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Supplemental Calcium Application Influences Potato Tuber Number and Size

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***Abstract*. Tuberization in potato is known to be under complex biochemical control involving hormones. A number of studies have provided evidence for a critical role of GA in tuberization. There is also evidence that GA in plants can be modulated by a Ca/calmodulin pathway. The purpose of the present study was to determine the influence of supplemental Ca fertilization on tuber size and tuber number. Plantlets of *Solanum tuberosum* 'Russet Burbank' raised in tissue culture were planted in 20-L pots filled with sandy loam field soil with the pH of 6.9 and exchangeable soil Ca level of 350 ppm. All treatments received the same total amount of N (equivalent to the rate of 280 kg·ha^{-1}). Four treatments were evaluated: nonsplit N (from ammonium nitrate), split N (from ammonium nitrate), split N+Ca (from calcium nitrate), split N+Ca (50% N from urea, 50% N from ammonium nitrate and Ca from calcium chloride). The total Ca was applied at the rate equivalent to 168 kg·ha^{-1} on a split schedule (equally split at four, six, eight and ten weeks after planting). Four months after planting tubers were harvested and evaluated. As expected tuber tissue Ca was increased by Ca application from 144 to 245 µg·g^{-1}. In general, the two Ca treatments had significantly lower tuber number per plant as compared to the nonsplit and split N treatments. A plot of mean tuber Ca and tuber number for individual plants showed a significant negative relationship. Both Ca treatments produced tubers with higher mean tuber weight compared to nonsplit N. This increase in tuber size with Ca application was not apparent when compared with split N treatment. These results show that Ca application to soil can decrease tuber number suggesting that soil Ca may influence tuberization in potato.**

Tuberization in potato (*Solanum tuberosum* L.) plants is a complex process that is known to be influenced by photoperiod, temperatures, and N nutrition (Batutis and Ewing, 1982; Ewing and Struik, 1992; Ewing and Wareing, 1978; Koda and Okazawa, 1983; Li, 1985; Menzel, 1985; Jackson, 1999; Snyder and Ewing, 1989). For example short days (longer than a critical length of the night period) promote tuberization (Batutis and Ewing, 1982; Ewing and Wareing, 1978; Jackson, 1999) whereas high temperatures and N inhibits tuberization (Li, 1985; Menzel, 1983, 1985). Although the exact mechanism of how environmental and nutritional factors affect tuberization is not known, many studies have implicated the role of plant hormones in modulating tuberization in potato (see for review Ewing, 1995).

Among the known hormones, the most convincing case for a critical role in the control of tuberization, has been made for gibberellin (Ewing, 1995; Jackson, 1999; Koda and Okazawa, 1983). High GA level inhibited tuberization and tuberization was promoted by reducing GA level. For example, Jackson and Prat (1996) were able to induce tuberization in long days (otherwise noninducing conditions) by inhibiting GA biosynthesis with ancymidol. Inhibition of tuberization by high temperatures has been linked to enhanced GA level and reduction in inhibitors such as ABA (Menzel, 1980). In follow up studies Menzel (1983, 1985) found that high temperatures promoted GA synthesis in the buds which reduced tuberization. Similarly the inhibition of tuberization by high N was explained in terms of increased GA level (Krauss, 1985; Krauss and Marschner, 1982). A recent study by Xu et al. (1998) also demonstrated a decrease in GA during tuber initiation in vitro cultured single node cuttings. From these studies the authors concluded GA to be a dominant regulator of tuber initiation and growth.

There is some evidence indicating the involvement of Ca in tuberization (Balamani et al., 1986). Tuberization was inhibited in a single node leaf cutting by Ca chelator EGTA and Ca ionophore A 23187. Tuberization was restored by including $CaCl_2$ in the medium. Poovaiah et al. (1996) developed a transgenic plant over expressing PCM1, a potato calmodulin isoform. These plants had reduced tuberization and exhibited a phenotype reminiscent of GA treated potato plants. Other studies on the changes in barley aleurone during germination contain evidence for the modulation of GA by Ca/calmodulin pathway (Bush et al., 1993; Gilroy and Jones, 1993). These studies have provided evidence for a powerful interaction between cytosolic Ca and GA action. Free cytosolic Ca has also been demonstrated to be a major metabolic regulator participating in the signal transduction (Hepler and Wayne, 1985; Marme, 1982; Poovaiah, 1985; Poovaiah and Reddy, 1987). In addition, the role of Ca in the maintenance of membrane integrity and cell wall strength is well established (Clarkson and Hanson, 1980; Marschner, 1995; Palta, 1996). There is also evidence for the presence of Ca-dependent and calmodulin-independent protein kinase which is thought to modulate plant growth and development (Roberts and Harmon, 1992). Thus, it is possible that Ca could regulate tuberization process in potato. In fact a recent review by Jackson (1999) suggested Ca/calmodulin to be a signaling pathway regulating potato tuberization. In the present study we report the influence of root zone Ca on tuberization.

Materials and Methods

Plants of 'Russet Burbank' were raised from micropropagated stem cuttings. For this purpose, single node cuttings were transferred to a sterile MS (Murashige and Skoog, 1962) culture media for 21 d under continuous light with about 60 µmol·m^{-2}·s^{-1} photosynthetic photon flux (PPF) from cool white fluorescent lamps (Steffen and Palta, 1986). Uniform rooted and single stemmed micropropagated plantlets were transplanted to 5 × 6 cm plant containers filled with Jiffy Mix (JPA, Chicago, Ill.). Transplants were kept covered with clear plastic for the first 2 d to minimize transplant shock and avoid desiccation. Two weeks after transplanting, plants were transferred to 20-L (30-cm-diameter) pots containing 1:1 (by volume) Plainfield loamy sand (sandy, mixed, mesic, Typic Udipsammet) and perlite. The soil for this purpose was collected from the top 15 to 20 cm layer at the University of Wisconsin–Madison Hancock Agricultural Research station. This soil is typical of that commercial production of potatoes in Wisconsin. Soil analyses gave values of 2 meq/100 g cation exchange capacity, 0.7% organic matter, and nutrients (mg·kg^{-1} soil) 66 (P), 160 (K), 350 (Ca), and 100 (Mg) (Standard soil analysis performed by University of Wisconsin Soil and Forage Laboratory). Based on a plant population of 35,960 plants/ha, the N P K requirement per plant were calculated on individual plant basis. This amounted to 7.81 g of N, 4.3 g of P and 4.3 g of K per plant. For each pot all of the P and K and some of N (1.09 g) was mixed with soil before planting.

The experiment was conducted in a greenhouse at the University of Wisconsin-Madison. A randomized complete block design with four nutrient treatments and eight replications per treatment was used. Each replication for every nutrient treatment consisted of one plant. Daily minimum and maximum temperatures were about 20/18 ºC during the experimental period. The photoperiod was 14 h with photosynthetically active radiation of 400 to 600 µmol·m^{-2}·s^{-1} at the top of the plant canopy from alternating high pressure sodium and metal halide lamps.

Two weeks after planting in the 20-L pots 3.12 g of N in the form of ammonium nitrate

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Table 1. Source and rate of N and Ca application for various treatments. All pots received the same total amount of N (7.81 g/plant equivalent to 280 kg·ha^{-1}). All Ca treated pots received same total amount of Ca (4.68 g/plant equivalent to 168 kg·ha^{-1}) from different source. Nitrogen at 0 and 2 weeks after planting in all treatments and all application times in split N and non-split N was from ammonium nitrate.

	Amount of N and Ca applied (g/plant) at various time of applications (weeks after planting)					
	0	2	4	6	8	10
Treatment	N	N	N/Ca	N/Ca	N/Ca	N/Ca
Nonsplit N	1.09	3.12	3.6/---	---	---	---
Split N	1.09	3.12	0.9/---	0.9/---	0.9/---	0.9/---
Split calcium nitrate	1.09	3.12	0.9/1.17	0.9/1.17	0.9/1.17	0.9/1.17
Split calcium chloride+UAN[z]	1.09	3.12	0.9/1.17	0.9/1.17	0.9/1.17	0.9/1.17

[z]UAN = mixture of 50% ammonium nitrate and 50% urea (28:0:0).

was given all the plants which was the equivalent to 112 kg·ha^{-1} N (Table 1). This coincided with the emergence application for field plants. The amount and time of N applications are presented in Table 1. All treatments received identical amounts (7.81 g) of total N (equivalent to 280 kg·ha^{-1}). However, the time of N application was different in different treatments as follows.

1) Nonsplit N, all N at 4 weeks after planting (similar to hilling in a commercial practice) from ammonium nitrate (34N–0P–0K).

2) Split N, four equal split application from ammonium nitrate.

3) Split calcium nitrate (9N–0P–0K–11Ca).

4) Split UAN (28N–0P–0K, 50% N from urea+50% N from ammonium nitrate) at 4, 6, 8, and 10 weeks after planting. These fertilizers were purchased from FS Cooperative, Wis.

All Ca treatments received the same total amount of Ca (4.68 g/plant equivalent to 168 kg·ha^{-1}) either from calcium chloride (0N–0P–0K–27.3Ca) or calcium nitrate (9N–0P–0K–11Ca) as four equal split applications at 4, 6, 8, and 10 weeks after planting. The amount and time of Ca applications are presented in Table 1. All nutrients were dissolved in water and given to the plants by pouring at the top of soil. Leachate from each pot if any was collected and given back to the same plant.

Tubers were harvested at 125 d after planting. At harvest, tubers from each pot were rinsed free of soil, weighed individually and graded (<56 g, ≥56g). After grading, five tubers (≥56 g) were collected for the determination of tissue calcium concentration. Samples for tissue calcium analysis were obtained by removing a 1-cm-thick longitudinal slice from the center of each tuber. The periderm and most of the cortex were removed from the tissue with a razor blade and discarded. The remaining nonperiderm tissue was prepared for Ca analyses as described by Kratzke and Palta (1986). For this purpose the samples were dried in an oven at 70 ºC, ground, weighed and ashed (450 ºC, 6 h). The ash was then dissolved in 2 N HCl. This solution was diluted with a lanthanum chloride ($LaCl_3 \cdot H_2O$) solution and distilled-deionized water to obtain samples in a final concentration of 0.2 N HCl and 2000 mg·L^{-1} of lanthanum chloride. Ca concentration was determined by atomic absorption spectrophotometry (Varian model Spectraa-20, Varian Associates, Inc., Sunnyvale, Calif.).

Analyses of variance (ANOVA) were performed to test treatment effects on tuber Ca concentration, total tuber yield, total tuber number, mean tuber weight and the proportion of tubers >56 g by using the general linear model procedure of Statistical Analysis System (version 7). Data were analyzed and effects were considered significant if $P \leq 0.05$. After completing the ANOVA, LSD test (alpha = 0.05) was used to compare treatment mean values.

Results

Application of Ca either from calcium chloride or calcium nitrate increased the Ca concentration of the tuber nonperiderm tissue as compared to split and nonsplit N controls (Fig. 1 and Table 2). Tissue Ca concentration was highest when calcium chloride was used together with UAN. The nonperiderm Ca concentration increased from 144 ppm in the nonsplit control to 245 ppm in the calcium chloride treatment. Although split N application tended to increase the average nonperiderm Ca concentration as compared to nonsplit N, this increase was not significant. There were no significant differences in total tuber yield (mass) per plant among treatments (Fig. 2 and Table 2).

Overall total tuber number per plant was significantly influenced by the application of Ca (Table 2 and Fig. 3). Plants given Ca produced fewer tubers than the nonsplit N and split N controls (Fig. 3). Split application of calcium nitrate produced the lowest number of tubers per plant (Fig. 3). However, there was no significant difference among the two sources of Ca for the tuber number per plant (Fig. 3). Average tuber number per plant was 15 in the calcium nitrate treatment as compared to 24 and 21 for the nonsplit and split N treatments respectively. Mean tuber weight was higher in the Ca treated plants as compared to the nonsplit N control but not when compared to split N control (Fig. 4 and Table 2). There was a significant difference among treatments for the proportions of tuber greater than 56 g at $p = 0.1$. However, this differences was not significant at $p = 0.05$ (Table 2). Average tuber weight was highest in the calcium nitrate treatment. In this treatment mean tuber weight was about 60 g as compared to 42 g in the nonsplit N treatment (Fig. 4).

In both the Ca treatments, nearly 50% of the tubers had tuber weight greater than 56 g (Fig. 5). However, only 29% of the tubers were >56 g in the nonsplit N control treatment. The split N treatment tended to produce larger tubers than the nonsplit N but these differences were not significant.

A scatter plot of tuber tissue Ca level and total tuber number for each individual plant is shown in Fig. 6. A quadratic fit showed a significant negative relationship between tuber Ca and tuber number per plant. As the mean tuber Ca content increased from 100 to 240 ppm the tuber number per plant decreased from about 25 to 15.

Discussion

Wisconsin soils routinely show ammonium acetate-extractable Ca levels of 250 to 1000 mg·kg^{-1} soil (Simmons and Kelling, 1987; Kleinhenz et al., 1999). The soil used in this study had a Ca level of 350 mg·kg^{-1}, which is considered adequate to satisfy vegetative plant demand for Ca (Simmons and Kelling, 1987; Kleinhenz and Palta, 2002). Consistent with this expectation, our plants grew normally without any Ca deficiency. Our results showed that in this soil split application of Ca at the equivalent to 168 kg·ha^{-1} from either calcium nitrate or calcium chloride increased tuber Ca concentration in nonperiderm tissue (Fig. 1). These results are

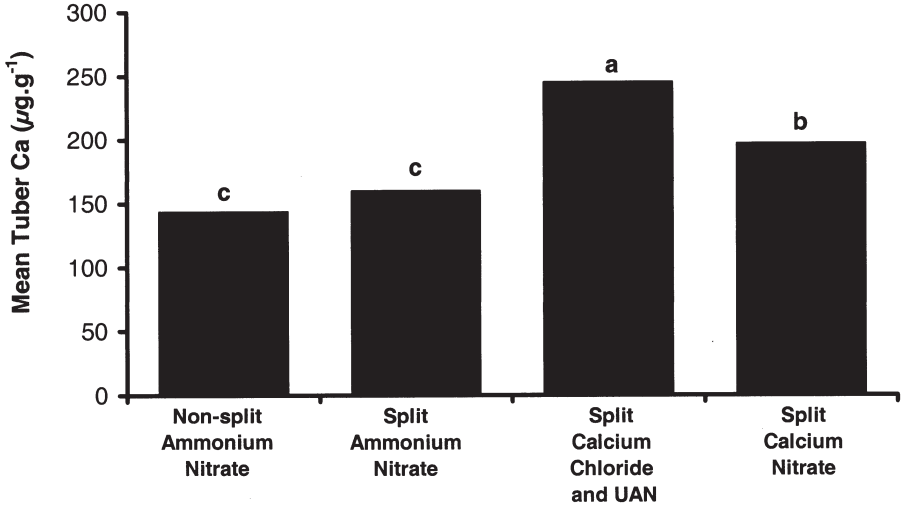

Fig. 1. Treatment effects on nonperiderm tissue Ca concentration of potato tuber. Plots depict the mean tuber Ca (μg·g^{-1} dry weight) for treatments. Mean values that have the same letter are not significantly different based on the SAS general linear model procedure. LSD (alpha = 0.05).See Table 1 for details of treatments.

Table 2. Analyses of variance (ANOVA) for treatment effects.

Variable	F value	*P*
Mean tuber calcium	8.81	0.0003
Total tuber yield	1.19	0.3328
Total tuber number	5.70	0.0035
Mean tuber weight	3.12	0.0418
Proportion of tubers >56 g	2.68	0.0658

consistent with previous studies (Kleinhenz et al., 1999) and show that application of soluble forms of Ca during the tuber bulking period can enhance the Ca level in nonperiderm tissue. Some tubers of the cultivar 'Russet Burbank' have been shown to have tiny roots growing directly out of the tubers during tuber growth and development (Kratzke and Palta, 1985; Struckmeyer and Palta, 1986). These functional roots were shown to be capable of supplying water and inorganic nutrients to the tubers (Kratzke and Palta, 1985). More recently direct evidence for the transport of soil Ca to the tuber via tuber and stolon roots has been presented using ^{45}Ca (Busse and Palta, 2003). Since Ca moves in the xylem along with water, tuber and stolon roots could carry nutrients such as Ca to the tubers (Palta, 1996). From these studies it was suggested that by the application of Ca in the soil surrounding the tuber one should be able enhance tuber Ca uptake. Later field studies confirmed this suggestion (Gunter et al., 2000; Karlsson et al., 2001; Kleinhenz et al., 1999; Ozgen et al., 2000). The results of our study (Fig. 1) are consistent with these previous studies and support the concept that tuber Ca concentration can be significantly increased by supplemental Ca application.

This study provides evidence that supplemental Ca application can alter tuberization. This research suggests that addition Ca to soil during the tuberization period can reduce tuber number (Table 2 and Fig. 3). This means that an increased Ca concentration in the soil may suppress the tuberization signal. The fact that both sources of Ca (calcium chloride and calcium nitrate) were able to reduce tuber number further suggests that the observed decrease in tuber number is due to Ca and not the counter anion. The mechanism by which soil Ca may alter tuberization is not known. The tuberization signal is known to be under complex biochemical control involving hormones (Ewing, 1995). There is strong evidence for a critical role of GA in tuberization (Ewing, 1995; Jackson, 1999; Koda and Okazawa, 1983; Xu et al., 1998). There is also evidence that GA in plants can be modulated by a Ca/calmodulin pathway (Bush et al., 1993; Gilroy and Jones, 1993). Thus, an increase in Ca concentration in the soil may be suppressing tuberization signal by increasing GA. Similarly a decrease in soil Ca may increase tuberization by decreasing GA levels. Further studies are needed to shed light on the mechanism(s) by which soil Ca may modulate tuberization in potato.

Although the main influence of soil Ca was on tuber number our data show that application of Ca during bulking increased tuber weight (Table 2, Figs. 4 and 5). If photosynthetic capacity of the plant remained constant one would expect larger tubers as tuber number

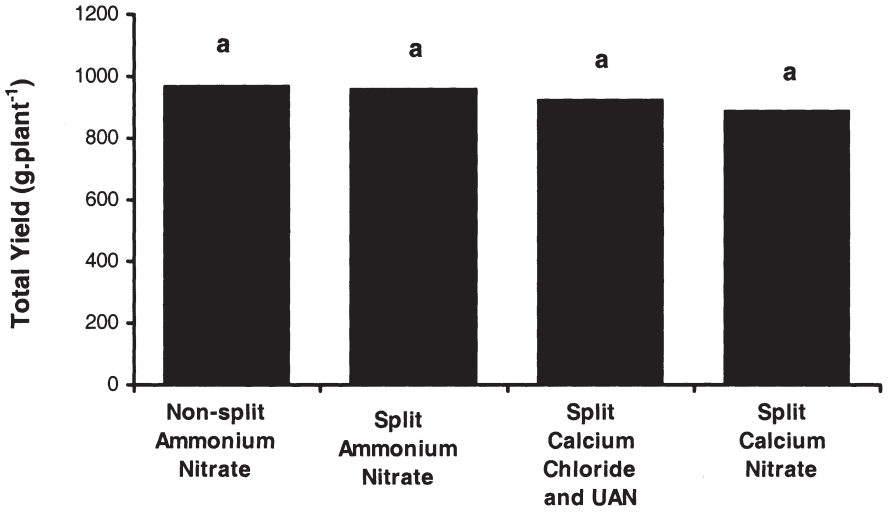

Fig. 2. Treatment effects on total tuber yield. Plots depict the total yield (g/plant) for treatments. Mean values that have same letter are not significantly different based on SAS general linear model procedure. LSD (alpha = 0.05).

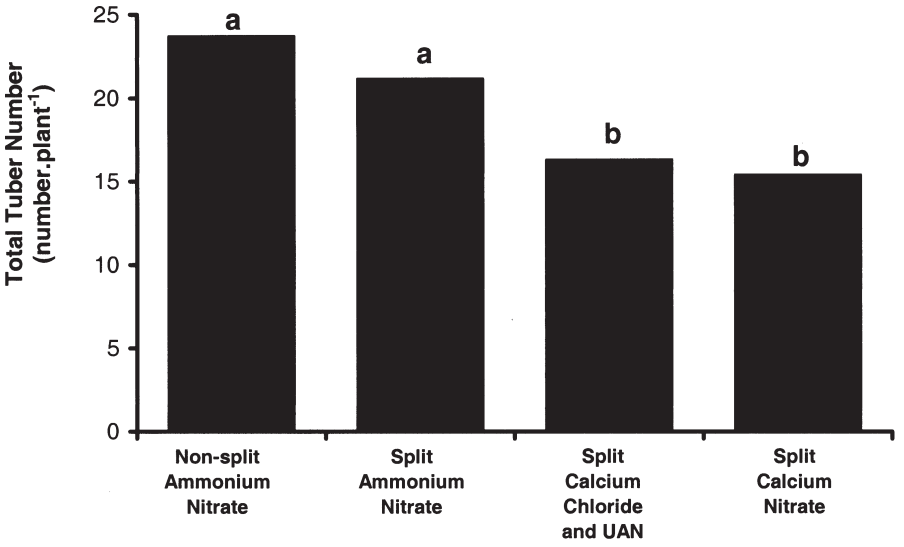

Fig. 3. Treatment effect on total tuber number. Plots depict the total tuber number (number of tubers/plant) for different treatments. Mean values that have same letter are not significantly different based on SAS general linear model procedure. LSD (alpha = 0.05).

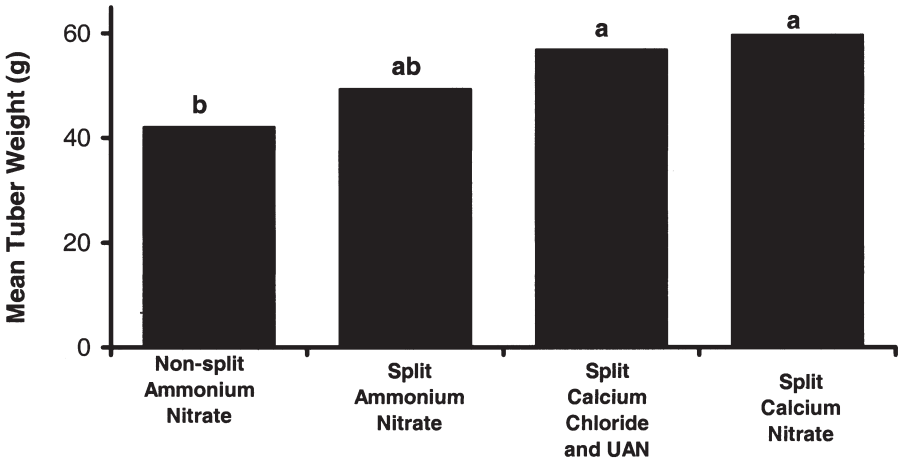

Fig. 4. Treatment effect on tuber weight. Plots depict the mean tuber weight (g) for different treatments. Mean values that have same letter are not significantly different based on SAS general linear model procedure. LSD (alpha = 0.05).

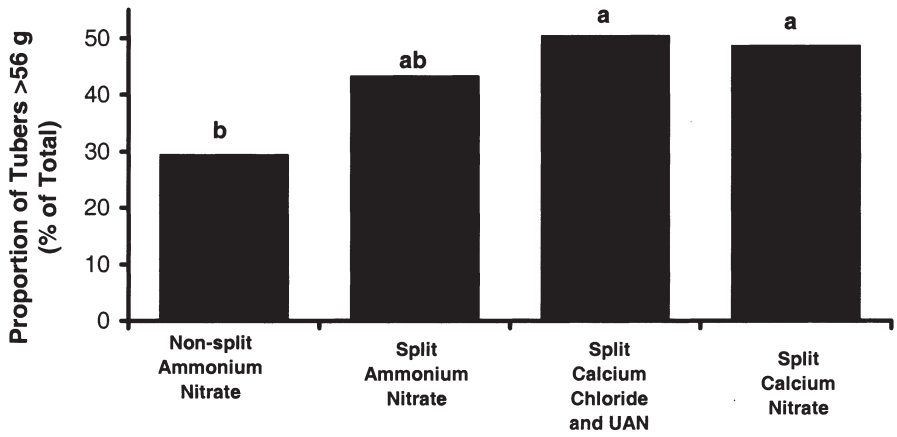

Fig. 5. Treatment effect on tuber grade. Plots depict the proportion of tuber >56 g (% of total) treatments. Mean values that have same letter are not significantly different based on SAS general linear model procedure. LSD (alpha = 0.05).

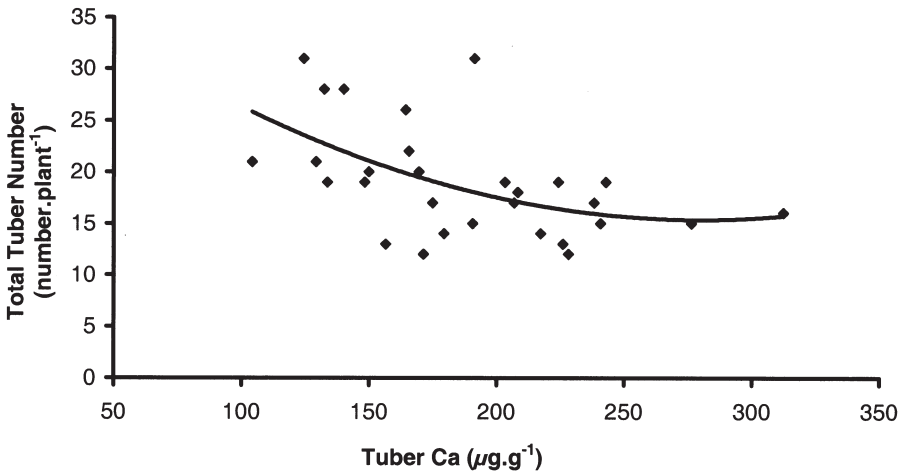

Fig. 6. Scatter plot of the relationship between non-periderm tissue Ca and total tuber number per plant. Each point indicates the tuber Ca concentration and tuber number of an individual plant. Quadratic equation (Pearson correlation) provided best fit for these data set. Model for the graph is $y = 0.0003x^2 - 0.1897x + 41.906$. $R^2 = 0.2782$. Significant at $P < 0.05$.

per plant decreased. The fact that total tuber yield was not affected by soil Ca application further supports that explanation. These results are also consistent with those reported by Simmons and Kelling (1987). They reported an improvement in tuber grade by supplemental Ca application under field conditions in a sandy soil. They however did not report any data on tuber number. Larger tuber size especially in the Russet varieties is commercially desired. However, seed growers desire larger number of small size tubers. Results of our study may have important implications for commercial production of potatoes. By manipulating soil Ca levels growers may be able to manipulate tuber number and size.

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