A MORPHOLOGICAL AND ANATOMICAL STUDY OF THE TOXIC EFFECT OF ALUMINUM ON CORN ROOTS

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ABSTRACT

A MORPHOLOGICAL AND ANATOMICAL STUDY
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Robert L. Hatch

Zea mays L., cv. Spring Gold roots showed symptoms of Al toxicity when grown in a nutrient solution containing $AlCl_3$. A comparative morphological and anatomical study of the damaged roots was undertaken with the use of the scanning electron microscope (SEM), light microscope (LM), transmission electron microscope (TEM) and the microprobe x-ray analyzer. Al was found to accumulate at the root surface and to a lesser degree in cells of the cortex with the endodermis serving as a barrier to further penetration. SEM pictures demonstrated the continuation of cellular division or elongation within the vascular cylinder after treatment whereas, cells exterior to the endodermis were arrested and subsequently sheared by the continued elongation within the vascular cylinder. Photomicrographs showed an increase in vacuole size of epidermal and cortical cells and a corresponding decrease in the number of vacuoles when exposed to Al. Ribosomes were tightly packed along the endoplasmic reticulum or aggregated as small polyribosomes. No changes were observed in other organelles. Large quantities of Al at the root surface were evident within 8 hr.

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Robert L. Hatch

A THESIS

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1973

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Sincere appreciation is expressed to all who have helped in any way throughout my education. The opportunity to study in the United States has been a most rewarding experience.

For his careful and critical review of my program of study and research, I thank my major professor, Dr. H. Paul Rasmussen. Working under his guidance has been an excellent opportunity.

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Readers:

The paper-format used for this thesis meets the requirements stipulated by the Department of Horticulture and the University. The thesis body has been prepared for publication in the Journal of the American Society for Horticultural Science and thus follows the manuscript style for this journal.

A Morphological and Anatomical Study of the Toxic Effect of Aluminum on Corn Roots

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Michigan State University, East Lansing

Anstract. Zea mays L., cv. Spring Gold roots showed symptoms of Al toxicity when grown in a nutrient solution containing $AlCl_3$. A comparative morphological and anatomical study of the damaged roots was undertaken with the use of the scanning electron microscope (SEM), light microscope (LM), transmission electron microscope (TEM) and the microprobe x-ray analyzer. Al was found to accumulate at the root surface and to a lesser degree in cells of the cortex with the endodermis serving as a barrier to further penetration. SEM pictures demonstrated the continuation of cellular division or elongation within the vascular cylinder after treatment whereas, cells exterior to the endodermis were arrested and subsequently sheared by the continued elongation within the vascular cylinder. Photomicrographs showed an increase in vacuole size of epidermal and cortical cells and a corresponding decrease in the number of vacuoles when exposed to Al. Ribosomes were tightly packed along the endoplasmic reticulum or aggregated as small polyribosomes. No changes were observed in other organelles. Large quantities of Al at the root surface were evident within 8 hr.

Poor yields on acid soils have been attributed largely to Al induced root damage (1, 5, 7, 8, 10, 12, 13, 20). Liming acid soils was beneficial because of increased soil pH and therefore decreased soluble Al (11). Species and cultivars vary in Al tolerance (1, 7, 8, 11, 13). Several authors have studied Al toxicity by observing changes in root structure at the cellular level. The light microscope (2, 4, 6) and more recently the microprobe (16, 17) have been used in these studies. The present study was undertaken to observe further morphological and anatomical changes of Al damage at the tissue, cellular and subcellular level using the SEM and TEM as well as the LM and electron microprobe x-ray analyzer.

Materials and Methods

Corn (Zea mays L., cv. Spring Gold) seeds were soaked in distilled water for 12 hr and germinated in white quartz sand. Seedlings were grown in a growth chamber with a day temperature of 21 C (16 hr day) and a night temperature of 19 C for 2 weeks. The seedlings were removed and transferred to a modified nutrient solution containing either 10^{-3}M $CaCl_2$ or 10^{-3}M $AlCl_3$ as described by Rasmussen et al. (17). Roots were excised and prepared for observation at 1/2, 2, 8, 24, 36, 48, 60 and 72 hr. intervals. Others were left in nutrient solution for 5 and 8 days before harvesting.

The gross morphology of the control and Al treated corn roots was recorded photographically prior to preparation for microscopic observation.

Roots for SEM studies were excised, washed and carefully dissected with a double edge razor blade. After dehydrating through an ethanol series, the tissue was transferred to a 50% solution of isoamyl acetate and absolute alcohol for 30 min, followed by 100% isoamyl acetate for 1 hr. The samples were critical point dried in a Denton DCP-1 using liquid CO_2. The dried roots were mounted on round glass cover slips with carbon Tube Koat (G. C. Electronics Co., Rockford, Ill.) and placed on SEM stubs. The roots were coated with 20 nm C followed by 20 to 40 nm of Au-Pd (60%/40%) in a vacuum evaporator (Ladd Research Industries) and viewed in the SEM (Advanced Metals Research Model 900) at 21 KV accelerating potential.

Thick sections (0.5-1 um) were cut from plastic blocks (prepared for TEM) for observation with the light microscope. These sections were

placed on glass slides with distilled water and dried at approximately 175 F on a warming plate. The sections were stained with toluidine blue (5-10 sec), washed with distilled water and air dried prior to examination. Photomicrographs were taken using phase contrast microscopy.

Representative root tips were harvested, fixed and killed in 5% glutaraldehyde and 2% OsO_4, dehydrated in alcohol and embedded in Epon 812. Thin sections (0.06-0.09 um), cut on a Porter-Blum MT-2 ultra microtome, were stained in uranyl acetate (30 min) and lead citrate (5 min) prior to TEM examination (Philips 300).

After washing root tips with distilled water, samples used for element localization were frozen at -20 C in Ames Tissue-Tek O.C.T. compound and sectioned on a CTD-International-Harris-Cryostat. Sections 16 um thick were placed on polished C discs and dried at room temperature. Cross-sections and longitudinal sections from the zone of differentiation and maturation were analyzed for Al, P, Ca, K, Mg and Fe distribution on an electron microprobe x-ray analyzer (Applied Research Laboratory Model EMX-SM). An accelerating voltage of 21 KV with a sample current of 0.05 ua was used throughout this study.

Three plants were randomly chosen from each treatment and the experiment was repeated twice.

Results and Discussion

Typical Al toxicity symptoms showing stunted roots with malformed secondary root formation were observed (11, 17, 18) (Figure 1).

Secondary roots appeared to discontinue elongation when exposed to Al, confirming the observations of Ruprecht (20). However, SEM pictures

Figure 1. Control and Al treated corn seedlings 5 days from treatment.

A) Comparison of control and Al treated.
B) Normal development of secondary roots.
C) Stunted secondary roots showing Al toxicity symptoms.

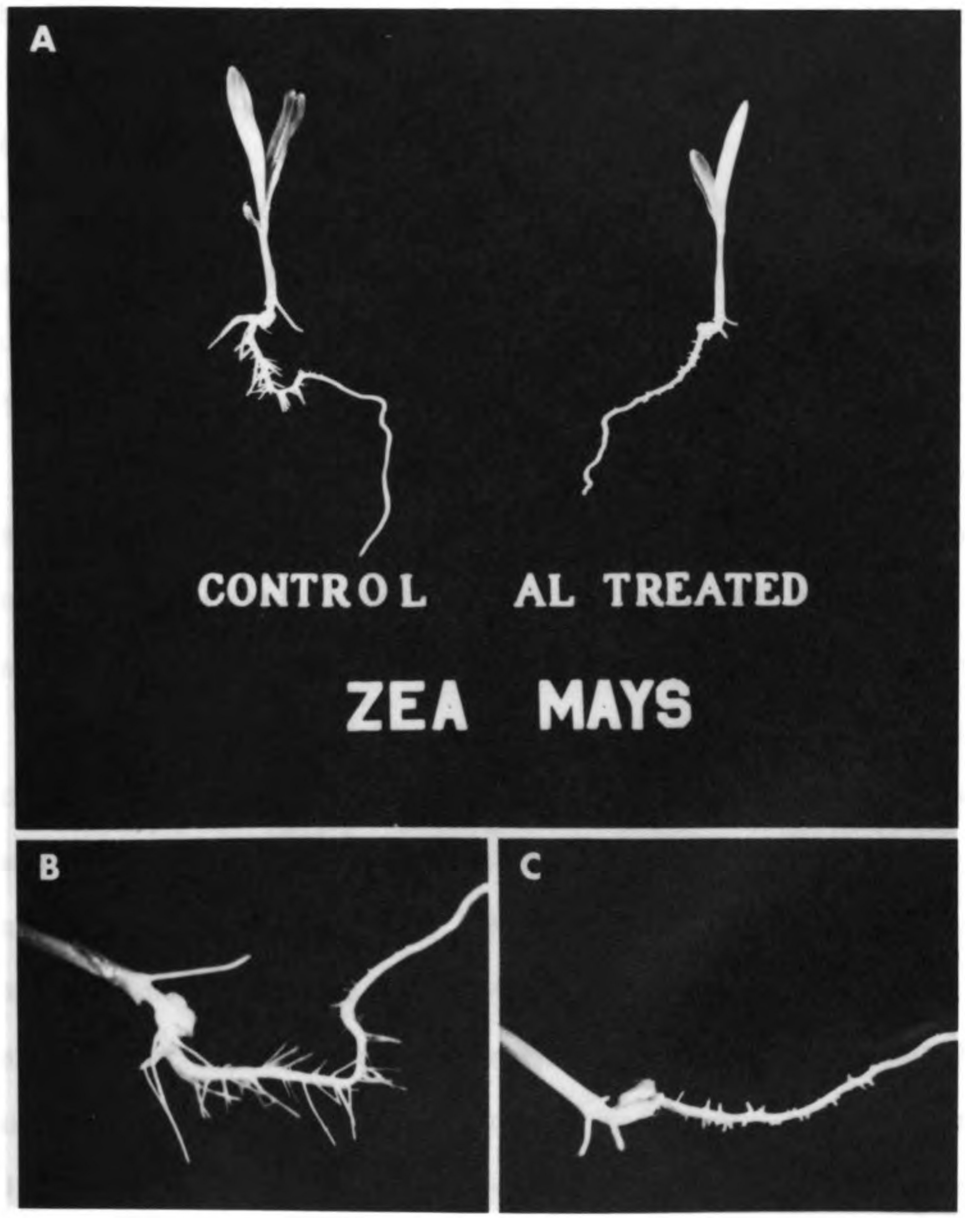

Figure 1

showed that cells interior to the endodermis continued to elongate. Although secondary roots continued to emerge injury was obvious. New secondaries continued to emerge basipetally and after 6 to 8 days exposure to Al emerged within 1 to 2 cm of the root cap. Similar results have been reported for wheat (6). No secondaries were evident below this point after 8 days.

Results obtained from the scanning electron microscope (SEM) clearly identify the mechanical injury to roots caused by Al. These data support work done at the cellular level and aid in interpretation of the morphological changes that occur. Figure 2 illustrates that elongation continued in the zone of differentiation interior to the endodermis and caused a shearing of cortical and epidermal cells which had been arrested by Al. This indicated that Al had not passed through the endodermis. Clarkson and Sanderson (4) suggested that the differential elongation of the cells interior and exterior to the endodermis may produce tensions which lead to collapse of cortical cells. This cracking and shearing of cells was most prevalent in the zone of elongation (Figure 3).

Corn roots examined 30 min and 2 hr after treatment resembled control roots at the organ, tissue, cell and subcellular levels. Small cracks near the root tip, extending over the surface were observed after 8 hr (Figure 4). Excess sluffing of root cap cells was also symptomatic of early injury (Figure 5a and 5b). Extreme cracking and sluffing of outer cells was evident in treated roots after 24 hr (Figure 5c and 5d).

Secondary roots after 24 hr showed similar results. Their development from initiation in the pericycle through the endodermis was normal.

Figure 2. Scanning electron micrographs of control and Al treated (5 days) corn root tips.

A) Surface view of control (RC-Root cap).
B) Surface view of treated primary root showing typical Al damage (arrow).
C) Longitudinal view of control with intact root cap (RC).
D) Longitudinal view of primary root tip damaged by Al (arrow).

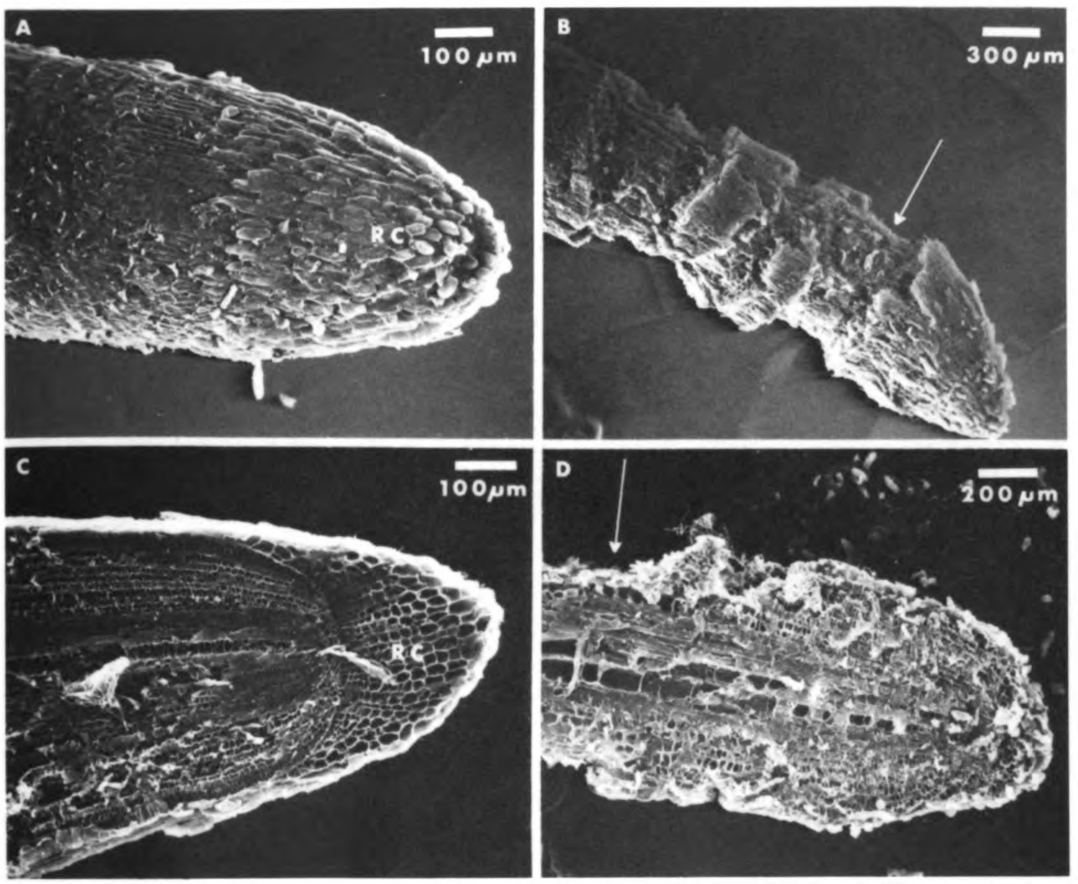

Figure 2

Figure 3. Scanning electron micrograph of Al treated (5 days) corn root tip showing excessive damage in zone of elongation.

X) Meristematic region.
Y) Zone of elongation.
Z) Zone of maturation.

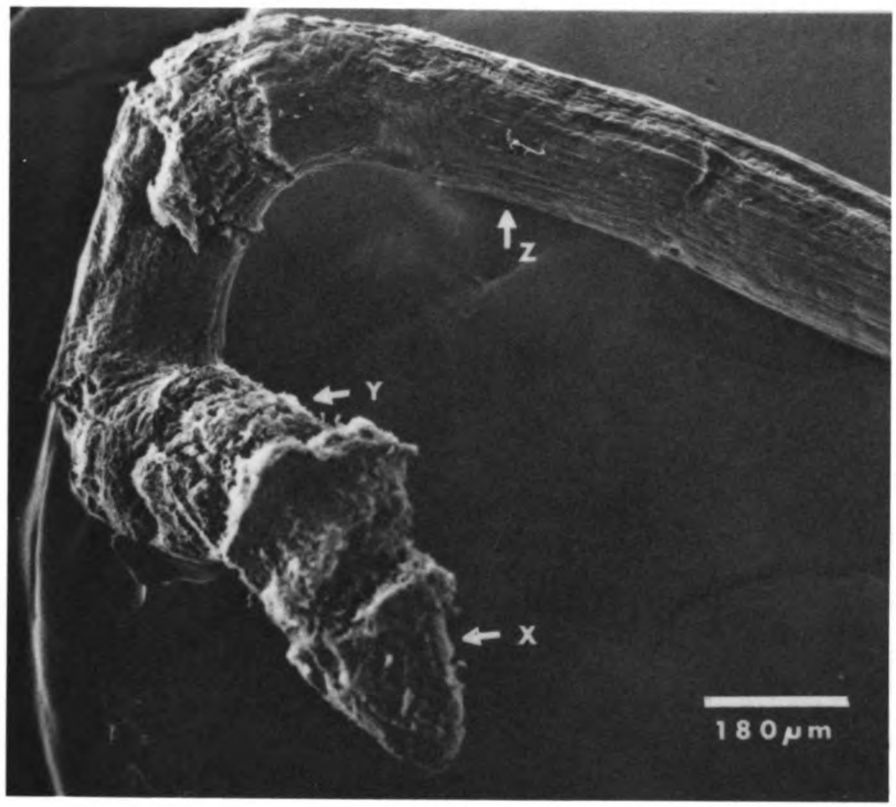

Figure 3

Figure 4. Scanning electron micrographs of corn root surfaces.

A) Normal secondary root tip of control plant.
B) Cracking over the surface (arrow) in zone of elongation (24 hr).
C) Close up showing break of epidermal layer in zone of elongation (36 hr).
D) Extreme cracking of Al treated secondary root behind root cap (60 hr).

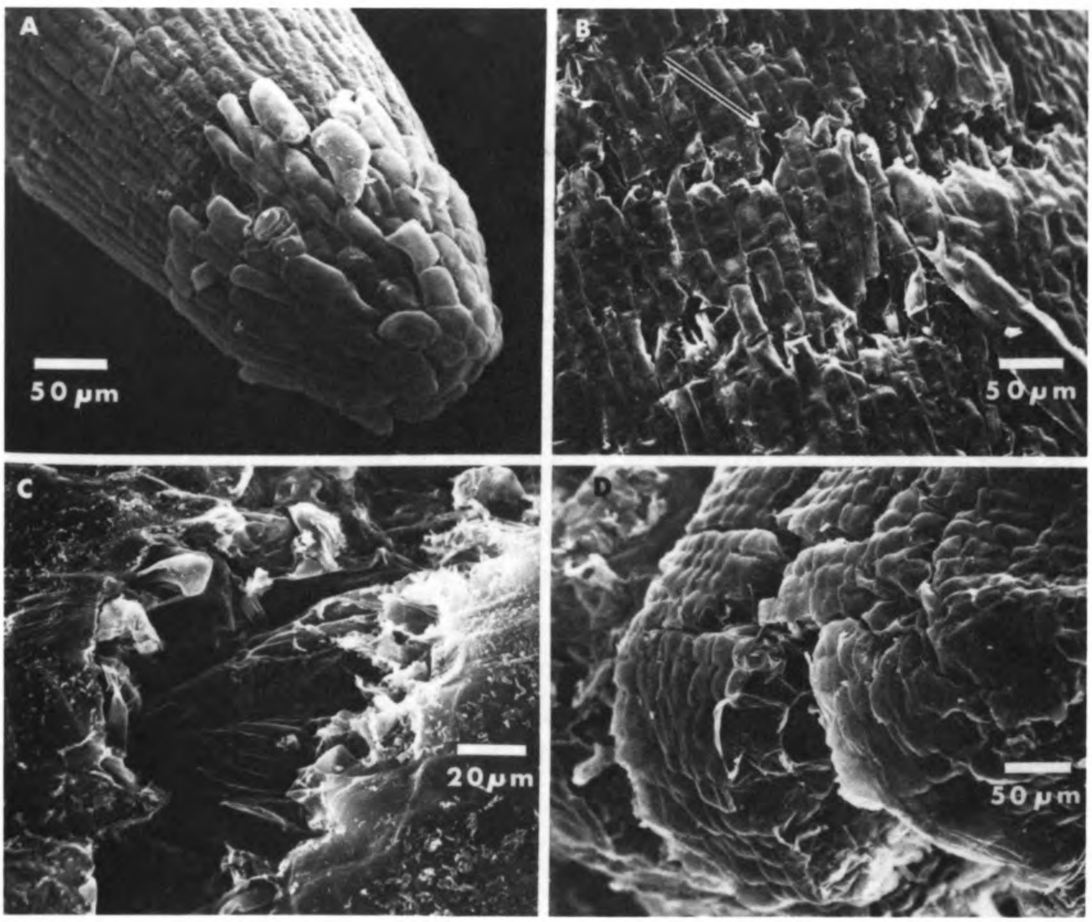

Figure 4

Figure 5. Scanning electron micrographs showing breakdown of corn root cap cells after Al treatment.

A) Surface view of intact control root tip.
B) Surface view of treated (24 hr) root showing individual cells detached (arrow) from the root cap.
C) Longitudinal view of control root tip.
D) Longitudinal view showing detached root cap (arrow) after 8 days treatment with Al.

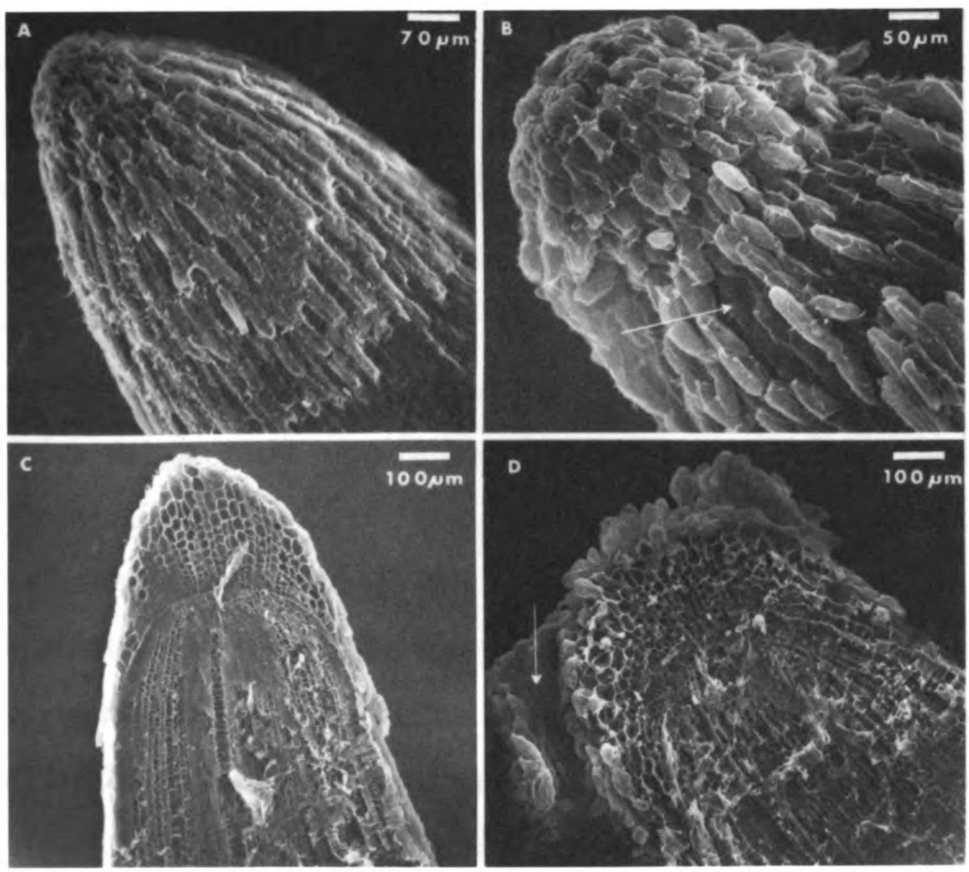

Figure 5

However, severe cracking of the roots occurred when they penetrated the epidermis and were exposed to high concentrations of Al (Figure 6). Rasmussen (16), using the microprobe, suggested that emerging secondary roots provided a means by which Al entered the plant. SEM pictures (Figure 7) support this theory.

Light and electron microscopy substantiated previous work (4, 6, 11, 14, 21) stating that most of the Al accumulated at the root surface and only small amounts moved into the epidermal and cortical cells. Further penetration was blocked by the endodermis. Thick transverse sections through the root cap and into the zone of maturation showed no differences between control plants and those grown in Al up to 2 hr. Epidermal and cortical cells of treated roots (4 hr or more) contained larger vacuoles and gave the appearance of having less cytoplasm than non-treated roots (Figure 8).

Transmission electron micrographs confirmed these findings. Cells of the zone of elongation and interior to the endodermis appeared normal (Figure 9). Increased vacuole size and slight plasmolysis of epidermal and cortical cells in the zone of elongation was readily noted after 8 hr (Figure 10). Such an early effect is understandable since Rorison (19) found that maximal uptake of Al by sainfoin roots was reached within 4 hr. Further, Clarkson (2) reported that elongation of onion roots was completely inhibited by 10^{-3} and 10^{-4}M $Al_2(SO_4)_3$ within 6 to 8 hr. At 24 hr nearly all small vacuoles had coalesced to form larger vacuoles. Al affected the integrity of the tonoplast causing it to tear apart and lose rigidity. A pulling away of the plasmalemma from the cell wall indicated a response to Al (Figure 11). Several workers (2, 9) reported

Figure 6. Scanning electron micrographs of corn secondary roots.

A) Normal secondaries of control plant.
B) Damaged secondaries (arrow) of Al treated plant (5 days).
C) Secondaries emerged while growing in Al (5 days).
D) Cracking (arrow) of emerging secondary upon contact with Al (5 days).

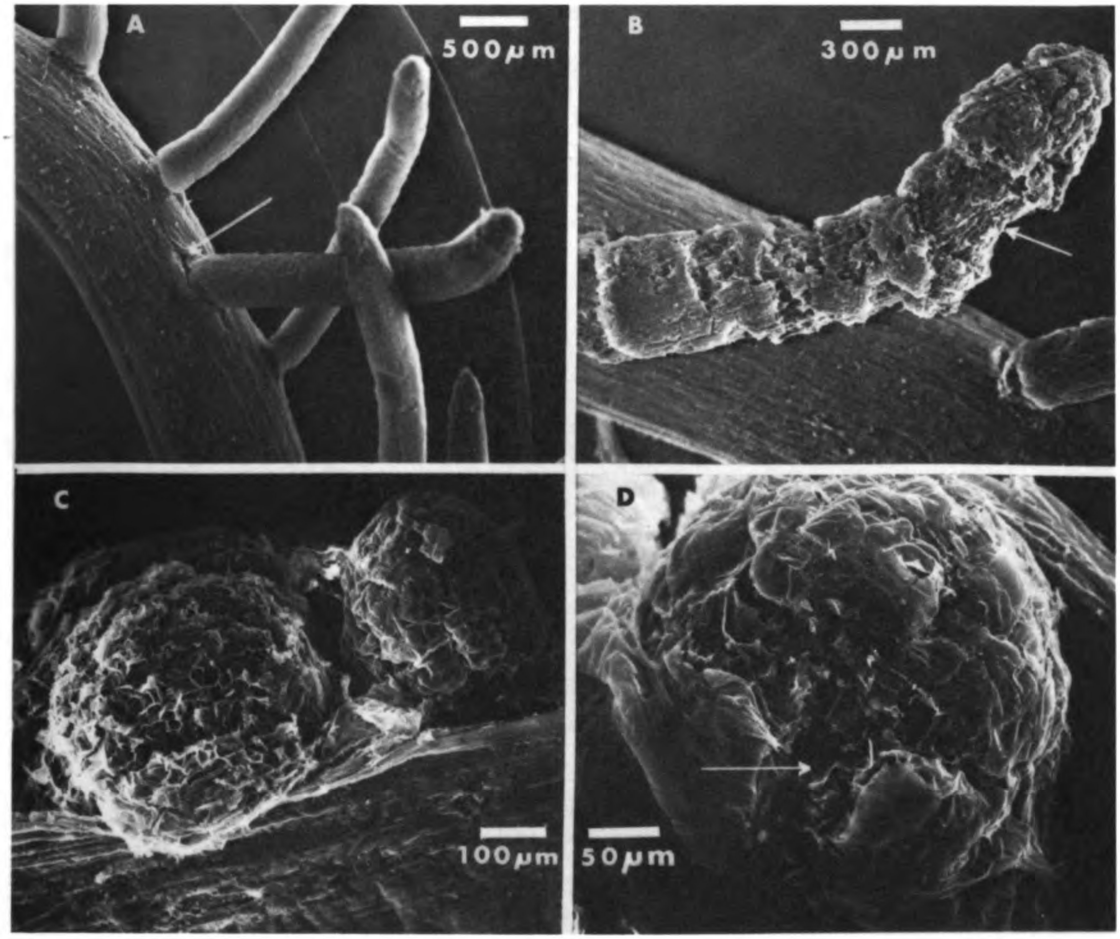

Figure 6

Figure 7. Scanning electron micrographs of corn roots illustrating secondary root initiation from pericycle and possible means of Al entry.

A) Emerging secondary root of control plant from zone of maturation.
B) Secondary root emergence of Al treated (5 days) plant 2 cm from tip. Arrows indicate channels through which Al may enter.

(Ct-cortex, End-endodermis, Pc-pericycle, VE-vessel element)

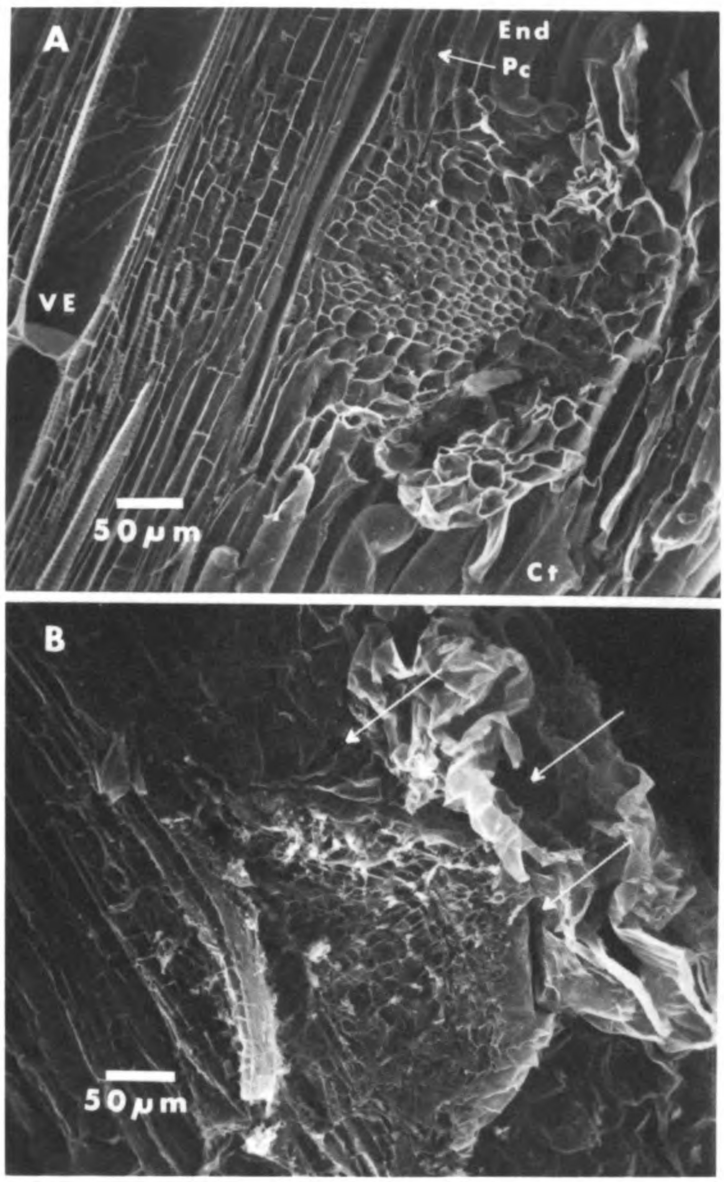

Figure 7

Figure 8. Photomicrographs of endodermal and cortical cells of corn root tips. Transverse view through the zone of elongation. Note difference in number and size of vacuoles. Arrows denote individual cells.

A) Numerous small vacuoles in cortical cells of control plant.
B) Large vacuoles in cells of cortex after 24 hr in Al solution.

(Ct-cortex, End-endodermis, Ep-epidermis, Pc-pericycle, VC-vascular cylinder)

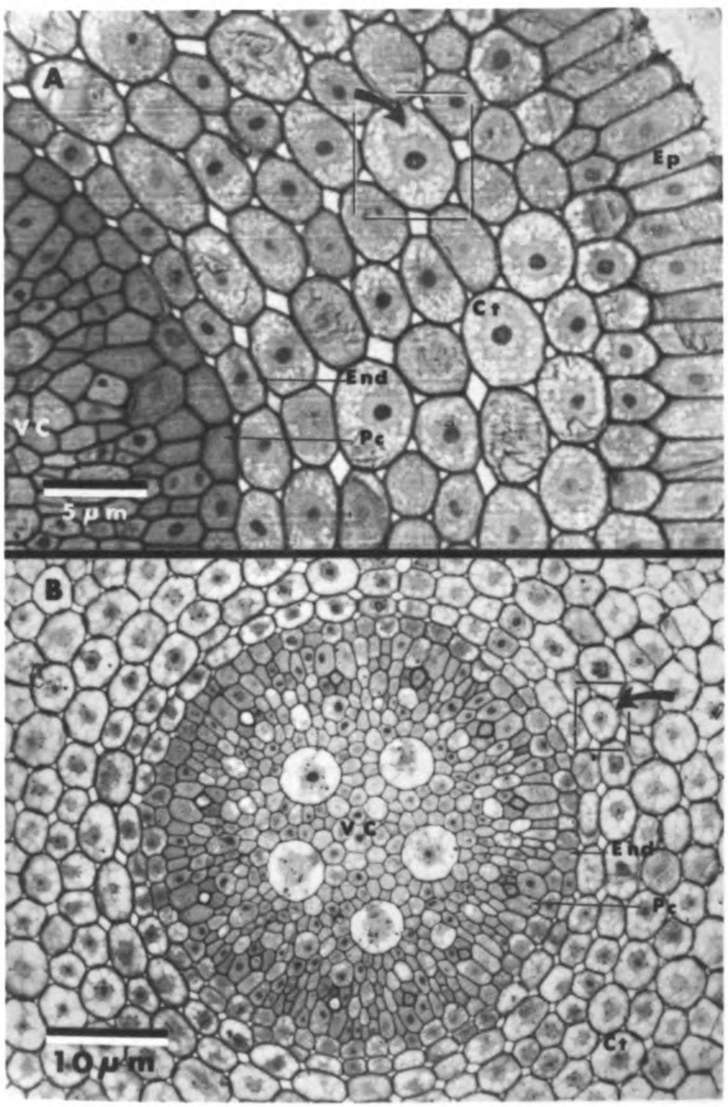

Figure 8

Figure 9. Transmission electron micrograph of Al treated (24 hr) cell through the zone of elongation and interior to the endodermis. Notice undamaged amyloplasts (Ap), endoplasmic reticulum (ER), mitochondria (M), nucleus (N), plasmalemma (Pl) and tonoplast (T).

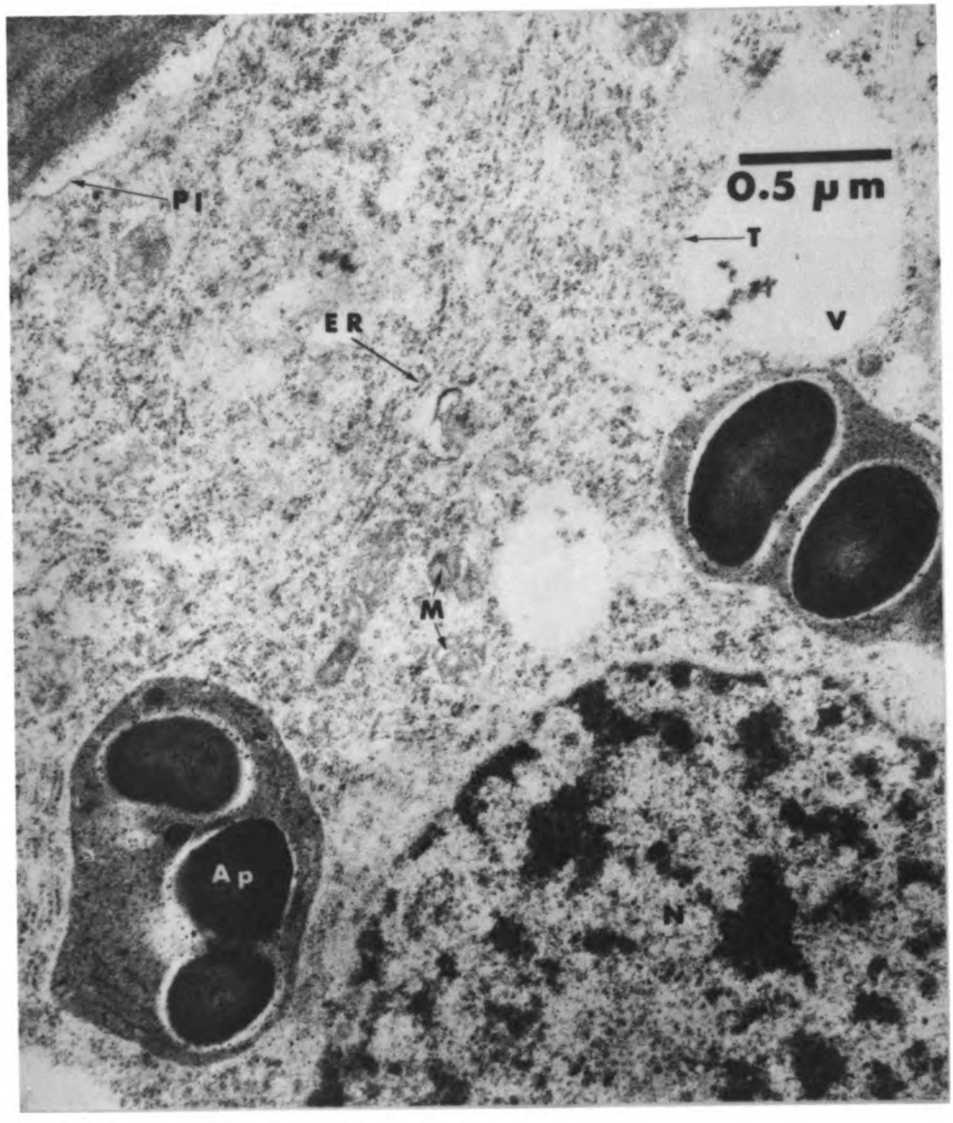

Figure 9

Figure 10. Transmission electron micrographs illustrating difference in vacuole size of epidermal and cortical cells through the zone of elongation.

A) Small but numerous vacuoles in epidermal cells of Zea mays roots (control).
B) Large vacuoles in epidermal cells of Al treated roots (60 hr).
C) Cell of cortex with normal vacuoles.
D) Disintegration and stretching of tonoplast of cortical cell resulting in larger vacuoles size (24 hr).

(N-nucleus, Nu-nucleolus, V-vacuole)

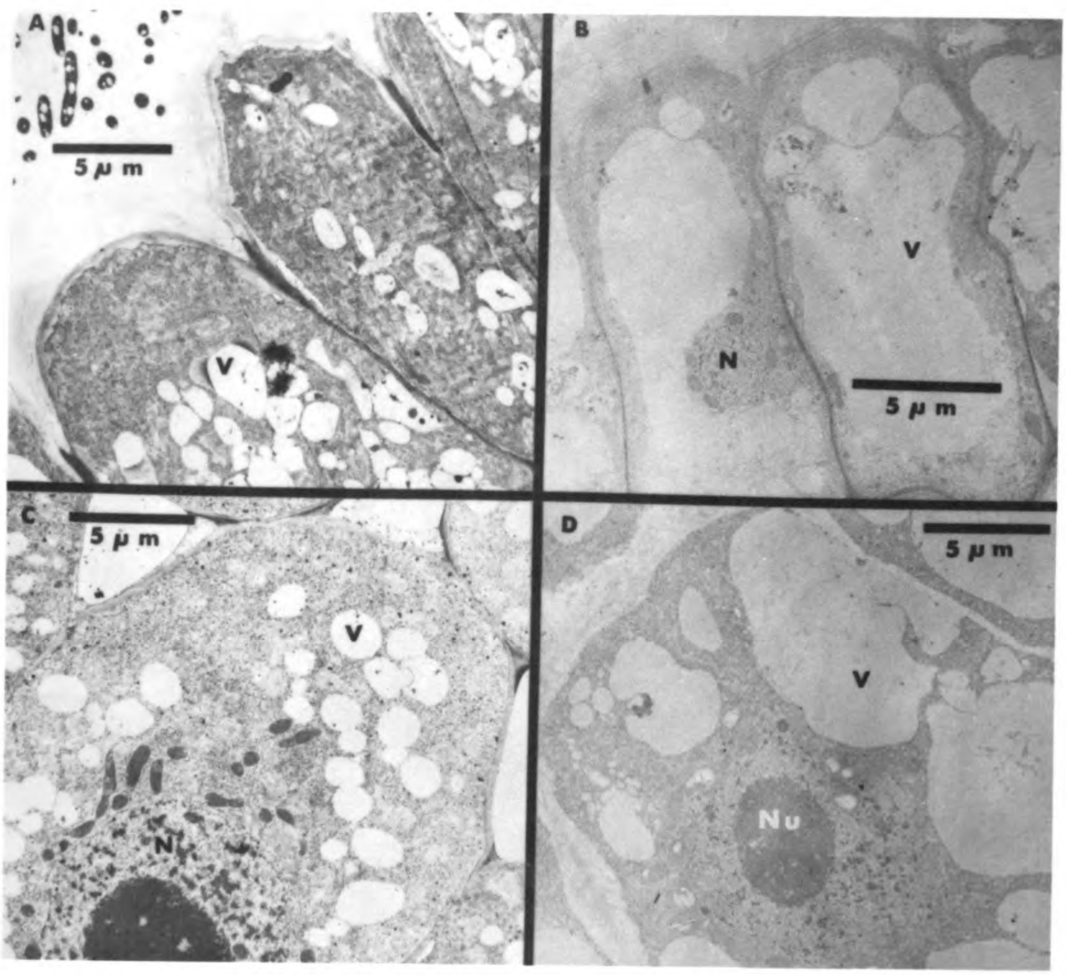

Figure 10

Figure 11. Transmission electron micrographs of Al treated (24 hr) cortical cells through the zone of elongation.

A) Plasmalemma pulling away from cell wall (arrow).
B) Breakdown and sluffing of plasmalemma from cell wall.
C) Plasmodesmata preventing further plasmolysis.

(CW-cell wall, Pl-plasmalemma, Pd-plasmodesmata, V-vacuole)

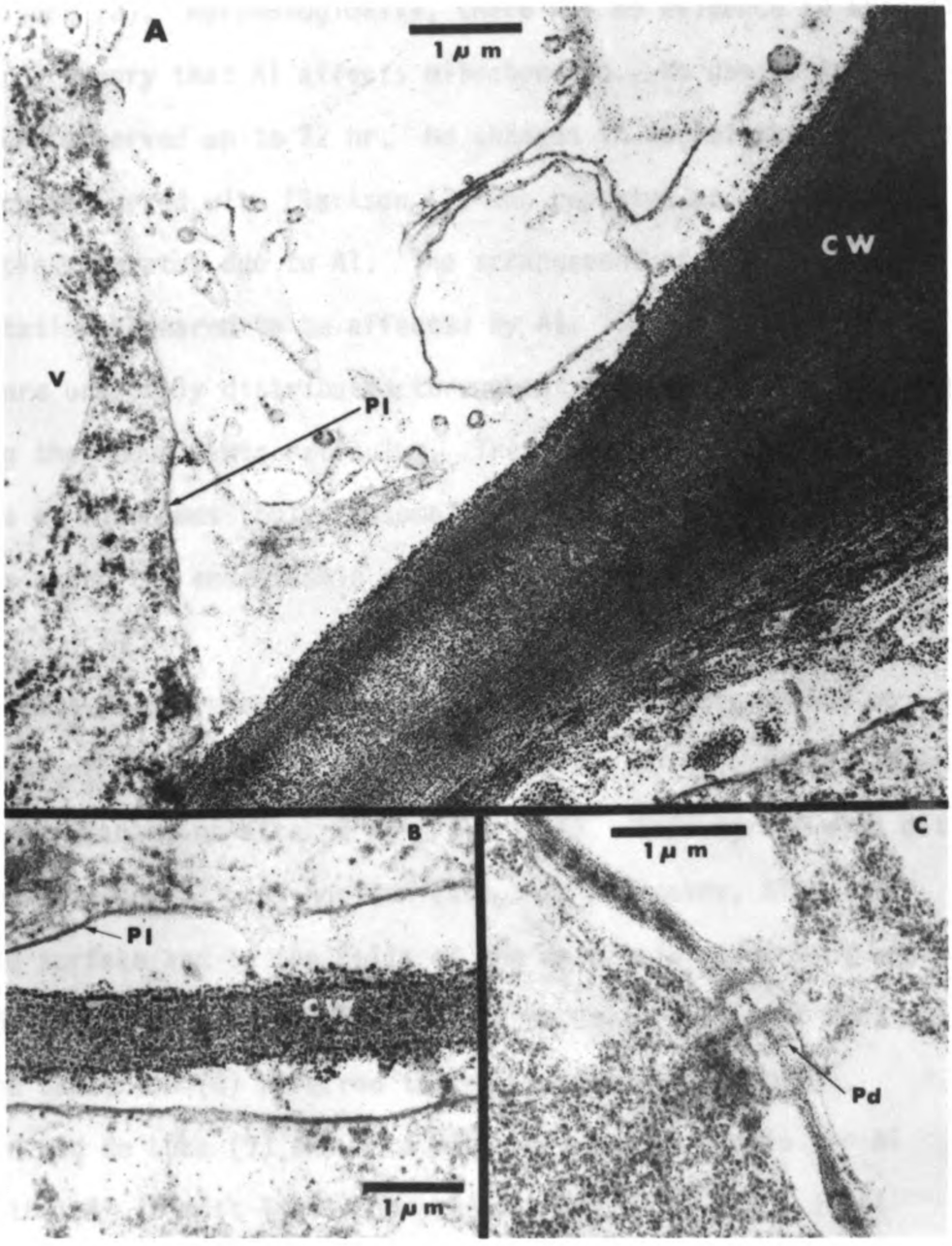

Figure 11

Al accumulated in the cell wall next to the plasmalemma, which may be an explanation of this phenomena. No damage of mitochondria and nuclei was observed (Figure 12). Morphologically, there was no evidence to support Clarkson's (3) theory that Al affects mitochondria. No damage to organelles was observed up to 72 hr. No changes in nuclei were observed, results which concurred with Clarkson (2) who reported no abnormalities of the mitotic apparatus due to Al. The arrangement of ribosomes and their orientation appeared to be affected by Al. In the absence of Al ribosomes were uniformly distributed throughout the cytoplasm and evenly spaced along the endoplasmic reticulum. Treated plants showed small aggregations of ribosomes (polyribosome) in the cytoplasm and a jamming of ribosomes along the endoplasmic reticulum (Figure 13A and B respectively).

Line scans of the electron microprobe x-ray analyzer showed no Al in the zone of elongation in plants treated for 30 min, traces after 2 hr and large quantities after 8 hr (Figure 14). This agrees with data presented by Clarkson (2) and Rorison (21). In all cases, Al accumulated at the surface and in the cells of the epidermis confirming earlier reports (16). Most of the Al detected at 2 hr could represent what Clarkson and Sanderson (4) referred to as superficial adsorption.

Joslyn and de Luca (9) showed a high affinity of pectin for Al indicating that Al is most likely adsorbed to the cell wall. In Al treated barley roots, Clarkson (2) noted that 85-90% of the Al was found in the cell wall. McClean and Gilbert (11) found Al localized in the protoplasm and nuclei. Data obtained with the microprobe showed higher concentrations of Al in the cell wall than in intracellular areas

Figure 12. Transmission electron micrographs of Al treated (24 hr) corn roots.

A) Normal mitochondria of root cap region.
B) Undamaged nucleus of cortical cell (zone of elongation).

(Ap-amyloplast, M-mitochondria, N-nuclei, V-vacuole)

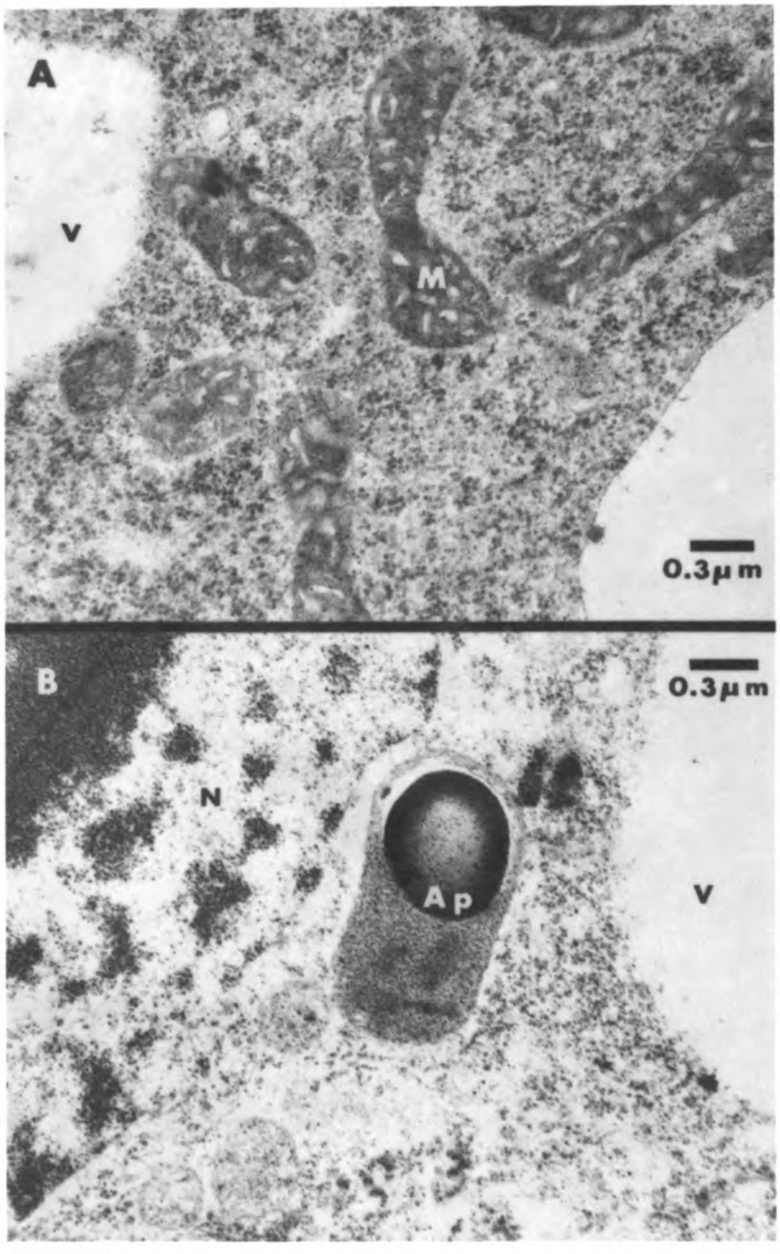

Figure 12

Figure 13. Transmission electron micrographs illustrating cellular ribosome arrangement in corn root tips.

A) Normal ribosome configuration along endoplasmic reticulum through zone of elongation.
B) Jamming of ribosomes along endoplasmic reticulum of Al treated (60 hr) cell.
C) Distribution of ribosomes throughout cytoplasm of control plant (root cap region).
D) Bunching of ribosomes when plant grown in Al solution 24 hr (root cap region).

(CW-cell wall, ER-endoplasmic reticulum, GA-Golgi apparatus, M-mitochondria, N-nucleus, V-vacuole)

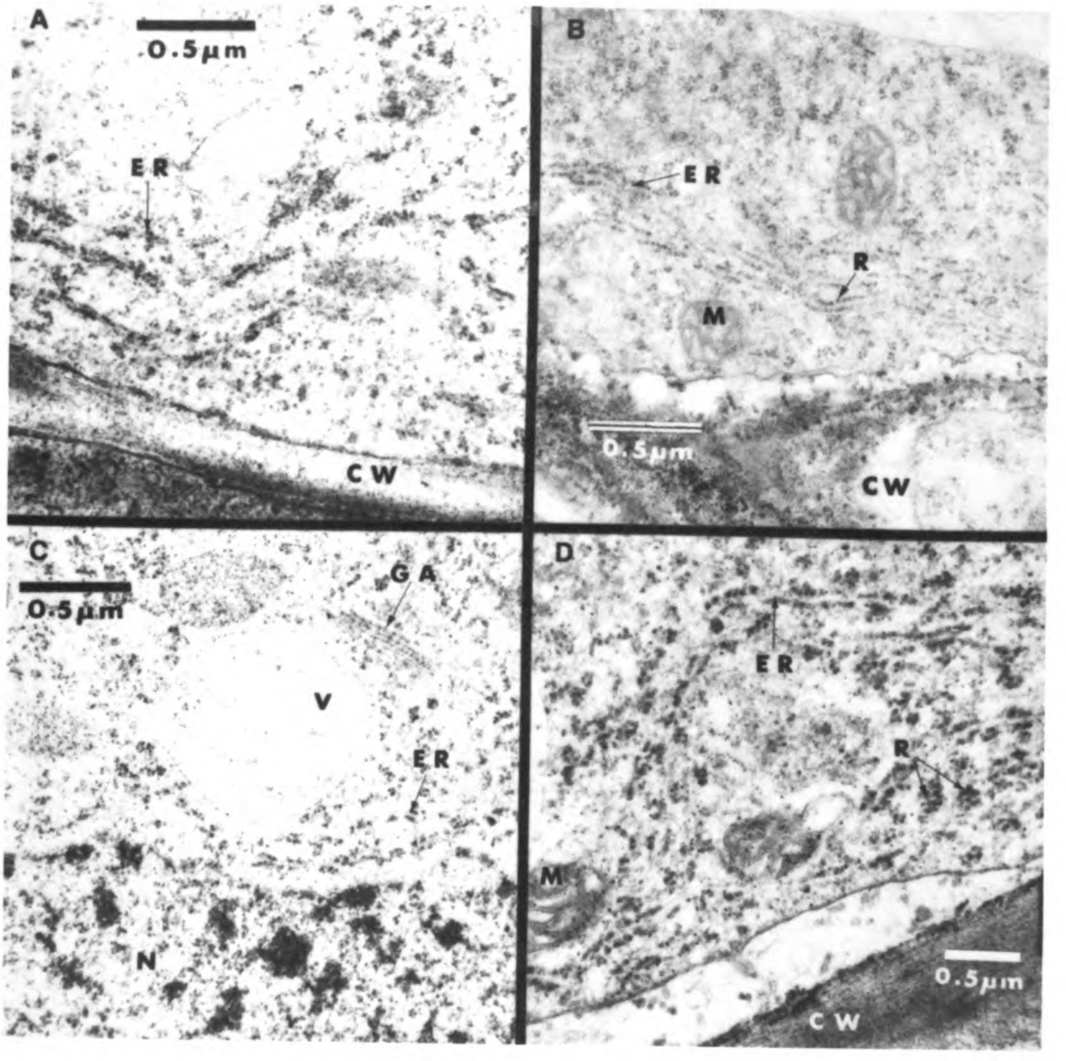

Figure 13

Figure 14. Line x-ray analysis of Al in corn roots treated with Al for 0, 2, and 8 hr. Transverse section from zone of elongation.

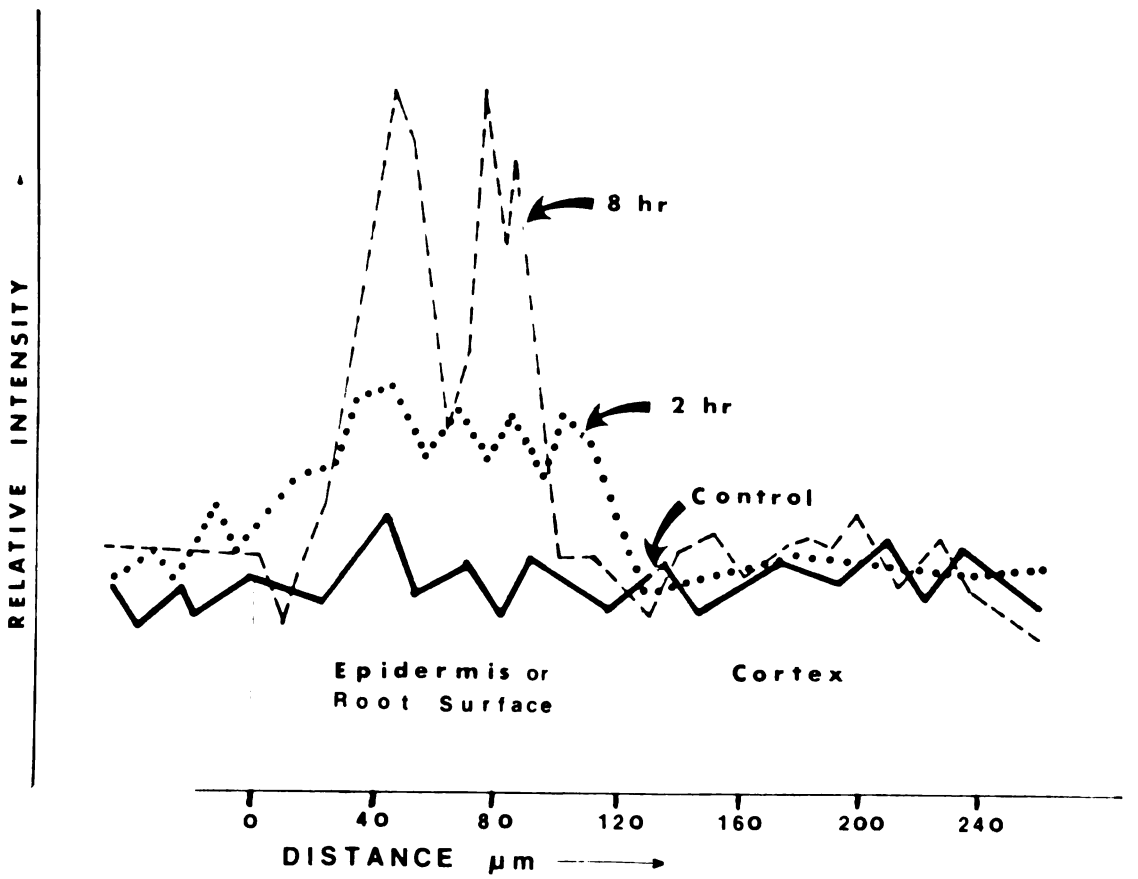
RELATIVE INTENSITY
8 hr
2 hr
Control
Epidermis or
Root Surface
Cortex
0
40
80
120
160
200
240
DISTANCE µm

Figure 14

(Figure 15). The Al may have moved toward the cell wall as the section air dried on the C disc, but even small quantities in the cytoplasm could have elicited a physiological response (15).

Micrographs obtained with the SEM reaffirmed previous work suggesting that Al accumulated largely in the epidermis and cortex of corn root tips. That the endodermis served as a barrier to further Al penetration was indicated by continued elongation of the vascular cylinder while outer cells were arrested and sluffed. Disintegration of the plasmalemma and tonoplast of cells exterior to the endodermis was observed with the LM and TEM. No cellular or subcellular differences were noted past this barrier when plants were grown in Al solution. The accumulation of ribosomes throughout the cytoplasm and their jamming along the endoplasmic reticulum indicated that Al may affect protein synthesis.

Figure 15. Line x-ray analysis for Al in Al treated (5 days) corn roots showing accumulation of Al at the root surface (RS) and in the cell walls (CW) of the cortex (Ct). Transverse sections from zone of elongation.

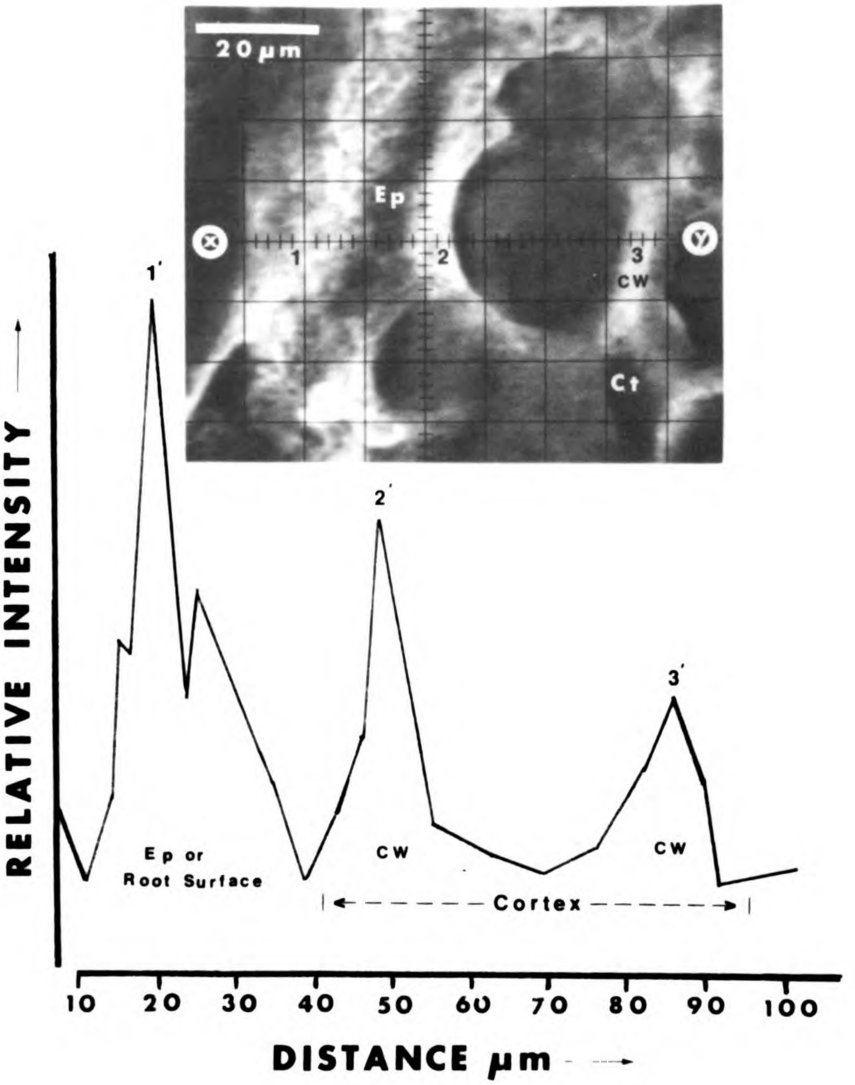
20 µm
Ep
1
2
3
CW
Ct
1'
2'
3'
RELATIVE INTENSITY
Ep or
Root Surface
CW
CW
Cortex
10
20
30
40
50
60
70
80
90
100
DISTANCE µm

Figure 15

LITERATURE CITED

LITERATURE CITED

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APPENDICES

APPENDIX A

GENERAL LITERATURE REVIEW

GENERAL LITERATURE REVIEW

Al is the third most abundant element (8.13%) in the lithosphere, preceded only by O_2 and Si (Hutchinson, 1943). Therefore, a study of the interactions of this element with plants is most appropriate.

In 1804, de Saussure (Stoklasa, 1918) reported 0.12% Al in the ash of Rhododendron and traces in other plants. Berthelot and Andre (1895) found Al in the ash of annual plants and noted that Al was absorbed mostly in the roots and translocated into the leaves only in small amounts.

A. Effects of Aluminum on Plants

Although Al is not generally considered essential for the growth of plants (McGeorge, 1925; Pratt, 1966), small amounts may stimulate plant growth. Sommer (1926) found a slight increase in seed production of peas and a marked increase in millet when Al was added to the nutrient solution. Pratt (1966) criticized Sommer's results because her work was done before several minor elements were recognized as being essential. He suggested the possibility that one of these elements was added as an impurity in the Al. Haas (1936) reported a beneficial effect of Al on the growth of Valencia orange leafy-twig cuttings. Liebig et al. (1942) reported that small amounts of Al eliminated the toxic effect of Cu on citrus. Lipman (1938) found that individual corn plants receiving small concentrations of Al were superior, in general, to those not receiving Al.

Field plots with low concentrations of Al have resulted in higher yields of alfalfa and red clover (McCleod and Jackson, 1965). Tea has been shown to grow best in soils containing soluble Al (Chenery, 1955). The beneficial effects of Al may however have been indirect. Since researchers often use high concentrations of Al to obtain significant results, Hackett (1962) felt that important effects of low concentrations of Al could possibly have been overlooked, effects which could be of ecological and physiological importance.

Rothert (1906) found many plant roots to be very sensitive to Al. Kratzmann (1914), Miyake (1916) and Stoklasa (1918) also suggested that Al in sufficient amounts was toxic to plants. In working on unproductive soils in Indiana, Abbott et al. (1913) found that $Al(NO_3)_3$ was the toxic compound affecting plant growth. They concluded that soluble Al, or lack of basicity, caused the unproductiveness of the soil. Corrective measures included the use of limestone, supplemented by phosphate and potash. Other workers substantiated these findings (Blair and Prince, 1927; Burgess and Pember, 1923; Hartwell and Pember, 1918; McGeorge, 1925; Ruprecht, 1915).

An opposing view that Al was not toxic to plants was shared by Denison (1922), Line (1926) and Magistad (1923). They maintained that Al compounds could not cause injury to plant growth due to insufficient concentrations of Al in the soil solution.

B. Anatomical and Morphological Changes Due to Aluminum Toxicity

Plants injured by high concentrations of Al are easily recognized. Although tops may be slightly stunted and show symptoms of P deficiency

(DeWaard and Sutton, 1960; Pratt, 1966), roots serve as an earlier and better indication of Al toxicity. An overall reduction of root area with stunted and malformed secondary root development is often observed (Clarkson, 1965; McClean and Gilbert, 1927; Rasmussen et al., 1968; Rorison, 1960).

C. Cellular Distribution

Early investigators were concerned with the toxic effects of Al and the distribution of Al within the plant. Ruprecht (1915) found stunting of the roots by Al and suggested it was due to the arresting of the development or killing of the first layer or two of cells and not to a poisoning of the entire root system. The development of secondary roots was stopped upon contact with Al. Studies indicated that cell division was severely affected (Clymo, 1962) or prevented (Sampson et al., 1965). The mechanism of cell division is highly sensitive to Al and may be permanently damaged by short exposures (Clarkson, 1965). Staining roots for Al indicated an accumulation mainly in root tips, surfaces, epidermal cells and cortical tissues with very little internal to the endodermis (Fleming and Foy, 1968; Wright and Donahue, 1953). Using microautoradiographic techniques, Clarkson and Sanderson (1969) noted that the endodermis restricted the entry of ^{46}Sc, a close analog of Al, into the stele. Using haematoxilin as a stain to indicate Al distribution in corn and cabbage roots, McClean and Gilbert (1927) found protoplasm and especially nuclei of epidermal cells heavily stained while cells of cortex, exterior to the endodermis, were only lightly stained. Using electron microprobe x-ray analysis, Rasmussen (1968) found high

concentrations of Al and P at the root surfaces and within the root cap. He further demonstrated that Al entered the conductive tissue through the break in the root surface caused by secondary root emergence. Clarkson (1966) suggested that the interaction of Al and P might occur 1) at the cell surface or 2) within the cell, possibly within mitochondria, which he postulated would result in a marked decrease in the rate of sugar phosphorylation by inhibiting hexokinase.

D. Hydrogen Ion Effect on Aluminum

Soluble and exchangeable Al in soils is influenced largely by soil acidity (pH). However, not all acid soils with the same pH have the same amount of soluble or exchangeable Al (Clark, 1966; McCleod and Jackson, 1967b; Pratt, 1966). At a given pH soils high in organic matter contain much less available Al than those low in organic matter (Pierre et al., 1932). The base saturation of the soil (Pierre, 1931) and the natural drainage of the subsoil (Ragland and Coleman, 1959) also influence Al content. Studies by Conner and Sears (1922), Hartwell and Pember (1918), MacLean and Chiasson (1966), Miyake (1916), Pierre (1931), Ruprecht (1915), Truog (1918) and Wright (1937) showed that the amount of soluble Al is more important in affecting plant growth than the H-ion. In fact, Gilbert and Pember (1930) observed no appreciable differences in dry weight yields of lettuce seedlings grown in a pH range of 3.2 to 7.5. Yet, Hutchinson (1943) criticized early work by Rothert (1906), Kratzmann (1914), Kiyake (1916) and Stoklasa (1918) because they did not control the H-ion concentration. Kerridge et al. (1971) suggested that a weakness in the use of many nutrient solutions dealing with

Al toxicity is the inadequate control of pH and P and thus Al concentration.

E. Tolerance

The tolerance of plants to Al varies widely. Two methods are used for determining tolerance levels; namely, soil and nutrient solutions. The advantages of nutrient culture are discussed by Kerridge et al. (1971). In classifying comparative resistance of certain plants to soil acidity and active Al, Burgess and Pember (1923) used the terms low (less than 300 ppm), medium (300-500 ppm) and high (greater than 500 ppm) resistance. According to McLean and Gilbert (1927) crops depressed with 2 ppm Al in nutrient solution were considered sensitive. Intermediate plants were injured by 7 ppm while tolerant crops could survive in concentrations of 14 ppm. Although these classifications may serve for crop plants, tolerance varies with cultivars (Armiger et al., 1968; Foy et al., 1965a, 1965b, 1967a, 1967b, 1967c, 1969, 1970; MacLean and Chiasson, 1966; McCleod and Jackson, 1967a; Neenan, 1960; Ouellette and Dessureaux, 1958; Reid et al., 1969; Vose and Randall, 1962). Barley, beets, leek and lettuce are generally considered very susceptible to Al injury. Plants which show intermediate effects are cabbage, rye and sorghum, while corn, turnips and redtop are rather resistant to Al. The degree of tolerance among plants however is controversial (Burgess and Pember, 1923; Foy and Brown, 1964; Hartwell and Pember, 1918; Lignon and Pierre, 1932, McLean and Gilbert, 1927). These discrepancies may be due to the cultivar used. Often cultivars have been selected because of properties associated with tolerance (Foy et al., 1965a, 1965b, 1967a, 1967b, 1967c).

F. Theories Explaining Tolerance

1. Interaction of Aluminum with Other Elements

According to Foy and Brown (1964) tolerance is related to the plant's ability to absorb and utilize P in the presence of high concentrations of Al. With the addition of phosphate to the soil, Al toxicity has been reduced (Blair and Prince, 1927; Conner and Sears, 1922; Hartwell and Pember, 1918; McLean and Gilbert, 1928). Pierre and Stuart (1933) observed that phosphate (monosodium and monocalcium) not only reduced Al concentration in soil solution, but also increased pH and thus precipitation of aluminum phosphate. On the other hand, they found superphosphate did not affect the pH, but lowered the concentration of Al in soil solution. Lettuce plants receiving Al had only 1/5 to 1/7 as much P as those which did not receive Al. Therefore, they suggested that Al inactivated P primarily in the roots and interfered with normal P metabolism.

Ouellette and Dessureaux (1958) suggested that the rate of Ca uptake by plants determined its degree of tolerance to Al. They found more total and water soluble Ca in so-called tolerant species. Foy et al. (1969) supported this hypothesis. Ruprecht (1915) realized the importance of Ca and reported that $Ca(CO_3)_2$ added to the soil precipitated Al. The inactivation of Al in the soil counteracted its harmful effect. Al has been shown to induce Ca deficiency (Armiger et al., 1968; Clarkson and Sanderson, 1971; Foy et al., 1967c, 1969; Hortenstine and Fiskell, 1961; Johnson and Jackson, 1964; McCleod and Jackson, 1965, 1967a; Munns, 1965). Others (Foy and Brown, 1963; MacLean and Chiasson, 1966) reported that Ca decreased in the tops of Al treated plants; however, there was increased absorption of Ca by the roots.

Rees and Sidrak (1961) found that the toxic effects of Al were correlated with its effect on the K/Ca balance. Al, as with Ca, depressed the uptake and translocation of K (DeWaard and Sutton, 1960; Harward et al., 1955; McCleod and Jackson, 1965, 1967a). Although Al decreased the amount of K in plants, Fawzy et al. (1954) and Foy and Brown (1963) showed that low concentrations of Al could also increase K uptake in roots.

Dios and Broyer (1962) found that a proper balance of Al and Mg resulted in no reduction in total dry weight of corn. Al generally decreased Mg uptake (DeWaard and Sutton, 1960; Lee, 1972; McCleod and Jackson, 1967a).

The uptake of B (Hortenstine and Fiskell, 1961) and Cu (Liebig et al., 1942) was not inhibited by Al. However, the manner in which Cu is rendered injurious by Al is not understood. Hiatt et al. (1963) demonstrated Cu inhibition in excised wheat roots with low concentrations of Al. The possibility of Al inactivating Fe within the cell was postulated by Rees and Sidrak (1961). Results showed that Al as EDTA complex markedly enhanced Fe absorption. They also noted that high concentrations of Al lowered Mn in leaves. Work by Lee (1972) established that Mn-induced Fe deficiency in nutrient solution cultures was associated with the Mn/Fe ratio. He found that additions of Al decreased this ratio and counteracted deficiency symptoms by increasing plant Fe content.

2. pH

In 1927, McClean and Gilbert noticed the tendency of crops to change the pH of solutions in which they grow. However, this tendency was not

correlated with the sensitivity of the crop to Al. Foy et al. (1965b) have shown that wheat cultivars resistant to Al can raise the pH of the nutrient solution in which they are grown while sensitive cultivars lower the pH. Foy et al. (1967c) later suggested that zones of differential pH around the roots varied with cultivars or that sensitive cultivars absorb more Al at the same pH or both. The ability of plants to produce organic acids which may act as chelating agents near the roots was suggested by Jones (1961). These acids could precipitate Al at physiological pH values thereby making it unavailable to precipitate P.

3. Cation Exchange Capacity

Al tolerance has been associated with low CEC of roots (Foy et al., 1967c; Vose and Randall, 1962). Vose and Randall found the CEC of legumes to be twice that of graminae. Within either group they found that species making the most demands on soil fertility tended to have the highest CEC. In accordance with the Donnan Theory (Huffaker and Wallace, 1958), which states that low CEC favors monovalent to divalent uptake, Vose and Randall (1962) postulated that the lower CEC of resistant selections might possibly be effective in increasing the uptake of monovalent cations at the expense of polyvalent Al cations.

Several interesting theories have been proposed regarding Al tolerance in plants. A better understanding of this problem could aid plant breeders in developing more tolerant cultivars of alfalfa (Ouellette and Dessureaux, 1958), barley (Foy et al., 1965a, 1967c, Reid et al., 1969, 1971), beans (Foy et al., 1967b, 1970) and cotton (Foy et al., 1967a). These crops would then have greater abilities to exploit acid, Al-toxic subsoils for both water and nutrients.

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APPENDIX B

ELECTRON DIFFRACTION FOR Al IN Al-TREATED CORN ROOT CELLS

ELECTRON DIFFRACTION FOR Al IN Al-TREATED CORN ROOT CELLS

Several authors (1, 2, 3) have suggested that Al precipitates P, primarily in the roots, and interferes with normal P metabolism. An attempt to show an accumulation of aluminum phosphate ($AlPO_4$ - rhombic form or $Al(PO_3)_3$ - tetragonal form) was undertaken by using electron diffraction on a Philips 300 transmission electron microscope. It was thought that small dense bodies (Figure 16) found in the vacuoles of epidermal cells from the zone of elongation might be deposits of aluminum phosphate.

While a diffraction pattern of an Al standard was obtained, no similar pattern was observed when the electron beam was focused on these bodies. Since no recognizable diffraction pattern resulted from focusing the beam on cell walls, cytoplasm, Golgi bodies, mitochondria, nuclei or vacuoles, it was concluded that if Al were within the cell it must be in an amorphous form.

Figure 16. Electron diffraction for Al.

A) Transmission electron micrograph of Al treated (24 hr) corn root tip showing dense material (arrow) within vacuole of epidermal cell (zone of elongation).
B) Electron diffraction pattern of Al standard.
C) Electron diffraction pattern of dense material (arrow) in vacuole of Figure 16-A.

(CW-cell wall, L-lysosomes, M-mitochondria, V-vacuole)

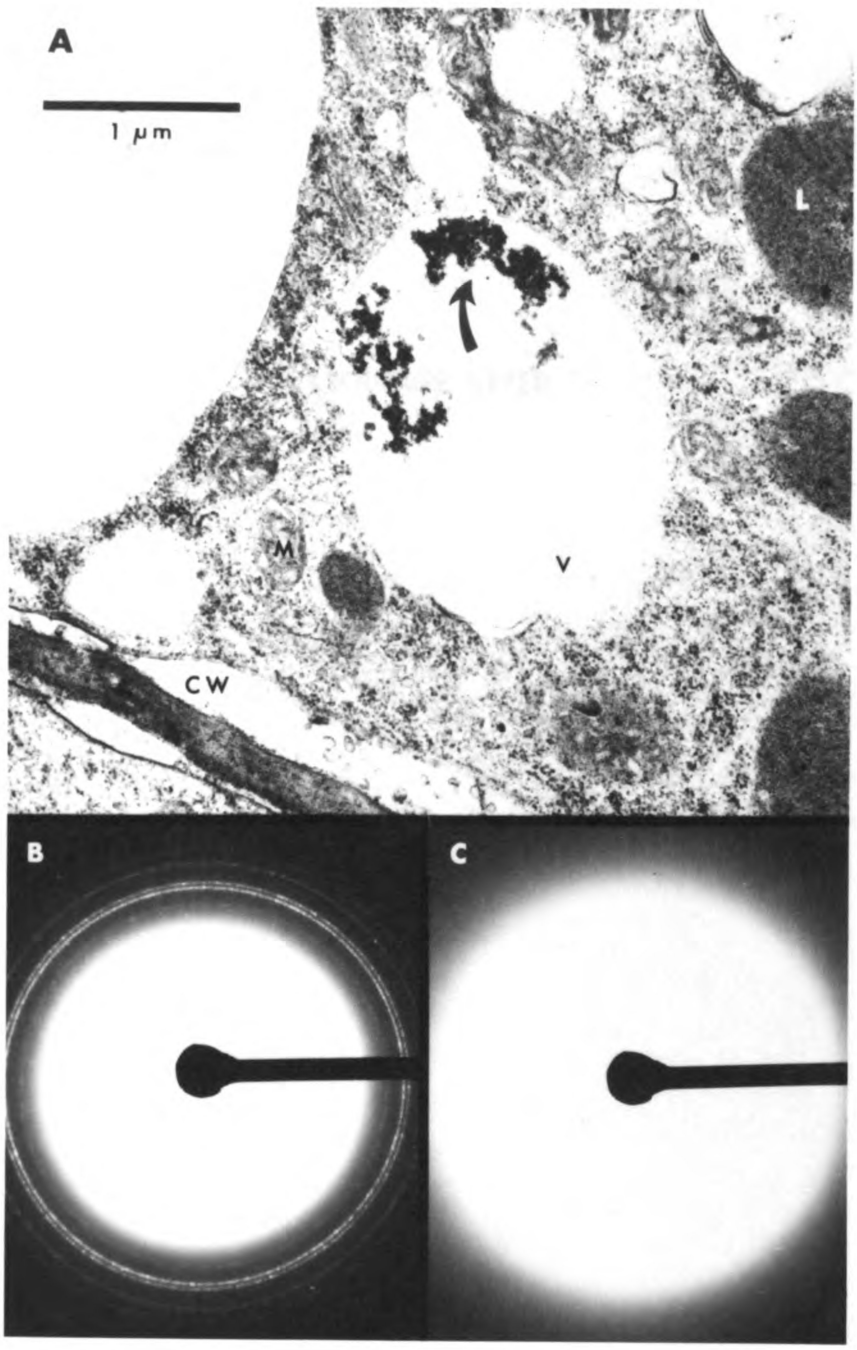

Figure 16

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