Relationship of Calcium to Potato Scab

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Maine Agricultural Research Station external publication 1524.
Accepted for publication 10 January 1991 (submitted for electronic processing).

ABSTRACT

Lambert, D. H., and Manzer, F. E. 1991. Relationship of calcium to potato scab. Phytopathology 81:632-636.

Field plots were treated with 4.5 MT/ha of dolomitic lime, an equivalent amount of gypsum (960 kg of Ca per hectare), or no Ca. At harvest, soil pHs in 1989 and 1990 were 4.4 and 4.4, 4.4 and 4.5, and 5.1 and 5.5 for nontreated, gypsum, and lime, respectively. In rows inoculated with *Streptomyces scabies*, incidences of tubers with scab lesions in 1989 and 1990 were 20 and 22, 18 and 22, and 53 and 80%, respectively, for the same treatments. Without reinoculation, scab incidences in 1990 were 0, 0, and 32%, respectively. Scab incidence was correlated with soil pH ($P \leq 0.001$), but was not correlated with Ca concentrations in the soil, healthy tuber periderm, or medulla tissue. Calcium concentrations were four to five times higher in scab tissue than in healthy periderm from the same tubers. Therefore, in low pH soils, higher tissue Ca concentration is an effect rather than a cause of increased scab. Lesion diameter was inversely correlated with tuber Mg and Mn concentrations. Tubers with high Ca concentrations were less susceptible to soft rot when inoculated with *Erwinia carotovora* subsp. *carotovora*, indicating that treatment differences were sufficient to alter host reaction in a disease system known to be calcium-affected.

Liming of low pH soils increases the severity of common scab of potato caused, in most cases, by *Streptomyces scabies* (17). The concept that calcium is directly responsible for some or all of this increase has been reviewed by Keinath and Loria (15). A number of investigations have concluded that soil H^+ concentration determines scab severity rather than soil Ca concentration or the ratio of Ca to other elements (3,8,14,28). Others have suggested that tuber Ca concentration affects resistance, or that soil Ca concentration is a better indicator of scab susceptibility than soil H^+ (5-7,11,13). Specific involvement of Ca in scab development implies a calcium-dependent mechanism in resistance, pathogenicity, or pathogen survival. Lack of involvement would allow growers to increase soil Ca levels to improve tuber quality. The primary benefit of increasing the Ca content of tubers is a reduction in susceptibility to Erwinia soft rot resulting from increased cross-linkage of pectate chains (16,21,22). This study was designed to test the hypotheses that increasing soil Ca increases scab and that soil or tuber Ca parameters are adequate indicators of scab development. Data from previous studies that support these hypotheses have also been reevaluated.

MATERIALS AND METHODS

Field plots. A field experiment was established at Presque Isle, ME, in 1989. Treatments were control, 6.4 MT/ha of gypsum (17% Ca, 2.4% Mg), and 4.5 MT/ha of dolomitic lime (24% Ca, 13% Mg). The latter two were broadcast just before planting on 31 May. Plots were replicated in four blocks and each contained four 20-m long rows, spaced 0.9 m apart. Plots were fertilized at planting with 1,000 kg/ha of 14-14-14 (140 kg of N, 60 kg of P, 116 kg of K) applied in bands. Soil at this site was a Caribou gravel-silt loam with an initial pH of 4.2 and a cation exchange capacity (CEC) (pH 4.2) of 5.5 meq/100 g. Plots were hand-planted with whole tubers of potato (*Solanum tuberosum* L.) cultivar Katahdin, a variety highly susceptible to scab. All seed tubers in the central 6-m long (20 hills) sections of the two inner rows were covered with 30 cc of inoculum prepared from actively growing trypticase soy broth cultures of *S. scabies* mixed with sufficient vermiculite to make the inoculum friable. Strains RL-30, RL-70, RL-174, RL-131, RL-W24, and RL-W46 (17) were isolated and tested for pathogenicity by R. Loria (Cornell University). After harvest on 21 September, lime and gypsum treatments were reapplied at the previous rates. On 5 June 1990, the plots were replanted as before. Twenty hills at one end of the two inner rows were reinoculated while the adjoining 20 hills were left uninoculated to assess the relative survival of *S. scabies* from 1989 to 1990. The boundary between these two areas was centered on the previous years' inoculum.

Scab ratings. Tubers from all inoculated hills were harvested, stored for 2 wk, washed, and separated into diseased and symptomless groups. Each group was weighed. Scabby tubers were further divided into severity classes with 1-10% and >10% surface area affected in 1989 or 1-20% and >20% surface area affected in 1990, when scab was more severe. In 1989, diameters of 100 discrete lesions were measured for each plot by using eight to 10 tubers from the 1-10% severity class.

Tissue and soil analyses. Six medium-sized healthy tubers were selected from each plot, rinsed in 1% HCl for 2 min, and peeled with a potato peeler (av. slice thickness ~1.1 mm). Approximately 10 g of medulla tissue taken from inside the vascular ring was saved from each tuber. These tissues were dried, ground, and analyzed for cation and P concentrations by the University of Maine, Plant and Soil Sciences Analytical Lab. In 1989, tuber samples in the 10-20% surface area severity class from the control and gypsum treatments (three to six tubers per plot) were taken from common storage (5 C) after 1 mo and were peeled. All the scabby periderm from each tuber was collected separately from peelings of healthy surfaces of the same tubers. In 1990, sampling was done immediately after washing with six tubers from each of the 12 plots. A total of 20 soil samples per plot from 15-cm deep cores of hilled soil were collected on 5 July 1989, 21 September 1989, and 19 July 1990. Samples were dried and analyzed by the Analytical Lab for pH (in H_2O), CEC, and phosphate and cations extractable by pH 3.0, 1 N ammonium acetate.

Soft rot. Resistance to soft rot was assayed after tubers were graded in 1989. Tubers were maintained at room temperature for two days, washed in 0.5% sodium hypochlorite, and rinsed. Two cores 3 mm in diameter and 20 mm deep were removed from eight tubers per plot. A suspension containing approximately 200 cells of *Erwinia carotovora* subsp. *carotovora* in 100 µl of distilled water was placed in each hole. Strain Ec 14 (24) was used as inoculum in one hole and a recently isolated strain of *E. c. carotovora* from a potato stem with blackleg was used in the second hole. Tubers were placed in a sealed 120-L container, flushed with nitrogen, and maintained in a positive-pressure

nitrogen atmosphere for 3 days. Tubers were removed, weighed, cut in half, washed to remove macerated tissue, blotted, and reweighed. The amount of macerated tissue was calculated as weight lost with washing.

Data analysis. Data were analyzed by two-way analyses of variance, regression, and correlation (Minitab, State College, PA); means were separated by Duncan's New Multiple-Range Test. Data in related papers (11,13) were taken from tables of means or by measurements from graphs and analyzed by regression or correlation.

RESULTS

Soil and tissue analyses. Lime treatment increased soil pH to 5.1 by September 1989 and to 5.5 by July 1990 (Table 1). Gypsum did not alter pH relative to the untreated control plots. Extractable P varied with treatment in 1989 but not 1990. Extracted Ca was higher in the gypsum treatment than in the lime treatment. Soil Mg was increased by the addition of Mg in gypsum and lime. In 1990, extractable K was highest in the untreated plots. Differences in element concentration within periderm or medulla tissue generally reflected differences in soil element contents and/or soil pH (Table 2). Concentrations of Ca, Fe, Al, and Mn were considerably higher in tuber periderm than in the medulla tissue.

TABLE 1. Element concentrations and pH of soils with different calcium treatments[y]

Element	Sample date	Untreated	Gypsum	Lime
Ca	7/89	956 a[z]	2,540 c	1,365 b
	9/89	967 a	1,726 c	1,640 b
	7/90	923 a	3,693 c	2,349 b
Mg	7/89	148 a	466 c	370 b
	9/89	120 a	337 b	466 c
	7/90	116 a	307 b	547 c
K	7/89	715 a	673 a	677 a
	9/89	350 a	317 a	251 a
	7/90	416 b	330 a	309 a
P	7/89	21 a	25 b	21 a
	9/89	34 b	37 b	29 a
	7/90	21 a	24 a	18 a
pH	7/89	4.23 a	4.23 a	4.60 b
	9/89	4.38 a	4.35 a	5.08 b
	7/90	4.40 a	4.45 a	5.53 b

[y] Concentrations in kilograms per hectare.
[z] Means within rows followed by the same letter do not differ significantly ($P \leq 0.05$) by Duncan's New Multiple-Range Test.

Scab incidence. In 1989, average scab incidences were 53, 20, and 18% in the lime, control, and gypsum treatments, respectively (Table 3). In uninoculated borders, incidence was 0.6%. Disease incidence in individual replicates was most associated with soil pH ($r = 0.91$; $P \leq 0.001$). There were also highly significant correlations with soil P ($r = 0.82$; $P \leq 0.01$), tuber Zn ($r = -0.74$; $P \leq 0.01$), and tuber B ($r = -0.73$; $P \leq 0.01$). However, these three parameters were more highly correlated with soil pH than with scab, and therefore a causal relationship can not be inferred. Periderm or medulla Ca concentrations from scab-free tubers were not correlated with scab incidence. In 1990, scab incidence averaged 22% in the reinoculated control and gypsum plots and 80% in the lime plots. In those portions of the plots not inoculated in 1990, disease incidences for these treatments were 0, 0, and 32%, respectively. Again, scab incidence was correlated with soil pH ($r = 0.96$; $P \leq 0.001$) but not with any Ca parameters. Other parameters correlated with scab were equally correlated with pH.

Element concentrations in scab lesions. Calcium was four- to fivefold higher in scab tissue than in healthy periderm from the same tubers (Table 4). Iron and aluminum concentrations showed similar differentials. Other elements, except for K, were 1.2- to 2.9-fold higher in scabby periderm.

Lesion size. Differences in lesion diameters were slight but significant in 1989, averaging 9.34, 9.20, and 9.08 mm in the control, gypsum, and lime treatments, respectively. The untreated control differed significantly from the lime but not the gypsum treatment. When lesion diameters were regressed on element concentrations, differences were most associated with tuber Mg

TABLE 2. Element concentrations in healthy periderm and medulla tuber tissue in potatoes grown in soils with different calcium treatments[y]

		Periderm			Medulla		
Element	Year	Control	Gypsum	Lime	Control	Gypsum	Lime
Ca	1989	0.43 a[z]	0.73 b	0.54 a	0.07 a	0.13 b	0.08 a
	1990	0.63 a	1.22 b	0.82 a	0.10 a	0.16 b	0.11 a
N	1989	24.4	25.4	24.1	14.8	15.5	14.8
K	1989	37.5	38.8	39.0	22.7	24.4	22.1
	1990	39.0	40.7	41.8	22.9	23.6	21.8
Mg	1989	1.71	1.70	1.88	1.02	1.07	1.12
	1990	2.05 a	2.04 a	2.33 b	1.22	1.17	1.32
P	1989	2.23	2.47	2.16	2.65	2.81	2.71
	1990	2.19	2.40	2.26	2.71	2.71	2.89
Al	1989	289	281	298	7	8	7
	1990	469	481	532	16	19	14
Fe	1989	277	266	298	31	34	25
	1990	415	486	515	28	32	33
Mn	1989	51	62	32	9	9	8
	1990	118 b	110 b	39 a	10 b	8 ab	7 a
Cu	1989	14	13	12	9	11	10
	1990	18	20	20	14	14	11
Zn	1989	22	22	11	18	19	18
	1990	26 ab	32 b	22 a	25	25	23
B	1989	13	13	13	5.1	5.1	4.7
	1990	18	17	15	6.2 b	5.6 ab	4.9 a
Ca/K	1989	0.011 a	0.019 b	0.014 a			
	1990	0.016 a	0.030 b	0.020 a			
Ca/P	1989	0.19 a	0.30 b	0.25 ab			
	1990	0.29 a	0.51 b	0.36 a			
Mo	1990	0.9 a	0.9 a	1.0 b	0.4	0.3	0.4

[y] Concentrations in milligrams per gram for Ca, N, K, and Mg; and in milligrams per kilogram for Al, Fe, Mn, Cu, Zn, B, and Mo.
[z] Means within rows followed by the same letter do not differ significantly ($P \leq 0.05$) by Duncan's New Multiple-Range Test. Means without letters do not differ significantly. Periderm and medulla tissues were analyzed separately.

($r = -0.72$; $P \leq 0.01$). Other significant negative correlations ($P \leq 0.05$) were with tuber Mn ($r = -0.63$) and periderm Mn ($r = -0.58$). Correlations between Mg and Mn were not significant, and the Mn relationship with lesion size appeared to be independent of Mg. Differences in tuber Mg were consistent with soil treatments (Table 1). Lesion diameter was not related to scab incidence or pH. Percentages of deep-pitted lesions, which averaged 17%, did not differ significantly among treatments in 1989.

Soft rot. Tissue loss to soft rot averaged 74, 57, and 68 grams per tuber for the control, gypsum, and lime treatments, respectively, with a significant difference ($P \leq 0.05$) between the control and gypsum treatments. Of the elements measured in medulla tissue, only Ca was correlated with soft rot loss ($r = -0.80$; $P \leq 0.01$).

DISCUSSION

Soil pH was the strongest predictor of disease, and only those factors correlated with pH were significantly related to disease incidence. Another line of evidence supporting the importance of pH is the sensitivity of *S. scabies* but not *S. acidiscabies* to pH values in agar medium below 5.0 (17,18). Substantial additions of Ca in the form of gypsum did not increase scab incidence or inoculum survival. Gypsum increased tuber Ca more substantially than lime and had a greater effect on soft rot reduction. Significance in soft rot response indicates that differences in Ca treatments were sufficient to alter host reaction in a disease system known to be affected by Ca. Small differences in lesion size among treatments were not related to Ca. Calcium concentrations in healthy periderm or medulla tissues were not correlated with scab incidence. However, Ca as well as Al and Fe concentrations were more than fourfold higher in scab tissue than in the healthy periderm of the identical tuber samples. Much of the Ca in tubers is associated with cell walls (22). Lesion tissue is particularly high in Ca because it is composed primarily of suberized cell walls with little dry matter from starch or cell contents. Both Houghland and Cash (14) and Lutman and Cunningham (20) reported twofold differences in Ca content of skin from healthy and scabby tubers. Lutman and Cunningham (20) found that the Ca concentration in the most superficial healthy periderm layer did not differ from that of scab tissue. The Ca concentration of peelings as thick as scab lesions, however, was only half that of healthy superficial periderm or scabby periderm. Deposition of additional Ca in scab lesions as a response to infection is another possibility and has been reported in other systems (2,29). Regardless of cause, this artifact is sufficient to explain substantial differences in periderm Ca between any treatments with differing effects on scab incidence. Excessive Fe and Al may be bound to the lignin- and suberin-rich material in lesions, or be from contaminating oxides or clays not completely removed by the acid wash. These two elements, like Ca, are much more concentrated in periderm tissue.

Several studies have reported a relationship of Ca with scab, and most of these have included gypsum treatments. The study generally cited as the earliest demonstration of a Ca–scab relationship (13) was done in a pH range of 4.6–6.2. Statistical analyses of the data were not reported. Our regresssion analyses of the study's calcium sulfate treatment means show no significant relationship of scab to tuber Ca ($r = 0.65$; $P > 0.1$), replaceable soil Ca ($r = 0.53$; $P > 0.2$), or added Ca ($r = 0.04$; $P > 0.2$). These relationships may have been significant in comparisons

TABLE 3. Percentages of tubers in each scab severity class from soil treated with gypsum or lime

	Inoculated and harvested 1989			Inoculated 1989 and harvested 1990			Inoculated 1989, 1990 and harvested 1990		
Treatment[x]	0%	1–10%	>10%	0%	1–20%	>20%	0%	1–20%	>20%
Control	80 b[z]	19 a	2 a	100 b	0 a	0 a	78 b	16 a	6 a
Gypsum	82 b	16 a	2 a	100 b	0 a	0 a	78 b	17 a	6 a
Lime	47 a	41 b	12 b	68 a	18 b	14 b	20 a	35 b	45 b

[x] Plots were inoculated in 1989 with or without reinoculation in 1990.
[y] Percentage of tuber surface affected.
[z] Means within columns followed by the same letter do not differ significantly ($P \leq 0.05$).

TABLE 4. Element concentrations in healthy or scabby tuber periderm tissue in 1989 and 1990[w]

		Control		Gypsum		Lime		
Element	Year	Healthy	Scabby	Healthy	Scabby	Healthy	Scabby	Ratio[x]
Ca	1989	0.44[y]	1.67	0.61	2.66	...	...[z]	4.1
	1990	0.64	3.43	1.07	5.85	0.74	3.67	5.3
K	1989	34.8	34.3	35.5	36.1	...	...	1.0
	1990	34.5	26.3	38.9	30.6	37.4	28.7	0.8
Mg	1989	1.59	2.62	1.61	2.56	...	...	1.6
	1990	1.84	3.11	1.83	3.28	2.10	3.63	1.7
P	1989	2.21	2.72	2.38	3.13	...	...	1.3
	1990	2.20	2.36	2.35	3.17	2.38	2.87	1.2
Al	1989	216	842	217	833	...	...	3.9
	1990	431	2,762	418	2,722	400	2,433	6.3
Fe	1989	212	878	214	795	...	...	3.9
	1990	430	2,697	408	2,440	407	2,330	6.0
Mn	1989	39	48	47	151	...	...	2.3
	1990	82	194	64	219	24	71	2.9
Cu	1989	17	29	15	31	...	...	1.9
	1990	15	41	17	43	17	42	2.6
Zn	1989	21	32	20	35	...	...	1.6
	1990	25	38	24	39	22	33	1.6
B	1989	15	26	15	26	...	...	1.8
	1990	18	37	19	35	13	26	2.0
Mo	1989	0.6	1.2	0.6	1.2	...	...	2.1
	1990	0.9	2.3	0.9	2.4	1.0	2.4	2.5

[w] Healthy and scabby periderm were peeled from identical sets of three to six tubers with 10–25% of their surface area affected. There were four replicates per treatment. Concentrations are in milligrams per gram for Ca, K, Mn, and P and micrograms per gram for Al, Fe, Mn, Ca, Ze, B, and Mo.
[x] Average concentrations in all scabby samples divided by average concentrations in healthy samples.
[y] Differences between healthy and scabby tissue were significant ($P \leq 0.05$) for all elements except K in 1989. Differences among soil treatments were significant for Ca in 1989 and for Ca, K, Mg, Mn, and Zn in 1990.
[z] Lime treatment not included in 1989.

of individual treatment means if variation among replicates was small. However, a substantial difference in scab incidence and tuber Ca concentrations between treatments differing only by 30 kg of gypsum per hectare suggests that random error in this experiment was at least moderate. Our multiple regression analysis of data from the lime-treated plots explained 94% ($F = 65.8$) and 3% ($F = 2.2$) of the variability in scab incidence by soil pH and tuber Ca concentration, respectively. Without statistical analysis, we feel that there is insufficient evidence for a Ca–scab relationship in these data.

Goto (11) compared scab incidence in uninoculated gypsum and lime-treated plots in two soils that had a pH in water of 4.5 and 4.8. Both Ca treatments increased soil pH values measured after consecutive fall and spring crops and were associated with substantial increases in scab. Lime treatments increased disease more than gypsum treatments containing equivalent amounts of Ca. The author did not state that Ca increased susceptibility to scab but concluded that measurement of extractable Ca was a better predictor of potential scab severity than soil pH. This was based on a lack of correlation between pH and scab in one of the soils when data from both harvests were analyzed together. When we analyzed data for each harvest separately, correlations of scab with pH for 1978 and 1979 were $r = 0.70$ ($P = 0.053$) and $r = 0.93$ ($P \leq 0.001$), respectively. For extractable Ca in 1978 and 1979, correlations were $r = 0.55$ ($P = 0.15$) and $r = 0.91$ ($P = 0.0015$), respectively. In this soil, pH and Ca were not correlated in 1978 ($r = 0.46$; $P > 0.2$), but were highly correlated in 1979 ($r = 0.97$; $P < 0.001$). Thus, to the extent that pH and extractable Ca were independent parameters, pH was the better predictor of scab incidence. Much of the predictive value of Ca resulted from its covariance with pH. Whether *S. scabies* was the streptomycete causing disease in this case is open to question, as it is unusual for natural populations of this species to persist and cause severe disease in this pH range without artificial inoculation.

Davis et al (5–7) monitored plant Ca concentrations in studies of various chemical and irrigation treatments that reduced scab in highly buffered, high Ca soils (pH 7.5–8.0). In the first experiment (5), gypsum significantly decreased scab severity and periderm Ca concentrations but increased medulla Ca by 9% (not significant). Frequent irrigations (7) or application of PCNB (pentachloronitrobenzene) decreased scab severity and petiole Ca concentrations (5). All scab-reducing treatments, including sulfur amendments (5) or fertilization with triple superphosphate (6) were associated with lower periderm Ca concentrations or Ca/P ratios. These analyses were interpreted as an indication of Ca involvement in scab susceptibility. Suppression of scab in wet soils has been explained by various other mechanisms (1,19). That the primary mode of action of the very toxic compound PCNB is a modest reduction in Ca uptake seems unlikely. While some treatments decreased Ca uptake, a more general explanation of the consistently lower periderm Ca concentrations in less scabby treatments (including gypsum) is the considerable difference in Ca concentrations between healthy and scabby periderm. In our study, e.g., 10% scab would have increased periderm Ca 30–40% over a healthy control. There are also important differences between low and high pH soils that affect scab. Suppression of scab by gypsum occurs only in alkaline soil (23). Development of *S. scabies* is inhibited at low pH but is optimal above pH 7 (17). In addition, host and pathogen physiological processes requiring Ca are presumably more affected by small changes in Ca concentration at a low pH when Ca nutrition is marginal, than at a high pH when Ca is sufficient. Streptomyces spores absorb considerable amounts of Ca, which is required for germination (10,12). For example, the optimum Ca concentration for *Streptomyces viridochromogenes* germination is 0.5 mM. The germination rate is reduced 50% at 0.15 mM Ca. Calcium concentrations are this low only in extremely acidic soils (26), and it is therefore unlikely that low soil Ca concentrations reduce scab in a nonparasitic phase of the disease cycle.

Potatoes may be grown at relatively low soil pH and Ca levels. Yield responses to Ca in low-calcium soils are not substantial (27), but Ca deficiency may affect quality, e.g., soft rot resistance (16,21,22), "internal rust spot" (4), and subapical necrosis (9). Crops grown in rotation with potato may also have higher Ca requirements. These considerations may provide justification for applying gypsum rather than lime in situations in which scab is an important consideration, a practice already followed for potatoes grown in acidic, low-calcium, South African soils (25).

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