# Emergence and growth of two non-nodulated soybean genotypes (*Glycine max* (L.) Merr.) in response to soil acidity*

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## Abstract

Toxic levels of extractable soil Al limit production of important crops in many areas of the world. The nature of the limitation in soybeans is not completely understood. Our objectives were to investigate the cause of acid-soil-induced delays in seedling emergence, the effect of acidity on productivity in non-nodulated soybeans and further test the Al tolerance of PI 416,937 compared to a sensitive control, Essex. Growth characteristics of the two genotypes through the flowering stage were measured on a Corozal clay (Aquic Tropudult) in Puerto Rico which had been differentially limed to provide a wide range of soil Al. Early growth was also studied in the laboratory using soil from the field experiment. Highly acidic soil conditions, coupled with high Al levels, reduced growth in both Essex and PI 416,937. The principal factor responsible for delayed emergence in the high Al soil was not delayed radicle initiation, but delayed initiation of hypocotyl elongation. Hypocotyl initiation was highly associated with rate of tap root growth, with the former possibly determined by the latter, because a minimum tap root length of 60 mm was required in both high and low Al soils before hypocotyl initiation commenced. In seedlings, the high acidity reduced root more than shoot growth. By 44 days after planting (DAP), however, soil acidity had reduced shoot growth greatly. Although the soybean plants were not nodulated, foliar N levels and shoot growth were decreased by high Al levels, indicating that interference with N fixation may not be the sole mechanism by which nitrogen accumulation and plant growth is reduced in the field.

## Introduction

The most productive soils of the world are already under cultivation, and areas available for agricultural expansion are often strongly acid,

possessing toxic levels of soil Al saturation. The pH of soil can be increased and Al toxicity reduced by liming, which can be expensive or, in the case of incorporation of lime into subsurface layers, requires specialized equipment.

The mechanism by which soil acidity reduces the yield of legumes is a subject of considerable interest. High levels of soil acidity have been observed to delay emergence of common bean (*Phaseolus vulgaris* L.) (R. Lemus, personal communication), and soybean (D. Layne, per-

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sonal communication). The delay could be due to delayed germination, delayed initiation of hypocotyl elongation or a reduction in the rate of growth of the hypocotyl. Stofella et al. (1991) reported that low pH did not delay the germination of bell peppers (*Capsicum annuum* L.), but did delay emergence, and Shoemaker and Carlson (1990) also found that germination times for eight bedding plant species were not delayed by low pH media.

Abruna et al. (1992) found that high levels of acidity severely reduced nodulation and yield of Hardee soybeans grown on an Aquic Tropudult in Puerto Rico. Board and Caldwell (1991) hypothesized that a major effect of soil acidity on soybean yield was a reduction in the ability of plants to fix $N_2$ gas, either by interfering with nodulation or reducing availability of Mo, and that in their study this explained the lower soybean seed yields observed in unlimed plots.

Although genetic variability for Al tolerance in soybean is not well characterized, studies published in the last 25 years have described considerable differences in response (Armiger et al., 1969; Board and Caldwell, 1991; Hanson and Kamprath, 1979). A selection from PI 416,937 has been shown to possess Al-tolerant characteristics in studies employing two contrasting soil types (Campbell and Carter, 1990; Foy et al., 1993).

The objectives of our study were to 1) elucidate the nature of acid-soil-induced delayed emergence in soybeans, 2) examine field responses of soybean to acidity in the absence of $N_2$ fixation, and 3) test the Al tolerance of PI 416,937 by subjecting it to severe acidity-Al stress under tropical conditions in comparison with a relatively Al-sensitive control genotype, Essex.

## Materials and methods

### *Experiment I. Emergence and early growth study*

Samples of surface soils from the zero lime treatment and the high lime treatment plots from the field experiment site (described in Experiment II) were collected, dried, mixed and screened. Properties are given in Table 1. After being moistened to approximate field capacity, a 45-mm layer of soil was placed in disposable transparent plastic drinking cups whose walls were 7 degrees from vertical. Six seeds of either PI 416,937 or Essex were placed on the soil at the edge of the container with the hilum facing outward, so that growth of root and hypocotyl could be observed through the wall. The seeds were overlaid with a 40-mm layer of soil, and cups were placed in plastic trays with a layer of water in the bottom. Each tray was covered with a plastic dome so that a high degree of humidity would be maintained. The domes were kept at 26°C in the laboratory, with a low photosynthetically active radiation level of about 5 $\mu$mol m$^{-2}$ s$^{-1}$, under a 12-h light 12-h dark regime.

The four best-growing plants per cup were selected for study. Tap root and hypocotyl positions were measured nondestructively several times per day with tap root measurement ceasing shortly after the bottom of the cup was reached. The plants were harvested after 11 days, and fresh weight and length of various plant parts measured.

The experimental design was a randomized complete block. The treatments were two levels of extractable soil Al (1.1 and 11.6 cmol$_c$kg$^{-1}$) and the two genotypes. A 2 × 2 factorial arrange-

*Table 1.* Chemical properties of soils with high and low levels of extractable Al used in seedling growth study

| Al | Ca | Mg | K | Mn | Al | pH |
|---|---|---|---|---|---|---|
| (cmol$_c$kg$^{-1}$) | | | | ($\mu$g g$^{-1}$) | saturation (%) | (CaCl$_2$) |
| 1.1 | 4.70 | 0.95 | 1.36 | 112 | 13.6 | 4.38 |
| 11.6 | 1.75 | 0.42 | 0.97 | 139 | 78.7 | 3.45 |

ment of Al level and genotype was randomly assigned to experimental units, which were the drinking cups. The subplot error terms (i.e., the seedling variation within a cup) were pooled with experimental errors when permitted according to the rules for significance testing of Carmer et al. (1969). Data were analyzed using the analysis of variance procedure (SAS, 1988).

### Experiment II. Field study

The field experiment was conducted on an Aquic Tropudult (Corozal clay), at the AES-UPR Corozal Substation in the central mountains of Puerto Rico. The site had no history of soybean production. Areas previously used for limed and fertilized experiments on plantains and bananas (*Musa* spp) were cleared and treated with approximately 6500 kg ha$^{-1}$ sulfur to lower the pH. After 8 months, five levels of limestone (0, 2385, 4760, 7136, and 11896 kg ha$^{-1}$) were assigned randomly to plots (245 m$^2$ each), applied, and incorporated in 2 applications. The field was moldboard plowed to a 23-cm depth between applications. Two fertilized crops of sweet potatoes (*Ipomoea batatas* (Lam.) L.) were grown and harvested.

Five plots representing a range of acidity levels were then selected for study (mean extractable soil Al = 9.37, 5.81, 5.40, 3.32, and 3.26 cmol$_c$kg$^{-1}$, corresponding to increasing lime applications) with each plot divided into 5 subplots to determine microvariability in pH within a whole plot. Each subplot was partitioned into two sub-subplots (1.44 × 6.10 m) with a genotype assigned randomly to each of the sub-subplots within a subplot. In this way five replicate comparisons of genotypes were obtained for each level of soil acidity and associated Al saturation.

On June 4, 1991, Essex or PI 416,937 soybeans were planted into the 50 subplots in 36-cm rows (4 rows per sub-subplot). The crop was thinned to 16.4 plants m$^{-1}$ at 20 days after planting (DAP). Stand and height were measured at several dates. Number of leaflets per plant was evaluated on two 3-m row segments of each sub-subplot at 23 days after planting. At 35 DAP random fully expanded leaflets (120 per sub-

subplot) were collected, oven-dried, weighed and ground for chemical analysis. At 44 DAP (the R1 growth stage; Fehr et al., 1971), the field was inspected on a row by row basis and seven subplots were discarded because of poor stand or atypical appearance. In each of the remaining 18 subplots (36 sub-subplots), an above-ground section was harvested and oven-dry weight and plant number determined. Harvest area within each sub-subplot (in most cases 3.51 m$^2$) was bordered by guard plants to minimize competition effects on vegetative yield estimates. In some sub-subplots, where plant stand was uneven, only those portions of rows with good stand were employed for sampling, resulting in a harvest area less than 3.51 m$^2$. To compensate for the small variation in sample area among sub-subplots, dry weight was expressed as kg ha$^{-1}$. Randomly selected plants from each whole plot were dug and roots examined for evidence of nodulation.

Soil samples were collected 48 DAP from each sub-subplot. These were air-dried, ground and analyzed. Soil pH in water and 0.01$M$ CaCl$_2$ (1:2 soil:water) were measured with a glass electrode. KCl-extractable Al was determined using an atomic absorption spectrophotometer and exchangeable cations were extracted with neutral 1$M$ NH$_4$OAc and similarly determined.

Foliar nitrogen content was determined on 10 mg samples using a Perkin-Elmer 2400 CHN elemental analyzer. Foliar concentration of other elements was determined by converting 0.5 g samples to dry ash, adding 0.5$N$ HCl solvent and analyzing with a Perkin-Elmer Plasma II emission spectrophotometer (ICP).

### Statistical analysis

Regressions, correlations, and analysis of variance were completed using GLM procedures (SAS, 1988). In the analysis of dry matter accumulation at 44 DAP, whole plots with extractable Al below 3.8 cmol$_c$kg$^{-1}$ were designated as moderate Al. Plots with Al levels between 3.8 and 6.58 cmol$_c$ kg$^{-1}$ were defined as moderate Al. Two subplots were eliminated because of aberrant soil Al values. Because neither genotype accumulated appreciable

amounts of dry matter in the plot with highest acidity (9.37 cmol$_c$kg$^{-1}$ extractable Al), this whole plot was eliminated from the analysis of genotypic comparisons. Genotypic and Al effects were considered fixed with replicate subplots within a whole plot random.

## Results and discussion

### Experiment I

#### Seedling emergence

To evaluate Al effects on the timing of physiological events, we plotted growth vs. time for each individual plant. Using the slopes of these growth curves we were able to calculate the time that each shoot emerged from the soil. In the most acid soil, both genotypes emerged at about the same time (163.2 and 164.4 hrs after planting for Essex and PI 416,937, respectively) while in the higher pH soil, Essex emerged at 106.7 hrs, and PI 416,937 at 132.9 hrs after planting (Fig. 1). For Essex, the total delay caused by the higher level of acidity was 56.5 hrs and for PI 416,937 it was 31.5 hrs, indicating a tolerance of the PI to the high Al saturation found in the more strongly acid soil. Genotypic, soil Al, and



*Fig. 1.* Times of radicle initiation, initiation of hypocotyl elongation and emergence for Essex and PI 416,937 soybeans growing in soils with high and low levels of extractable Al.

interaction effects were all statistically significant ($p < 0.05$).

The observed delay in seedling emergence, induced by high acidity, was composed of three factors. Eleven percent of the delay was due to increased time required for radicle initiation, 66% was attributable to the time between radicle initiation and initiation of hypocotyl elongation (IHE), and 23% to the time from IHE to emergence. Thus, the major effect of low pH-Al toxicity on emergence was to delay the time from germination to IHE. The two genotypes differed little ($< 2$ hrs) in their response to soil acidity with respect to time of radicle initiation and hypocotyl growth rate (Table 2). The PI and Essex differed substantially in the time from radicle initiation to IHE; the PI was much less affected by soil acidity than Essex (17.3 vs 43.9 hrs delay). This difference accounted for the previously noted tolerance of the PI to acid soil with respect to emergence.

The PI may have emerged more slowly than Essex in the absence of Al stress because of its somewhat larger-than-normal 100-seed weight (the PI and Essex are 20 and 14 g, respectively). Employing a soil environment, Edwards and Hartwig (1971) demonstrated that genotypes with seed size similar to that of the PI have development rates up to 50% slower than normal genotypes in the first few days after radicle initiation.

#### Early tap root growth

Rate of tap root growth in the high extractable Al soil was less than half that in the low Al soil (0.67 mm h$^{-1}$ vs 1.52 mm h$^{-1}$). No genotypic differences or interactions were detected. As can be noted in the plot of tap root and shoot lengths vs. time (Fig. 2), IHE began when tap roots reached about 60 mm, regardless of soil acidity level. We postulate that IHE was linked to some event associated with the plants reaching this root length. The reduced tap root growth rate in the more highly acidic soil may have retarded IHE indirectly. Pan et al. (1988) theorized that the high association between root and shoot growth is related to cytokinin production in the roots. Aluminum damage to the roots disrupts cytokinin production, resulting in insufficient cytokinin for proper leaf expansion. A similar
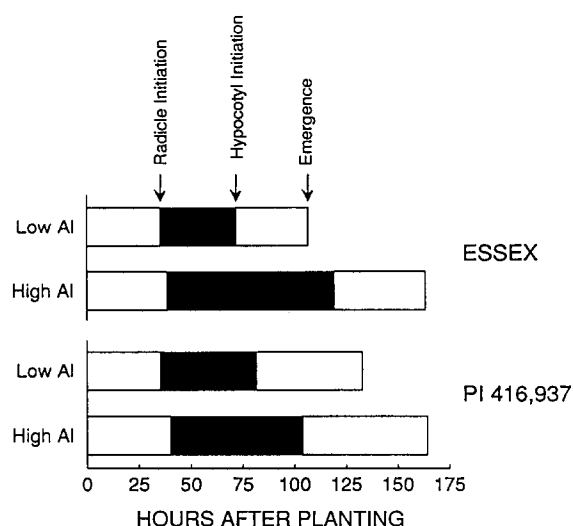
*Table 2.* Characteristics of soybean genotypes 11 days after planting and reductions associated with high extractable soil Al

| | Essex Al (cmol$_c$kg$^{-1}$) 11.6 | 1.1 | Reduction (%) | PI 416 937 Al (cmol$_c$kg$^{-1}$) 11.6 | 1.1 | Reduction (%) | Mean reduction (%) | Statistically significant terms at $p \leqslant 0.05$ |
|---|---|---|---|---|---|---|---|---|
| **Length (mm)** | | | | | | | | |
| Root tip to soil surface | 110 | 232 | 52.5 | 120 | 179 | 33.1 | 43 | Al, Al × g[a] |
| Surface to top of plant | 182 | 294 | 38.3 | 185 | 274 | 32.4 | 35 | Al |
| **Fresh weight (g)** | | | | | | | | |
| Tap root | 0.102 | 0.137 | 25.6 | 0.115 | 0.142 | 18.9 | 22 | Al |
| Lateral roots | 0.030 | 0.108 | 72.2 | 0.085 | 0.271 | 68.7 | 70 | Al, g, Al × g |
| Total root | 0.132 | 0.245 | 46.2 | 0.200 | 0.413 | 51.6 | 49 | Al, g, Al × g |
| Total shoot and underground stem | 0.999 | 1.39 | 28.0 | 1.09 | 1.61 | 32.2 | 30 | Al, g |
| **Other Characteristics** | | | | | | | | |
| Rate of early tap root growth, mm h$^{-1}$ | 0.742 | 1.54 | 51.9 | 0.592 | 1.48 | 60.1 | 56 | Al |
| Rate at emergence of hypocotyl growth mm h$^{-1}$ | 1.65 | 1.60 | −3.1 | 1.51 | 1.56 | 3.2 | 0 | |
| Time from planting to germination, h | 38.6 | 35.4 | −9.0 | 40.3 | 35.4 | −13.8 | −11 | Al |
| Time from planting to emergence, h | 163.2 | 106.7 | −53.0 | 164.4 | 132.9 | −23.7 | −38 | Al, g, Al × g |
| Time from planting to appearance of unifoliate leaves, h | 174.5 | 154.4 | −13.0 | 174.4 | 156.1 | −11.7 | −12 | Al |

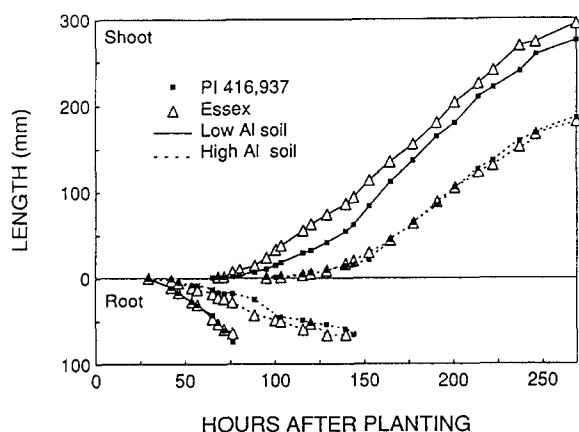[a] Al = extractable soil aluminum, g = genotype.

*Fig. 2.* Mean lengths of hypocotyl and root of Essex and PI 416,937 soybeans growing in soil with high and low levels of extractable Al as a function of time.

type of hormonal mechanism may exist with respect to hypocotyl initiation.

### Plant characteristics 11 days after sowing

Soil acidity significantly decreased growth of each trait except rate of hypocotyl elongation at emergence (Table 2). The most severely affected characteristics were fresh weight of lateral roots and rate of early taproot elongation. In general shoot factors were less affected than root factors.

The outstanding difference between the two genotypes was in lateral root growth, which for PI 416,937 was more than twice as much as that observed in Essex (Table 2). The two genotypes responded similarly to increased acidity, except for lateral root weight, tap root length, and total root weight, where the interaction effects were significant. In the low extractable Al soil, PI 416,937 showed considerably better lateral root growth than Essex, but Essex had longer tap roots. At low Al, PI 416,937 lateral root weight was 191% of the tap root weight, while in Essex it was only 79% of the tap root weight. In the high Al soil the ratios fell to 74% for PI 416,937 and 30% for Essex. The propensity of PI 416,937 to grow more lateral roots than Essex may help explain the drought tolerance noted for the PI in acid soils (Goldman et al., 1989; Hudak and Patterson, 1990; Sloane et al., 1990).

### Experiment II

#### Emergence

Soil Al had a marked effect on emergence. At 6 DAP, plant number per m row (STAND) was predicted well by the regression equation, STAND $= 17.6 - 1.93$ Al $(cmol_c kg^{-1})$ $(R^2 = 0.51$ $p = 0.0001$   n $= 50)$. Predicted stand at $9.0\ cmol_c kg^{-1}$ soil Al was only 2% of that predicted for $0.5\ cmol_c kg^{-1}$ soil Al (the two extremes of sub-subplot extractable Al concentration encountered in the field). By 14 DAP many more plants had emerged and the predicted stand at high Al was 77% that at low Al (STAND $= 27.1 - 0.734$ Al,  $R^2 = 0.12$  $p = 0.015$). By 20 DAP there was no significant relation between STAND and soil Al ($R^2 = 0.02$ $p = 0.37$). The reduced early stand we observed was therefore due to delayed emergence rather than to reduced seedling viability.

*Table 3.* Relationship between soil properties and KCl-extractable Al $(cmol_c kg^{-1})$ in 50 field sub-subplots

| Regression equation | $R^2$ | Significance level |
|---|---|---|
| pH $(H_2O) = 5.1439 - 0.15455$ Al | 0.96 | 0.0001 |
| pH $(CaCl_2) = 4.4565 - 0.09950$ Al | 0.92 | 0.0001 |
| Ca $= 6.6291 - 0.5497$ Al | 0.91 | 0.0001 |
| Mg $= 0.9156 - 0.0553$ Al | 0.77 | 0.0001 |
| K $= 1.167 - 0.0424$ Al | 0.55 | 0.0001 |
| Mn $= 60.584 + 1.556$ Al | 0.01 | 0.4378 |
| Al saturation $= 0.0673 + 0.07749$ Al | 0.97 | 0.0001 |

*Table 4.* Relation between above-ground dry matter production (DM) 44 days after planting and soil characteristics in 36 sub-subplots

| Regression equation | $R^2$ | Significance level |
|---|---|---|
| DM $= 2373.0 -$ 247.34 Al $(cmol_c kg^{-1})$ | 0.95 | 0.0001 |
| DM $= 2532.2 - 3109.57$ Al Sat. | 0.93 | 0.0001 |
| DM $= -5543.7 + 1524.85$ pH $(H_2O)$ | 0.92 | 0.0001 |
| DM $= -8062.9 +$ 2314.01 pH $(CaCl_2)$ | 0.87 | 0.0001 |
| DM $= -466.8 +$ 410.16 Ca $(cmol_c kg^{-1})$ | 0.86 | 0.0001 |
| DM $= -1190.4 + 3562.84$ Mg $(cmol_c kg^{-1})$ | 0.76 | 0.0001 |
| No relationship between DM and Mn | 0.00 | 0.9763 |

## Soil and plant responses to lime

The reduced levels of extractable Al resulting from liming were closely associated with increased pH, Ca, and Mg (Table 3), and with increased dry matter production (Table 4). The level of exchangeable Mn was apparently more related to variation in soil parent material in the experimental area than to acidity because there was no significant relationship between extractable soil Al and Mn (Table 3). Soil Bray II P values (Bray and Kurz, 1945) averaged 30 mg kg$^{-1}$, which is more than adequate for the tropical soil under study.

Dry matter production and plant height were reduced and trifoliolate emergence and flowering delayed with increased soil Al levels. Plant characteristics and regression equations relating them to soil Al are given in Table 5. The detrimental effect of Al on plant height was noted early (presumably related to delayed emergence) and became more severe as plants grew older. The calculated reductions caused by a 10.5 cmol$_c$kg$^{-1}$ increase in extractable soil Al in above-ground growth observed between 23 and 44 DAP in the field range from 76 to 103% (Table 5). These reductions are more severe than the 30%–35% reductions in shoot growth observed for a similar increase in soil Al during seedling growth in Experiment I (Table 2). The seedlings in the early growth stage are able to utilize nutrients from the cotyledons and are therefore less sensitive to nutrient limitations imposed by poor root growth that occur later. This is consistent with the observation that acidity-caused reductions in early shoot growth were generally less marked than reductions in early root growth, which ranged from 43 to 70% (Table 2).

At 41 DAP, Essex plants were approximately 5 cm taller than PI 416,937 in the absence of toxic Al effects (data not shown). Analysis of variance revealed that overall dry matter accumulation by PI 416,937 significantly ($p < 0.05$) exceeded that of Essex (Table 6). Although the genotype × Al interaction was not significant, the trend was for the PI to accumulate 20% more dry matter than Essex under moderate Al stress conditions, with smaller genotypic differences in dry matter accumulation in the absence of stress. The magnitude of genotypic differences we observed was similar to that reported in pot studies

*Table 6.* Dry matter accumulation (kg ha$^{-1}$) of soybean genotypes at 44 days after planting under low and moderate extractable soil Al levels

| Genotype | Soil Al level[a] | | Percent of control |
| --- | --- | --- | --- |
| | Low | Moderate | |
| PI 416,937 | 2213 | 1137 | 51 |
| Essex | 2071 | 950 | 46 |
| LSD (0.05) | 198 | 115 | |

[a] Mean Al levels for low and moderate designations were 1.14 and 5.14 cmol$_c$kg$^{-1}$, respectively.

*Table 5.* Relationship between plant characteristics and soil Al (cmol$_c$kg$^{-1}$) for 50 sub-subplots and calculated % reduction between low and high soil Al levels, pooled over the two genotypes

| Characteristic | Regression equation | R$^2$ | Significance level | Calculated value at | | Reduction (%) |
| --- | --- | --- | --- | --- | --- | --- |
| | | | | Al = 0.5 | Al = 11.0 | |
| Height 20 DAP (cm) | C = 18.1 − 1.22 Al | 0.78 | 0.0001 | 17.5 | 4.7 | 73 |
| Height 23 DAP (cm) | C = 20.7 − 1.45 Al | 0.79 | 0.0001 | 20.0 | 4.8 | 76 |
| Height 28 DAP (cm) | C = 26.9 − 1.89 Al | 0.84 | 0.0001 | 26.0 | 6.1 | 76 |
| Height 35 DAP (cm) | C = 40.1 − 3.24 Al | 0.82 | 0.0001 | 38.5 | 4.5 | 88 |
| Height 41 DAP (cm) | C = 55.7 − 4.69 Al | 0.89 | 0.0001 | 53.4 | 4.1 | 92 |
| Percent plants with trifoliolate leaf 14 DAP | C = 25.6 − 2.74 Al | 0.20 | 0.0014 | 24.2 | −4.5 | 118 |
| Number of leaflets per plant 23 DAP | C = 9.5 − 0.56 Al | 0.73 | 0.0001 | 9.2 | 3.3 | 64 |
| Mean plant weight 28 DAP (g) | C = 1.108 − 0.1035 Al | 0.81 | 0.0001 | 1.06 | −0.03 | 103 |
| Leaflet weight 35 DAP (mg) | C = 142.4 − 12.87 Al | 0.86 | 0.0001 | 136 | 0.8 | 99 |
| Percentage plants flowering 35 DAP | C = 96.0 − 8.01 Al | 0.53 | 0.0001 | 92 | 8 | 91 |

*Table 7.* Relationship between dry matter production in kg ha$^{-1}$ (DM) and foliar mineral concentration for 22 representative subplots

| Regression equation | $R^2$ | Significance level |
|---|---|---|
| DM = -1403.6 + 2414.3 Ca (%) | 0.82 | 0.0001 |
| DM = -8363.2 + 1671.6 N (%) (Essex) | 0.75 | 0.0001 |
| DM = -7607.5 + 1671.6 N (%) (PI 416,937) | | |
| DM = 2415.4 - 2.2566 Al (mg kg$^{-1}$) | 0.60 | 0.0001 |
| DM = 2069.9 - 0.9585 Mn (mg kg$^{-1}$) | 0.60 | 0.0001 |
| DM = 5752.1 - 43.490 Zn (mg kg$^{-1}$) | 0.63 | 0.0001 |
| DM = 2697.0 - 3.7373 Fe (mg kg$^{-1}$) | 0.39 | 0.0019 |
| No relationship of DM with Mg | 0.01 | 0.5907 |

by Campbell and Carter (1990) and Foy et al. (1993).

### *Foliar mineral concentration relationships*

Foliar analyses were obtained from 22 subplots with a wide range of extractable soil Al levels (0.6 to 9.6 cmol$_c$kg$^{-1}$). Dry matter accumulation was highly correlated with foliar Ca ($R^2 = 0.82$) and with Al, Mn, N, Zn, and Fe, but not with Mg (Table 7). Including foliar Al, Mn, Zn, Mg, or N with foliar Ca in the regression did not significantly improve the correlation.

The concentrations of foliar Ca, N, Al, Mn, Zn, and Fe were correlated with extractable soil Al (Table 8). The critical levels for toxicity of 200 mg Mn kg$^{-1}$, 300 mg Fe kg$^{-1}$, and 200 mg Al kg$^{-1}$ (Plank, 1988) were exceeded in nearly all the subplots; foliar levels for Ca in one high-extractable-Al subplot fell below the deficiency critical level of 0.5%. Foliar N decreased 0.1%

*Table 8.* Relationship between foliar mineral concentration and extractable soil Al (cmol$_c$kg$^{-1}$) for 22 representative subplots

| Regression equation | $R^2$ | Significance level |
|---|---|---|
| Ca (%) = 1.524 - 0.0903 Al | 0.85 | 0.0001 |
| N (%) = 6.278 - 0.11389 Al (Essex) | 0.77 | 0.0001 |
| N (%) = 5.841 - 0.11389 Al (PI 416,937) | | |
| Al (mg kg$^{-1}$) = 193 + 69 Al | 0.59 | 0.0001 |
| Mn (mg kg$^{-1}$) = 63 + 168.9 Al | 0.65 | 0.0001 |
| Zn (mg kg$^{-1}$) = 85.4 + 3.859 Al | 0.66 | 0.0001 |
| Fe (mg kg$^{-1}$) = 264 + 26.4 Al | 0.37 | 0.0027 |
| Mg (%) = 0.34 - 0.00076 Al | 0.01 | 0.75 |

for each cmol$_c$kg$^{-1}$ of extractable soil Al, but did not reach the deficiency level of 4.25%.

Genotype had a significant effect on two foliar nutrients. Nitrogen levels averaged 5.7% in Essex and 5.3% in PI 416,937 ($p = 0.038$); foliar Mg was 0.31% in Essex and 0.35% in PI 416,937 ($p = 0.006$). The lower N levels found in PI 416,937 are consistent with the slightly more yellowish green color they showed in the field.

Board and Caldwell (1991) reported decreased N concentrations in soybeans grown on acid soils, and suggested that the main effect of reduced soil pH on yield was reduced ability of the plants to fix N$_2$ gas. The soybeans in our study were not nodulated, but did show a marked reduction in foliar N as well as other nutrients as soil Al increased, suggesting that decreased root development induced by acidity is sufficient to cause poor soybean growth even in the absence of detrimental effects on N fixation.

### Conclusions

Highly acidic soil conditions reduced soybean growth in both Essex and PI 416,937 soybeans. The principal factor responsible for delayed emergence in the high extractable Al soil was not delayed radicle initiation, but delayed initiation of hypocotyl elongation. Hypocotyl initiation was associated with rate of tap root growth, with the former possibly determined by the latter, because a minimum tap root length of 60 mm was required in both high and low Al soils before hypocotyl initiation commenced. In seedlings, the high Al soil reduced root growth more than shoot growth. By 44 DAP, however, soil acidity had reduced shoot growth greatly. Although the soybean plants in this study were not nodulated, foliar N levels and shoot growth were decreased by high Al saturation and strong acidity, indicating that interference with N fixation may not be the sole mechanism by which nitrogen accumulation and plant growth is reduced in the field.

The PI 416,937 tended to be more tolerant to Al stress during seedling emergence than was Essex. A high concentration of extractable soil Al (9.4 cmol$_c$kg$^{-1}$) quickly overwhelmed both genotypes as they began subsequent growth, however. Under more moderate Al stress (ap-

proximately $5.1\,cmol_ckg^{-1}$) both genotypes grew and flowered, but the PI tended to accumulate somewhat more dry matter than Essex.

## Acknowledgements

## References

Abruna F, Rodriguez J, Badillo-Feliciano J, Silva S and Vicente-Chandler J 1978 Crop response to soil acidity factors in Ultisols and Oxisols in Puerto Rico, III. Soybeans. J. Agric. Univ. P. R. 62, 90–112.

Armiger W H, Foy C D, Fleming A L and Caldwell B E 1969 Differential tolerance of soybean varieties to an acid soil high in exchangeable aluminum. Agron. J. 60, 67–70.

Board J E and Caldwell A G 1991 Response of determinate soybean cultivars to low pH soils. Plant and Soil 132, 289–292.

Bray R H and Kurtz R T 1945 Determination of total organic and available forms of phosphorus in soils. Soil Sci. 59, 39–45.

Campbell K A G and Carter Jr T E 1990 Aluminum tolerance in soybean. I. Genotypic correlation and repeatability of solution culture and greenhouse screening methods. Crop Sci. 30, 1049–1054.

Carmer S G, Walker S G and Seif R D 1969 Practical suggestions on pooling variances for F-test of treatment effects. Agron. J. 61, 334–336.

Edwards Jr C J and Hartwig E E 1971 Effect of seed size upon rate of germination in soybean. Agron J. 63, 429–430.

Fehr W R, Caviness C E, Burmood D T and Pennington J S 1971 Stages of development descriptions for soybean. Crop Sci. 11, 929–931.

Foy C D, Carter, Jr T E, Duke J A and Devine T E 1993 Correlation of shoot and root growth and its role in selecting for aluminum tolerance in soybean. J. Plant Nutr. 16, 305–325.

Goldman I L, Carter Jr T E and Patterson R P 1989 Differential genotypic response to drought stress and subsoil aluminum in soybean. Crop Sci. 29, 330–334.

Hanson W D and Kamprath E J 1979 Selection for aluminum tolerance in soybeans based on seedling-root growth. Agron. J. 71, 581–586.

Hudak C M and Patterson R P 1990 Evaluation of a soybean plant introduction for drought tolerance under field conditions. Agron. Abst. p. 123.

Pan W L, Hopkins A G and Jackson W A 1988 Aluminum inhibited shoot development in soybean: A possible consequence of impaired cytokinin supply. Comm. Soil Sci. Plant Anal. 19, 1143–1153.

Plank C O 1988 Plant Analysis Handbook for Georgia. Cooperative Extension Service, University of Georgia College of Agriculture, Athens, Georgia. 64 p.

SAS Institute 1988 SAS/STAT User's Guide. SAS Institute, Inc, Cary, NC.

Shoemaker C A and Carlson W H 1990 pH affects seed germination of eight bedding plant species. HortScience 25, 762–764.

Sloane R J, Patterson R P and Carter Jr T E 1990 Field drought tolerance of a soybean plant introduction. Crop Sci. 30, 118–123.

Stoffella P J, DiPaola M L, Pardossi A and Tognoni F 1991 Rhizosphere pH influences early root morphology and development of bell peppers. HortScience 26, 112–114.

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