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X-RAY MICROANALYSIS OF HOLLOW HEART POTATOES

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Abstract

Electron microprobe and X-ray fluorescence techniques were used to study elemental gradients associated with the physiological disorder hollow heart in potato tubers. Gradients were found along the length and across the width of mature tubers. These were not related to the disorder, however. Tubers with advanced symptoms of the disorder had elemental levels and gradients similar to those in healthy, control tubers. The results suggest that if the disorder is initially caused by an elemental deficiency, as has sometimes been proposed, the deficiency is temporary and no longer exists in mature tubers with advanced hollow heart. Radial gradients were associated mainly with two contrasting tissues, the central pith and the surrounding perimedullary zone. Tissue differences are critical in microprobe studies involving small samples. Microprobe studies of developing tubers containing incipient stages of hollow heart, employing strip samples restricted to the central pith where the disorder originates and taken so as to traverse the small lesions, showed a dramatic increase in Mg in lesion areas. It is suggested that a nutrient imbalance may trigger the onset of the cell necrosis that characterizes the initiation of hollow heart in potato. A localized Mg toxicity or Ca deficiency due to high Mg:Ca ratio is implicated.

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Introduction

Hollow heart in potato is a physiological disorder that causes serious economic losses some years. It has been associated with sudden, very active vine growth following cool temperatures shortly after tuber set (Van Denburgh et al. 1979; Timm, 1981). Such growing conditions apparently alter the physiological balance of the plant so that foliar increases are at the expense of tuber growth. A popular theory is that certain important nutrients may become limiting, leading to the death of some pith cells (Krantz and Lana, 1942; Levitt, 1942; Kallio, 1960; Arteca et al. 1980). The histological events associated with hollow heart development, from a few necrotic cells in the pith of the young tuber to the well-known advanced stages in the mature tuber, have been described in detail (Levitt, 1942). Some results on elemental gradients in potatoes showing advanced hollow heart symptoms compared with healthy tissue have been reported (Levitt, 1942; Macklon and De Kock, 1967; Arteca et al. 1980). The present work extends these studies and takes into account the large compositional differences between pith and perimedullary tissue, a point often overlooked. Incipient as well as advanced stages of hollow heart were studied, the former being particularly important to an understanding of any nutrient imbalances associated with the disorder's inception. Electron microprobe and X-ray fluorescence techniques employed at the histological level were used for most of the analyses.

Materials and Methods

Plant Material

Early phases of the work were carried out on mature potatoes. These were obtained from the University of California, Davis, coordinated varietal trials. The tubers were cut in half longitudinally along the central pith and those revealing hollow heart were retained. In these mature tubers the hollow heart was nearly always of the advanced type (Figs. 1b and 1c). For each hollow heart tuber found, a healthy tuber (no hollow heart symptoms) of the same cultivar and comparable in size, shape, and pith dimensions was also retained.

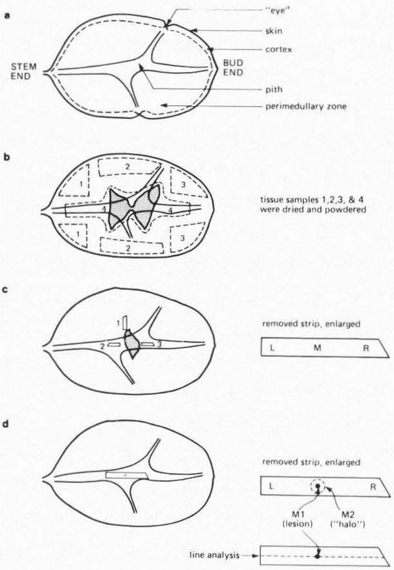

Figure 1. Schematic of potato tubers cut longitudinally along pith showing (a) major tissue parts; (b) zones (tuber with advanced hollow heart) sampled for X-ray fluorescence analysis; (c) location of strips taken (tuber with advanced hollow heart) for electron microprobe analysis, and test sites on strips; and (d) location of strips taken (tuber with incipient hollow heart) for electron microprobe analysis, and test sites on strips. Tissue samples were also taken from tubers with no visually-detectable hollow heart ('controls') at locations comparable to those shown in (b), (c), and (d).

Later phases of the work were carried out on young, developing potato tubers, cultivars Red La Soda and Pontiac. In early May, 1981, the Bakersfield area of California experienced a sudden change to higher day-time temperatures (25-30^{o}C) following a cool period (15-20^{o}C), during which time the tubers were still at a relatively early stage of enlargement. Tubers hand-harvested two weeks before commercial harvest operations from these naturally-stressed potato plants revealed, on cutting, a considerable number showing very early symptoms of hollow heart. For each hollow heart tuber found, a corresponding control was selected, i.e., a tuber of the same cultivar, grown in the same location, and of comparable size, shape, and internal tuber anatomy. Typical internal anatomy of a potato tuber is shown in Figure 1a.

Tissue Samples for X-Ray Fluorescence Analysis

Blocks of tissue from the four main tuber zones (Fig. 1b) were removed from each tuber, utilizing both halves. Care was taken during this and subsequent steps to avoid elemental contamination of the cut tissue surfaces from hands, scalpel and other objects. After recording fresh weights, the tissue samples were dried at 70^{o}C, weights recorded, and ground to a fine powder using a mortar and pestle. Circles 6 mm in diameter of powdered sample were attached to mylar film (untouched by hands) held in place in plastic photographic slide holders. Clear protective coating aerosol spray was used to fasten the powder to the mylar. Sheets of paper with circular cutouts placed over the mylar-slide facilitated precise application of the spray, followed immediately by application of the powdered sample. For each sample, two successive applications of spray and powdered sample ensured a uniform distribution of sample over the 6 mm circular area. Powdered samples of National Bureau of Standards Orchard Leaves were similarly prepared for use as standard reference material. Blanks consisted of 2 coatings of the aerosol spray on mylar film. The samples were analyzed using a Kevex 7000 energy dispersive spectrometer employing rhodium tube source and direct excitation mode, secondary targets Gd, Sn, Ag, Ge, Fe, and Ti and a Si(Li) detector. Data were recorded in counts per second.

To confirm the X-ray fluorescence results, powdered samples were also analyzed for the elements of interest using standard atomic absorption methods.

Tissue Samples for Electron Microprobe Analysis

An approximately 25 mm cube of tissue from the middle part of the tuber, containing the region of interest, was sectioned on a sliding microtome to produce slices 400 μm thick. Before sectioning the slice used for subsequent sampling, the knife blades were cleaned with distilled water and wiped dry. The slice was placed on a clean sheet of hard filter paper. Using a clean scalpel, strips 2 mm wide and 12 or 20 mm long were removed. The 12 mm long strips were taken at the sites shown in Figure 1c. These were: (1) adjacent to the hollow, in the case of the hollow heart tuber, extending radially outward into the perimedullary region; (2) along the central pith in the direction of the stem end; and (3) along the central pith in the direction of the bud end. Strips were also taken at comparable sites in healthy, control tubers. The 20 mm long strips were taken at the sites shown in Figure 1d. These were taken along the longitudinal length of the central pith traversing the small dark lesion(s) characterizing the first visible symptom of hollow heart. The entire strip was taken carefully from within the central pith core, avoiding the surrounding perimedullary tissue. Strips were also taken at comparable sites in healthy, control tubers.

To assist in identifying and orienting the strips, one end was taper-cut. Any handling, by means of forceps, was done at that end. The tissue strips were allowed to air-dry while being prepared. They were mounted on 25 mm diameter round glass microprobe slides, using electrical circuit copper print as the adhesive. The mounted samples were placed in a 30°C oven for final drying and held in a desiccator until analyzed.

Elemental spectra at a few sites on the strips (Fig. 1c and upper strip in Fig. 1d) were obtained using an ARL EMX/SM electron microprobe, with the operating voltage 15kV, beam current 300 nA, and beam diameter 35 μm. X-ray counts for 100 sec live time were collected using a Kevex 7000 energy dispersive spectrometer. This gave preliminary information on the elements present and their relative levels at selected sites on the strips.

The entire length of some tissue strips (lower strip in Fig. 1d) was analyzed for selected elements using the more critical line analysis method. This was done with the electron microprobe with wavelength dispersive crystal spectrometers utilizing RAP (Mg Kα), ADP (Cl Kα), and LiF (Ca Kα) crystals.

Results

Major Parts of Tuber

The dry matter content of pith tissue was much lower than that of the surrounding perimedullary tissue (Fig. 2). It changed little from stem to bud end of the tuber's perimedulla, although it was slightly lower in the bud end than in the stem or mid-tuber zones. The dry matter content of hollow heart tubers was similar to that of tubers without hollow heart.

X-ray fluorescence analysis of dried powdered tissue samples from the different zones of the tuber detected the elements Cl, K, and Ca in significant quantities (Fig. 3). From stem to bud end of the tuber's perimedulla, there was a decrease in Cl and an increase in K. Calcium tended to be lower in the stem end than elsewhere. Atomic absorption analyses (not reported here) confirmed these gradients.

Elemental content of the pith was considerably higher than that of the perimedullary tissue when expressed on a dry weight basis. On a fresh weight basis, this difference was reduced considerably.

Differences in levels of detectable elements between tubers with and without hollow heart were

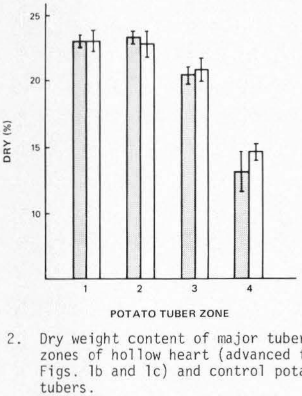

Figure 2. Dry weight content of major tuber zones of hollow heart (advanced type, Figs. 1b and 1c) and control potato tubers.
Shaded bars represent hollow heart tubers; empty bars represent control tubers.
Tuber zones 1-4 represent, respectively, the stem end perimedulla, mid-tuber perimedulla, bud end perimedulla, and central pith (Fig. 1b). Each bar is the mean of 9 tuber replicates, with standard error shown at top of bar.

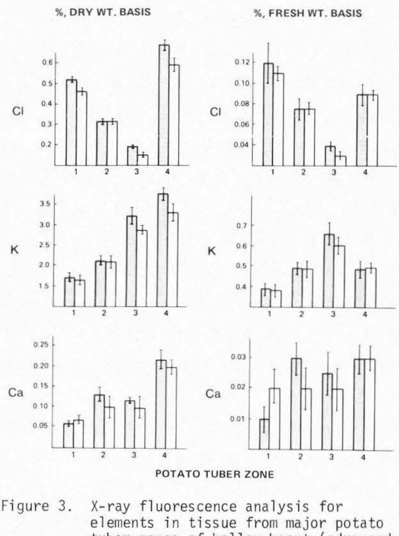

Figure 3. X-ray fluorescence analysis for elements in tissue from major potato tuber zones of hollow heart (advanced type, Fig. 1b) and control tubers. Shaded bars represent hollow heart tubers; empty bars represent control tubers.
Tuber zones 1-4 represent, respectively, the stem end perimedulla, mid-tuber perimedulla, bud end perimedulla, and central pith (Fig. 1b). Each bar is the mean of 9 determinations using 9 different tubers, with standard error indicated at top of bar.

relatively minor and not significant in most cases.

Advanced Hollow Heart in Mature Tubers

Elements detected in significant quantities by electron microprobe analysis of tissue strips were K, Cl, S, P, and Mg. The results are shown in Figure 4. The "1" strips, taken radially from the pith region towards and extending into the perimedulla, showed a considerable decrease in level of all elements along the strip. In "2" and "3" strips, taken entirely within the central pith and extending from the middle of the tuber towards the stem and bud ends, respectively, there were no such gradients along the length of the strips. Test sites restricted to pith tissue (L, M, and R in "2" and "3" strips) or very close to pith tissue (L in "1" strips) had much higher elemental levels than those in the high starch, lower moisture perimedullary tissue (M and R in "1" strips).

Differences in elemental levels between hollow heart and control tubers were not considered significant, although levels of some elements (Cl, Mg, and K) tended to be higher in tissue samples of hollow heart tubers.

Incipient Hollow Heart in Developing Tubers

Amongst these field-stressed, Red La Soda and Pontiac cv. developing tubers, many were found on cutting to have hollow heart symptoms. No symptoms were detectable in tubers weighing less than 80 g and they occurred most frequently in large (>150 g) tubers. Most of these were in the early stages of the disorder. A few contained a single very small (2-3 cells in diameter) dark spot characteristic of the first visible symptom. Others had a slightly more advanced, but still early, stage consisting of a patch of small dark lesions. They were always contained within the central pith, usually about half way between stem and bud ends of the tuber. Scanning electron micrographs (Fig. 5) showed that the cells forming a lesion were distorted and had thickened walls. These and surrounding cells were deficient in starch, while cells further away from the lesion had the normal complement of starch granules for pith cells.

Preliminary elemental analyses were carried out at selected points along each strip using the electron microprobe's energy dispersive X-ray spectrometer. The same samples were then analyzed along the entire length of each strip, using the wavelength dispersive method. Results obtained by the two methods were essentially the same, therefore only wavelength dispersive results are reported. One element in particular, Mg, was present in much higher levels in and around the incipient lesions than in healthy tissue further away from the lesion area or in comparable sites of control tubers (Figs. 6, 7). Moreover, the 'halo' zone immediately surrounding the lesion (M2 in Fig. 6 depicting a single lesion sample), and areas between lesions in a multi-lesion sample (M2 in Fig. 7), had much higher Mg levels than the lesion itself (M1 in Figs. 6, 7). Other tissue strips of the same cultivar, and of certain other cultivars tested, revealed similar gradients for Mg, leaving no question as to the validity of the examples presented here.

Potassium and Cl gradients (not shown here) in the region of the lesion resembled those for Mg in that the 'halo' zone gave higher counts than the inner part of the lesion. However, there was little or no gradient in K or Cl between the lesion and healthy tissue at either end of the strip, as was the case with Mg. Calcium levels were below detectable limits using either the energy dispersive or wavelength dispersive methods of analysis with the electron microprobe.

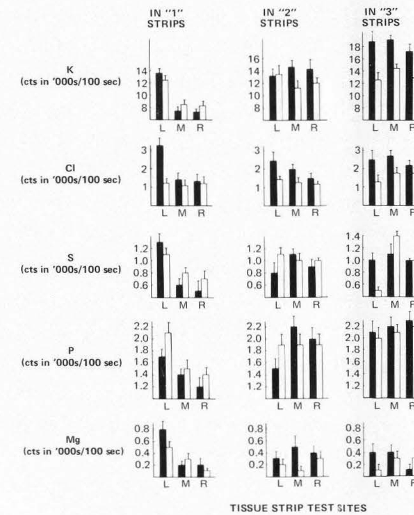

Figure 4. Electron microprobe analysis for the localization of elements in potato tuber tissue from hollow heart (advanced type, Fig. 1c) and control tubers.
Tissue strips 1-3 were taken adjacent to the hollow (and comparable sites in control tubers) extending, respectively, radially into the perimedulla, along the pith in the direction of the stem end, and along the pith in the direction of the bud end (Fig. 1c). Left, middle, and right (L, M, R) sites on each strip were analyzed. Shaded bars represent hollow heart tubers; empty bars represent controls. Each bar is the mean of 11 tubers for "1" strips, 7 tubers for "2" strips, and 3 tubers for "3" strips, with standard error indicated at top of bar.

Tissue strips from comparable sites of control tubers, similarly analyzed, gave results (not shown here) almost identical to those of the healthy L and R portions of strips containing hollow heart. Not only were their levels of Mg, K, and Cl the same as the healthy ends of tissue strips containing hollow heart, but no gradients were evident along the length of the strips. As with strips containing lesions, no Ca was detected in strips from control tubers.

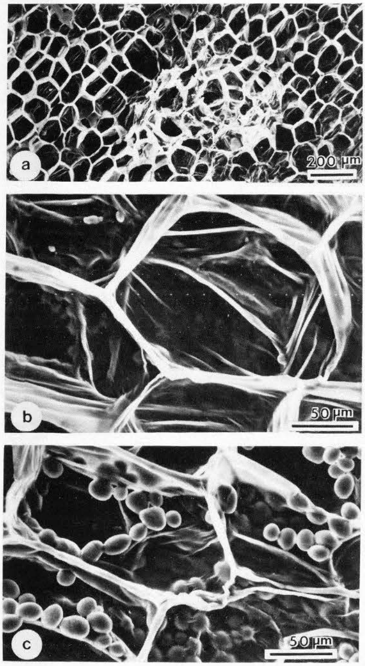

Figure 5. Scanning electron micrographs of potato tuber pith tissue with incipient hollow heart showing (a) thickened walls of a group of distorted cells forming a small lesion in middle of picture, (b) starch-deficient cells in and immediately surrounding the lesion, and (c) normal cells containing starch granules in tissue further away (4-5 mm) from the lesion.

Discussion and Conclusions

The dried and powdered samples used for X-ray fluorescence analysis represented relatively large areas of the fresh tuber. This method is well suited to compositional study of the tuber's major zones. The results, confirmed by atomic absorption analysis, were similar to those reported for mature potato tubers by other workers using other analytical methods (Macklon and DeKock, 1967; Johnston et al. 1968; Arteca et al. 1980). Potato tubers have elemental gradients along their length and width in response to metabolic changes that occur during their development and maturation on and off the plant (Weaver et al. 1978). Lengthwise gradients probably reflect to a large extent these metabolic changes in the tuber relative to total plant needs at a particular period in the life of the tuber. Radial gradients, while also varying with the tuber's metabolism, are mainly associated with two contrasting tissues (Mohr, 1972). The central pith (high moisture, low starch) and the surrounding perimedulla (low moisture, high starch) contain very different elemental levels, the extent of the difference depending on whether results are expressed on a dry or fresh weight basis. These fundamental tissue differences must be taken into account in any meaningful study of elemental gradients associated with an internal disorder.

Mature tubers displaying advanced hollow heart had essentially the same elemental composition as mature tubers without hollow heart. This was indicated by both analytical methods - the X-ray fluorescence method in which the tissue samples represented fairly large areas of the tuber (Fig. 3) and the electron microprobe method employing localized strip samples (Fig. 4). The gradients obtained in the tissue strips extending radially from the edge of the hollow ("1" strips in Fig. 4) are probably gradients between tissue types, and not related to specific tissue disorder. It is felt that the inclusion of more than one tissue in microanalytical studies of this kind is a source of error that has not always been fully appreciated. From the preliminary work which dealt with mature tubers, we concluded that (1) by the time tubers reach the mature stage, those with and without hollow heart do not differ appreciably in elemental composition, (2) any further attempt to establish elemental imbalances associated with hollow heart should be focused on incipient rather than mature stages of the disorder, (3) the microprobe technique should be used, with the tissue strips carefully restricted to the central pith and taken so as to include affected (lesion) and nonaffected tissue, and (4) it was important to continue to work with paired tuber samples - with and without hollow heart, each pair being of the same cultivar, grown under the same conditions, and comparable in size and internal anatomy.

Our observations of the histological origin and development of hollow heart in the tuber correspond with those reported by others. The discoloration of necrotic hollow heart cells is believed to be due to melanin discoloration of

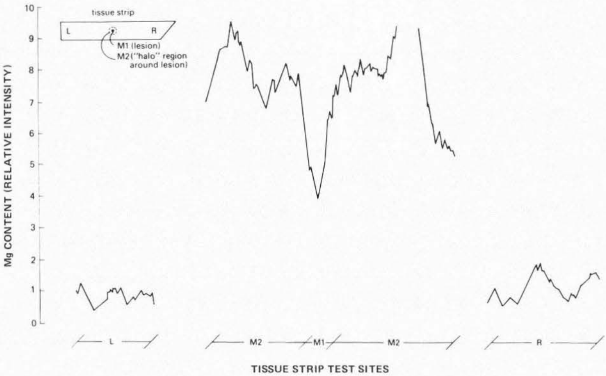

Figure 6. Segments of an electron microprobe line analysis for magnesium along the pith traversing a small lesion (Fig. 1d) characterizing incipient, potential hollow heart of potato tuber tissue (cv. Red La Soda).

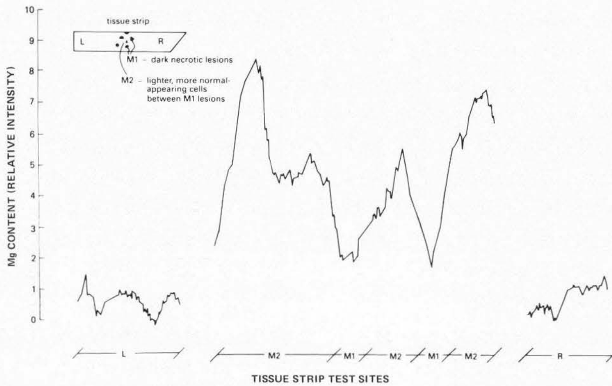

Figure 7. Segments of an electron microprobe line analysis for magnesium along the pith traversing a patch of several small dark necrotic lesions characterizing an early, potential stage of hollow heart of potato tuber tissue (cv. Red La Soda).

the cellular protoplasmic contents and cell walls, and perhaps also to accumulation of polyphenols such as chlorogenic acid and tyrosine (Reeve, 1968). The thickening of lesion cell walls results from their suberization and increased hemicellulose and pectin content (Reeve, 1968). Starch depletion in the lesion area, particularly in the cells immediately around the lesion, seems to be related to the formation of wound tissue (Ilker et al. 1977). It is logical that any finding of mineral imbalances in these regions could be associated with one or more of these histochemical changes.

That a mineral imbalance may be the cause of the initial necrosis which eventually leads to hollow heart has been suggested frequently in the literature. Levitt (1942) found a lower content of all elements tested (Ca, Mg, K, Cu, Fe, and Mn) in hollow heart tubers than in controls. Arteca et al. (1980) found a lowered Ca content in hollow heart tubers. However, both of these studies dealt only with mature tubers. In our work with mature tubers, there was no evidence of a lowered mineral content of tissue in hollow heart tubers. This variance with the results of the above authors could be due to the particular combination of tuber growth and maturation properties involved. Our work with mature tubers suggests that if any mineral imbalance existed at an early stage of the disorder's inception, it no longer exists in mature tubers showing advanced hollow heart symptoms.

In young, developing tubers containing incipient hollow heart, the increase in Mg in the immediate vicinity of the small, forming lesions was dramatic. It seems likely that a nutrient deficiency associated with possible Mg toxicity triggers the onset of the cell necrosis in the pith; rapid growth expansion of the tuber then results in the familiar large hollow regions. Because of the well-known interaction between Mg and Ca, it may be a Ca deficiency that causes the initial cellular breakdown and necrosis. The role played by Ca in membrane and cell wall integrity is well known. In a study of bitter pit in apple, Hopfinger and Poovaiah (1979) also found a Mg:Ca imbalance and concluded that localized Mg toxicity or localized Ca deficiency causes this physiological disorder. However, it has also been documented that mineral elements and other constituents tend to accumulate in the vicinity of injured or necrotic tissue (Yarwood, 1967; Faust et al. 1968; Ford, 1979). It is possible that the observed mineral imbalances are coincidental to, rather than the cause of, the development of hollow heart. The fact that our study included lesions only a few cells in diameter lends some support to, but does not prove, the theory that mineral imbalances initiate the disorder.

Experiments involving the addition of Ca and other elements as soil fertilizers to field-grown potatoes, cv. Red La Soda, are now in progress. These may help to resolve the above question. Hopfinger and Poovaiah (1979) were able to show that bitter pit symptoms in apple fruit could be induced by vacuum-infiltrating the fruit with Mg and that they could be totally prevented by adding Ca, lending support to their conclusion that mineral imbalances caused the disorder.

Potatoes contain only about 0.002 - 0.012% Ca on a fresh weight basis, with most of that being contained in the outer parts of the tuber (Johnston et al. 1968; Bretzloff, 1971). The low levels in the pith are below the 0.05 - 0.1% range needed for detection by the electron microprobe technique used in our work thus far, which has emphasized analyses at the histological level. In future work it may be possible to follow Ca levels associated with specific cellular structures such as cell walls (using a microprobe interfaced with an electron microscope, and appropriate tissue preparation) in order to verify the role of Ca in the initiation of hollow heart.

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Discussion with Reviewers

N.S. Wright: If an imbalance in Mg and Ca initiates hollow heart, would you not expect some control tubers (those predisposed to develop hollow heart) to show abnormally high Mg and

abnormally low Ca in the M2 region?
Authors: Yes, but there is the problem of finding it. The M2 ('halo') region around the incipient lesion is small in area relative to the total region of the pith in which the lesion could develop. Furthermore, the incidence of hollow heart in a given tuber population may not be high when one wants to study it, so that even exhaustive analysis of the pith of some tubers does not necessarily prove anything. The tubers tested might not be the ones to develop hollow heart, or might not be at the stage of tuber development to show it. We did not detect an imbalance between Mg and Ca in any of our analyses of control tubers, but these analyses were limited in number. The approach mentioned in your question is sound and should be investigated further. By testing all parts of the central pith of developing tubers of susceptible cultivars that have received stress conditions usually resulting in hollow heart, it may be possible to detect a Mg:Ca imbalance corresponding with a potential M2 (or M1) region if, in fact, the imbalance precedes the lesion.

D.A. Walker: Why would the relatively high Mg level be restricted to the region immediately surrounding the lesions?
Authors: The 'halo' region immediately surrounding the lesion probably reflects gradients in relation to the necrotic cells, with the lesion as the locus. For example, the lesion could change the pH and, therefore, the solubility of various elements (Ca being very susceptible to pH changes).

D.A. Walker: What would account for the mineral imbalance in the early stages of the disorder being rectified in the mature tuber?
Authors: The large split or hollow region present in the mature tuber is believed to be due to continued expansion of the tuber after the dead cells of the incipient lesion in the developing tuber are no longer capable of enlarging. The disorder tends to develop in large-sized tubers. Expansion of the tuber would tend to deplete, or physically 'dilute', a previously existing mineral imbalance.

D.A. Walker: What factors would contribute to possible Mg toxicity or Ca deficiency?
Authors: Any number of stress factors, especially those affecting root growth activity, could affect Mg and Ca source-sink relationships. Temperature stress or water stress (deficiency or flooding) are among these. Also, because of its smaller atomic weight, Mg is more mobile than Ca and, when Ca is deficient, Mg may readily substitute for it.

D.A. Walker: Would a difference in water content between pith and perimedullary region account for the dissimilarity in elemental composition when measured by dry versus fresh weight?
Authors: The water component of plant tissues such as potato tuber is normally low in Mg and Ca, these minerals generally being present in association with cellular structures. Therefore, the water component per se should have little or no direct bearing on the pattern of results. The other major component of potato tubers is the starch granules which make up a large part of the dry weight. Perimedullary tissue contains considerably more starch than does pith tissue. The mineral content of starch granules from several plant sources tends to be rather low (Gracza, 1965). Presumably, the Mg and Ca content of potato starch is low too. This would tend to lower the levels of these minerals present in the perimedulla as compared with the pith, especially when calculated on a dry weight basis. Variations in mineral levels of the starch granules from the pith versus perimedulla might also play a role in affecting the results.

N.S. Wright: Can you envisage your methods being used to determine the predisposition to hollow heart of potato seedlings?
Authors: Not at this stage of the work. Before considering this application, it should be confirmed that the mineral imbalance exists before, and is therefore the probable cause of, the formation of the lesion. One way of investigating the latter point might be to treat susceptible pith tissue with added Mg and Ca, as Hopfinger and Poovaiah (1974) did in their study of the physiological disorder bitter pit in apple fruit. These authors showed that bitter pit symptoms could be induced by vacuum-infiltrating the fruit with Mg and that they could be totally prevented by adding Ca, lending support to their conclusion that mineral imbalances caused the disorder.

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