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ABSTRACT

Eastern gamagrass, *Tripsacum dactyloides* L., has been reported to tolerate a wide variety of soil conditions, including drought, flooding, and acidity, but its specific tolerance to aluminum (Al) has not been tested. One strain of this species, PMK Select Lot 94 SFG-1, was tested for its tolerance to excess Al in an acid, Al-toxic Tatum subsoil (clayey, mixed, thermic, Typic Hapludult) and in nutrient solutions containing Al. Roots were able to penetrate unfertilized Tatum subsoil at pH levels as low as 4.1-4.2 (1:1 soil-water), at Al saturations of 64 to 77% of CEC, and to tolerate Al concentrations in nutrient solution that would be lethal for many crop plants. For example, with 4 mg Al L^{-1} and a final solution pH of 4.67, shoot and root dry weights were 75 and 76%, respectively, of those with no Al. Even with 24 mg Al L^{-1} and a final solution pH of 4.13, shoot and root dry weights were 45 and 46%, respectively, of those for the no Al check treatment. Hence, this strain of gamagrass shows promise for use on soils having acidic, Al-toxic subsoil layers that act as root barriers and predispose plants to injury by drought. Roots of gamagrass are also reported to penetrate hard clay pans and to create root channels for subsequent crops that lack this ability. Current studies indicate that the strain tested was susceptible to a chlorosis resembling iron

(Fe) deficiency when grown in a Jiffy Mix potting mixture or with excess Al in nutrient solutions. Hence, gamagrass is tentatively being classified as a calcifuge [Al tolerant-Fe-inefficient]. In the current experiment, considerable plant to plant variability was noted regarding susceptibility to this chlorosis factor and to a purpling symptom resembling phosphorus (P) deficiency. Results indicate that an exhaustive screening of gamagrass populations could identify strains that are more suitable for specific soil situations.

INTRODUCTION

Shallow rooting is a serious yield-limiting factor for crops in soils throughout the world. In many soils, rooting depth and proliferation are believed to be limited by acidic (Al-toxic) subsoil layers (Foy, 1992), and soil acidity is generally increased by long-term nitrogen (N) fertilization (Darusman et al., 1991). When the pH of the sub-plow layer of soil is below 5.0 (1:1 soil-water), Al toxicity is likely to occur in Al-sensitive plants (Foy, 1974,1984,1988; Kamprath and Foy, 1985). In most soils, lime applied to the plow layer-does not move downward at satisfactory rates to neutralize subsoil Al, and mixing lime with acidic subsoil to detoxify Al is generally not cost effective. Plant species and genotypes/cultivars within species differ widely in their tolerance to excess soluble Al (Foy, 1993). Hence, an alternative approach is to lime and fertilize the plow layer of soil as usual and grow plants having the abilities to send their roots into acidic, potentially Al-toxic subsoil horizons. Such plants would be more tolerant to drought and more effective in using subsoil water and nutrients, particularly N, which might otherwise become a groundwater pollutant.

Eastern gamagrass, *Tripsacum dactyloides* L., shows promise as a tool for ameliorating both acidic and compact subsoils. This long-lived perennial was a popular forage crop during the 1800's (Magoffin, 1831, 1843), but due to plowing and overgrazing, the species practically disappeared as a crop for over a century. Currently, the species is making a comeback as a forage crop (Faix et al., 1980; Brejda et al., 1987; Hardin, 1994; Dickerson and van da Grinten, 1990). The species occurs naturally from the northern United States to Paraguay and Bolivia (Harlan and deWet, 1977). According to Hitchcock and Chase (1971), it grows from Massachusetts west to Michigan, Iowa and Nebraska, and south to Florida, Texas and the West Indies. Although *Tripsacum* is a small genus, it contains great variability (Kindiger and Dewald, 1996). Some forms are reportedly adapted to swales of the North American prairies, eastern coastal plains, deep sandy soils, semi-arid regions in Mexico, rocky outcrops, tropical rain forests, and river banks (Harlan and deWet, 1977).

Exceptional drought tolerance in one strain of eastern gamagrass (observed by Dan Shepherd, Clitton Hills, Missouri) led to a seed production enterprise (Eaheart, 1992). This species has many other traits that would be desirable in sustainable agriculture. These include high protein content (up to 17% in forage and 30% in grain), high yields (8 tons·acre^{-1}), high palatability and digestibility (Faix et al.,

1980; Schwendiman and Hawk, 1973; Burns et al., 1992) as well as adaptation to a wide range of soil conditions. Evidence based on nitrogenase production indicates that eastern gamagrass can meet some of its N requirement through associative N fixing bacteria (Brejda et al., 1994). After considering all of its desirable features, C.L. Dewald (personal communication, 1995), considers eastern gamagrass "queen of the grasses".

Roots of eastern gamagrass are reported to penetrate clay pans that serve as root barriers to corn and soybeans in soils of Missouri (McGinty and Alberts, 1995). In some cases, where roots penetrated to depths of 2 m or deeper, the soil was sufficiently acidic (pH below 5.0 in water) that Al toxicity could limit root growth of sensitive crop plants (Clark et al., 1996). However, to my knowledge, the specific Al tolerance of this species has not been tested. Roots of gamagrass growing in and below clay pans had large amounts of aerenchyma or air filled voids that probably enabled them to tolerate perched water tables that often occur in these soils (Clark et al., 1996). These investigators also noted that under soybeans following old stands of eastern gamagrass, roots were found to a depth of 150 cm, but roots of soybean following row crops were only 40 to 60 cm deep. However, subsequent exam inations showed that at least some of the roots found under soybeans following eastern gamagrass were old gamagrass roots that were not yet completely decomposed. Water retention characteristics of the soil that had been in gamagrass for 50 years showed that root channels created by this species were persistent, and hence might reduce the physical restriction of clay pans for roots of subsequent crops.

The objective of this study was to test the tolerance of eastern gamagrass to excess Al in acidic soil and nutrient solution, and hence determine its ability to tolerate and ameliorate acidic subsoils.

MATERIALS AND METHODS

Four greenhouse experiments were conducted during June to September 1994 at Beltsville, MD. One experiment was in fertilized, acid Tatum subsoil (clayey, mixed, thermic, Typic Hapludult), two experiments in a split medium, and one in nutrient solutions containing Al.

Experiment 1: Fertilized Tatum Subsoil

The growth medium was a Tatum clay loam subsoil having a pH of 4.66 (1:1 soil-water) before fertilization. This subsoil is used routinely to screen plants for Al tolerance (Foy and Peterson, 1994). Before planting, the soil was fertilized with a standard treatment that produces good plant growth on Tatum subsoil that is limed to pH of 5.5, or higher. The treatment consisted of 100, 109, and 137 $\mu g \cdot g^{-1}$ of N, P, and potassium (K), respectively, added as ammonium nitrate (NH_4NO_3) and monopotassium phosphate (KH_2PO4) in solution and mixed throughout the soil, along with lime treatments. Each pot was mixed separately.

TABLE 1. Lime response of eastern gamagrass on Tatum subsoil (Experiment 1).

$CaCO_3$ added mg kg^{-1}	Final [+] soil pH	% Al sat.[++]	Shoot dry weight g pot^{-1}	Root dry weight g pot^{-1}	Relative shoot weight %	Relative root weight %
0	4.15	77	0.68	0.29	39.3	37.5
375	4.25	64	1.20	0.66	69.3	83.5
750	4.42	59	1.13	0.61	64.7	78.4
1500	4.57	44	1.38	0.61	79.3	78.3
3000	4.98	14	1.74	0.80	100.0	100.0
	Lsd 5%		0.33	0.16	19.1	17.3

[+]pH in 1:1 soil water suspensions.
[++](KCl extr. Al)/(KCl extr. Al + NH_4OAc extr. Ca, Mg, K, and Na) x 100 = %.

Lime rates were 0, 375, 750, 1,500, and 3,000 mg·kg^{-1} calcium carbonate ($CaCO_3$), resulting in final soil pH values of 4.15 to 4.98 and Al saturation values of 77 to 14% of CEC (Table 1). The experimental design was a randomized complete block with five lime rates with three replications. Six stratified (pre-germinated) seeds of eastern gamagrass (PMK Select Lot 94 SFG-1) were planted in 1-kg pots, and the stand was thinned to three plants after establishment. Thirty-three days after planting, shoots and roots were harvested, photographed, dried, and weighed. Dry matter were subjected to analysis of variance, and statistically significant differences between means were evaluated by an LSD at 5%.

Experiment 2: Split Medium—Jiffy Mix Above/Unfertilized Tatum Subsoil Below

In a preliminary, single pot, split medium study, Jiffy Mix (a commercial plant bedding mixture) was placed in the upper portion and Tatum subsoil with no fertilizer or lime, with fertilizer alone, and with fertilizer plus lime sufficient to neutralize Al. Final pH values for the subsoil were 4.6, 4.2, and 5.0, respectively. Roots penetrated the Tatum subsoil in each of the three treatments (Figure 1). In a parallel test with single pots, the roots of the Al-tolerant Dayton and Al-sensitive Kearney barley (*Hordeum vulgare* L.) cultivars and Al-tolerant Perry and Al-sensitive Chief soybean [*Glycine max.* (L.) Merr.] cultivars failed to penetrate unlimed Tatum subsoil. Roots of Al-tolerant Atlas 66 wheat (*Triticum aestivum* L.) made limited growth into the unlimed subsoil, but those of Al-sensitive Scout 66 wheat made none. In similar preliminary studies, a single-cross maize (*Zea mays* L.) hybrid, reported to tolerate acid soils in Brazil, made more root growth in the unlimed Tatum subsoil than one that is reportedly more sensitive to soil acidity. These preliminary results indicated that eastern gamagrass has a higher tolerance to Al than many other plant species, and this observation prompted the replicated study of Experiment 2.

In Experiment 2, three eastern gamagrass plants per pot were grown for 28 days in a split medium consisting of fertilized Jiffy Mix (above) and unfertilized Tatum subsoil (below) treated with 0, 375, 750, 1,500, 3,000 and 4,000 mg·kg^{-1} $CaCO_3$ to give a final subsoil pH range of 4.4 to 5.7 and Al saturation values from 77 to 4% of CEC (Table 2). The experimental design was a randomized complete block with six lime rates and four replications. Holes were punched in the bottoms of the pots in the upper part of the split medium to permit roots to penetrate the subsoil in the lower containers. Pots containing Jiffy Mix or Tatum subsoil were watered to field moisture capacity, initially, and weighed daily to determine water use and loss by evaporation. For the first five days, the combined pot units were adjusted to field moisture capacity daily. For the next five days, only one-half of the daily water loss was restored to encourage rooting in the subsoil. On day 12, pots were restored to field moisture capacity. For the remainder of the experimental period, only one-half of the daily water loss was replaced. During this time, plants showed early signs of wilting, but recovered when watered. Dry matter data were treated as in Experiment 1.

FIGURE 1. Eastern gamagrass on a split medium composed of Jiffy Mix (upper) and Tatum subsoil (lower). Top photo: Plants in nested containers. Bottom photo: Roots in Jiffy mix (top) and in Tatum subsoil (bottom) with (left to right) no treatment, fertilizer alone and fertilizer plus 3000 mg $CaCO_3$ kg^{-1}. Final subsoil pH values were 4.6, 4.2, and 5.0, respectively (single pots).

TABLE 2. Shoot and root growth of eastern gamagrass in a split medium. Upper portions of nested cups contained fertilized Jiffy Mix and the lower portions contained unfertilized Tatum subsoil treated with different levels of $CaCO_3$ (Experiment 2).

$CaCO_3$ added to subsoil mg kg^{-1}	Final⁺ pH of subsoil	% Al sat.⁺⁺	Shoot dry weight in Jiffy Mix g pot^{-1}	Root dry weight in Jiffy Mix g pot^{-1}	Root dry weight in subsoil g pot^{-1}	Relative weight in subsoil %
0	4.4	77	13.1	3.01	0.75	57.2
375	4.5	66	15.4	3.25	1.09	83.4
750	4.6	54	15.3	3.67	1.30	100.0
1500	4.7	39	14.1	2.75	0.92	70.6
3000	5.1	11	14.8	3.44	1.29	99.0
4000	5.7	4	10.0	2.17	0.79	60.3
	Lsd 5%		5.8	1.20	0.52	20.0

⁺pH in 1:1 soil-water suspensions.
⁺⁺(KCl extr. Al)/(KCl extr. Al + NH_4OAc extr. Ca, Mg, K, and Na) x 100 = %

Experiment 3: Split Medium—Potting Soil Above/Unfertilized Tatum Subsoil Below

The upper portions of the split medium were fertilized potting soil at pH 6.6, and the lower portions were unfertilized Tatum subsoil treated with 0, 375, 750, 1,500, 3,000, and 4,000 mg·kg^{-1} $CaCO_3$ to give a final subsoil pH range of 4.2 to 5.6 (Table 3). Three plants were grown for 35 days before being photographed, harvested, dried, and weighed. The experimental design was a randomized complete block with six subsoil lime rates and four replications. Dry weights of shoots and roots were treated as in Experiments 1 and 2.

Experiment 4: Nutrient Solutions Containing Aluminum

A preliminary, unreplicated experiment showed that the roots of eastern gamagrass were not seriously injured by 4 mg·L^{-1} Al in nutrient solutions at pH 4.0 (Figure 2). This result prompted the replicated study of Experiment 4 with higher concentrations of Al. Pregerminated seeds were planted in Jiffy Mix and plants were grown for seven days before the roots were washed clean and the plants transferred to the experimental solutions. The basal nutrient was a 1/5 Steinberg described previously (Foy et al., 1967; Taylor and Foy, 1985), which has been used routinely in Al tolerance tests. The nutrient solution containers were 8-L buckets, equipped with aerators, and enclosed in wooden boxes to exclude light. Each container top had four holes and four corks, each of which supported one plant (four plants per container). The experimental design was a randomized complete block with 0, 4, 8, 16, and 24 mg·L^{-1} Al with four replications. Nutrient solution pH was adjusted to 4.0 initially, and then on every other day thereafter for the duration of the experiment. After 25 days in the solutions, the plants were photographed, harvested, dried, and weighed. Dry matter data were statistically analyzed as in the earlier experiments.

RESULTS

Experiment 1: Fertilized Tatum Subsoil

Shoot and root dry weights were significantly increased by liming the Tatum subsoil from pH 4.15 to 4.98, at Al saturation values between 77 and 14% of CEC (Table 1 and Figure 3). Dry weights of both shoots and roots were significantly higher at pH 4.25 to 4.57 than at 4.15, and those of shoots were significantly higher at pH 4.98 (14% Al sat.) than at all other pH levels. Relative shoot and root dry weights (wt at pH 4.25/wt at pH 4.98 x 100) were 69 and 83%, respectively, when the soil Al saturation was 64% of CEC. Roots penetrated the unlimed soil, even at pH 4.15 (Al sat. 77%), and maintained a normal white color (Figure 3). Hence, this strain of eastern gamagrass appeared more tolerant to the Al-toxic soil than many other species. For example, compare the lime response of gamagrass as shown in Figure 3 with that of Sordan [cross between grain sorghum, *Sorghum*

TABLE 3. Shoot and root growth of eastern gamagrass in a split medium. Upper portions of the nested cups contained fertilized potting soil at pH 6.61. Lower portions contained unfertilized Tatum subsoil treated with different levels of $CaCO_3$ (Experiment 3).

$CaCO_3$ added to subsoil mg kg^{-1}	Final [+] pH of subsoil	Shoot dry weight in potting soil g pot^{-1}	Root dry weight in potting soil g pot^{-1}	Root dry weight in subsoil g pot^{-1}	Relative weight in subsoil %
0	4.2	12.9	2.88	2.21	64.1
375	4.5	12.5	2.48	3.07	89.0
750	4.5	13.2	2.92	3.07	89.0
1500	4.9	12.5	2.14	3.44	99.7
3000	5.1	13.7	2.72	3.45	100.0
4000	5.6	16.2	3.20	2.96	85.8
	Lsd 5%	3.6	1.05	0.81	20.0

[+]pH in 1:1 soil-water suspensions.

FIGURE 2. Response of eastern gamagrass to Al in nutrient solution. Left to right: 0, 1, 2, and 4 mg Al L^{-1} at initial pH 4.0 (single pots).

bicolor (L) Moench, and Sudangrass] as shown in Figure 4. Also note that even with a higher pH range for the plants shown in Figure 4, Sordan was more sensitive to the acid soil than the gamagrass plants shown in Figure 3.

With no lime added at pH 4.15, plant shoots were stunted, some old leaf tips were necrotic, and some purpling leaf symptoms resembling P deficiency were noted. Although growth improved with liming, some of these symptoms persisted, even at pH 4.98 where plant dry weights were maximal and where little or no Al toxicity would be expected. The fertilizer applications used indicated that absolute P deficiency was not growth-limiting; however, P availability may have been sub-optimal at pH 4.98.

Experiment 2: Split Medium—Jiffy Mix Above/Unfertilized Tatum Subsoil Below

When Jiffy Mix was the top portion of the split medium, roots of gamagrass penetrated the unfertilized, unlimed Tatum subsoil at pH 4.4 (Table 2 and Figure 5). Liming the subsoil to a pH range of 4.5 to 5.1 significantly increased absolute root dry weights and relative weights (wt with no lime/wt with lime x 100) in the subsoil portion of the split medium, but these parameters were decreased at pH 5.7 (Table 2). Low lime response and good root development and color in unfertilized soil at pH 4.4 confirmed the Al tolerance of the gamagrass noted in

FIGURE 3. Lime response of eastern gamagrass on acid, Al-toxic, fertilized Tatum subsoil. Left to right 0, 375, 750, 1,500, and 3,000 mg $CaCO_3$ kg^{-1}. Final soil pH values were 4.13, 4.25, 4.42, 4.57, and 4.98, respectively. Corresponding Al saturation values were 77, 64, 59, 44, and 14% of CED, respectively (Experiment 1).

Experiment 1. Some leaf chlorosis was observed at both low and high subsoil pH, with the least chlorosis occurring at pH 4.6 and 5.1.

Experiment 3: *Split Medium—Potting Soil Above/Unfertilized* Tatum Subsoil Below

When the top portion of the split medium was potting soil at pH 6.61, shoot dry weights in the potting soil were not significantly affected by liming of the Tatum subsoil to pH 5.6, but root weights in the potting soil tended to be highest at pH 5.6 (Table 3). Although roots penetrated the unfertilized, unlimed Tatum subsoil and showed little injury at pH 4.2 (Figure 6), absolute root dry weights were significantly increased as the subsoil pH was increased to the range of 4.5 to 5.1. Relative root dry weights (wt with no lime/wt with lime x 100) showed a similar pattern (Table 3); however, treatment differences did not reach statistical significance at the 5% level. Results support the conclusions obtained from

FIGURE 4. Lime response of Sordan (sorghum-Sudangrass hybrid) on an acid, Al-toxic Tatum subsoil. Left to right: 0, 375, 750, 1,500, 3,000, and 6000 mg $CaCO_3$ kg^{-1}. Final soil pH values were 4.3, 4.3, 4.4, 4.6, 5.2, and 6.3, respectively. Corresponding Al saturation values were 76, 64, 64, 51, 29, and 0.1%, respectively (single pots).

Experiments 1 and 2 that gamagrass has considerable tolerance to excess Al in the acid Tatum subsoil.

Experiment 4: Nutrient Solutions Containing Aluminum

Shoot dry weights were significantly reduced by Al concentrations of 4 $mg{\cdot}L^{-1}$ or above, but these reductions were significantly greater at 24 mg Al than at 4 or 8 $mg{\cdot}L^{-1}$ (Table 4). Even Al at 24 $mg{\cdot}L^{-1}$, shoot and root dry weights were 45 and 46%, respectively, of those with no Al. At 4 mg Al L^{-1}, the corresponding values were 75 and 66%, respectively, for shoots and roots. Although root dry weights were reduced by Al, roots were still able to grow and maintain a white color at combinations of Al and pH that would be lethal to many crop species (Figure 7). Hence, results of the nutrient culture study supported the conclusions from the subsoil studies in Experiments 1, 2, and 3 that gamagrass has a relatively high degree of Al tolerance. This conclusion is further strengthened by the fact that solution pH did not exceed 4.7 for the Al treatments during the experiment and

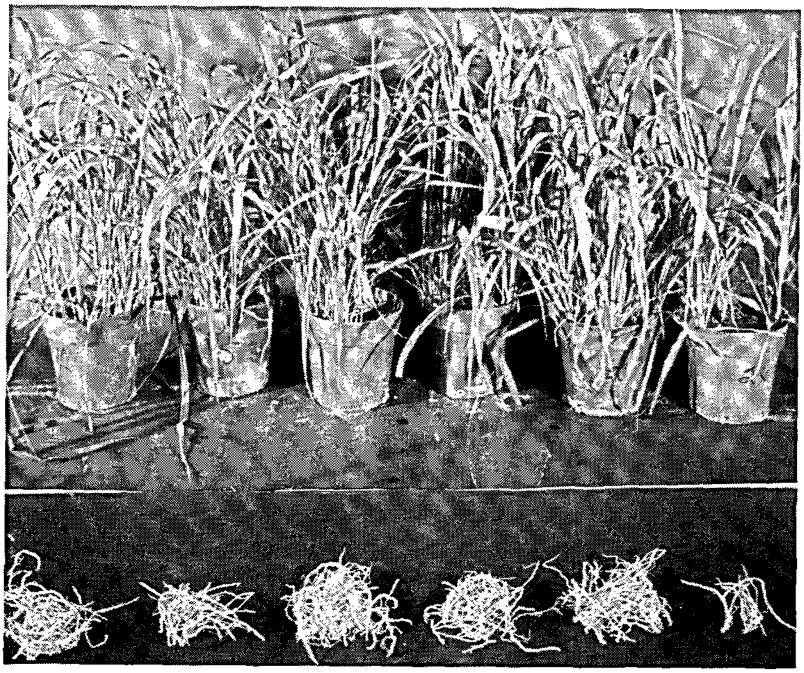

FIGURE 5. Shoot and root growth of eastern gamagrass in a split medium composed of fertilized Jiffy Mix (upper) and unfertilized Tatum subsoil (lower). The subsoil was treated with (left to right) 0, 375, 750, 1,500, 3,000, and 4,000 mg $CaCO_3$ kg^{-1}. Final subsoil pH values were 4.4, 4.5, 4.6, 4.7, 5.1, and 5.7, respectively. Corresponding Al saturation values were 77, 66, 54, 39, 11, and 4% of CEC, respectively (Experiment 2).

was generally maintained within the range of 3.7 to 4.5 (data not shown). This means that roots were always exposed to relatively high concentrations of soluble Al. Solution pH values for the no Al treatments were also maintained below 4.5 for the first 14 days of the experiment, but then rose abruptly to values above 6.0 after 17 days (Table 4).

When growing in Jiffy Mix prior to exposure to Al solutions, gamagrass showed chlorosis with considerable plant to plant variability. Although the Jiffy Mix potting mixture supposedly contained balanced fertility, the addition of Peters 20-20-20 fertilizer with Fe caused the plants to turn green. Plants that were green in Jiffy Mix also greened up when placed in nutrient solutions containing 1 mg Fe L^{-1} as FeEDTA. At first, this greening occurred in both the no Al and plus Al treatments. Later, the no-Al plants remained green while those treated with increasing concentrations of Al showed increasing degrees of a leaf striping chlorosis resembling Fe deficiency. This condition was particularly severe in plants grown at the 24 mg Al L^{-1} treatment level.

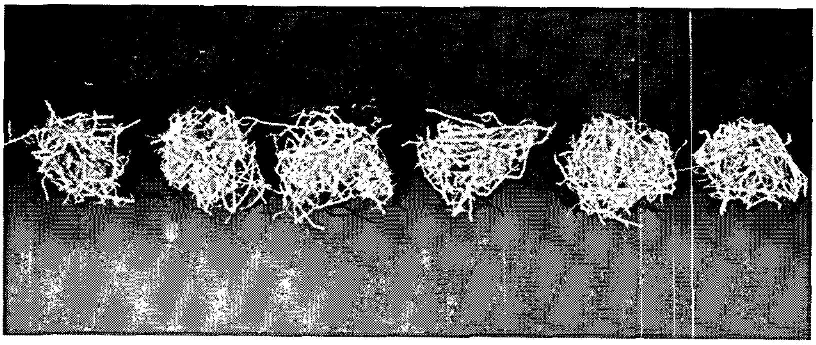

FIGURE 6. Root growth of eastern gamagrass in the Tatum subsoil portion of a split medium. The top portion of the medium was fertilized potting soil (pH 6.61). Unfertilized Tatum subsoil was treated with (left to right) 0, 375, 750, 1,500, 3,000, and 4,000 mg $CaCO_3$ kg^{-1}. Final subsoil pH values were 4.2, 4.5, 4.5, 4.9, 5.1, and 5.6, respectively (Experiment 3).

DISCUSSION

Four experiments, conducted in an acid, Al-toxic Tatum subsoil and in nutrient solutions containing Al, showed that gamagrass had a high degree of Al tolerance. Hence, it is a prime candidate for use in soils having acidic, Al-toxic subsoil layers that serve as root barriers and predispose plants to injury by drought. In many acid soils, these subsoil layers may also reduce rooting depth by mechanical impedance (not soil hardness, *per se*, but restricted conductivity for oxygen, water, and nutrients). McGinty and Alberts (1995) and Clark et al. (1996) reported that roots of gamagrass can penetrate hard clay pans and perhaps create root channels for subsequent crops that lack this ability. Hence, it may be a suitable tool for ameliorating problems of Al toxicity and/or mechanical impedance in subsoils.

The appearance of chlorosis in gamagrass growing in the Jiffy Mix potting mixture indicates that this species can be tentatively classified as a calcifuge (Al tolerant-Fe inefficient). Plant to plant variability in the expression of chlorosis indicated that screening gamagrass populations for Fe efficiency may be profitable. Variability within the strain tested in the Al solutions also suggested variable susceptibility to Al-induced Fe deficiency chlorosis as has been reported for wheat (Foy and Fleming, 1982). Purpling symptoms in gamagrass on the acidic Tatum subsoil and in Al-containing solutions suggested the possibility of a variable P efficiency within the strain tested. Similar observations were made in field plantings on a low P soil at Beltsville, MD (C.D. Foy, unpublished data); however, the symptoms have not been positively identified as P deficiency. Kindiger and Dewald (1996) and C.L. Dewald (personal communication, 1996) have pointed

TABLE 4. Response of eastern gamagrass to aluminum in nutrient solution (Experiment 4).

Al added mg L^{-1}	Final [+] solution pH	Shoot dry weight g pot^{-1}	Root dry weight g pot^{-1}	Relative shoot weight %	Relative root weight %
0	6.47	8.85	1.65	100.0	100.0
4	4.67	6.55	1.08	74.6	66.3
8	4.44	5.22	0.96	59.2	58.5
16	4.25	4.45	0.82	50.9	50.5
24	4.13	3.89	0.74	45.2	46.5
	Lsd 5%	1.23	0.28	10.1	12.4

[+]Solution pH was initially 4.0 and was readjusted to 4.0 on alternate days thereafter. Solution pH did not exceed 4.7 for the Al treatments during the experiment and was generally maintained within the range of 3.7-4.5. Solution pH values for the no Al treatment were also maintained below 4.5 for the first 14 days of growth, but rose abruptly to values above 6.0 after 17 days.

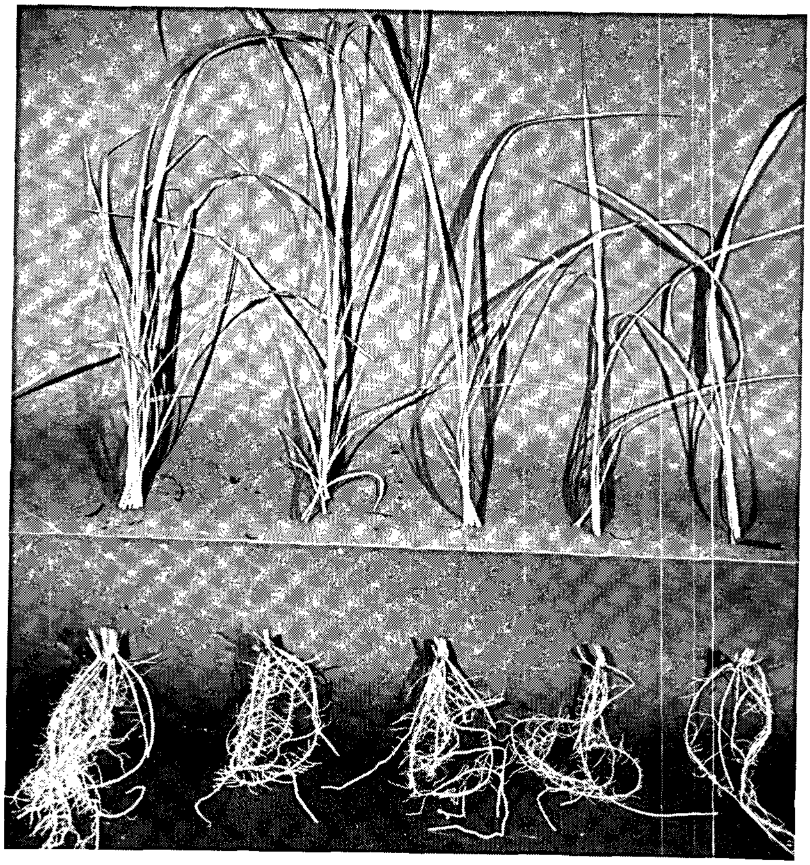

FIGURE 7. Response of eastern gamagrass to Al in nutrient solution. Left to right: 0, 4, 8, 16, and 24 mg Al L^{-1}. Solution pH was adjusted to 4.0, initially, and readjusted to 4.0 on alternate days thereafter. Final solution pH values were 6.47, 4.67, 4.44, 4.25, and 4.13, respectively (Experiment 4).

out that present varieties of gamagrass reproduce by sexual means and that each seed has the possibility of being genetically different. Hence, it seems that a more exhaustive screening of gamagrass populations for tolerances to different stress factors could reveal genotypes that are more suitable for specific soil situations.

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