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Impact of Source and Timing of Calcium and Nitrogen Applications on 'Atlantic' Potato Tuber Calcium Concentrations and Internal Quality

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Abstract. **Three Ca sources and two application schedules were compared for their effectiveness for increasing tissue Ca concentrations in 170 to 284 g field-grown tubers of 'Atlantic' potato (*Solanum tuberosum* L.). Additional observations were made of internal physiological defects. Paired measures of tissue (periderm and nonperiderm) Ca concentration and internal quality (±hollow heart, ±internal brown spot) were made on individual tubers produced in plots fertilized with N at 224 kg·ha^{-1} and Ca at either 0 or 168 kg·ha^{-1}, supplied from either gypsum, calcium nitrate or NHIB (9N–0P–0K–11Ca, a commercial formulation of urea and $CaCl_2$). Application of N and Ca at emergence and hilling (nonsplit) was compared to application at emergence, hilling, and 4 and 8 weeks after hilling (split). Tuber yield and grade were unaffected by treatments. Split Ca application (from either calcium nitrate or NHIB) increased mean tuber nonperiderm tissue Ca concentrations and the percentage of tubers with an elevated Ca concentration in both years compared with non-Ca-supplemented controls. Split Ca application also resulted in greater increases in Ca in nonperiderm tissue than nonsplit Ca application in 1994. Although the correlation coefficient between Ca level in periderm and nonperiderm tissue of >400 individual tubers was highly significant in both study years, linear regression analyses suggested the Ca level in the two tissues were poorly related. Split application was associated with a 37% reduction in the incidence of internal tuber defects, relative to nonsplit application in 1994. Calcium application did not affect tuber internal quality based on means analysis, but chi-square analysis suggested that Ca concentration and internal quality of individual tubers may be related. The incidence of internal defects was 16.4% in tubers with nonperiderm tissue Ca ≤100 μg·g^{-1} dry weight compared to 10.6% in tubers with nonperiderm tissue Ca >100 μg·g^{-1} dry weight. These data suggest that 1) it is feasible to increase tuber Ca levels by field applications of moderate amounts of Ca, 2) tuber quality is impacted by N and Ca application schedule, and 3) Ca concentrations in tuber periderm and nonperiderm tissues may be controlled independently.**

Increases in plant tissue Ca concentration are more likely to result from altered flux of Ca in xylem sap than from increasing Ca supply to roots (Kirkby, 1979; Marschner, 1995). However, previous reports suggest that this hypothesis does not apply to Ca in potato (*Solanum tuberosum*) tubers (Kratzke and Palta, 1985, 1986; Simmons et al., 1988). For example, Kratzke and Palta (1985) demonstrated that water taken up by the main basal roots of the potato plant bypasses tubers and is delivered to aboveground tissue. The same authors then used a split-pot approach to fertigate zones containing either developing tubers or main roots of individual plants separately (Kratzke and Palta, 1986). Tuber Ca levels were affected by the Ca supply to the region containing developing tubers, but not main roots (Kratzke and Palta, 1986). These studies were instrumental in developing the hypothesis that tuber Ca concentrations are dictated primarily by the amount of Ca taken up by roots arising directly from stolons and tubers (Kratzke and Palta, 1986), in addition to direct tuber uptake from soil solution (Marschner, 1995). If true, the form, placement, and timing of Ca application would impact the efficacy of field-based Ca treatments intended to increase tuber Ca (Kratzke and Palta, 1986). The available evidence suggests the Ca concentration of the soil solution surrounding, but not beneath tubers, dictates primarily tuber Ca concentration (Kratzke and Palta, 1986).

Seasonal applications of N in combination with adequate soil moisture availability probably optimizes tuber yields and quality of 'Russet Burbank' potato (McCann and Stark, 1989; Ojala et al., 1990; Stark et al., 1993), especially in years when leaching occurs. Water potential gradients between foliage and tubers also affect tuber Ca levels (Win et al., 1991). Because moisture and fertility requirements change during crop development, a goal of in-season management is to supply adequate soil moisture and fertility at each crop stage, thereby avoiding excessive inputs, which reduce profits and increase the likelihood of groundwater contamination (Ojala et al., 1990).

Localized tissue Ca deficiencies are implicated as a mechanism initiating cell death and tissue necrosis (Bangerth, 1979; Collier et al., 1980; Levitt, 1942; Olsen et al., 1996). Necrotic lesions in potato tubers referred to as brown center, internal brown spot, internal heat necrosis, and internal rust spot may also

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be induced or exacerbated by temperature and/or moisture stress (Olsen et al., 1996; Van Denburgh et al., 1979, 1980, 1986; Win et al., 1991). Small necrotic lesions in pith tissue of immature tubers may initiate the development of large, often irregularly shaped cavities in pith tissue referred to as hollow heart (Crumbly, 1970; Dinkel, 1960; Levitt, 1942). Disproportionate and inconsistent tuber and plant growth rates after certain cultural practices also may exacerbate the incidences of hollow heart (Rex and Mazza, 1989). The relative incidence of necrotic lesions and hollow heart is genotype-specific. Tubers of 'Atlantic' are susceptible to these defects (Ehlenfeldt, 1992; Rex and Mazza, 1989; Sterrett et al., 1991; Wannamaker and Collins, 1992). When prevalent, brown center and hollow heart reduce tuber marketability and the profits, of growers. Hollow heart and brown center produce no external symptoms, and no effective method exists to identify affected tubers (Rex and Mazza, 1989; Watts and Russell, 1985).

Our objectives in these studies were to 1) compare the effectiveness of several Ca sources for increasing tuber Ca, 2) evaluate the impact of nutrient application timing on tuber yield and quality, and 3) examine the relationship between tuber Ca content and the incidence of hollow heart and brown center. We used unique methodology based on precise nutrient application and tissue Ca analysis of 839 mature tubers individually.

Materials and Methods

Plot establishment and maintenance. Certified, whole B-grade seed tubers of 'Atlantic' potato were planted on a Plainfield loamy sand (sandy, mixed, mesic, Typic Udipsamment) in 1993 and 1994 under center-pivot irrigation at the Univ. of Wisconsin-Madison Hancock Agriculture Research Station, Hancock. Soil pH was ≈6 and cation exchange capacity (CEC) ≈3 meq/100 g. Seed tubers were planted in three groups of nine rows separated by 3-m-wide drive alleys. Total length of each row was ≈70 m at planting. In-row seed tuber and between-row spacing was 30 and 91 cm, respectively. Individual plots were marked within each group of nine rows before plant emergence. The center row in each nine-row group was nontreated and used to separate experimental plots, which consisted of four adjacent rows 6 m in length. Treatments are listed in Table 1. A completely randomized design and a randomized complete block design with eight replications were used in 1993 and 1994, respectively.

Relevant preplant soil and season environmental information are presented in Table 2. Irrigation was applied as needed to replace soil water lost due to evapotranspiration. The minimum/maximum average daily air temperature for the period starting with 50% plant emergence to the time of vine desiccation was 14/26 °C in both study years. Low weed, disease, and insect pest pressures were maintained by using cultivation and minimal amounts of agrichemicals common to commercial practices in the Central Sands region of Wisconsin.

Nutrient sources. Treatments and controls consisted of eight combinations of source and application timing (Table 1). All N in the control plots and any additional N needed in Ca-treated plots was supplied as commercial-grade ammonium nitrate (34N–0P–0K). Calcium nitrate, gypsum, and NHIB, a commercially available Ca source (9N–0P–0K–11Ca) was supplied by Hydro-Agri North America (Tampa, Fla.), U.S. Gypsum (Ontario, Cal.), and Stoller Enterprises (Houston, Texas), respectively. For applications made at emergence and hilling in the calcium nitrate treatments, solid calcium nitrate (15.5N–0P–0K–19Ca) was applied. For applications made 4 and 8 weeks after hilling, liquid calcium nitrate (9N–0P–0K–11Ca) was applied. All gypsum (0N–0P–0K–20Ca) was finely granulated. For applications at emergence in the NHIB treatments, a liquid formulation (11N–0P–0K–8Ca) was used. For applications at hilling, and 4 and 8 weeks after hilling in the NHIB treatments, 75% of the Ca was supplied as liquid NHIB (11N–0P–0K–8Ca), and 25% was supplied as laboratory-grade calcium chloride ($CaCl_2 \cdot 2H_2O$).

Nutrient application. Combinations of N and Ca were applied to all four rows within each experimental plot. For all but the gypsum treatments, the material(s) required for a specific row were dispensed from a calibrated container to a single 7.5-L watering can and mixed vigorously with 6 L of irrigation water. The entire solution was then dispensed to the top of the hill uniformly along the entire length of the row and with minimal foliar contact. Runoff into the furrow was minimal due to slow application and rapid infiltration in this soil. Application was repeated in this way for all rows within each plot. Nitrogen for the gypsum-treated rows was applied in the manner, but gypsum was applied dry in bands at the base of each side of the row. Hills were mechanically reformed immediately after completion of the second application on dates listed in Table 1. Nutrient application dates listed in Table 1 coincided with the crop stages; emergence,

Table 1. Source, timing, and rate of N and Ca application to individual rows in plots of 'Atlantic' potato. All plots received the same total amount of N (224 kg·ha^{-1}) and the same total Ca (168 kg·ha^{-1}), if Ca was applied. Nutrient sources and application methods are described in the materials and methods.

	Date and rate of Ca application (kg·ha^{-1})			
Treatment	10 June 1993 and 2 June 1994	24 June 1993 and 16 June 1994	22 July 1993 and 13 July 1994	19 Aug. 1993 and 3 Aug. 1994
Nonsplit application schedule[z]				
Control	---	---	---	---
Calcium nitrate	34	134	---	---
NHIB	34	134	---	---
Gypsum	34	134	---	---
Split application schedule[y]				
Control	---	---	---	---
Calcium nitrate	34	44	45	45
NHIB	34	44	45	45
Gypsum	34	134	---	---

[z]All plots received N at 82 kg·ha^{-1} at emergence and 142 kg·ha^{-1} at hilling.
[y]All plots received N at 82 kg·ha^{-1} at emergence, 48 kg·ha^{-1} at hilling, and 47 kg·ha^{-1} at hilling + 4 weeks and hilling + 8 weeks.

Table 2. Preplant soil, season, and environmental information for experiments conducted at Hancock Agricultural Experiment Station (Waushara County, Wis.) in 1993 and 1994.

	Year	
	1993	1994
Soil information		
Preplant		
Soil type	Plainfield loamy sand (Typic Udipsamment)	
Previous crop	Cucumber (*Cucumus sativus* L.)	Alfalfa (*Medicago sativa* L.)
pH (in water)	7.0	5.9
Organic matter (%)	0.4	0.8
Average test P–K–Ca ($mg \cdot kg^{-1}$)	135–95–410	105–115–350
K application ($kg \cdot ha^{-1}$)[z]	117	112
At planting N–P–K application ($kg \cdot ha^{-1}$)[y]	28–25–146	34–30–168
Season information		
Dates		
Plant	14 May	5 May
Emergence (50%)	10 June	2 June
Vine kill	31 Aug.	18 Aug.
Harvest	14 Sept.	1 Sept.
Total days	110	105
Precipitation and irrigation[x]		
Precipitation		
Episodes	39	33
Events with > 2.5 cm	6	3
Total (cm)	47	33
Irrigation		
Episodes	11	23
Total (cm)	13	31
Total (cm)	60	64

[z]Applied broadcast as 0N–0P–50K on 13 Apr. 1993 and as 0N–0P–60K on 4 Apr. 1994.
[y]Applied banded about 5 cm to each side of seed tuber as 5N–10P–30K, impregnated with Di-syston 8 (Disulfoton, 0,0-Diethyl S-[2-(ethylthio)ethyl]phosporodithioate) insecticide in 1994 only.
[x]All information for the period from the time when 50% of plants emerged to vine kill.

hilling, and 4 and 8 weeks after hilling, respectively.

Harvest and grading. Two weeks after chemical vine desiccation, tubers were removed from the two inner rows of each experimental plot with a single-row harvester. Tubers from each of the 128 experimental rows were kept separate and, within 1 d of harvest, tubers were rinsed free of soil and graded into cull (misshapen, green, decayed), B-grade (<57 g, passing a 4.75-cm screen), and A-grade classes (57 to 114 g, 114 to 170 g, 170 to 284 g, 284 to 369 g, 369 to 454 g, and >454 g) with an electronic grader. Immediately after grading, 10 tubers from the 170 to 284 g A-grade class of each experimental row were chosen randomly and transferred to controlled storage (5 °C, ≈60% relative humidity) in Madison for measure of tissue Ca concentration and evaluation of internal quality.

Measure of tuber tissue Ca and internal quality by using individual tuber samples. All procedures described in this section were performed on individual tubers from each experimental row. After a 3- and 1-month storage period in 1993 and 1994, respectively, tubers were rated for internal quality, and tissue was sampled for Ca analysis. Individual tubers from a single experimental row were washed with a minimum volume of distilled water and peeled using an automated vegetable peeler (Dazey Stripper, model DVS 5; Rival Corp. Kansas City, Mo.). The periderm and ≈1 to 3 mm of attached cortical tissue were removed during peeling and constituted samples referred to as periderm. To ensure periderm samples of uniform thickness, peeler blades were changed after use on 30 tubers. Peeled tubers were halved lengthwise and the presence or absence of hollow heart and brown center were noted. Hollow heart was defined as a cavity (≥3 mm diameter) in the central pith region of the tuber. Brown center was defined as a dark patch (≥3 mm diameter) of necrotic tissue in the central pith region of the tuber. Cavities and necrotic lesions in all tubers examined were confined to the central, lignified, relatively translucent tissue of the pith.

One-half of each tuber was bisected longitudinally a second time after rating for internal quality. Periderm from the entire tuber and nonperiderm tissue from the quarter tuber (including defected tissue, if present) were retained and prepared for Ca analysis. Nonperiderm tissue, as defined in this study, contained all tuber tissue exclusive of periderm and 1 to 3 mm of adjacent cortical tissue. Nonperiderm samples contained the central pith but were composed primarily of parenchymous storage tissue as described elsewhere (Sieczka and Thornton, 1993). The procedure described by Kratzke and Palta (1986) was used for Ca analysis. Samples for Ca analysis were dried (70 °C, 48 h), ground to pass a 40-mesh (0.635 mm) screen, weighed, ashed (450 °C, 8 h), dissolved in 2 N HCl, and diluted with a lanthanum chloride ($LaCl_3 \cdot XH_2O$) solution and distilled–deionized water to obtain samples in 0.2 N HCl and in La at 2000 $\mu g \cdot mL^{-1}$. Duplicates of each tissue sample were prepared beginning at the weighing stage. Calcium concentration was determined by atomic absorption spectrophotometry (model SpectrAA-20; Varian Associates, Inc., Sunnyvale, Calif.).

Sampling from the ten 170 to 284 g tubers from each row

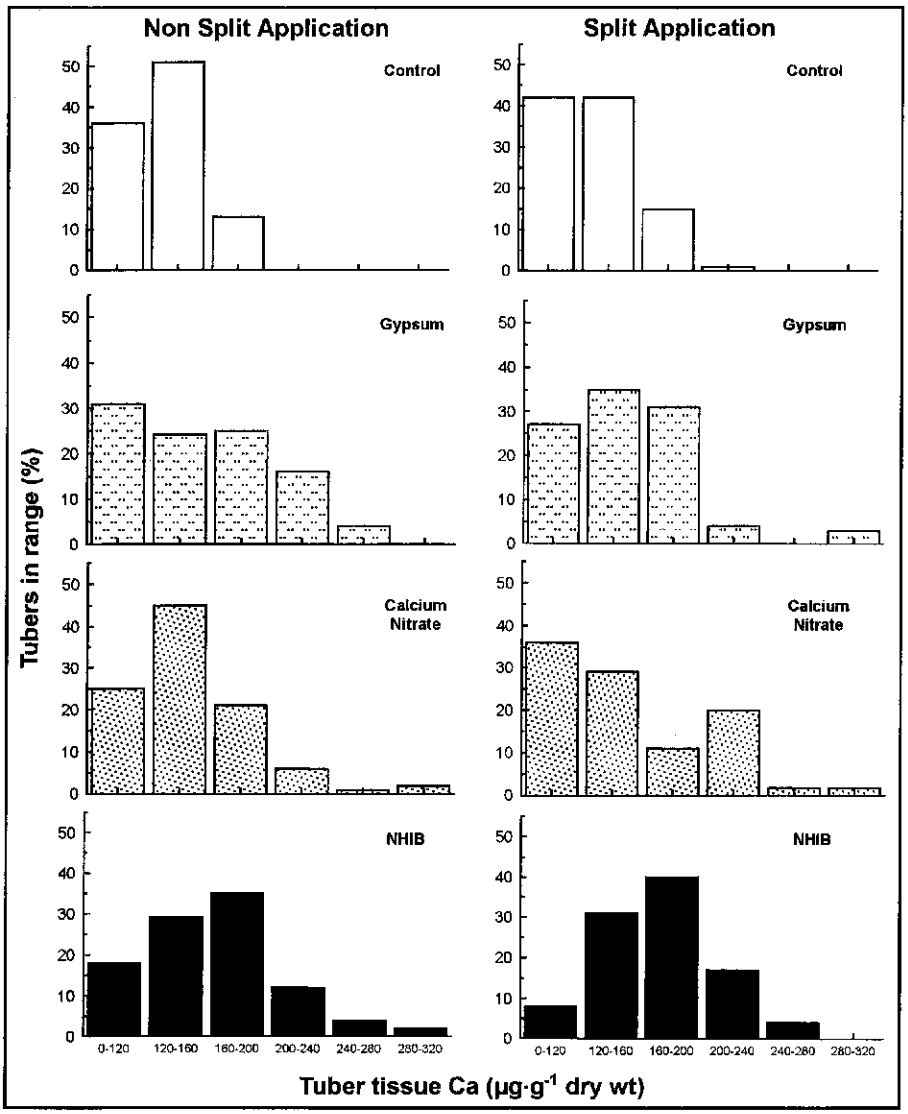


Fig. 1. Treatment effect on the distribution of Ca level values for individual tubers in 1993. Total nonperiderm tissue Ca concentration was measured in 48 to 53 separate tubers per treatment after field application of N ± Ca. Plots depict the percentage of tubers within a given range of Ca level. Left column, nutrient application at emergence (E) and hilling (H). Right column, nutrient application at E, H, and 4 and 8 weeks after hilling. See Table 1 for details.

retained at harvest continued until three tubers free of internal defect were obtained. Therefore, in both study years, 384 defect-free tubers were analyzed (3 tubers × 64 plots × 2 rows). The number of defected tubers obtained was 18 in 1993 and 53 in 1994. A total of 768 defect-free and 71 defected tubers were analyzed in this study.

Means comparison tests of average yield and Ca variables. Mean replicate values, averages of data from the two rows in each replicate (plot), were obtained for the following yield variables: total and A-grade yield (kg·ha^{-1}), percentage crop A-grade (57 to 369 g). Similarly, replicate mean values of Ca concentration in tuber periderm and nonperiderm were obtained from individual measures. Individual tuber values also permitted testing treatment effects on the variability of Ca concentration values. Variability of Ca concentration values within each treatment was estimated by calculating the mean Ca concentration for both tissue types in each treatment, and within each replicate, the absolute value of the deviation of individual tuber values from the treatment mean. The average deviation within each treatment replicate was then used in statistical analysis.

By using replicate mean values, analyses of variance (ANOVA) were performed to test nutrient application schedule and treatment effects on yield, Ca concentration, and internal quality variables by using the General Linear Models Procedure of Statistical Analysis System (SAS, version 6.09, Cary, N.C.). Data from each year were analyzed separately, and effects were considered significant if $P \leq 0.10$. Individual treatment effects were evaluated only within nonsplit and split treatment groups (i.e., among-group treatment comparisons were not made). After completing the ANOVA, Fisher's LSD test ($P = 0.05$) was used to compare treatment group mean values, and Duncan's multiple range test ($P \leq 0.05$) was used for comparisons among the four treatments within each group.

Descriptive statistics of the distribution of Ca values. Histograms depicting the percentage of tubers within specific Ca concentration ranges were prepared for each treatment by using values from the analysis of Ca in ≥48 individual tubers per treatment in each year. Concentration ranges were chosen by dividing the experiment-wide range in each year into six subranges equal in magnitude. For each treatment, the percentage of tubers within each subrange was determined and plotted (Figs. 1 and 2).

Correlation between periderm and nonperiderm tissue Ca. Paired measures of periderm and nonperiderm tissue Ca concentration were used to test the correlation in Ca concentration between the two tuber tissues. Plots of periderm Ca level by nonperiderm Ca level for >400 individual tubers per year were prepared and r values calculated.

Relationship of internal quality to nutrient application timing, treatment, and tissue Ca. Observations of internal quality in 437 individual tubers in 1994 permitted initial description of effects of field treatments and tuber Ca on the incidence of hollow heart and brown center. Data from 1993 were not included due to the low incidence (4.5%) of defected tubers. To determine the relationship between tissue Ca and internal quality, tubers were separated in two groups, tubers with a Ca level and either below or above the 25th percentile of the entire experimental range in 1994 (Ca at 100 µg·g^{-1} dry weight).

Results

Precipitation, irrigation, and season temperature. Although the relative contribution of rainfall and irrigation to total crop water input differed by year, the sum of rainfall and irrigation for the period starting with 50% plant emergence to the time of vine desiccation was similar in 1993 and 1994 (Table 2). Less rainfall in 1994 compared to 1993 required a greater amount of and more frequent irrigation in 1994 compared to 1993 (Table 2).

Storm events >2.5 cm occurred six times during the growing season in 1993 but only three times in 1994. The different irrigation schedule in the two study years resulted primarily from lower precipitation in 1994 (Table 2) and not due to frequent or prolonged elevated temperatures (data not shown).

Yield. Although ANOVA indicated that nutrient application schedule (treatment group) affected crop value in 1993, there was no difference between groups. Nonsplit treatments affected total and A-grade yield and crop value in 1993, but no differences existed among split treatments (data not shown). Treatment group, block, or treatment within treatment group did not affect any yield variable in 1994 (data not shown). The average total tuber yield was 54.3 and 50.4 t·ha^{-1} for the 1993 and 1994 seasons respectively.

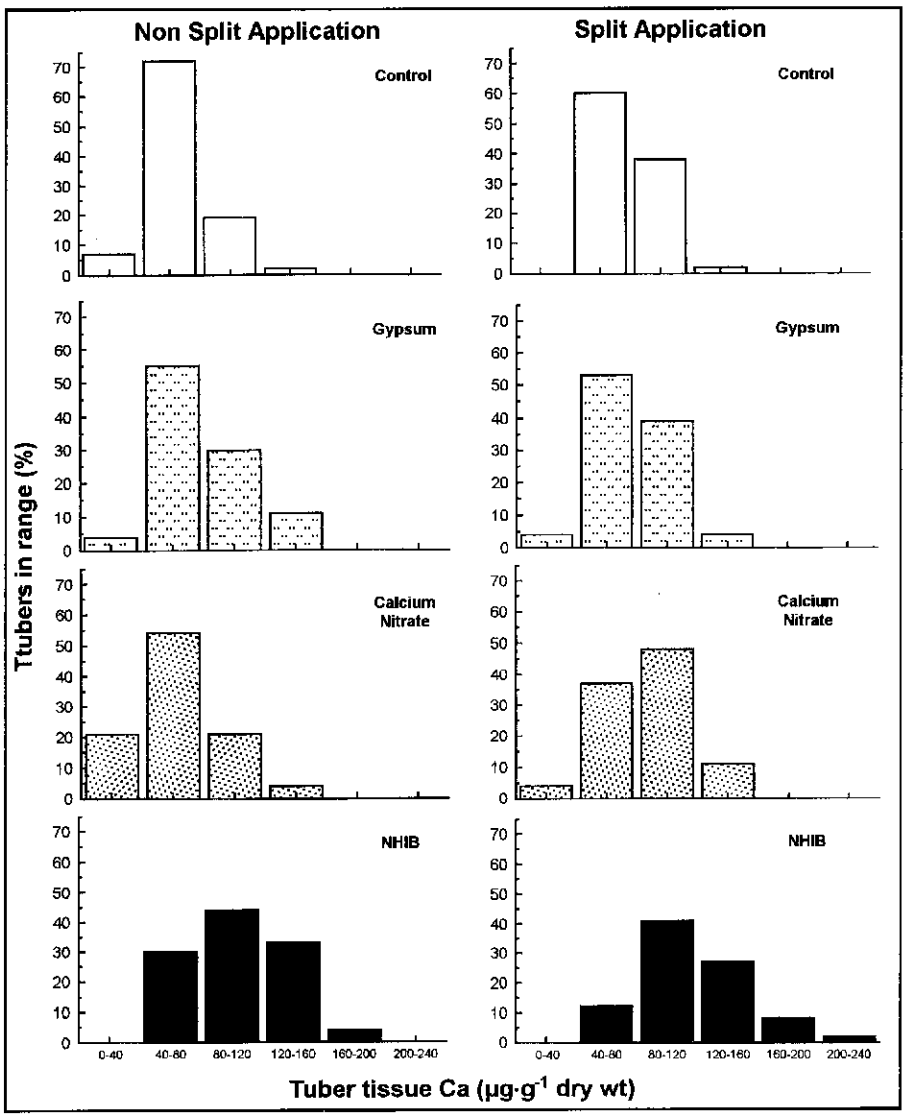
Tuber tissue Ca concentration. Split application resulted in an increase in average Ca concentration of nonperiderm tissue in 1994, but not in 1993, compared to nonsplit application (Tables 3 and 4). Treatment within both schedules affected nonperiderm Ca concentration and deviation in both study years (Tables 3 and 4) and periderm Ca concentration and deviation in 1993 (Table 3). Treatment within the nonsplit group in 1994 also significantly affected periderm Ca concentration and deviation (Table 4).

With one exception (calcium nitrate applied on the nonsplit schedule in 1994), all Ca treatments had Ca in nonperiderm tissue than those of the controls for nonperiderm tissue Ca level (Tables 3 and 4). However, differences were not always significant (Tables 3 and 4). In 1993 and 1994, tubers grown in plots treated with NHIB on the split schedule had the greatest mean nonperiderm Ca concentration value and percentage increase over the control (Tables 3 and 4). The same trend was noted for periderm Ca concentration in 1993 (Table 3) but not in 1994 (Table 4). In 1993, the rank order of treatments within both treatment schedule groups was nearly identical for Ca concentration in both tissue types; i.e., the concentration response to treatment was similar for both nonperiderm and periderm tissue in 1993 (Table 3). This was not seen in 1994 (Table 4). The rank order of treatments within both schedule groups was nearly identical for Ca concentration in both tissue types in 1993 (Table 3), but this was not the case in 1994 (Table 4). Periderm tissue had higher Ca concentrations and higher standard deviations for individual tuber values as compared to the nonperiderm Ca concentrations (Table 3 and 4).

Distributing tuber tissue Ca concentration values. The Ca concentration in like-treated tubers varied substantially (Figs. 1 and 2) and as noted above, Ca concentrations in nonperiderm tissue in nontreated tubers were distributed over a more narrow range than in tubers from Ca-treated plots. Compared to tubers from Ca-treated plots, most grown in control plots had Ca levels in the lower third of the observed experiment-wide range (Figs. 1 and 2). Calcium application in both years generally led to more tubers with greater Ca levels and broader ranges of Ca values (Figs. 1 and 2). The proportion of tubers with greater nonperiderm tissue Ca levels was higher in NHIB and calcium nitrate treatments, compared to controls (Figs. 1 and 2). For example, the NHIB, calcium nitrate, and gypsum treatments had 57%, 35%, and 38%, respectively, of the tubers with Ca > 160 µg·g^{-1} dry weight in the nonperiderm tissue as compared to only 15% of the tubers for the control treatment (Fig. 1). Gypsum and calcium nitrate treatments tended to show similar distributions. The range in overall Ca concentration in nonperiderm tissue was greater in 1993 than in 1994 (Figs. 1 and 2). Similar results were obtained for periderm Ca concentration values (data not shown).

Correlation between tuber tissue Ca concentration of periderm and nonperiderm tissue. A generally positive relationship ($P = 0.05$) between Ca in nonperiderm and periderm tissue of individual tubers existed (Fig. 3). However, substantial variability was evident, especially in 1994 (Fig. 3).

Fig. 2. Treatment effect on the distribution of Ca level values for individual tubers in 1994. Total nonperiderm tissue Ca concentration was measured in 48 to 53 separate tubers per treatment after field application of N ± Ca. Plots depict the percent of tubers within a given range of Ca level. Left column, nutrient application at emergence (E) and hilling (H). Right column, nutrient application at E, H, and 4 and 8 weeks after hilling. See Table 1 for details.



Incidence of internal quality defects. Nutrient application schedule and internal quality were associated in 1994 (Table 5). The chi-square test of the association between nonperiderm tissue Ca level and internal quality of 437 individual tubers was significant in 1994 (Table 5). Among tubers with <100 $\mu g \cdot g^{-1}$ dry weight, 16.4% showed internal defects, but only 10.6% of the tubers with >100 $\mu g \cdot g^{-1}$ dry weight were defective.

Discussion

To our knowledge, this is the first report to include data from paired measures of tissue Ca level and internal quality for a large number of mature, individual tubers. Measuring the Ca concentration in 839 individual tubers allowed us, through informative descriptive statistics, to identify treatment effects that remain unknown when bulked tuber samples are employed. For example, it is possible to describe the distribution and range of Ca concentration among tubers by using individual tuber analysis. Approaches used in previous work with individual tubers differ from our methods. For example, Arteca et al. (1980) and Mohr et al. (1984) examined comparatively fewer tubers, and Levitt (1942) analyzed Ca and internal quality in small, immature tubers. In another report, relationships among fertility regimen, tuber ionic composition, and tuber internal quality were based on bulked samples in which portions of many tubers were combined to make a single sample for Ca analysis (Clough, 1994). Alternatively, tuber internal quality and tissue Ca level were measured on different groups of tubers (Clough, 1994; Silva et al., 1991). It is not clear whether individual or bulked samples were used in other studies (Olsen et al., 1996; Tzeng et al., 1986). The average tuber Ca concentration in bulked samples may correlate with the percentage of defected tubers in the same or a different group of similarly treated tubers (Clough, 1994; Olsen et al., 1996; Tzeng et al., 1986). Data presented herein suggest that paired observations of Ca level and internal quality of many individual tubers may be an important technique in constructing inferences regarding the complex relationship between the two variables.

The first objective of this study was to determine if the Ca concentration of tuber tissue can be increased by field application of a moderate amount of Ca. The high native Ca content of many soils in Wisconsin potato production areas may make increases in tuber Ca levels after Ca application unlikely. Wisconsin soils routinely show ammonium acetate–extractable Ca levels of 500 to 1000 $mg \cdot kg^{-1}$ soil (Simmons and Kelling, 1987), and the soil used in this study had a Ca level of 350 to 410 $mg \cdot kg^{-1}$ soil. Although low for this region, Ca levels in soils used in this study exceeded those commonly thought necessary to satisfy vegetative plant demand for Ca. In this study, split application of Ca at 168 $kg \cdot ha^{-1}$ calcium nitrate or NHIB (except calcium nitrate in 1993) resulted in an increase in mean tuber Ca concentration in nonperiderm tissue (Tables 3 and 4). These results suggest that application of water soluble forms of Ca during the tuber development period can be effective in raising Ca level of the nonperiderm tissue. Internal defects in tubers occur in the nonperiderm tissue and raising nonperiderm Ca level appears to lower the incidence of internal defect (Table 5). Thus, it appears

Table 3. Treatment group and individual treatment effect on average 'Atlantic' tuber nonperiderm and periderm tissue Ca concentration in 1993. Absolute value of deviation of individual tuber values from treatment mean value is included as a measure of tuber variability within treatment. Although data of individual tubers from within two separate rows of each replicate were collected, replicate means within each treatment were employed in statistical analyses.

		Tissue Ca ($\mu g \cdot g^{-1}$ dry wt)			
		Nonperiderm		Periderm	
Group	N	Concn	Deviation[z]	Concn	Deviation
N and Ca application timing					
Nonsplit[y]	32	149.6 a	31.34 a	827.8 a	214.7 a
Split[x]	32	149.3 a	31.11 a	749.8 a	188.2 a
LSD[w]		14.4	6.41	90.2	50.0
ANOVA $P > F$		NS[v]	NS	NS	NS
Nonsplit application					
Control	8	131.0 b	20.77 b	728.6 b	150.3 b
Calcium nitrate	8	147.9 ab	30.10 ab	783.9 b	229.7 ab
Gypsum	8	153.0 ab	38.92 a	784.3 b	192.4 ab
NHIB	8	166.6 a	35.56 a	1014.7 a	286.5 a
Duncan's test		28.7	12.31	195.3	120.2
ANOVA $P > F$		0.0725	0.0159	0.0145	0.1014
Split application					
Control	8	128.0 b	22.96 b	669.2 c	138.1 b
Calcium nitrate	8	149.5 ab	41.44 a	803.5 b	164.7 ab
Gypsum	8	148.2 ab	31.19 ab	741.0 bc	214.2 ab
NHIB	8	171.7 a	28.86 ab	965.3 a	235.7 a
Duncan's test		29.7	12.98	129.8	84.9
ANOVA $P > F$		0.0268	0.0291	0.0002	0.0628

[z]For both tissue types, average absolute value of deviation of individual tuber values from treatment mean.
[y]Nutrient application at emergence and hilling (see Table 1).
[x]Nutrient application at emergence, hilling, and 4 and 8 weeks after hilling (see Table 1).
[w]Means within the same column and effect and followed by the same letter are not significantly different according to the test listed (Fisher's LSD test or Duncan's multiple range, $P \leq 0.05$).
[v]Indicates $P > F$ value > 0.10.

that application of calcium nitrate and NHIB during the tuber development period might lower the incidence of tuber internal defects.

Gypsum, calcium nitrate, and NHIB were similarly effective at increasing mean tuber Ca (Tables 3 and 4). The soluble source NHIB (especially on a split schedule) tended to result in larger mean tissue Ca content values, but differences between the soluble sources and gypsum usually were not significant (Tables 3 and 4). However, it is interesting to note that soluble sources, especially NHIB applied on the split schedule in 1994, tended to produce higher proportions of tubers with increased Ca levels in nonperiderm tissue compared to gypsum (Figs. 1 and 2). It is possible that frequent rainfall and irrigation events soon after the only applications of nonsplit calcium nitrate in 1994 leached this soluble Ca below the tuber zone and reduced its effectiveness compared to less-soluble gypsum (Table 4). This interpretation is consistent with the low CEC and moisture holding capacity of these soils and known aspects of tuber Ca uptake. The Ca concentration in the adjacent soil solution surrounding developing tubers determines tuber flesh Ca content (Kratzke and Palta, 1986). Tubers may not compete for Ca in the transpiration stream due to differences in water potential between tubers and foliage (Win et al., 1991).

Paired measures of Ca in the nonperiderm and periderm tissue of >800 tubers permitted us to examine closely the association between Ca levels in both tissues. A previous report suggested the Ca concentration in tuber skin and flesh are related, and that an increase in Ca level in one tissue corresponds to an increase in Ca in the other tissue (McGuire and Kelman, 1984). Calcium in the skin and Ca in the flesh of 'Russet Burbank' potato were highly correlated, but the magnitude and direct evidence for this at the individual tuber level were not presented (McGuire and Kelman, 1984). The extent and consistency of the relationship between tissue Ca levels have important implications. For example, inaccurate conclusions may be reached if measures of Ca in one tissue are used to infer Ca elsewhere. Furthermore, relationships between tissue Ca levels provide information regarding whether Ca in different tissues is controlled by different factors. For example, previous reports of genotypic differences in tuber Ca levels (Bamberg et al., 1993; Locascio et al., 1992) suggest that tuber Ca is under partial genetic control. It will be interesting to find out if the accumulation of Ca in the periderm and nonperiderm tissue is under separate genetic control.

Our data are inconclusive regarding the association between nonperiderm and periderm tissue Ca concentration. Linear regression analysis suggests the Ca concentration in nonperiderm and periderm tissue of individual tubers was poorly related (r^2 = 0.26 and 0.30 for 1993 and 1994 respectively; Fig. 3). The variable nature of Ca in both periderm and nonperiderm tissue suggests that strict reliance on calculated r values for individual data sets may overestimate the extent to which nonperiderm and periderm tissue Ca levels are truly related. Since the relationship between periderm and nonperiderm Ca was poor (Fig. 3), our data suggest that different factors may be responsible for accumulating Ca in these tissues. Furthermore, supplemental Ca application did not always result in a consistent effect on periderm and

Table 4. Treatment group and individual treatment effect on average 'Atlantic' tuber nonperiderm and periderm tissue Ca concentration in 1994. Absolute value of deviation of individual tuber values from treatment mean value is included as a measure of tuber variability within treatment. Although data of individual tubers from within two separate rows of each replicate were collected, replicate means within each treatment were employed in statistical analyses.

		Tissue Ca ($\mu g \cdot g^{-1}$ dry wt)			
		Nonperiderm		Periderm	
Group	N	Concn	Deviation[z]	Concn	Deviation
N and Ca application timing					
Nonsplit[y]	32	116.4 b	20.57 a	793.0 a	226.2 a
Split[x]	32	129.9 a	21.88 a	785.9 a	216.3 a
LSD[w]		9.3	4.0	72.7	43.2
ANOVA $P>F$		0.0054	NS[v]	NS	NS
Nonsplit application					
Control	8	104.8 c	14.76 b	770.6 ab	188.3 b
Calcium nitrate	8	104.1 c	21.15 a	884.5 a	186.4 b
Gypsum	8	119.0 b	22.21 a	763.8 ab	230.2 ab
NHIB	8	137.7 a	24.19 a	753.0 b	299.9 a
Duncan's test		14.5	6.01	127.8	93.3
ANOVA $P>F$		0.0001	0.0120	0.1028	0.0410
Split application					
Control	8	114.6 c	14.37 b	822.2 a	159.3 b
Calcium nitrate	8	129.7 b	23.55 ab	732.2 a	232.2 ab
Gypsum	8	120.8 bc	21.58 ab	812.7 a	224.3 ab
NHIB	8	154.4 a	28.01 a	776.5 a	249.5 a
Duncan's test		13.7	9.64	147.9	85.0
ANOVA $P>F$		0.0001	0.0332	NS	NS

[z]For both tissue types, average absolute value of deviation of individual tuber values from treatment mean.
[y]Nutrient application at emergence and hilling (see Table 1).
[x]Nutrient application at emergence, hilling, and 4 and 8 weeks after hilling (see Table 1).
[w]Means within the same column and effect and followed by the same letter are not significantly different according to the test listed (Fisher's LSD or Duncan's multiple range test, $P \leq 0.05$).
[v]Indicates $P > F$ value > 0.10.

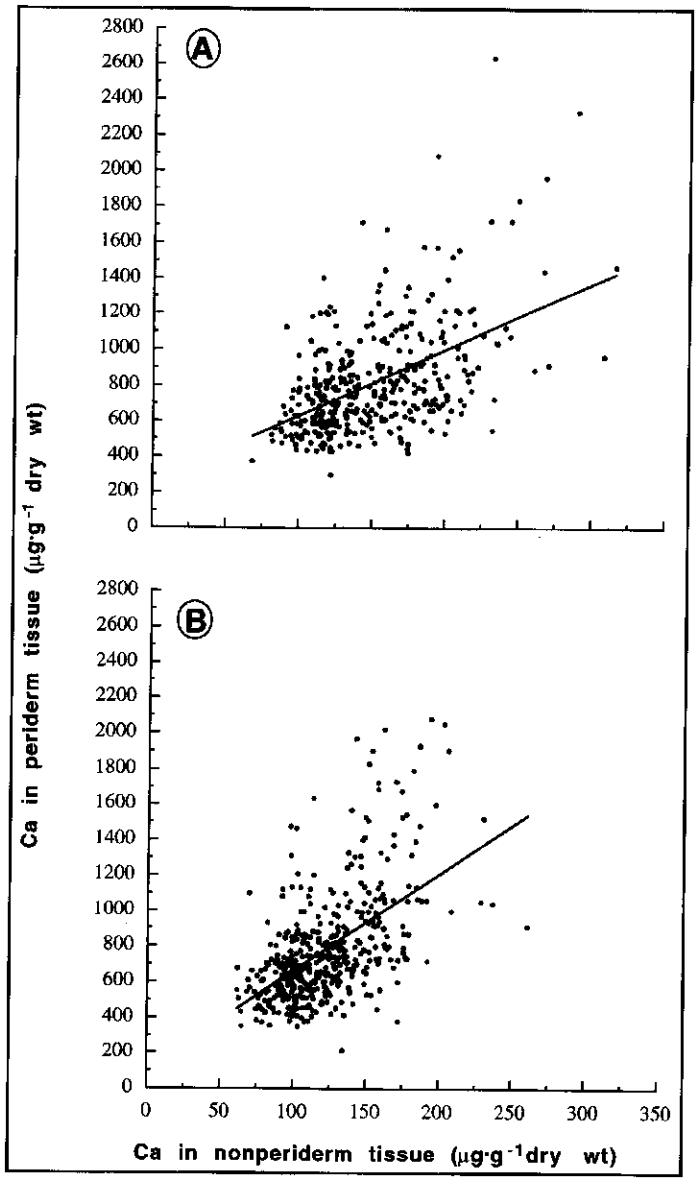


Fig. 3. Scatter plot of the relationship between periderm and nonperiderm tissue Ca level in 'Atlantic' tubers. Each point indicates the Ca level in the two tissues for 383 individual tubers measured in (**A**) 1993 and, for 437 individual tubers measured in (**B**) 1994. Tissue composition as described in materials and methods. Lines derived using linear regression with equations (**A**) y = 3.68x + 260.5, r^2 = 0.26 and (**B**) y = 5.49x + 111.7, r^2 = 0.30.

nonperiderm tissue Ca (Tables 3 and 4). For example, in 1994 split application of calcium nitrate and NHIB resulted in an increase in the Ca level of nonperiderm tissue only (Table 4). Thus, our results suggest that Ca fertility may have differential effects on Ca in tuber peel and flesh. In support of this suggestion, Olsen et al. (1996) noted that Ca fertility affected Ca in peel more than in nonperiderm tissue.

Split application of calcium nitrate and NHIB, produced a higher proportion of tubers with greater Ca level, as compared to controls (Figs. 1 and 2). For example, the split calcium nitrate and NHIB treatments had ≈35% and 57%, respectively, of the tubers with Ca> 160 µg·g^{-1} dry weight as compared to only 15% in controls (Fig. 1). Variability in Ca concentration among like-treated tubers was also evident (Figs. 1 and 2). For example, individual tubers with a given treatment (e.g., calcium nitrate or NHIB) had Ca levels < than 100 µg·g^{-1} dry weight to over 200 µg·g^{-1} dry weight. Differences among individual tubers in Ca concentration may have resulted from soil- and plant-based factors governing tuber Ca uptake or from the nonuniform distribution of Ca within the hill from a specific treatment. Variability in Ca level among tubers from identically treated plots has important implications and suggests that novel methods may be required to evaluate the relationship between application methods, tuber Ca concentration, and internal quality.

Paired measures of Ca level and internal quality on many individual tubers were useful to assess Ca internal quality relationships. After categorizing all 437 paired observations from 1994 based on Ca content, chi-square analysis provided preliminary evidence that the incidence of internal defects may be related to the Ca concentration of individual tubers. A disproportionately high number of defected tubers was found in the group of tubers with Ca at ≤100 µg·g^{-1} dry weight (Table 5). This may be evidence that the nonperiderm tissue Ca concentration of individual tubers is among the factors which influence the likelihood that tubers will develop internal defects. Future studies may benefit from tissue nutrient analysis at the inception of internal defect development (Levitt, 1942; Olsen et al., 1996). Such data would aid in determining whether the observed relationship between low Ca concentrations and internal quality defects is coincidental.

Others have reported negative relationships between tuber flesh (Clough, 1994) or periderm (Silva et al., 1991; Tzeng et al., 1986) tissue Ca levels and the incidence of internal defects or lower Ca concentrations in defected tubers (Arteca et al., 1980; Mohr et al., 1984; Olsen et al., 1996). But, based on our data, we question the advantage of relating tuber internal quality to skin Ca levels. The relationship we found between nonperiderm and

Table 5. Chi-square tests of associations between independent variables and the incidence of internal defects in 'Atlantic' tubers in 1994. Scoring for the presence or absence of defects in 437 individual tubers permitted grouping observations into categories listed below. Chi-square analysis tests the probability that random sampling from a common population could produce similar data. A probability value ≤0.10 suggests the independent variable and internal quality are associated.

Independent variable	No. of tubers			Chi-square probability
	Total	Without defect	With defect[z]	
Nutrient application schedule				0.087
Nonsplit	224	191	33	
Split	213	193	20	
Tuber nonperiderm tissue Ca concentration (µg·g^{-1} dry weight)				0.102
≤100	116	97	19	
>100	321	287	34	

[z]Tubers containing brown center and/or hollow heart internal defects.

periderm tissue Ca levels was inconsistent. In addition, tuber flesh Ca levels probably are more important than periderm Ca levels in development of necrotic tissue in the flesh. In spite of evidence that hollow heart and brown center may be induced by environmental stress and/or nutrient imbalances (Levitt, 1942; Mohr et al., 1984; Olsen et al., 1996; Rex and Mazza, 1989; Sterrett et al., 1991), few have succeeded in inducing these defects experimentally (Van Denburgh et al., 1979, 1980, 1986). Definitive evidence regarding mechanisms responsible for the initiation of the defects is lacking. Current information suggests that hollow heart and brown center result from general declines in cell and tissue health induced by several interacting physiological factors (Ehlenfeldt, 1992; Olsen et al., 1996; Van Denburgh et al., 1986; Win et al., 1991). Because potato tubers are deficient in Ca, improved tuber health by increased Ca level is expected (Palta, 1996). Our data are consistent with this premise.

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