan Palta, potato researcher from the University of Wisconsin. Data from several studies also suggests that higher calcium tubers store better and have reduced incidence and severity of soft rot. Recently Palta and his graduate student, Chris Gunter, have also investigated the influence of seed tuber calcium contents on seed piece performance.

“We have obtained some evidence that in some cultivars the seed piece tuber quality can be improved through calcium application. In this study we found that seed-piece tubers given calcium nitrate during their development gave higher yield in the following season,” explained Palta.

In addition to these issues they have also investigated practical means of delivering soluble calcium products, timing and source of application of calcium. Since the common water soluble products (calcium nitrate, N-Plus and NHIB) supply calcium and nitrogen, they have also investigated the interaction of calcium and nitrogen application on quality and yield.

WHY CALCIUM?

Calcium has long been known to play an important role in the growth and development of plants. It has been well recognized that the cell membrane health is very crucial to the survival and health of the plant cell. It is now well established that the health of the cell membranes cannot be maintained in the absence of a critical level of calcium around the membranes. If the level of calcium associated with the membranes is reduced, the membranes become leaky resulting in an unabated loss of cellular salts and organic compounds. Such loss, if not reversed, leads to the eventual death of the cell.

The tuber is botanically a stem tissue. As compared to the above-ground stem portion of the plant, tubers contain very little calcium. On average, calcium concentration in the tuber is less than one fifth of the calcium of the stem tissue. Transpiration is the main driving force for calcium transport in plants. Calcium, therefore, moves along with water in the xylem. Tubers, being surrounded by moist soil, will have much less transpiration as compared to the above-ground part of the plant. Consequently low transpiring organs, such as tubers, accumulate much less calcium per unit fresh weight than leaves.

More than four years ago, Palta and his graduate student, Marian Kratzke, provided evidence for the existence of functional roots on the tuber and at the tuber-stolon junction.

“In a follow-up study, we showed that these roots displayed normal root

Potato tuber showing root system.

The main root system supplies nutrients and water to the foliage, not the tuber.
anatomy and they appear to derive from parenchyma cells adjacent to the vascular tissue,” Palta said. By feeding a water-soluble dye, it was demonstrated that these roots were able to supply water to the tuber whereas the main root system supplied water to the top part of the plant. Since water and calcium are known to move together, they suggested that these tuber and stolon roots supply nutrients such as calcium to the tuber as shown by the dye.

Potatoes during bulking with calcium fertilizer. Prior to our research, growers used to complete fertilization at hillling. This was a necessity, since no nutrient application could be made by tractor after hillling without damaging the plants. Our results show applications of calcium need to be made much later in the season. This can be easily achieved by injecting calcium fertilizer directly into the irrigation line. Since tubers develop during the late part of the season it would be important to add supplemental calcium during bulking, which is even more critical in sandy soils,” Palta added.

Due to low-moisture-holding capacity, sandy soils are irrigated two-to-three times a week. Thus, the top portion of the hill is continuously washed by the irrigation and rain, with water moving soluble nutrients to the lower portion of the hill. These nutrients remain accessible to vegetative growth via the main root system. However, the tubers developing during late season will not have access to these nutrients via the tuber and/or stolon roots.

**SOURCE, QUANTITY**

Calcium should be applied in water-soluble form to facilitate uptake by the tuber. Lime and gypsum, common sources of calcium used in agriculture, are not water soluble. Thus they have studied water soluble calcium products such as calcium nitrate, N-Plus and NH4H and found them to be effective at improving tuber calcium contents.

**CALCIUM AND TUBER QUALITY**

Internal defects such as brown center and hollow heart produce no external symptoms on effected tubers and, therefore, cannot be culled out before sale. They have examined the impact of calcium fertilization on internal defects over several seasons. Individual tubers were analyzed for the defects as well as for calcium contents. They found, in general, a reduction in the internal defects by calcium application.

“However, it is important to point out that at a given level of tuber calcium there is a large variability (especially at low calcium concentration) among tubers for the incidence of internal defects. In other words, in addition to calcium there are other factors that contribute to development of internal defects. Furthermore, there are variations among cultivars in terms of the incidence of internal defects, suggesting genetic control for these traits,” he said.

Other recent studies also suggest that timing of nitrogen application and interaction between calcium and nitrogen may influence the incidence of tuber-internal defects.

**HEAT STRESS**

Heat stress is known to reduce plant growth and reduce partitioning of photosynthate to the tubers. Although there are differences among cultivars in their response to heat stress, in general, heat tends to increase stem length and branches while reducing the leaf size and total leaf. In addition, high temperatures also reduce the net photosynthesis. The overall result of heat stress is a decrease in plant growth and tuber yield.

Recent studies by Palta and his graduate students, Ahmed Tawfiq and Matt Kleinhenz, have shown that calcium applications can mitigate heat stress effects on potato plants. Although they do not know a mechanism by which calcium is able to mitigate heat stress effects on potatoes, their results provide some insight.

“For example, we found that stomatal conductance was higher in calcium-treated than control plants under heat stress. Maintenance of stomatal opening could be important in avoiding heat stress effects via enhanced transpirational water loss. We found a decrease in the calcium concentration in leaves of plants exposed to heat stress but the calcium concentration was maintained at the same level as prior to heat stress in the leaves of plants given calcium fertilization during heat stress,” he added.

“It appears that during heat stress calcium is able to sustain cell division and cell elongation in the apical meristem. We are currently investigating the mechanisms by which calcium is able to do this and mitigate heat stress effects on a plant,” he concluded.

(Editor’s Note: Dr. Jiwan Palta is a potato researcher for the University of Wisconsin. Photos courtesy of Jiwan Palta, UW Madison.)
"Effect of N Fertilizer Source and Rate on the Yield, Quality and Storability of Potatoes"

1) CN-9® vs. UAN-32 on Atlantic and Russet Norkotah potato varieties.
2) Rates of 100 lbs. to 350 lbs. of N / acre.
3) Applied in 9 weekly applications through sprinkler irrigation beginning at tuber initiation.
4) In 1998: CN-9® out yielded UAN-32 potatoes at the higher fertility rates for both varieties.
5) In 1999: CN-9® out yielded UAN-32 potatoes at all fertility rates for both varieties.
Supplemental calcium fertilization of potatoes has been shown to increase the percentage of US1 grade potatoes (Simmons, et al., 1988) and decrease the incidence of internal brown spot before and after storage, and sub-apical necrosis after storage (Tzeng, et al., 1986).

The primary objective of this study was to evaluate the effects of N fertigation rate as provided by UAN and CN on potato yield, quality and storability.

MATERIALS AND METHODS

A field study was conducted in 1998 and 1999 at the New Mexico State University, Agricultural Science Center, Farmington, on a Wall sandy loam soil (coarse-loamy, mixed, calcareous, mesic Typic Camborthid). The profile is deep, well-drained, and highly permeable. Soil electrical conductivity ranges from 2.5 mmhos/in. in the top 18 in. to about 17.8 mmhos/in. below 35 in. Soil surface pH averages 8.1 and organic matter content is less than 1.0%. Average annual precipitation depth at the study site is 7.6 in. and the average temperature is 52°F.

A duplicated triple sprinkler line-source (TLS) design was used to provide N fertigation gradients to two potato varieties (Atlantic and Norkotah Russet) during 1998 and 1999 using both UAN and CN as N sources. The TLS design (Lauer, 1983), a modification of the single line-source design (Hanks et al., 1976), consists of three equally spaced sprinkler laterals that provide near uniform irrigation to a crop planted between the outer laterals when the system is operated under appropriate conditions. Injection of liquid N fertilizer into the center line only, provides a continuous decreasing gradient of sprinkler-applied N away from, and on each side of the center line. Our design consisted of ten individually valved sprinkler laterals (five on each side of a main feed line) that provided four TLS replicates. The two outer laterals and the center line of each five-lateral set provided water only to the potato plots throughout the entire season. During fertigation events, the center lateral of each TLS applied both water and N fertilizer to the crop. This provided eight separate N application gradients (one on each side of the four injection lines) superimposed over a plot area of uniform irrigation. To evaluate the effects of N source, and possible benefits of Ca on potato growth, two laterals were injected with UAN and the other two with CN at volumes required to provide equal N application gradients with either source. The initial fertigation was applied near tuber initiation each year (June 11, 1998 and June 4, 1999). Nine additional fertigations were subsequently applied at weekly intervals. All injections were applied at an equal volume necessary to provide a per event fertigation rate of 20 lbs N/acre to plots closest to the injection line (2 rows away). Potato seed pieces were planted at a 6-inch spacing in mid-April of both years on 18, 34-inch raised beds parallel to, and between, each sprinkler line. The plot length planted to each variety (Atlantic or Norkotah) was 40 feet. Prior to each fertigation, five catch-cans were set between laterals in furrows spaced 8.5 feet apart (every three rows) to collect irrigation samples for analysis of N and Ca using the LECO and ICP methods, respectively.
Prior to planting, 11-52-0, 0-0-60, and 34-0-0 were broadcast to the plot area and incorporated to a depth of about 4 inches with a disk at rates of 106 lbs N, 197 lbs P₂O₅, and 155 lbs K₂O in 1998 and 34 lbs N, 160 lbs P₂O₅, and 235 lbs K₂O in 1999. For weed control, a mixture of metolachlor (70%) and metribuzin (15%) at a rate of 2 pts of product/acre was sprayed on the soil surface and irrigated in just prior to plant emergence in both years.

Potatoes were harvested in early October, 1998 and mid-September, 1999 using a two row potato digger. Five, 2-row (68 in), 30 foot long plots within each variety and fertigation gradient were picked up by hand after digging. Tubers were weighed, counted and graded using USDA standards (1972). Ten tuber sub-samples were dissected and examined for internal defects caused by disease while sub-samples consisting of US 1 grade tubers were put into winter storage and then re-examined for quality in March. Fertilizer, yields and other parameter values were based on the average of four observations obtained at equal distances away from the injection laterals.

RESULTS AND DISCUSSION

Fertilizer treatment levels ranged from 170 to 336 lbs N/acre in 1998 and from 101 to 284 lbs N/acre in 1999. These rates included the N fertilizer applied at planting (106 and 34 lbs N/acre in 1998 and 1999, respectively). Marketable tuber yields (tubers greater than 1 7/8 inches in diameter without defects) of both varieties generally increased with increasing N rate in both 1998 and 1999 with CN as the N source and in 1999 with UAN as the N source (Fig. 1). In 1998 however, yields were similar or decreased in both varieties with increased UAN fertilization (Fig. 1). In 1998, maximum yields of Atlantic and Norkotah tubers (495 and 467 cwt/acre, respectively) occurred at the highest level of CN fertilization (300 lbs N/acre). At an equal rate of N fertilization with UAN, yields averaged about 14% less. In 1999, tuber yields of both varieties increased up to a N fertilizer rate of about 250 lbs/acre but averaged about 9% lower at equal N rates when fertilized with UAN than with CN (Fig. 1).

The effect of N rate and source on tuber quality (expressed as weight per tuber) varied between varieties (Fig. 2). The average size of Atlantic tubers, while differing between years, (6.6 ounces in 1998 and 5.4 ounces in 1999) was not affected by N rate or N source (Fig. 2). The observed differences in Atlantic marketable yields between N rates then, were primarily the result of N effects on the number of marketable tubers produced rather than tuber size. For example, when averaged over both fertilizers, the number of marketable Atlantic tubers produced per acre at the highest and lowest rates of N fertilization, were 114,000 and 100,000/acre, respectively. In the Norkotah variety, there was a general trend of increasing tuber size with increased rate of N fertilization, at least when fertilized with CN (Fig. 2) and this corresponded to the observed variability in yield. The average number of Norkotah tubers produced per acre at the high and low N rates were 82,000 and 80,000, respectively.

The percentage of tubers infected with disease at harvest (primarily internal browning), or after storage (brown spot and soft rot), was not affected by N rate or source, but did
differ between varieties. Internal browning at harvest in the Atlantic variety averaged 12% over all N rates, N sources, and years. After storage, the percentage of disease rose only slightly to about 15%. In Norkotah Russet, less than 2% of the tubers were infected with disease both at harvest and after storage.

REFERENCES


Fig. 2. Average weight per marketable potato tuber (v. Atlantic and v. Norkotah) at various levels of N fertilization provided by calcium nitrate (CN) and urea ammonium nitrate (UAN) during 1998 and 1999.
"Calcium’s Role in Tuber Quality"

1) George Clough, Oregon State University, recommends 80 lbs. Ca to preplant incorporated into the hills and 60 lbs. Ca sidedressed in 2 applications early in the season.

2) Jiwan Palta, University of Wisconsin, recommends 100 lbs. to 200 lbs. Ca split applied through the irrigation water during early bulking.

3) Calcium is taken into the tuber by tiny root hairs on the tuber or stolon only.

4) Soil calcium is not always available, and calcium is immobile within plants once it is taken up and translocated to the growing point.
Evidence continues to mount that there is a direct link between calcium and potato quality, and that providing soluble calcium to plants should be a regular part of a grower's regimen.

"If I were to make a recommendation, it would be 80 pounds of actual calcium in a preplant band incorporated into hills, and 60 pounds of actual calcium sidedressed in two applications early in the season," says George Clough, Associate Professor of Horticulture at the Hermiston Agricultural Research and Extension Center in Hermiston, Oregon.

Jivan Pallla, Associate Professor of Horticulture at the University of Wisconsin, has the same idea but prefers a different approach. In sandy to sandy-loam soils, he would spoon feed 100 to 200 pounds of calcium to tubers during the early bulking period. He would apply the calcium through irrigation water, and split it between three or four applications.

The recommendations have filtered down to growers from some two decades of research by teams around the world.

Clough ran three years of trials in the early 1990s. Russet Burbanks were planted each of the three years. Frontier was planted for two years, and Atlantic was planted one year.

Clough applied 0, 80, 160, or 240 pounds of calcium per acre prior to planting and side-dressed 0, 30, or 60 pounds of calcium per acre.

In Russet Burbanks, Clough found reduced brown center; improved fresh fry color; an increase in tuber phosphorous, potassium, and calcium; and no increase after storage in the severity of internal brown spot (IBS) or percentage of tubers with IBS and brown center. In addition, hollow heart incidence decreased in storage one year, while brown center incidence decreased in storage two years.

In Atlantics, the percentage of tubers with IBS in the bud end dropped from 6.25 to 3.33, the overall percentage of tubers with IBS dropped from 7.42 to 3.75, and the percentage with tubers with IBS and brown center was lower after storage than at harvest.

In Frontier, Clough observed reductions in IBS severity, the (continued)
percentage of tubers with IBS in the center, bud-end IBS severity, and the overall percentage with IBS. After storage, IBS severity and the overall percentage of tubers affected were lower among the potatoes that had received supplemental calcium.

"Tuber yield and size were not affected by the calcium treatments, but we did see definite effects on quality even though soil tests showed adequate levels of calcium," Clough remarks. "Other researchers have shown the same thing. We were just picking up where the University of Wisconsin had left off."

At Wisconsin, Palta and graduate student Marian Kratzke discovered that potato tubers have tiny roots themselves, and that these roots are an important channel for the tubers to take in nutrients. Previously, it was thought that nutrients came in through the potato plant's roots, were transported to the leaves and then downward to the tubers. Palta and Kratzke discovered that each tuber has small hairlike roots that are the primary conduit into the tuber for many nutrients. The frequency at which these tuber roots occur and the role they play in plant nutrition are still the subjects of intense debate by potato researchers.

Soil calcium is not always available to a plant, and calcium is immobile within plants once it is taken up and translocated to the growing point. Calcium moves in the transpiration stream so plant parts such as tubers that are not part of the transpiration stream are more subject to calcium deficiency.

The work at Wisconsin demonstrated that the calcium must be in soluble form, and it must be applied close enough for the tuber to take it in itself.

"To improve calcium uptake by tubers, additional calcium should be placed so that as much calcium as possible comes in contact with the stolon and tuber region and not the basal roots of the plant," writes Palta. He recommends applying calcium to the upper portion of the hill where tubers develop.

Also, writes Palta, "we have found that calcium should be applied in water soluble form to facilitate calcium uptake by the tuber," Palta recommends applying the supplemental calcium during early tuber bulking.

Clough's work was done during three years of relatively light IBS pressure so he was unable to test calcium against the environmental conditions that are most conducive to IBS. At Washington State University, however, graduate student Nora Olsen conducted experiments in the greenhouse that deliberately introduced temperate stress.

"In the first experiment, I harvested tubers at tuber initiation, early tuber bulking, late tuber bulking, and maturity," reports Olsen. "I wanted to see how early IBS might show up. In this experi-

Potato tubers have tiny roots themselves, and these roots are an important channel for the tubers to take in nutrients. Previously, it was thought that nutrients came in through the potato plant's roots, were transported to the leaves and then downward to the tubers.

ment, I saw it as early as tuber initiation, which is earlier than many people suspected."

In the second experiment, we added heat stress at tuber initiation, tuber bulking, and maturity. There were a total of seven days with elevated soil temperatures, including five days above 90 degrees. I saw no IBS in the tubers that received calcium, and 5% to 75% IBS in the tubers without calcium fertilization. A high soil temperature stress at tuber maturity with no calcium fertilization did increase the incidence and severity of IBS, she concludes.

The unanswered questions are enough to cause Larry Hiller to be cautious in recommending a large investment of supplemental calcium. However, Hiller, Associate Professor of Horticulture at Washington State University, emphasizes that growers should at least manage their crops in a way that is most conducive to calcium uptake.

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1) Some of the detrimental effects of heat stress to plant growth and stomatal function may be alleviated by Calcium Nitrate applications during the heat stress period.

2) Mitigation of heat stress by Calcium Nitrate application may maintain productivity when optimum growing temperatures are restored.

3) Application of calcium and nitrogen as Calcium Nitrate during heat stress resulted in greater tuber yield than applications of nitrogen alone.
APPLICATION OF CALCIUM AND NITROGEN FOR MITIGATING HEAT STRESS EFFECTS ON POTATOES

Ahmed A. Tawfik¹, Matthew D. Kleinhenz², and Jiwan P. Palta³

Abstract

This study was designed to investigate the effect of calcium and nitrogen application during heat stress on leaf calcium concentration, transpiration rate, membrane thermostability, and biomass accumulation and partitioning. Micropropagated Russet Burbank potato (Solanum tuberosum L.) plants were transplanted into 20 L pots containing 1:1 (v/v) soil: perlite and exposed to 30/20°C (D/N) temperatures for four weeks (weeks 9-12 after transplanting) in a controlled-environment growth room. The maximum temperature was maintained for 6 hr during the middle of the 14 hr photoperiod. The nutrition treatments were N before stress (NBS), N during stress (NDS) and Ca and N during stress (Ca+NDS). Calcium was supplied as Ca(NO₃)₂. All treatments received the same total amount of nitrogen. Native soil Ca level without amendment (550 mg Ca/kg soil) was sufficient for potato plant growth under normal temperatures.

Plants given Ca and N during heat stress had the highest leaf Ca concentration and transpiration rate during and 2 weeks after conclusion of the heat stress period. When measured after 4 weeks of heat stress, area and fresh and dry weight of the most recently mature leaf was significantly greater in NDS and Ca+NDS plants compared to NBS plants. Cellular membrane thermostability (measured as ion leakage from heat-treated leaf disks) was not affected by any treatment prior to heat stress. However, leaf tissue from Ca+NDS plants exhibited significantly higher membrane thermostability compared to NBS plants after 2 and 4 weeks of heat stress. At harvest, NDS and Ca+NDS plants had significantly higher leaf/stem (fresh weight ratio) values compared to NBS plants. Also, Ca+NDS plants had significantly greater total tuber and biomass values than NBS and NDS plants. Results of this study suggest that some detrimental effects of heat stress on plant growth and stomatal function may be alleviated by Ca and N application during heat stress. The data also suggest that mitigation of heat stress by Ca and N application during heat stress may maintain plant productivity when optimum growing temperatures are restored.

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ADDITIONAL KEY WORDS: Solanum tuberosum, Russet Burbank, calcium nutrition, nitrogen nutrition, heat stress, stomatal resistance, membrane thermostability, leaflet calcium concentration.
Compendio

El presente estudio fue diseñado para investigar el efecto de la aplicación de calcio y nitrógeno en la concentración de calcio en las hojas, tasa de transpiración, termo-estabilidad de membrana, y acumulación y distribución de biomasa durante estrés producido por altas temperaturas. Plantas de papa de la variedad Russet Burbank (*Solanum tuberosum* L.) fueron micropropagadas y luego transplantadas en macetas de 1 litro de capacidad conteniendo suelo y perlita (1:1 volumen). Las plantas fueron expuestas a temperaturas de 30/20°C (D/N) durante 4 semanas (9-12 semanas después de haber sido transplantadas) en una cámara de crecimiento con todos los factores medioambientales controlados. La temperatura máxima fue mantenida por 6 horas a la mitad del fotoperíodo de 14 horas. Los tratamientos fueron nitrógeno antes del estrés (NBS), durante el estrés (NDS) y calcio y nitrógeno durante el estrés (Ca+NDS). El calcio fue aplicado en forma de nitrato de calcio (Ca(NO₃)₂). Todos los tratamientos tuvieron la misma cantidad total de nitrógeno. Los niveles de calcio del suelo sin alteración (550 mg/Kg suelo) fueron suficientes para el crecimiento de las plantas de papa bajo temperaturas normales.

Las plantas tratadas con calcio y nitrógeno tuvieron la concentración más alta de calcio en las hojas así como también la tasa más alta de transpiración durante y hasta dos semanas después del período de estrés causado por altas temperaturas. Después de 4 semanas del período de estrés, el área total así como los pesos seco y fresco fueron medidos en hojas de reciente maduración. Los resultados indicaron que éstos fueron significativamente mayores en plantas NDS y Ca+NDS que en plantas NBS. La termo-estabilidad de la membrana celular (cuya medida es basada en la pérdida de iones de discos de hojas sometidas a altas temperaturas) no fue afectada por ningún tratamiento antes del estrés. Sin embargo, el tejido foliar de las plantas Ca+NDS exhibió una mayor termo-estabilidad de membrana comparado con la de las plantas NBS después de 2 y 4 semanas de estrés causado por altas temperaturas. En la cosecha, las plantas NDS y Ca+NDS tuvieron valores de hoja/tallo (tasa de peso fresco) significativamente mayores comparados con los de las plantas NBS. Asimismo, las plantas Ca+NDS tuvieron valores de biomasa y número de tubérculos significativamente mayores que los de las plantas NBS y NDS. Los resultados del presente estudio sugieren que algunos efectos negativos del estrés causado por altas temperaturas en el crecimiento de la planta y en la función de los estomas pueden ser aliviados mediante la aplicación de calcio y nitrógeno durante el estrés. Los datos también sugieren que dicho alivio puede mantener la productividad de la planta cuando las temperaturas óptimas para el crecimiento son restauradas.

Introduction

The cultivated potato (*Solanum tuberosum* L.) is adapted to regions with moderate climates. High temperature (> 28/18°C, day/night) is con-
sidered a major physiological constraint resulting in reduced plant growth (13) and limited tuberization (6, 15). High temperature also alters photosynthesis, respiration, membrane permeability (1, 18, 20) and photosynthetic partitioning to tubers (7).

Potato plants grown under high temperatures often produce leaves with reduced area compared to cool-grown plants (7, 19). Reduced potato leaf size may be due to reduced cell division such as observed in other crops (14, 24, 25), alteration in cell membrane permeability (5, 11), or lowered stomatal conductance and reduced CO₂ supply for assimilate production (7). The impact of calcium and nitrogen nutrition on heat stress responses of potato has not been investigated.

In this study, measures of leaflet Ca concentration, transpiration rate, membrane thermostability, and plant biomass accumulation and partitioning were taken on plants simultaneously exposed to differential Ca and N nutrition and high temperature.

Materials and Methods

Plant Material and Growing Media

Micropropagated Russet Burbank (Solanum tuberosum L.) plantlets were transplanted to 10 cm (diameter) pots containing Jiffy Mix (JPA, East Chicago, IL) and acclimated to growth room conditions. One week after transplanting, plants were transferred to 20-liter pots containing 1:1 (v:v) loamy-sand soil (Typic Udipsamment) and perlite. Soil was collected from the top 25-30 cm layer at the University of Wisconsin-Madison Hancock Agricultural Research Station. Soil analyses of CEC (meq/100 g), organic matter (%), and nutrients (mg/kg soil) P, K, Ca, and Mg produced values of 3, 1, 35, 130, 550 and 130, respectively. It is important to note that the soil used in the present study contained 550 mg/kg total extractable calcium. This Ca level has been shown to be sufficient for potato production on this soil (23). Also, in our previous studies conducted on the same soil type containing native total extractable Ca levels of 350-550 mg/kg, we have found no significant yield differences among Ca treatments (10, 28). Required amounts of N, P and K per plant were calculated as 1, 1.5 and 5.2 g, respectively (9) and added to the growing mix at transplanting.

Environmental Conditions and Nutrient Applications

The experiment was conducted in a controlled environment growth room (3.7m x 2.6 m) at the University of Wisconsin-Madison Biotron. A randomized complete block design with three nutrition treatments and four replicates was employed. Replicates consisted of a single plant. Data were analyzed using General Linear Model procedures (21) and Duncan’s Multiple Range test (α = 0.05) was used to separate treatment means. Daily temperature minima and maxima were 20/15C weeks 1-3, 25/15C weeks 4-8, 30/20C weeks 9-12 (heat stress period), 25/15C weeks 13-14,
20/15C weeks 15-16. Temperature minima and maxima were reached after gradual temperature changes each day. Maximum temperatures were maintained for 6 hr during the middle of the light period and the relative humidity was maintained at ca. 60% throughout the experimental period. Vapor pressure deficit during the heat stress period (30/20C. day/night) was 1.6/0.9 kPa during day/night. The photoperiod was 14 hr (460-480 μmol m⁻² s⁻¹, PPF) under cool-white fluorescent lamps.

Nutrition treatments included 3 combinations of Ca and N supplementation before and during the heat stress period (Table 1). The total amount of applied N was identical in all treatments while one treatment received additional Ca during the heat stress period (Table 1). Nutrient sources were dissolved in distilled water (ca. 400 ml) and applied between irrigations. Plants were drip-irrigated with distilled water 4 times per day and 50% of the leached water from each pot was pumped back once per week to the same pot using an attached pump. Plants were irrigated one day per week with a complete nutrient solution (excluding N, P, K, Ca) to ensure an adequate supply of other nutrients during plant growth.

Leaf Area, Weight, Transpiration Rate, and Calcium Concentration; Total Plant Fresh Weight

After 0, 2, and 4 weeks of heat stress, measures of area, fresh weight, dry weight, and transpiration rate were taken on leaf 5 or 6 of all plants. Prior to leaf removal for destructive measures, transpiration rate was recorded on the fully-expanded terminal leaflet using a LI-COR steady state porometer (model LI-1600; LI-COR, Inc., Lincoln, Nebraska, USA). Transpiration rate readings were repeated 2 weeks after the conclusion of heat stress. Total leaf area (cm²) was measured with an area meter (model LI-1300; LI-COR, Inc., Lincoln, Nebraska, USA). After fresh weight readings, all leaflets were removed from each leaf and prepared for Ca analysis as one sample. Samples were dried (70C, 48-72 hr), weighed, ground to pass a 40-mesh screen, ashed (450C, 8 hr), dissolved in 2N HCl, and diluted with a lanthanum chloride solution and distilled-deionized (dd) water to obtain samples in 0.2N HCl and 2000 mg L⁻¹ LaCl₃. Calcium concentration was determined by atomic absorption spectrophotometry (Varian model SpectrAA-20, Varian Associates, Inc., Sunnyvale, California, USA).

To determine the impact of Ca and N nutrition on biomass accumulation and partitioning, fresh weight (g/plant) of leaves, stems, and tubers were determined at harvest (16 weeks after transplanting).

Membrane Thermostability

Cellular membrane thermostability (MT) of leaf tissue was estimated after 0, 2, and 4 weeks of heat stress. Membrane thermostability was estimated using fully expanded terminal leaflets of recently mature leaves (leaves 2, 3 and measures of electrical conductivity as described previously.
TABLE I. — Nutrient application schedule and temperature regimen.

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</tbody>
</table>

<sup>1</sup>In Ca+NDS, N supplied as NH₄NO₃ + Ca(NO₃)₂ and Ca supplied as Ca(NO₃)₂p.<br><sup>2</sup>Heat stress was initiated at the beginning of week 9 and ended at the conclusion of week 12. Daily temperature maxima/minima for the experimental period beginning at transplanting: 20/15C (weeks 1-3), 25/15C (weeks 4-8), 30/20C (weeks 9-12, heat stress), 25/15C (weeks 13-14), 20/15C (weeks 15-16).

(3, 18). Leaflets were placed in open plastic bags and on ice for 15 min prior to sample preparation. Leaf disks (10 mm diameter) were obtained using a cork borer from the center of the leaflet but avoiding heat-injured tissue and the midvein. For each treatment, four disks were placed in a stoppered culture tube (25 x 200 mm). Disks were washed thoroughly with three changes of dd H₂O to remove electrolytes adhering to the tissue and released from cut cells at the periphery of leaf discs. After rinsing, all tubes were drained, 2 ml of dd H₂O were added (to prevent desiccation of tissue during heat treatment) and tubes were covered with plastic wrap. Heat treatment (T) tubes were incubated in a temperature regulated water bath for 1 hr at 45C, whereas control (C) tubes were placed at room temperature (ca. 25C) for the same period. As suggested previously (2, 3), the treatment temperature was chosen after preliminary experiments to determine the temperature producing the greatest effect. After heat treatment, 20 ml of dd H₂O were added to both control and heat-treated tubes. All tubes (T and C) were incubated for 24 hr at ca. 10C to allow diffusion of electrolytes from leaf disks in proportion to heat damage. Tubes were then transferred to a water bath at 25C and shaken for 15 min to mix tube contents prior to conductivity measurement. The initial conductivity of tube contents (C<sub>T</sub> or T<sub>T</sub>) was determined with an electrical conductivity meter (YSI Model 32, Yellow Springs, OH). Tubes were autoclaved (121C, 15 min), equilibrated to 25C in a water bath, and shaken before the final
Table 2.—Effect of calcium and nitrogen application before or during heat stress on fresh weight of different plant parts 16 week after transplanting. Measurements included all leaves, stems and tubers per plant. Nutrient applications were at 3, 8, 10 and 12 weeks after transplanting (Table 1). Treatments NBS, NDS and Ca+NDS described in Methods and Table 1.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Leaves</th>
<th>Stems</th>
<th>Leaf/stem</th>
<th>Tubers</th>
<th>Total foliage</th>
<th>Tubers+ Tuber/Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g/plant</td>
<td></td>
<td></td>
<td>Total foliage</td>
<td></td>
<td></td>
</tr>
<tr>
<td>NBS</td>
<td>173.4 b</td>
<td>144.9 a</td>
<td>1.2 b</td>
<td>611.7 b</td>
<td>318.3 a</td>
<td>930.1 b</td>
</tr>
<tr>
<td>NDS</td>
<td>202.1 ab</td>
<td>121.8 b</td>
<td>1.7 a</td>
<td>699.8 b</td>
<td>322.9 a</td>
<td>1023.7 b</td>
</tr>
<tr>
<td>Ca+NDS</td>
<td>248.7 a</td>
<td>132.3 ab</td>
<td>1.9 a</td>
<td>1000.3 a</td>
<td>381.0 a</td>
<td>1381.3 a</td>
</tr>
</tbody>
</table>

Means within the same column followed by the same letter are not significantly different (α=0.05; Duncan’s Multiple Range test).

F Fresh weight of leaves and stems.

Fresh weight of tubers and foliage.

Conductivity readings (C2 or T2) were recorded. The level of injury was calculated as relative injury (RI) as described previously (3):

RI (%) = 1 - {[(1 - (T1/T2)) / (1 - (C1/C2))]} * 100

where T and C refer to conductance values of heat-treated and control tubers, respectively, and subscripts 1 and 2 refer to initial and final (autoclaved) conductance readings, respectively.

Results

Visual Observations

All experimental plants were similar in size at initiation of the heat stress period. During the heat stress period only, new emerging leaves in the NBS treatment, but not in the NDS or Ca+NDS treatments, showed symptoms of Ca deficiency such as tip burn and leaflet curling and rippling. In contrast, none of the plants showed symptoms of nitrogen deficiency.

Fresh Weight of Leaves, Stems and Tubers at Harvest

Dramatic differences among treatments in biomass accumulation and partitioning were observed at harvest (Table 2). Leaf fresh weight of Ca+NDS plants was 30% and 19% greater than NBS and NDS plants, respectively, but the difference between Ca+NDS and NDS treatments was not significant. Similarly, the leaf/stem fresh weight ratio was significantly increased in NDS and Ca+NDS plants compared to NBS plants. Fresh weight of tubers and total biomass (foliage + tubers) was significantly greater in the Ca-NDS treatment compared to the other treatments. None of the treatments affected total foliage (leaves + stems) fresh weight.
Table 3.—Influence of calcium and nitrogen application on cellular membrane thermostability as determined by ion leakage (electrical conductivity test) following exposure of leaf disks to 45 C for 1 hr (details in Methods).

<table>
<thead>
<tr>
<th>Nutrition treatment</th>
<th>Before heat stress</th>
<th>2 weeks of heat stress</th>
<th>4 weeks of heat stress</th>
</tr>
</thead>
<tbody>
<tr>
<td>NBS</td>
<td>61.4 a</td>
<td>58.6 a</td>
<td>52.2 a</td>
</tr>
<tr>
<td>NDS</td>
<td>65.2 a</td>
<td>49.3 b</td>
<td>47.0 ab</td>
</tr>
<tr>
<td>Ca+NDS</td>
<td>61.8 a</td>
<td>47.8 b</td>
<td>44.2 b</td>
</tr>
</tbody>
</table>

Means within the same column followed by the same letter are not significantly different (α=0.05; Duncan’s Multiple Range test).

Also, tubers comprised a significantly higher percent of total biomass in Ca+NDS plants compared to NBS, but not NDS, plants (Table 2).

Leaf Ca Concentration and Transpiration Rate

At all points of measure, leaf Ca concentration and transpiration rate were greatest in Ca+NDS plants (Fig. 1). At the conclusion of heat stress, NDS leaves had higher Ca levels than NBS leaves (Fig. 1A). When measured two weeks after the conclusion of the heat stress period, leaf Ca concentration had declined further in NBS and NDS plants but concentrations in Ca+NDS plants had increased (Fig. 1A). Ca+NDS plants maintained nearly constant transpiration rates which were significantly greater at all points of measure than rates of NBS and NDS plants (Fig. 1B). However, transpiration rates of NBS and NDS plants declined dramatically but were comparable during the heat stress period (Fig. 1B). But, when measured two weeks after conclusion of the stress period, the transpiration rate of NDS plants had increased and was significantly greater than NBS plants (Fig. 1B).

Area, Fresh and Dry Weight of Recently Mature Leaves

None of the treatments affected leaf area or weight prior to heat stress (Fig. 2). However, NDS and Ca+NDS plants displayed ca. 35% greater leaf area than NBS plants after exposure to heat stress (Fig. 2A). The difference between NDS and Ca+NDS treatments in leaf area was not significant during heat stress (Fig. 2A). Fresh (Fig. 2B) and dry (Fig. 2C) weights of the same leaves (leaf used for area measurement) showed trends similar to leaf area (Fig. 2A) throughout the heat stress period.
FIG. 1. Nutrient application effect on leaflet Ca concentration and transpiration rate measured during and after a heat stress period. The same leaflet was used for both measures. Values are the mean of 4 single-leaf replicates ± S.D. Values within the same time and labelled with the same letter are not significantly different by Duncan's Multiple Range test (α=0.05). NBS [], NDS (O), Ca+NDS (○).
FIG. 2. Nutrient application effect on leaf area and fresh and dry weight measured during heat stress. The same leaf was used for all measures. Values are the mean of 4 single-leaf replicates ± S.D. Values within the same time and labelled with the same letter are not significantly different by Duncan's Multiple Range test (α=0.05). NBS ( ), NDS ( ), Ca+NDS ( ).
Cellular Membrane Thermostability

Membrane thermostability, expressed as relative injury (RI), was not influenced by nutrition treatment before the initiation of heat stress (Table 3). Although NDS and Ca+NDS plants had similar RI values during heat stress, Ca+NDS plants consistently had the lowest RI values and significantly greater membrane thermostability than NBS plants after four weeks of heat stress (Table 3).

Discussion

Results of the present study suggest that the impact of heat stress on some aspects of potato growth can be mitigated by Ca and N application during stress. Although we do not know the mechanisms by which Ca and N nutrition during heat stress might benefit plant growth, our results provide some insight into these mechanisms. For example, the N application method may have contributed to the greater leaf area values observed in NDS and Ca+NDS plants compared to NBS plants. All plants received the same total amount of N but 33% of the total N in NDS and Ca+NDS plants was applied during heat stress, whereas all N was applied before heat stress in NBS plants. It is possible that NBS plants used proportionally more N than other plants before and during the early part of the heat stress period. This may have led to lower N in the soil for the NBS plants later in the heat stress period compared to N available for NDS and Ca+NDS plants. It is possible, then, that NDS and Ca+NDS plants benefitted from greater rhizospheric N levels during heat stress. Of course, measures of soil N (not completed in the present work) would be required to clarify this issue. However, it is important to note that no systematic effects of N application timing on potato tuber yield have been found under normal field growing temperatures (8, 10, 16, 28).

Our results show that Ca and N application during heat stress resulted in greater membrane thermostability in leaf tissue compared to N application before stress (Table 3). Membrane thermostability was affected by treatment only during the heat stress period (Table 3). Cell membranes are thought to be a site of cellular and sub-cellular response to heat stress (2, 17) since maintenance of differential membrane permeability is a fundamental requirement for normal metabolism and plant survival. Calcium may reduce heat-induced ion leakage by stabilizing cell membranes and allowing normal function of ion transport mechanisms (5, 17, 29). Since young leaves of NBS plants developed advanced calcium deficiency symptoms during heat stress, higher Ca levels may be beneficial under these stress conditions.

In this study, greater leaf Ca levels and transpiration rates were recorded in plants supplied with additional Ca during heat stress. A mechanistic relationship among these variables is unknown but accepted aspects of Ca nutrition may be relevant in this regard. For example, Ca transport in the xylem is primarily by mass flow and the delivery rate to
leaves is influenced by transpiration rate (4). Our data support the hypothesis that plants with higher transpiration rates will accumulate comparatively higher levels of calcium. Low levels of Ca may hinder stomatal function since the selectivity of potassium uptake by guard cells has been found to be enhanced by Ca (30). Also, there is evidence that the plasma membrane H⁺-ATPase, thought to be involved in stomatal opening, is regulated through phosphorylation by a protein kinase shown to be stimulated by Ca in vitro (22). Similar activity of a protein kinase was detected in guard cell protoplasts (12). It is possible that elevated leaf Ca levels are required early in a heat stress period to reduce the likelihood that low Ca-related disruptions of cell function will occur. Sufficient Ca during heat stress may assist in stabilizing stomatal function, promote additional Ca accumulation, and allow for greater transpirational cooling and carbon fixation.

Our data demonstrate a significant increase in tuber yield in plants supplemented with Ca and N during heat stress (Table 2). Exposure to heat stress after tuber initiation likely minimized the inhibitory effect of heat stress on tuberization (6) in this study. Therefore, differences in tuber yield may have resulted from plants' differential ability to fix carbon and partition photosynthate to tubers. Greater tuber yield in the Ca+NDS, but not NDS, treatment compared to the NBS treatment demonstrates that N application alone during heat stress was insufficient to maintain tuber yield in this study. These results suggest that the combination of Ca and N nutrition may have a specific role in maintaining tuber yield under heat stress. The proposed effect of calcium on stomatal function (30) may be important in this regard.

We have conducted parallel studies in the Biotron facility under heat stress and non-stress conditions using the same soil and plant material as used in the present study. In previous experiments, neither Ca nutrition nor nitrogen application timing significantly affected biomass accumulation or partitioning under non-stress conditions (26, 27). Furthermore, in our field studies, tuber yield was significantly affected by Ca and N application during tuber bulking only in the hot and dry 1988 season (17). No yield differences were apparent in normal seasons (10, 28).

In conclusion, results of this study suggest that the negative effects of heat stress: (i) on potato leaf growth can be mitigated by application of Ca or N during the stress period; and (ii) on stomatal function can be mitigated by Ca and N application during the stress period. In addition, plants given supplemental Ca and N during heat stress had significantly greater tuber yield at the completion of the study.

Literature Cited


"Calcium Accumulation in Potato Tubers: Role of the Basal Roots"

1) Calcium taken in by basal roots is transported into the plant, but not into the tubers.

2) Calcium taken in by tuber roots and stolon roots is transported into the tuber.
Calcium Accumulation in Potato Tubers: Role of the Basal Roots

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Additional index words. Solanum tuberosum, potato tuber roots, stolon roots, calcium placement

Abstract. Using a divided-pot system, the supplies of Ca to the tuber region and to the basal root region of potato plants (Solanum tuberosum L.) were controlled separately. Addition of Ca to the basal root region did not increase the Ca concentration in the tubers over that of the field-grown tubers. Addition of Ca to the stolon and tuber region, however, resulted in an over 3-fold increase in the Ca concentration of the tuber peel and medullary tissue. These results suggest that a) the main root system (basal roots) does not contribute to Ca accumulation in the potato tuber and b) tuber Ca content can be increased by placing Ca in the tuber and stolon area.

Potatoes are much lower in Ca than the above-ground vegetative portion of the plant (4). While most soils provide sufficient Ca for healthy plant growth, recent studies indicate many potential benefits, such as reduced incidences of internal rust spot (2), sprout subapical necrosis (5), and soft rot during storage (9) from increasing Ca concentration in potato tubers.

Previous work has shown that there are different types of roots applying water to the potato plant (7). The basal roots (BR) and stem–stolon junction roots (ST, Fig. 1) that arise from the main stem were found to supply water primarily to the above-ground vegetative portion of the plant. However, small roots growing from the stolons and tubers were found to transport water to tubers under field conditions (7). Since Ca moves primarily with the water flow in the xylem (1), Ca uptake by the tuber may be affected greatly by the location of Ca additions. The purpose of this investigation was to determine if the placement of Ca in different root areas affects the amount of Ca accumulated by the tubers. Specifically, the contribution of the basal roots to tuber Ca was studied.

Potato plants (cv. Red Pontiac) were started from tissue culture to ensure genetically uniform plants. The plants were grown in sand in a growth chamber for 6 weeks. At this time, stolons had initiated. The intact plants were then removed from the sand and placed in a divided pot (Fig. 1). Five-gallon (18.9-liter) pots (30 cm in diameter) were separated horizontally into 2 sections by a plastic bag. A slit of about 0.5 cm was cut in the center of the bag and the plant was threaded through the slit until the basal roots were in the bottom half of the pot and the tubers and stolons were in the top half of the pot (Fig. 1). The bottom half of the pot was filled with a peat–vermiculite mixture (Jiffy Mix, JPA, East Chicago, Ill.). The top half of the pot was watered with a chloride tube placed along the side of the pot (Fig. 1). The top half was cut directly from the surface. The lower half had drainage holes at the bottom of the pot, and drainage holes were cut in one side of the pot. The plants were grown in a greenhouse with supplemental light to provide a 14-hr day.

For the first 3 months, each half of the pot was watered with 750 ml of half-strength Hoagland's nutrient solution 6 times every 3rd day. During the 3rd month, the same amount of nutrient solution was added every other day. This nutrient solution contained Ca at 100 mg·liter⁻¹. In order to prevent leakage of nutrients from the top half into the bottom half, the peat–vermiculite mixture in the top and bottom halves was never saturated. After the 3rd month, the pots were divided into 3 groups. Three pots were watered with half-strength Hoagland's solution and were designated as controls. The top halves of 3 other pots were watered with half-strength Hoagland's solution that contained CaCl₂ at 3000 mg·liter⁻¹, while the bottom half was watered with normal half-strength Hoagland's solution containing 100 mg·liter⁻¹. In the last 3 pots, the bottom half of the pot was watered with the 3000 mg·liter⁻¹ solution while the top half was watered with normal half-strength Hoagland's solution. The plants were harvested one month later. Tubers >2 cm long were sampled from each pot.

The tubers were rinsed in distilled water after harvest and stored in a cool, dark room until analysis.

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1Graduate Student.
2Associate Professor.

Table 1. Calcium content of outer layers of potato tubers.

<table>
<thead>
<tr>
<th>Calcium concentration (mg·liter⁻¹) in the nutrient solution applied to</th>
<th>Calcium concentration in tubers (mg·g⁻¹)</th>
<th>Peel tissue</th>
<th>Medullary tissue</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stolon and tuber area</td>
<td>Basal root area</td>
<td></td>
<td></td>
</tr>
<tr>
<td>100</td>
<td>100</td>
<td>0.09 ± 0.07</td>
<td>0.05 ± 0.02</td>
</tr>
<tr>
<td>100</td>
<td>300</td>
<td>0.09 ± 0.07</td>
<td>0.05 ± 0.01</td>
</tr>
<tr>
<td>0.07 ± 0.03</td>
<td>0.18 ± 0.02</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field-grown</td>
<td>0.08 ± 0.02</td>
<td>0.04 ± 0.04</td>
<td></td>
</tr>
</tbody>
</table>

Mean ± SD.

Results are the average of 9 different samples. Each sample consisted of a separate potato. Three potatoes were sampled from each pot. For comparison, Ca content of field-grown potatoes also is presented.

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at 4°C until they could be processed. The Ca concentrations of the surface and medullary tissue were determined. For this purpose, the tubers were peeled to obtain about 1 mm of outermost layer of the tuber. Two additional 1-mm-thick layers were then peeled and collected from each tuber. These latter layers contained the cortical tissue under the skin and included the xylem ring of the tuber. This tissue was termed the medullary layer. The samples were dried in an oven at 60°C, ground to pass a 20-mesh screen, ashed at 450°C, and the ash was dissolved in 2 N HCl. This solution was diluted with a lanthanum chloride solution to obtain a resulting solution in 0.2 N HCl and LaCl₃ at 2000 mg·liter⁻¹. The Ca concentration of the samples was determined by atomic absorption spectrophotometry.

The field plants were grown at the Univ. of Wisconsin Experimental Station at Hancock, in Summer 1984. The soil at the Hancock location is a sandy loam with a pH of 5.9. The soil Ca level was about 650–750 kg·ha⁻¹. No additional Ca was added. The fertilizers applied were 400 kg·ha⁻¹ of 0N-0P-50K as preplant broadcast, 600 kg·ha⁻¹ of 6N-24P-24K at planting, and 300 kg·ha⁻¹ of 34N-0P-0K at emergence and hilling. Irrigation was based on the evapotranspiration loss and averaged to about 0.5 cm per day for the entire season.

The divided pot method successfully separated the basal roots from the rest of the underground portion of the plant. Only one pot had a few tubers growing in the bottom section, and these were not used in the analysis. The Ca concentration of the greenhouse-grown controls was close to the concentration of the field potatoes (Table 1). In the treatment in which extra Ca was added to the basal root region, the tubers had the same Ca concentration as that of control tubers (Table 1). The similarity of Ca levels in these treatments suggests that the basal roots did not contribute to Ca accumulation by the tubers. These results were anticipated from our previous study, which showed that the water from the basal roots was transported almost exclusively to the above-ground vegetative portion of the plant, bypassing the tubers (7). Wiersum also showed that movement of soil-applied ⁴⁵Ca was primarily to the leaves (10).

When Ca at 3000 mg·liter⁻¹ was added to the tuber and stolon region, there was a more than 3-fold increase in the Ca concentration of the peel and medullary tissue over that in all other treatments (Table 1). There are 2 possible explanations for this result. First, soil directly through the epidermis of the tuber. Second, the Ca could have moved with water to the tuber via the tuber roots and the stolon roots.

Kraus and Marschner (8) reported increased Ca accumulation by the tuber when Ca was added to the tuber and stolon area in a quartz sand media. Following the direct application of ⁴⁵Ca solution to the tuber surface, a rapid uptake of Ca by the tuber also was reported in this study (8). They concluded that enlarging natural conditions take up large quantities of Ca directly from the soil. Recently Davies and Millard (3) detected a high amount of ⁴⁵Ca, applied to soil, in tuber vascular ring (predominantly xylem). They estimated that about 60% of the Ca entered through the stolon roots. These results strengthen our suggestion that tuber and stolon roots play an important role in Ca uptake by the tuber. The results of the previous study (3, 8) and present study suggest that Ca uptake by the tuber roots, stolon roots, and periderm.

On a practical level, the results of the present study indicate that placement of Ca fertilizer on the plant is important for enhancing tuber Ca content. To improve Ca uptake additional Ca should be placed so that as much Ca as possible comes in contact with the stolon and tuber region and not the basal roots of the plant. For example, Ca fertilization may be more beneficial if applied to the soil surface when the plant is killed or if killed at later stage of growth.

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