Root Development in Aluminous Hawaiian Soils[1]

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ABSTRACT: Roots of *Rhodomyrtus tomentosa* and *Melastoma malabathricum* were excavated in three soil series from the bauxitic area of Kauai. Root systems of *R. tomentosa* and *M. malabathricum* in Kapaa and Halii soils were very shallow, with tap roots turning laterally at shallow depth and with long lateral roots very close to the soil surface. Deeper tap-root penetration of *R. tomentosa* and *M. malabathricum* was observed in the Koolau soil.

Lime and phosphorus treatments were added to bauxitic subsoils of the Kapaa and Halii series in pots and *Leucaena glauca* (L.) was planted in the pots. Tap roots of *L. glauca* were stimulated by phosphorus treatment, but were restricted in untreated subsoils. Increased root development with phosphorus treatment seemed to be more related to phosphorus supply than to decreased aluminum effects. No evidence of root damage due to aluminum was found.

L. glauca roots were sectioned with a freezing microtome and stained, using hematoxylin without a mordant. Although all staining obtained could not be attributed to aluminum, since other metals can act as mordants for hematoxylin, intensity of staining was assumed to be related to aluminum concentration in the tissues. Cell walls, nuclei, and cytoplasm stained in all tissues, and outer walls of epidermal cells stained very heavily. Staining was more intense in roots from check and P-treated plants than in roots from lime-treated plants.

STUDIES of the root development of natural plant communities (Weaver 1920, Weaver and Albertson 1943, Weaver and Darland, 1949) and of cultivated plants (Weaver, 1926; Troughton, 1957; Crider, 1955) under a variety of conditions and treatments, are well known to ecologists. Normally, a well-developed root system is essential to the vigorous growth and successful competition of the dominants in most plant associations. Shallow-rooted plants, however, are known from many different habitats, especially those with poor physical properties but also from those with a low nutritional status with respect to nitrogen, phosphorus, calcium (Fox, Weaver, and Lipps, 1953) and potassium (Haynes, 1943). Root damage and restricted root development in such crop plants as barley and tobacco have been associated with high levels of soil aluminum, but little is known of root development in uncultivated plants growing in soils with high concentrations of active aluminum.

In a study of vegetation on gibbsitic Hawaiian soils Moomaw and Takahashi (1960) reported shallow root systems, but detailed studies of root development and distribution in these

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soils were not made at that time. Two particularly aggressive plant species, *Rhodomyrtus tomentosa* (Ait.) Hassk. and *Melastoma malabathricum* L., are known to grow well on Hawaiian bauxitic soils, where *Rhodomyrtus* tends to form dense thickets excluding all other vegetation. These two species were introduced on Kauai about 50 years ago and *Rhodomyrtus* has now been declared a noxious weed. It is the object of this study to characterize root growth and distribution of these and other tap-rooted species on the bauxitic soils of Kauai.

Aluminum has been shown to be toxic to plants. One of the frequently-reported toxic effects of aluminum is root injury (Lignon and Pierre, 1932; McLean et al., 1926; Bortner, 1935) in which roots may be brown in color with few rootlets and discolored root tips (Gilbert and Pember, 1931) or with root tips blackened and thickened to twice normal size (Bortner, 1935). Restricted lateral root development in rye has been reported using water cultures (Magistad, 1925). Trenel and Alten (1934) concluded that aluminum may be a root poison. Using a divided-root technique corn plants were exposed to nutrient solutions with and without aluminum. Injury was restricted to roots in the high-aluminum solutions. Nagata (1954) found that over 5 ppm aluminum in culture solutions hindered barley growth and that aluminum seemed to accumulate in the roots. Growth hindrances were decreased by adding phosphorus or calcium. He concluded that translocation of phosphorus from the root to the top in the barley plant was hindered by aluminum in culture solutions.

The precipitation of phosphate and aluminum in the plant as an aluminum phosphate has been suggested. Burgess and Pember (1923) proposed that aluminum was fixed as relatively insoluble aluminum phosphate in plants, especially in roots. McGeorge (1925) suggested that internal precipitation of aluminum by phosphorus may be important in plants but listed no specific location.

Wright (1937) divided root systems of barley plants, placing each half in different culture solutions with and without aluminum. Plant analysis indicated plant damage resulting from poorly developed root systems in solutions containing aluminum, and internal precipitation of phosphorus and aluminum where large amounts of aluminum and phosphorus were present in roots. Wright (1943) found a higher percentage of phosphorus in aluminum-treated barley plants than in nontreated; this was particularly marked in the roots. The water-soluble phosphorus in the aluminum-treated plants was low, while a H_2SO_4 solution (pH 3.0) extracted practically all P from untreated plants but much smaller amounts from plants grown in contact with Al. The precipitation was listed as occurring primarily in roots, and sharp reductions in yield were attributed to P deficiency in meristematic regions due to root precipitates. Wright (1945), using microchemical tests to determine inorganically and organically bound P, found abundant inorganic P in roots grown in contact with Al and little or none in roots from solutions without Al.

Problems of plant growth on acid soils have long been ascribed to the "active" Al in the soil and to problems of phosphate nutrition due to fixation of phosphates by Al. Longnecker and Merkle (1952) studied root development of crimson clover in relation to lime placement and found most root growth in layers which had been limed. The beneficial effect of liming was attributed to decrease in solubility of Al and Mn and an increase in solubility of P. Ragland and Coleman (1959) applied lime at several rates to subsoils of the Norfolk catena in pots and found grain sorghum root growth into unlimed subsoils was related inversely to amounts of exchangeable Al. Root growth into subsoils increased substantially with lime treatment. Root development of sorghum grown in suspensions of acid clay was restricted severely unless 80% of the acidity was neutralized.

DESCRIPTION OF EAST KAUAI

The area studied is referred to by McDonald et al. (1960) as the Lihue Depression. It is a nearly circular basin with the rim being formed by the Haupu ridge on the south, the main mountain mass of central Kauai on the west, the Makaleha mountains on the north, and Nonou and Kalepa ridges on the east. The basin is floored with lavas of the posterosional Koloa volcanic series. Two vents from the Koloa volcanic series, Hanahanapuni Crater and Kilohana Crater, lie within the basin.

The general topography of the basin is of gently sloping to moderately steep ridges and plains dissected by perennial streams, notably the Wailua River and its tributaries.

The average annual rainfall in the Lihue Depression ranges from 40 or 50 inches near the ocean to over 170 inches near the mountains. Rainfall is usually highest in winter months but there are no months during which no rain falls.

Mean monthly temperatures from nine stations below 300 ft elevation on Kauai range from 69 F in February and March to about 77 F during August through October (McDonald et al., 1960). Although no temperature records are available for higher elevations, there is a decrease in temperature with increase in elevation, of about 3 F for each 1,000 ft.

Prevailing winds are the northeast trade winds but cyclonic storms occasionally upset this pattern, especially in winter months.

DESCRIPTION OF SOILS STUDIED

Three soils occurring in the Lihue Depression were selected for study. These soils are located in or near the main area of infestation of *R. tomentosa* and *M. malabathricum* and either comprise or are associated with the major bauxitic soils of East Kauai. The principal mineral form of Al present in these bauxitic soils is gibbsite, the trihydrate of aluminum oxide (Sherman, 1958). Detailed soil descriptions have been made by the Soil Conservation Service (Womack, 1960).

Kapaa Series

The Kapaa series is a deep, well-drained, Aluminous Ferruginous Latosol developed on gently sloping to steep uplands on Kauai. These soils occur mainly in association with the Halii soils which lie above, and Puhi soils which lie below. The Halii series is developed from parent material similar to that of the Kapaa series, namely the melilite and nepheline basalts of the Koloa volcanic series. The Kapaa soils occur between 200 and 1,000 ft elevation with mean annual rainfall from 60 to 100 inches. They are clayey in texture but feel like silty clay in the A horizon (0–6 inches) owing to the strong, very fine granular structure. They are extremely hard when dry but sticky and plastic when moist, containing many roots and few pebbles in the surface layers. With depth, some mottling occurs on the blocky structures and pebbles are more numerous. These soils are used mainly for pasture, nonirrigated sugar cane, and pineapple.

Halii Series

The Halii series is a deep, well-drained Aluminous Ferruginous Latosol on gently sloping to moderately steep uplands on Kauai. This series is associated with the Koolau series at higher elevations and with Kapaa series below. It occurs in belts at about 300 to 1,000 ft elevation with mean annual rainfall from 80 to 120 inches. The A horizon (0–9 inches) of this series is a gravelly clay that feels like silty clay and is grayish-brown in contrast to the yellowish-brown of the Kapaa series. It is somewhat less hard when dry and more plastic when wet than the Kapaa. It is used principally for nonirrigated sugar cane and small acreages of pineapple.

Koolau Series

The Koolau series is a deep, poorly-drained Hydrol Humic Latosol developed on gently sloping to moderately steep uplands. It is associated with the Halii soils, and occurs between 400 and 4,000 ft elevation with mean annual rainfall of 120 and 200 inches. Most of the Koolau series is covered by rain forest, but some is used for sugar cane and pasture.

The Koolau series is a grayish-brown clay that feels like a silty clay loam, with a structure that appears to be massive to very weak medium granular. It is only slightly sticky and plastic when moist, with matted roots and many worm holes and casts making it quite porous. Lower horizons have distinct strong brown mottles.

EXPERIMENTAL PROCEDURE

Roots of *Melastoma malabathricum* and *Rhodomyrtus tomentosa* were excavated in the Halii, Koolau, and Kapaa soil series and descriptions and measurements were made of depth of penetration of tap roots, location and length of lateral roots, relation of roots to soil profile, and possible evidence of causes of thicket formation. A few plants of Norfolk Island pine (*Araucaria excelsa*) (Lamb.) R. Bn. were also excavated in the Wailua Game Refuge.

Root description and measurement were also made of *R. tomentosa* seedlings used in a pot experiment designed to measure plant and soil Al. Notes taken included color, thickening, black tips, number of lateral roots, length of tap roots, and number of active buds.

Because tap roots were observed turning laterally in Halii and Kapaa soils in the field, a pot experiment was established using the soil layer in which these roots turned as "subsoils." These soils were collected from horizons where tap roots were observed to turn laterally and were sacked carefully to prevent dehydration. They were screened through wire mesh containing approximately 4 meshes to the inch. Weighed samples of the screened soil were used to form the "bottom" 5-inch soil layer in 11-inch plastic pots, and were treated with six lime and phosphate treatments. After the treatments were mixed thoroughly in the subsoils, a 5-inch layer of untreated Kapaa surface soil was added. *Leucaena glauca*[5] seeds were planted in the surface soil and after germination plants were thinned to two per pot.

At harvest the soils were carefully removed from the pots and washed from the roots. Measurements of tap-root penetration and lateral root development were made. Roots were examined for blunted and blackened tips, and root tips from each treatment were preserved for staining studies. Yields of tops and roots were recorded and plant Al concentrations were determined. The pH, extractable Al, exchangeable calcium, and cation exchange capacity were determined for each soil.

Root tips of *L. glauca* plants from treated pots were sectioned on a freezing microtome and stained, using hematoxylin without a mordant (Johansen, 1940). Slides of the root sections were made and photomicrographs were taken.

[5] In a personal communication Dr. F. R. Fosberg has indicated the correct name for this plant should be *Leucaena leucocephala.*

FIG. 1. *Rhodomyrtus tomentosa* excavated in the Kapaa soil series, Wailua Game Refuge. The tap root turned laterally at 4-inch depth and lateral roots penetrated diagonally before ascending toward the surface.

RESULTS

Six *R. tomentosa* plants were excavated in the Kapaa soil series. All plants were extremely shallow-rooted, with tap roots turning laterally at depths of from 3 to 10 inches below the surface (Fig. 1). Lateral root development in these plants was especially pronounced and one large 10-ft shrub had a lateral root 24 ft long. Lateral roots displayed a tendency to grow downward and outward for 2 to 4 inches and then to ascend toward the surface. Lateral roots were frequently found just at, or slightly under, the soil surface.

Two thickets of *R. tomentosa* were excavated in the Kapaa soil series. These thickets contained shrubs up to 10 ft in height with trunks 1.5 to 2.25 inches in diameter. Roots were observed with diameters up to 2 inches. Tap roots turned at a depth of 10 inches and no roots of the thickets were found below this depth. There was no evidence of root fusion.

M. malabathricum plants excavated in the Kapaa soil were found to have root development similar to that in *R. tomentosa,* with tap roots turning laterally at shallow depth and long lateral roots. One plant (Fig. 2) had a small, twisted and deformed tap root with 2 main lateral roots 5 ft long. Fibrous roots were almost lacking in both *R. tomentosa* and *M. malabathricum.*

Norfolk Island pine trees (*A. excelsa*) planted about 10 years ago in the Kapaa soils were excavated to determine root development in species planted in these soils. Tap roots of these trees penetrated to what appeared to be the bottom of the planting hole before turning upward toward the surface.

Two individual plants and a thicket growth of *R. tomentosa* were excavated in the Koolau soil near Hanahanapuni Crater. Tap roots of the two individual plants penetrated 9 inches downward before turning diagonally for 1 or 2 inches. Small plants of *M. malabathricum* nearby, like the *R. tomentosa,* had tap roots which penetrated from 8 to 10 inches.

The main tap root of the *R. tomentosa* thicket penetrated 24 inches downward in the Koolau soil without turning, even though water from the soil filled the hole at a depth of 1 ft, placing it well below the water table at the time of sampling. One lateral root of this thicket was observed from which numerous stems had arisen. This was the only observation of this type in the plants excavated. It is possible that this "root" could have been a stem buried by road construction since the thicket was located close to a forest preserve road. The Koolau soil in this area has a grey surface 8 to 10 inches in thickness with a reddish-brown, yellow-mottled layer below.

A 5-ft *M. malabathricum* plant about 20 ft from the *R. tomentosa* thicket was also excavated and the tap root was traced to a depth of 18 inches where water rapidly filled the trench.

A series of *R. tomentosa* plants in the Halii soil series were excavated on the northern slopes of Kilohana Crater. These plants had extremely shallow root systems with tap roots turning laterally at about a 4-inch depth and with lateral roots almost at the soil surface (Fig. 3). *R. tomentosa* shrubs in this area were easily pulled up without digging, and tracing of lateral roots was accomplished by pulling. Excavation of such roots was difficult because of long overlapping lateral roots of surrounding plants. One 40-inch plant had a lateral root which arose from the tap root about 2 inches below the soil surface and which was traced at depths of 1 inch or less for 11 ft.

FIG. 2. *Melastoma malabathricum* excavated in the Kapaa soil series, Wailua Game Refuge. Note the shallow lateral roots and the small tap root.

FIG. 3. Plants of *Rhodomyrtus tomentosa* from the Halii soil series on Kilohana Crater, Kauai. The lateral root of the larger plant was 11 ft long.

No evidence of root injury was found in *R. tomentosa* plants grown in pots except for an unusual blunting of root tips in the Halii soil. This blunting is best described as a curving and thickening of the root tip which then resembled a miniature chicken's head. Some blackened tips were also found in the Halii soil, but since the concretionary iron-rich surface of the Halii soil was used in these pots it is doubtful that these root abnormalities were due to Al injury.

The only evidence for thicket formation of *R. tomentosa* in this pot study was the presence of a number of buds on the tap root just below the soil surface. Young shoots were observed arising from these buds and often 6 to 10 young shoots were growing simultaneously on one plant. The number of shoots arising from buds increased with time. Bud numbers of single plants ranged from 5 to 30.

Root Development of Leucaena glauca

Root development of *Leucaena glauca* in treated subsoils of the Halii and Kapaa soil series was investigated separately in pots. In both the Kapaa and Halii subsoils root development was usually restricted to the untreated topsoil if subsoils were untreated. The greatest root development in subsoils was produced by P treatments. Treatments in which lime was added in addition to P stimulated root growth more than lime alone. The addition of 1,000 lb of elemental P without lime produced the most root penetration into the subsoils and also the highest plant yields.

Comparative root systems produced by treatments in the Kapaa subsoil are illustrated in Figure 4. Tap roots of *L. glauca* in the P treatments were straight and penetrated to the bottom of the pot. Tap roots of check plants did not develop in the untreated subsoils. The effect of treatment on tap-root penetration and root development in treated Kapaa subsoil ranked as follows: P > lime plus P > lime > check.

Figure 5 shows comparative root systems in Halii subsoils. Roots of check plants in the Halii subsoils penetrated slightly into the subsoil, but total root development in the check was much less than total development in subsoils treated with P and with lime plus P.

Two types of tap-root development with treatment were observed. A long straight tap root was characteristic of P treatment, while a branching tap root was characteristic of the lime plus P treatment.

FIG. 4. Plants of *Leucaena glauca* grown in treated subsoils of the Kapaa series. Treatments from left to right are: 500 lb P, 1,000 lb P, 5 tons lime, 5 tons lime plus 1,000 lb P, and check.

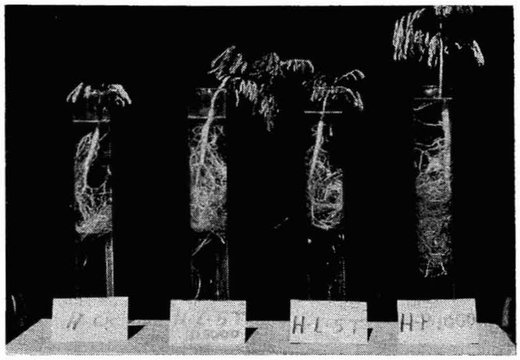

FIG. 5. Plants of *Leucaena glauca* grown in treated subsoils of the Halii series. Treatments from left to right are: check, 5 tons lime plus 1,000 lb P, 5 tons lime, and 1,000 lb P.

An interesting result of treatments added to Halii subsoils was the number of nodules produced on roots of *L. glauca.* Most nodulation occurred with lime plus P, but lime alone also stimulated nodule formation. Only one nodule was found with P treatment, and no nodules were found in the check.

Staining of Leucaena glauca *Root Tips*

Hematoxylin staining of cell walls, nuclei, and cytoplasm was evident (Fig. 6*d*). Outer walls of epidermal cells were especially heavily stained (Fig. 6*a, b*), which may indicate a precipitation of aluminum in this region. In P-treated plants two darkly stained areas at the periphery of the stele were observed, which may also represent areas of aluminum precipitation. One of these areas is shown in Figure 6*c*. The cells of the stele appeared to stain more intensely than those of the cortex (Fig. 6*a, b*), but the stelar cells are less highly vacuolated and thus contain more stainable material per unit volume than the cortical cells.

Staining was more intense in roots from the check (Fig. 6*a*) than in roots from lime-treated soils (Fig. 6*b*). Phosphate-treated roots stained more heavily than lime-treated roots. Roots treated with a combination of 5 tons lime plus 1,000 lb P stained more deeply than those treated with lime alone, but in most cases stained less deeply than those treated with P alone. Staining of nuclei was especially pronounced in the 1,000 lb P treatment.

The results obtained in this study differ from those reported by McLean and Gilbert (1927) for corn and cabbage, and by Wright and Donahue (1953) for barley, in that cells from stelar regions stained readily in all our preparations. Although McLean and Gilbert noted staining of nuclei and cytoplasm, this staining was restricted to the epidermis and outer cortex, and none of the stelar cells were stained. Wright and Donahue found that staining occurred from the epidermis to the outer wall of the endodermis, but that there was very little staining in the stelar region.

DISCUSSION

The importance of the effect of high soil Al on root growth cannot be minimized, but shallow root development in the Halii and Kapaa soil series was not interpreted as resulting from "Al toxicity." High soil Al can cause conditions in the soil which may limit root development, however. From previous work, it is known that Al can interfere with phosphate nutrition of the plant both by precipitation of phosphorus in the soil and possibly by precipitation within the plant. In addition, Al is thought to contribute to the acidity of the soil. If high alumina content of these subsoils is important in limiting root development of plants in bauxitic soils, any decrease in extractable Al and plant Al

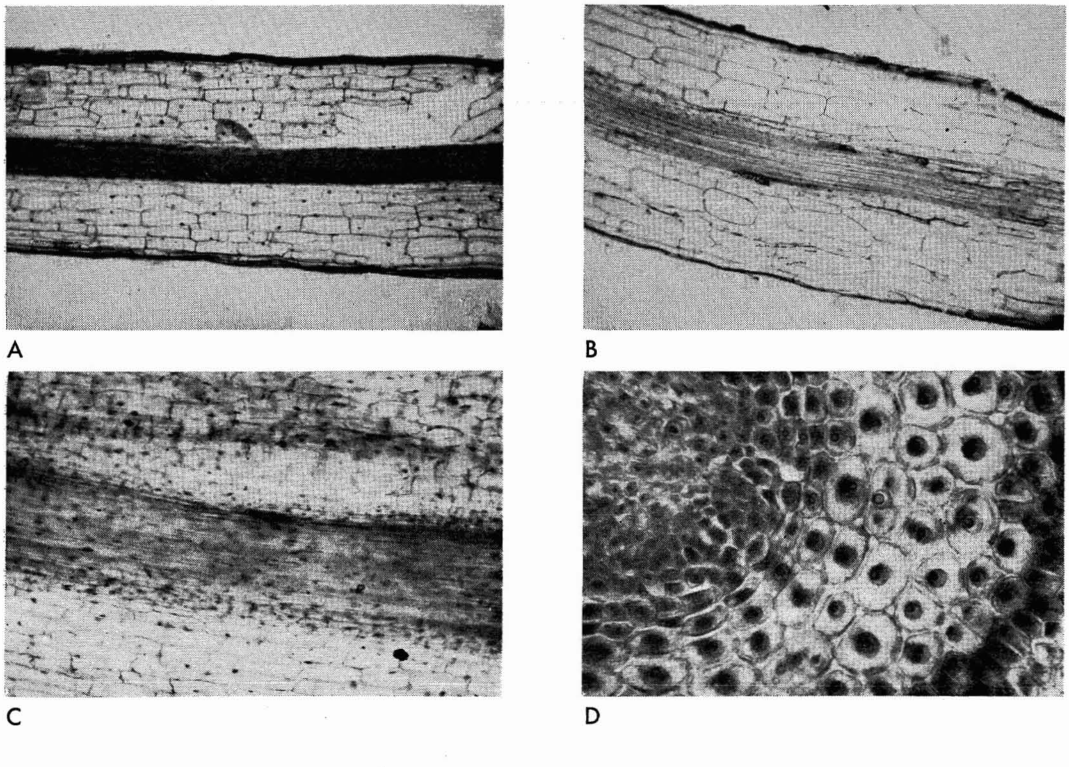

FIG. 6. Photomicrographs of *Leucaena glauca* roots sectioned and stained with hematoxylin. *A,* Root section from the untreated (check) subsoil of the Kapaa soil series. *B,* Section from Kapaa subsoil treated with 2.5 tons lime. *C,* Root from Kapaa subsoil treated with 500 lb P. Note heavily stained area in xylem region. *D,* Cross-section of root from Kapaa subsoil treated with 5 tons lime plus 1,000 lb P. Note staining of nuclei, cell walls, and cytoplasm.

should result in stimulated root growth. An examination of results of liming treatments shows, however, that although pH was increased and extractable Al and plant Al concentrations were decreased by liming, no marked stimulation of root development or plant growth of *L. glauca* occurred with liming. The increased root development of *L. glauca* in P-treated Halii and Kapaa subsoils in pots is interpreted more as a response to P than a decrease in Al effects. In addition, of course, a mass-action effect may be operating in which active aluminum in the soil is being supplied with enough phosphorus to permit complete precipitation as aluminum phosphate with enough remaining to supply the plant with adequate P.

Deep tap-root development in the Koolau soils was unexpected because of the extremely poorly-drained condition of this soil. Root growth in the wet Koolau soil in pots also appeared normal even though figures for extractable Al were high.

The lack of root damage in plants used in this study was probably related to the evolutionary background of the plants, which seem to thrive in areas of low fertility and high rainfall. Roots of plants sensitive to Al, like rye or barley, would probably be severely injured in these soils. But *Leucaena glauca,* like many other tropical plants, does not respond markedly to lime.

Thicket formation in *R. tomentosa* is probably caused by the large number of adventitious shoots which arise from buds on the tap root just below the soil surface.

Heavy staining of roots with hematoxylin cannot be definitely attributed to Al alone, since iron and other metals may also act as a mordant for hematoxylin. However, since in the present study chemical analysis showed Al to be present in large amounts, much of the staining obtained is attributed to Al. The particularly intense staining of the outer walls of the epidermis, and of two areas in the outer part of the stele, are interpreted as an indication that Al precipitation may have occurred in these areas.

Our results appear to differ significantly from those of McLean and Gilbert (1927) and of Wright and Donahue (1953). The reasons for these differences are not immediately apparent. In all three studies root sections were stained in hematoxylin without the addition of a mordant, and the staining which occurred was interpreted as an indication that aluminum was already present in the tissues.

REFERENCES

BORTNER, C. E. 1935. Toxicity of manganese to Turkish tobacco in acid Kentucky soils. Soil Sci. 39:15–33.

BURGESS, P. S., and F. R. PEMBER. 1923. Active Al as a factor detrimental to crop production in many acid soils. R. I. Agri. Expt. Sta. Bull. 194. 40 pp.

CRIDER, F. J. 1955. Root growth stoppage resulting from defoliation of grass. USDA Tech. Bull. 1102. 23 pp.

FOX, R. L., E. J. WEAVER, and R. C. LIPPS. 1953. Influence of certain soil profile characteristics upon the distribution of roots of grasses. Agron. J. 45:583–589.

GILBERT, B. E., and F. R. PEMBER. 1931. Further evidence concerning the toxic action of aluminum in connection with plant growth. Soil Sci. 31:4, 267–273.

HAYNES, J. L. 1943. Effects of pasture practices on root distribution. J. Amer. Soc. Agron. 35:10–18.

JOHANSEN, D. A. 1940. Plant Microtechnique. McGraw-Hill, New York.

LIGNON, W. S., and W. H. PIERRE. 1932. Soluble Al studies, II. Soil Sci. 34:307–322.

LONGNECKER, D., and F. G. MERKLE. 1952. Influence of placement of lime compounds on root development and soil characteristics. Soil Sci. 73:71–75.

MAGISTAD, O. C. 1925. The Al content of the soil solution and its relation to soil reaction and plant growth. Soil Sci. 20:181–225.

MCDONALD, G. A., D. A. DAVIS, and D. C. COX. 1960. Geology and Groundwater resources of the Island of Kauai, Hawaii. Hawaii Div. Hydrogr. Bull. 13.

MCGEORGE, W. T. 1925. The influence of Al, Mn, and Fe salts upon the growth of sugar cane, and their relation to the infertility of acid island soils. Hawaiian Sugar Planters' Assoc. Expt. Sta. Bull. Agri. Chem. Sec. 49.

MCLEAN, F. T., and B. E. GILBERT. 1927. The relative aluminum tolerance of crop plants. Soil Sci. 24(3):163–174.

MOOMAW, J. C., and M. TAKAHASHI. 1960. Vegetation on gibbsitic soils in Hawaii. J. Arnold Arb. 61:4, 391–411.

NAGATA, T. 1954. Influence of Al-ion concentration on the absorption of nutrients by plants. I, II. J. Sci. Soil Manure Japan 24: 255–262. (C. A. 48, 7710).

PLUCKNETT, DONALD L. 1961. Root growth in bauxitic soils. Hawaii Farm Sci. 10(1):8–9.

RAGLAND, J. L., and N. T. COLEMAN. 1959. The effect of soil solution aluminum and calcium on root growth. Soil Sci. Proc. 23:355–357.

SHERMAN, G. D. 1958. Gibbsite-rich soils of the Hawaiian Islands. Hawaii Agri. Expt. Sta. Bull. 166.

TRENEL, M., and F. ALTEN. 1934. Die physiologische Bedeutung der mineralischen Bodenazidität. Angew. Chem. 46:313–320.

TROUGHTON, A. 1957. The underground organs of herbage grasses. Commonwealth Bur. Pastures and Field Crops Bull. 44. 163 pp.

WEAVER, J. E. 1920. Root development in grassland formations. A correlation of root systems of native vegetation and crop plants. Carnegie Inst., Wash. Publ. 292. 151 pp.

——— 1926. Root Development of Field Crops. McGraw-Hill Book Co. Ltd., N. Y. 291 pp.

——— and F. W. ALBERTSON. 1943. Resurvey of grasses, forbs, and underground plant parts at the end of the great drought. Ecol. Monogr. 13:63–117.

——— and R. W. DARLAND. 1949. Soil-root relationships of certain native grasses in various soil types. Ecol. Monogr. 19:303–338.

WOMACK, DURWARD W. 1960. Tentative Description Legend of the Soil Survey of the Island of Kauai. May, 1960. Soil Conservation Serv., State of Hawaii. (Mimeo.)

WRIGHT, K. E. 1937. Effects of phosphate and lime in reducing aluminum toxicity of acid soils. Plant Physiol. 12(1):173–181.

——— 1943. Internal precipitation of P in relation to Al toxicity. Plant Physiol. 18:708–712.

——— 1945. Aluminum toxicity: Microchemical tests for inorganically and organically bound phosphorus. Plant Physiol. 20:310–312.

——— and B. A. DONAHUE. 1953. Aluminum toxicity studies with radioactive phosphorus. Plant Physiol. 28:674–680.