Eastern Gamagrass Root Penetration in Adverse Subsoil Conditions

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ABSTRACT

Eastern gamagrass [*Tripsacum dactyloides* (L.) L] (EG) is reported to exhibit acid tolerance and root penetration through claypans. To study its root growth in these conditions, a greenhouse column study was conducted under simulated soil stress conditions, using EG and sordan [*Sorghum* × *drummondii* (Steud.) Millsp. & Chase] as a comparison species. Treatments consisted of incomplete factorial combinations of plant species (EG and sordan), soil water potential (−10 and –300 kPa), lime (pH 3.5 and 4.8), and soil bulk density (D_b) (1.3 and 1.7 g cm^{-3}). The treatments were arranged as a randomized complete block design (RCBD). For some of the response variables that were analyzed at different depths, depth was considered as a subplot factor. Treatments were applied to Al-toxic Tatum Bt horizon material (clayey, fine, mixed, semiactive, thermic Typic Hapludults) used in the middle 30-cm section of 15 by 60-cm polyvinyl Cl (PVC) columns. Soil strength was determined at harvest by cone penetrometer resistance. Results indicated that EG tolerated acid, Al-toxic conditions, while sordan roots were sensitive to the low pH conditions. Eastern gamagrass roots penetrated high soil strength layers that inhibited sordan root growth. The characteristics of acid, Al tolerance, and penetration of high soil strength make EG valuable in establishing grassed buffers, vegetative conservation barriers, and pastures in extremely acid or dense soils.

Eastern gamagrass is a perennial warm-season C_4 grass native to eastern North America. At maturity, it is 2 to 3 m tall. In the 1800s, EG grew in unforested areas across the eastern half of the continental USA, and as far west as Texas (Beitelspacher, 1998). Farmers of that period appreciated EG as a resilient high-yielding, and nutritious forage crop, but over time, overgrazing and increasing acreage under cultivation drove it nearly into extinction (O'Brien, 1997; Polk and Adock, 1964).

Recently, EG has received attention as a forage crop, a grass for vegetative hedges, and a crop to ameliorate marginal soils. As a forage grass, EG is relatively palatable and high yielding (Roberts, 1992). Reported yields range from 11.2 to 21.3 Mg ha^{-1} per year (Dewald et al., 1996; Dickerson and van der Grinten, 1990). Eastern gamagrass has a long lifespan potential, thick stems, and dense overlapping growth, making it appropriate for use in vegetative hedges, a soil conservation technique for slowing the flow of runoff water and retaining eroding soils (Ritchie et al., 2000).

Similar to the roots of wetland plant species, EG roots contain aerenchyma, providing continuous gas-filled spaces that can transport O_2 for root respiration in inundated soils (Schussler and Longstreth, 1996). Drew et al. (2000) reported that aerenchyma forms constitutively in EG, without external stimulus. This is contrary to aerenchyma formation in some species which occurs when roots are subjected to hypoxia, causing cortical cells to disintegrate, leaving strips of cell wall material connecting inner and outer cortical cells (He et al., 1996; Schussler and Longstreth, 1996).

Eastern gamagrass is especially useful because of its tolerance to adverse subsoil conditions, such as extreme acidity and compaction. Foy (1997) showed that EG tolerates acid and Al-toxic conditions in both nutrient solution and soil. In the field, EG appeared to grow normally in Al-toxic compact soils and did not respond to liming at pH levels from 5.1 to 5.8 (Foy et al., 1999).

If EG roots can penetrate compacted soils, they may be able to ameliorate restrictive soils layers by providing channels for root development of subsequent crops (Clark et al., 1998; Dexter, 1991; Elkins, 1977). Clark et al. (1998) measured EG root distribution in two soil profiles and observed substantial root growth in clayey, acid, high Al subsoil layers. They also saw deeper root penetration of crop roots grown in fields subsequent to stands of EG, with crop roots following channels made by EG. Therefore, in addition to its use as a forage crop and in vegetative erosion barriers, EG may have potential for use in reclamation of marginal field soils because of its ability to penetrate layers of soil prohibitive to other crops.

The ability of EG to withstand drought and grow through soils with high soil strength and low pH needs further clarification. Kemper et al. (1998) hypothesized that EG avoids, rather than tolerates, drought because it can reach water below the claypan, a subsoil layer of clay accumulation that can impede the root growth of other species. Do EG roots penetrate compacted soils when they are water saturated and soft (exhibiting low soil strength) because of an ability to tolerate hypoxic conditions? Or do EG roots penetrate claypans and dense soil layers because of their ability to exert high penetration pressure? By studying EG root penetration through soil layers with controlled impeding conditions, the mechanisms of its root penetration may be better understood.

The objectives of this study were to determine how EG root growth is affected by extreme soil acidity (pH <4.5), compaction ($D_b = 1.7$ g cm^{-3}), and wetness ($\theta_m =$ 0 to -50 kPa). The three root inhibiting factors were evaluated both alone and in combination (Table 1). These effects also were assessed by comparison to sordan, a warm season forage grass known to be especially

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Published in Soil Sci. Soc. Am. J. 66:931–938 (2002).

Abbreviations: CEC, cation-exchange capacity; D_b, bulk density; EG, eastern gamagrass; PVC, polyvinyl Cl; RCBD, randomized complete block design.

Table 1. Treatment combinations for growth of eastern gamagrass and sordan in polyvinyl Cl (PVC) columns under simulated soil stress conditions in the greenhouse.

Treatment	Target soil pH	Bulk density	Target soil water potential	Soil limed	Soil strength treatment†	Interpretation of root-inhibiting conditions
		g cm^{-3}	kPa			
1	4.8	1.3	0 to −50	Yes	Low	Noninhibiting
2	4.8	1.7	0 to −50	Yes	Medium	Dense, low air-filled porosity
3	4.8	1.7	−400 to −600	Yes	High	Dense
4	3.5	1.3	0 to −50	No	Low	Acid
5	3.5	1.7	0 to −50	No	Medium	Acid, dense, low air-filled porosity
6	3.5	1.7	−400 to −600	No	High	Acid, dense

† Low, medium, or high soil strength with penetrometer resistances at harvest of 0.36 ± 0.25, 1.15 ± 0.51, or 1.88 ± 0.76 MPa, respectively.

intolerant of the three factors studied. The expected responses were:

1. Eastern gamagrass roots can penetrate acid subsoil layers because they tolerate high levels of exchangeable Al.
2. Eastern gamagrass roots can penetrate dense clayey subsoil layers because they tolerate the low O_2 conditions associated with these layers when their soil strength is low because of near saturation with water.

MATERIALS AND METHODS

Study Site

The study was conducted from July through October 1999, in a glass-covered greenhouse at the USDA Beltsville Agricultural Research Center, Beltsville, MD. Environmental conditions were controlled using a computer system (Wadsworth Control Systems MicroSTEP/SA[1]; Wadsworth Control Systems, Arvada, CO) to maintain 30 to 25 ± 2°C day to night temperatures. An overhead curtain provided shading when solar radiation exceeded 500 W m^{-2}. Plants were grown under supplemental incandescent lights to maintain a 16-h photoperiod during the experiment.

Treatments and Experimental Design

Treatment combinations resulted from the factorial arrangement of two plant species (EG and sordan), and two levels of soil water potential (−10 and −300 kPa), soil pH (3.5 and 4.8), and soil D_b (1.3 and 1.7 g cm^{-3}). A full factorial arrangement of the three soil factors at two levels each would produce eight treatment combinations, but we used only six of them (Table 1) for each plant species. This was done to include the most important soil treatment combinations, while reducing treatments to a feasible number.

The treatments were applied to microcosms (described later) utilizing a RCBD. Four blocks (also serving as four replicates) were based on four distinct locations within the greeenhouse. This blocking was used throughout the study to block for other nontreatment factors (such as harvesting schedule and initial plant size) to minimize within-block variations. Measurements were made at different depths within individual microcosms. Therefore, each microcosm served as a main plot for the combination of plant and soil characteristics and depth was considered as a subplot factor.

[1]Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the University of Maryland or the USDA and does not imply their approval to the exclusion of other products or vendors that may also be suitable.

Plant Material

Plant material consisted of 'Pete' EG and Sordan 79. Seeds were germinated in trays containing a peat-vermiculite mix and placed on a thermostatically controlled propagating mat (Progrow Supply Corp., Brookfield, WI) which maintained daytime temperature at 30°C. Germtec-treated seeds of 'Pete' EG and Sordan 79 (Lot 9729) were obtained from the Gamagrass Seed Co. (Falls City, NE) and Norvatis Seed Inc. (New Deal, TX), respectively. On 18 Aug. 1999, 7-wk-old EG seedlings and 5-wk-old sordan seedlings were selected for uniform size and vigor and transplanted into the microcosms (hereafter referred to as columns). Because EG is generally slower than sordan to germinate and establish, the two species were nearly equal in size at this time, sordan having five to six leaves, and EG four to six leaves.

Soil Material

Seedlings were transplanted into the top sections of the columns as described below. The top and bottom column sections were filled to a D_b of 1.3 g cm^{-3} with Galestown sandy loam (siliceous, mesic Psammentic Hapludults) collected from the A_p horizon of a field at the Beltsville Agricultural Research Center. The field was planted with corn (*Zea mays* L.) at the time of collection and had been used for field crops including soybean (*Glycine max* L. Merr.), corn and alfalfa (*Medicago sativa* L. ssp. sativa) rotations for the previous decade. The soil was autoclaved, then passed through a 5-mm mesh to remove crop residues. A controlled release (15-5-11) fertilizer, Osmocote Plus (Scotts-Sierra Horticultural Products Co.; Marysville, OH), was added to the Galestown soil used in the top 20-cm section at a rate of 3.1 mg cm^{-3} to meet plant nutrient requirements. Galestown sandy loam was used for the top and bottom sections so that its textural contrast with the Tatum soil used in the middle sections would create a barrier to capillary water flow, facilitating the maintenance of differing water regimes in the top and middle sections.

The middle 30-cm column section contained the test soil, collected from the B_t horizon of Tatum clay loam near Orange, VA, less than a month before we started the experiment. The Tatum soil was passed through a steel blade hammermill, which broke large peds into aggregates smaller than 20 mm in diameter. Rocks, roots, and debris were removed at this time. The cation-exchange capacity (CEC) of unlimed and limed Tatum soil was measured using the compulsive exchange method for acid soils described by Rhoades (1982). Particle-size distributions of the Tatum and the Galestown soils were determined with a modified sedimentation method. Particle density was determined using the pycnometer method described by Blake and Hartge (1986).

Soil pH in 1:2 soil/water suspensions (pH_w) was determined for Tatum and Galestown soils using samples taken from the columns at the end of the experiment. The exchangeable Al

of limed and unlimed Tatum soil samples was determined in a 1 *M* KCl extract using an atomic absorption spectrophotometer with a N_2O flame.

For the lime treatment factor, Tatum soil for limed treatments was amended with 3.2 g kg^{-1} $Ca(OH)_2$ to raise the soil pH to 4.8. This was according to a preliminary soil titration in which 25-g soil samples were mixed with 0 to 550 mg $Ca(OH)_2$ and incubated for 18 d. Unlimed treatments were left unamended, with a pH_w of 3.5 ± 0.1.

Moist Tatum soil was tamped into the middle section of each column to establish the second treatment factor, D_b of either 1.3 or 1.7 g cm $^{-3}$. A D_b of 1.3 g cm^{-3} is considered to be a nonrestrictive bulk density and 1.7 g cm^{-3} is considered to be potentially root-restricting compaction for a clay soil (Veihmeyer and Hendrickson, 1948; Zimmerman and Kardos, 1961). The soil was incubated under greenhouse conditions for 1 wk to allow the pH of the soil to equilibrate.

The third treatment factor, soil water potential, was adjusted to create two levels of soil strength and O_2 availability. Columns maintained at high water potentials close to saturation (0 to −50 kPa) were intended to contain little or no air-filled pore space, and to exhibit low soil strength. High bulk density combined with high water potential yielded potentially hypoxic conditions unsuitable for most root growth. Columns with low water potentials (−400 to −600 kPa) were intended to provide adequate water while maintaining well aerated, higher soil strength conditions.

Using a tension table and a pressure plate apparatus, soil water release curves were developed for the Tatum soil at both high and low bulk densities, and for the Galestown sandy loam at the bulk density used. The air-filled porosity was estimated from the soil water release curves and soil particle density measurements, using the equations for porosity:

$$f_t = 1 - D_b \times D_p^{-1} \quad [1]$$

and

$$f_w = \theta_m \times D_b \times D_w^{-1} \quad [2]$$

where f_t equals total soil porosity, f_w is water-filled porosity, D_b is soil bulk density, D_p is particle density, D_w is the density of water, and θ_m is gravimetric soil water content.

Columns

Twelve plant and soil treatment combinations and four blocks required 48 columns. The columns were constructed using schedule 40 PVC pipe with 7-mm thick walls and 15-cm i.d. Each column was split lengthwise to facilitate opening at harvest. Each column was divided horizontally into three sections (Fig. 1). The top section was 20 cm in height, the bottom was 10 cm and the middle section was 30 cm. Circular cuffs with deep flanges were fashioned from stainless steel to hold circles of screening to the base of each column. Two to three layers of 1.4-mm mesh fiberglass screen were placed within each base to allow drainage but check the loss of soil. Steel rings and plastic pull-ties were used to belt the two halves of each section of column together, and duct tape was used to connect the three sections. Portholes (13-mm diam.) were drilled into the sides of the columns for the insertion of E_H and pH electrodes, and for the installation of drip emitters (Chapin Watermatics, Inc., Watertown, NY) for the irrigation system. Five holes (16-mm diam.) in each column were threaded for the installation of mini-elbow tensiometers (1.5-cm ceramic tip) (Soil Measurement Systems, Tucson, AZ). Portholes not in use were sealed with rubber stoppers. The columns were arranged 30 cm apart on two adjacent moveable

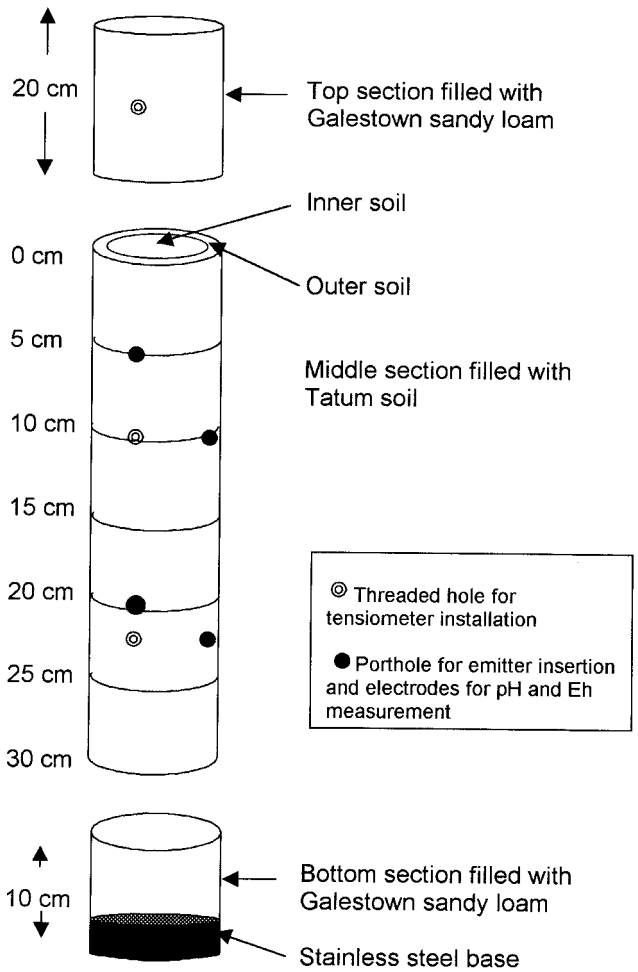

Fig. 1. Diagram for Polyvinyl-Cl columns used in greenhouse study, vertical view. Threaded holes and neighboring portholes are repeated on the opposite side of the column at the same heights.

greenhouse benches. Two replicates of the experiment were set up on each bench.

A timing system for irrigation was set up to operate on a 24-h cycle. Three 1-h timers were controlled by a 24-h clock. Toggles on the 1-h timers allowed watering applications for periods of 2 to 3 s, each emitter applying 5 mL s^{-1}. One timer controlled the irrigation of the top section for all columns via two emitters placed over the top edge of each column, one controlled the irrigation of the low water test soil, and one controlled the irrigation of the high water test soil. The water was delivered via two emitters inserted in the side of the middle section of each column (Fig. 1). Pipe and emitter tube lengths and elevations were kept equal for all columns to avoid variability in water pressure.

Soil water potential was monitored on randomly selected columns (representing an equal number of all treatment combinations, using three mini-elbow tensiometers in each column. Soil water potential was monitored daily using a Tensimeter transducer (Soil Measurement Systems, Tucson, AZ) to measure the vacuum under each tensiometer septum. Irrigation amount and timing were adjusted to maintain desired water potentials in the top and treatment sections. Once a week, E_H and pH measurements were made on the Tatum soil by inserting either a Pt electrode (Model 96-78; Orion Research Inc., Cambridge, MS) or a flat-tip pH electrode (Gel-filled Combination Electrode, model number 34105-026;

Table 2. Means comparisons of lime and soil strength (SS) effects ($P \leq 0.10$) on the average interior root density and total root weights of eastern gamagrass and sordan grown in polyvinyl Cl (PVC) columns under simulated soil stress in the greenhouse.

	Eastern gamagrass		Sordan	
	Average interior root density†	Total root weight per 60-cm column	Average interior root density†	Total root weight per 60-cm column
	g cm^{-3}	g col^{-1}	g cm^{-3}	g col^{-1}
		Lime × soil strength interactions		
Treatment				
1-L, Low SS	0.11a‡	10.3a	0.63a	70.6a
2-L, Med SS	0.10a	11.3a	0.13c	68.7a
3-L, High SS	0.13a	13.4a	0.42ab	48.7a
4-U, Low SS	0.08a	10.5a	0.00cd	52.5a
5-U, Med SS	0.04a	11.4a	0.29bc	45.2a
6-U, Med SS	0.10a	19.4a	0.01cd	57.3a
		Lime effect		
Limed§	0.09a	11.6a	0.45a	62.7a
Unlimed	0.07a	13.7a	0.05b	51.6a
		Soil strength effect		
Low SS¶	0.09a	10.4b	0.38a	61.5a
Med SS	0.07a	11.3b	0.15c	57.0a
High SS	0.11a	16.6a	0.21b	53.0a

† Mean for 5- to 30-cm depth of Tatum soil in the column.
‡ Means with the same letter within a column are not significantly different at the $P \leq 0.10$ level.
§ L = Limed, pH = 4.8 ± 0.7. U = Unlimed, pH = 3.5 ± 0.1.
¶ Low, medium, or high SS with penetrometer resistances of 0.36 ± 0.25, 1.15 ± 0.51, or 1.88 ± 0.76 MPa, respectively.

VWR Scientific Instruments, Bridgeport, NJ) into the soil through a porthole in the column and twisting the electrode to establish a soil slurry around the tip. Only columns given high water treatments were wet enough to allow measurement of E_H and pH in this manner.

Plant Harvest

Harvest of plants began 4 wk after transplanting. Because of logistical limitations not all treatment combinations across the four blocks could be harvested and analyzed at once. Therefore, harvesting was done on a block per week basis. This avoided confounding of a possible time effect with treatment effects (i.e., any possible time effect was confounded with the block effect and therefore removed from experimental error).

At harvest, plant height was measured from the soil surface to the tips of the three tallest leaves. Plants were cut 1 cm above the soil surface, placed in brown paper bags, dried at 80°C in a forced draft oven for 3 d and then weighed. The tape holding the top section to the middle section was removed and a serrated knife was used to cut the soil and roots at the joint. Penetrometer readings were taken on the middle section, using a penetrometer with a 2-cm^2 tip (Eijkelkamp Agrisearch Equipment, Glesbeek, The Netherlands). Readings were taken at 5-cm intervals down the length of the section. Two sets of readings were taken, in opposite halves of the column.

The middle section then was separated from the bottom section. The outer 1 cm of the middle soil section was separated from the inner core of the middle section in 5-cm horizontal increments using a steel ring and a serrated knife. The inner and outer portions of each 5-cm depth increment were sampled separately for determination of root mass and density and soil mass. Two soil samples of ~10 g each were taken from both the top and bottom sections of each column, and from each of the 5-cm layers of inner soil into which the middle section had been partitioned. The soil samples were placed in small manilla envelopes and weighed immediately. They were dried at 80°C for 3 d and then weighed again to determine soil water content. These soil samples were saved for determination of pH and exchangeable Al.

The inner and outer portions of the Tatum soil layers and the Galestown soil top and bottom sections were placed in water to soak for 48 h to loosen surrounding soil. After 48 h of soaking, the soil core with its intact segment of the root system was placed on a 20-cm diam. sieve with 2-mm openings. A stream of tap water was used to wash the soil from the roots, which were then retained on the sieve and collected with tweezers. The washed roots were soaked for an additional

Table 3. ANOVA results (P-values) for lime and soil strength effects on average interior root density, average interior root density for 5-cm increments of Tatum soil, total interior root weight, and total root weight per column.

		Eastern gamagrass		Sordan	
Parameter	Units	Lime‡	Soil strength§	Lime‡	Soil strength§
		P-values			
Mean interior root density (5–30 cm)	g root cm^{-3}	0.030*	0.141	0.000**	0.000**
5–10 cm	g root cm^{-3}	0.874	0.202	0.067†	0.492
10–15 cm	g root cm^{-3}	0.446	0.142	0.002**	0.802
15–20 cm	g root cm^{-3}	0.030*	0.643	0.000**	0.254
20–25 cm	g root cm^{-3}	0.066†	0.954	0.001**	0.028*
25–30 cm	g root cm^{-3}	0.031*	0.964	0.010**	0.067†
Total interior root weight	g root in 5–30 cm Tatum soil	0.099†	0.096†	0.000**	0.067†
Total root wt	g root column^{-1}	0.303	0.054†	0.241	0.751

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.
† Significant at the 0.10 level of probability.
‡ pH of 4.8 ± 0.7 or 3.5 ± 0.1 at harvest.
§ Low, medium, or high soil strength with penetrometer resistances of 0.36 ± 0.25, 1.15 ± 0.51, or 1.88 ± 0.76 MPa, respectively.

24 h, rinsed, patted dry, and weighed. They were then dried at 80°C for 48 h and reweighed.

Interior root density was calculated as the dry root weight in the interior portion of the 5-cm layers of Tatum soil divided by the volume of the sample of soil. This was done because of some variation in the size of samples. This volume was calculated as $(7.5\text{ cm})^2 \times 3.14 \times 5\text{ cm} \times$ (grams of inner soil for layer $\times$ grams of total soil for layer^{-1}).

Statistical Analyses

Statistical analyses were done using SYSTAT software (SPSS Inc., 1997). Treatment effects were considered significant at $P \leq 0.10$.

Since the first 5 cm of Tatum soil was mixed with varying amounts of Galestown soil from the top section, only the 5- to 30-cm depth of the test section was considered in analyses of interior root density and mean interior root density. Only in the ANOVA of total root weight in the 60-cm column were the roots of the 0- to 5-cm depth of the test section included.

Because of significant heterogeneity of variances between the two species, interior root density and total root weight in the Tatum soil test section were normalized. These normalized variables were calculated by dividing the original value for each species by the maximum species value for each block. These values then were used for direct comparison of treatment effects between the two species.

For nonnormalized variables including total root weight and interior root density, ANOVA was done separately for each species because of heterogeneity of variances of the two species. Root weight and interior density were analyzed both as the sum for a column and for individual intervals within a column. If the depth effect was significant, post hoc hypothesis testing was carried out using the Boniferroni test for significant differences between individual soil depths. Limed and unlimed treatments across the three levels of soil strength and the effect of soil strength across the liming conditions were compared using contrasts. Soil strength contrasts were based on theoretical considerations of bulk density and soil water content as well as penetrometer resistance measurements taken at harvest (Busscher et al., 1997). Using these considerations, the six treatments were assigned to either low, medium, or high soil strength (Table 1).

Soil water release curves for the Galestown soil and Tatum soil at high and low D_b were determined by distance weighted least squares regression of data for soil water content and soil water potential (SPSS Inc., 1997).

RESULTS AND DISCUSSION

Species Effect

For each of the four harvests, EG interior root density was approximately one third that of sordan (Table 2). Lime and soil strength effects were of greater number and magnitude for sordan root parameters than for those of EG (Tables 2 and 3). The mean total root weight of sordan was approximately five times that of EG, with compensatory growth in the top and bottom sections greatly increasing sordan root weight (data not shown). An ANOVA of normalized interior root density data (Table 4) showed a significant difference between species as well as a significant interaction of species $\times$ lime and species $\times$ soil strength. An ANOVA of normalized total root weight data also revealed significant differences because of pH and soil strength, a significant two-way interaction of species $\times$ lime and a significant three-way interaction of species $\times$ soil strength $\times$ lime.

Table 4. ANOVA results (P-values) of normalized interior root density and total root weights of eastern gamagrass and sordan grown in the greenhouse in polyvinyl Cl (PVC) columns with several soil stress factors‡.

Treatment	Normalized mean interior root density in 5–30 cm Tatum soil	Normalized total root weight in 5–30 cm Tatum soil
	P-value	
Lime§	0.001**	0.000**
Soil strength¶	0.008**	0.052†
Species	0.020*	0.281
Lime × Soil strength	0.521	0.867
Species × Lime	0.054†	0.002**
Species × Soil strength	0.052†	0.349
Species × Soil strength × Lime	0.865	0.018*

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.
† Significant at the 0.10 level of probability.
‡ Normalized by dividing value by species' maximum for the block.
§ Limed, pH of 4.8 ± 0.7, or unlimed, pH of 3.5 0.1 at harvest.
¶ Low, medium, or high soil strength with penetrometer resistances of 0.36± 0.25, 1.15± 0.51, or 1.88± 0.76 MPa, respectively.

Soil pH and Aluminum Toxicity

The unlimed Tatum soil used was naturally acidic, with a pH measured at plant harvest of 3.5 ± 0.1. The limed Tatum soil had a pH at plant harvest of 4.8 ±

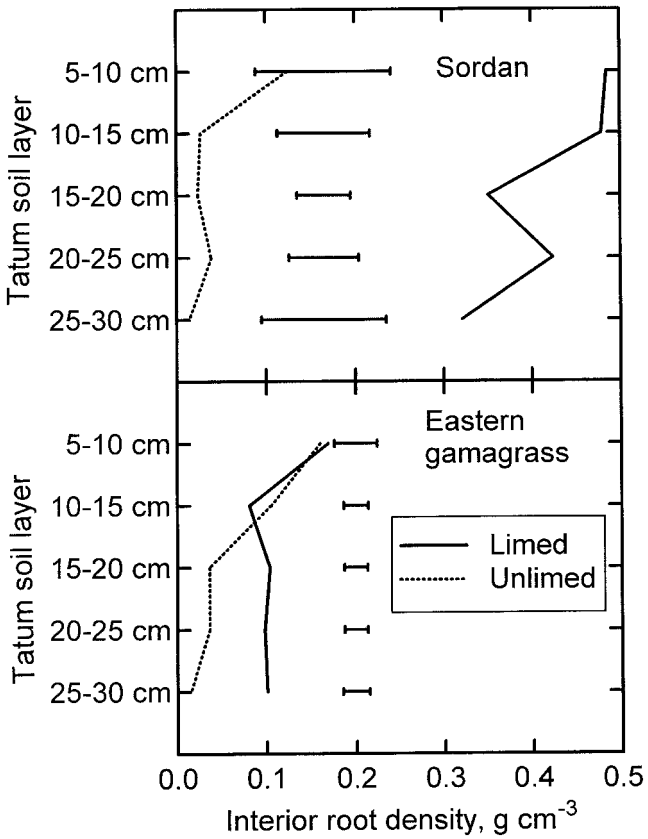

Fig. 2. Lime effect on interior root density of eastern gamagrass and sordan. Bars denote 1 standard error. The depth × lime interaction was significant at the $P < 0.10$ level.

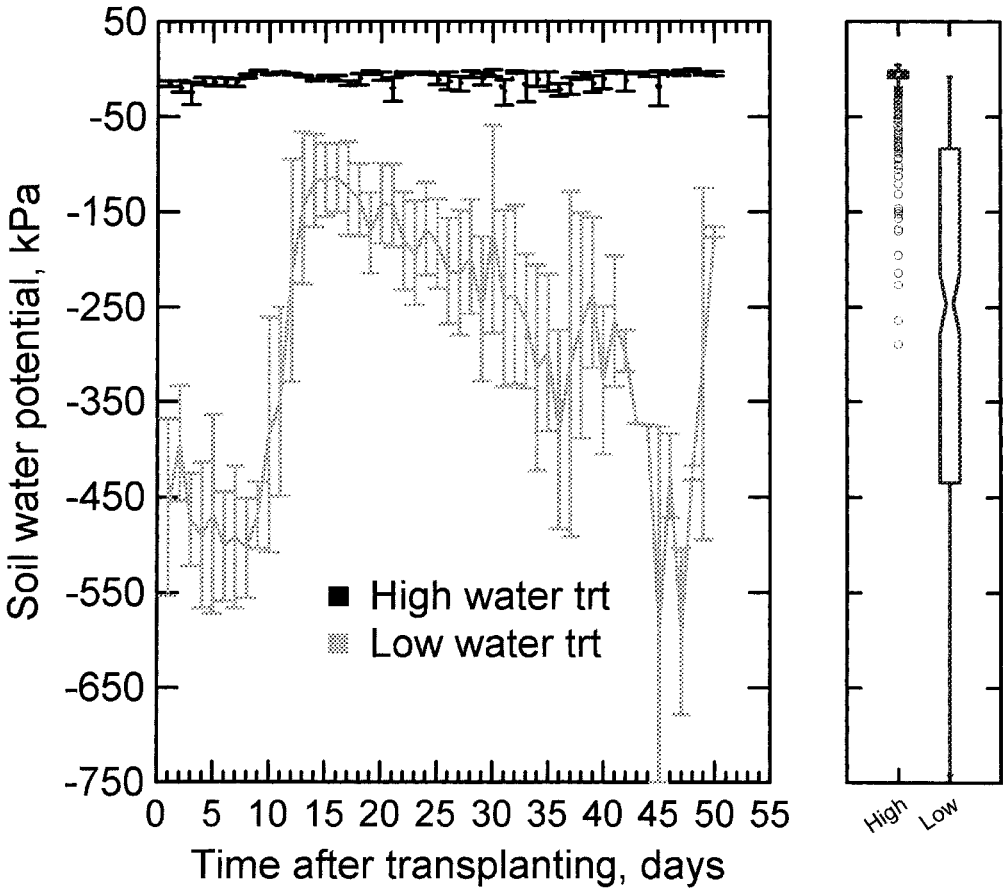

Fig. 3. Tensiometer readings (soil water potential, kPa) of Tatum soil in high and low water treatments over the course of the experiment, with the 95% confidence interval treatment means averaged over the experiment given in the box graph at right. The notched box shows the central 50% of the values, with the median at the center of the notch.

0.7. With a CEC of 8.4 ± 0.7 cmol(+) kg^{-1}, unlimed Tatum was 50 to 60% Al-saturated, a level considered to be Al toxic to sensitive cultivars (Evans and Kamprath, 1970; Foy, 1992). Eastern gamagrass showed tolerance to the acid Al-toxic conditions of unlimed treatments. Observations of EG roots at harvest showed no symptoms of Al toxicity. Lime had no effect on EG total root weight by column. However, lime did increase EG total interior root weight, mean interior root density, and interior root density at depths of 15 to 30 cm in the Tatum soil (Table 3 and Fig. 2). The tolerance of EG to acid Al-toxic conditions seen here agrees with findings reported by Foy (1997) and Foy et al. (1999).

Lime dramatically affected the root growth of sordan plants in Tatum soil, significantly increasing both total interior root weight and mean interior root density (Tables 3 and 4). Sordan roots in unlimed treatments showed the stubby and darkened morphology typical of Al toxicity, while those in limed treatments were normal in appearance. The comparative effects of liming on interior root density for sordan and EG at different depths of Tatum soil are shown in Fig. 2 and Table 3. In unlimed treatments with high bulk density, complete inhibition of sordan root growth was observed, with all roots confined to the top Galestown soil section.

Soil Strength

Tatum particle density was measured to be 2.95 g cm^{-3}. Using Eq. [1], the total porosity was calculated to be 0.42 for the high and 0.56 cm^3 cm^{-3} for the low D_b soil. Scheduled irrigation and supplemental applications of water resulted in mean matric potentials of −10.7 ± 25.7 and −299.7 ± 189.2 kPa for the high and low water treatments respectively, over the course of the experiment (Fig. 3). At harvest, high water treatments resulted in 18% higher average water contents than the low water treatments, with gravimetric soil water contents of 0.34 ± 0.04 cm cm^{-3} versus 0.28 ± 0.04 cm cm^{-3} (data not shown).

Using Eq. [2], total porosity and gravimetric soil water contents, the air-filled porosity was calculated as 0.21 ± 0.13 for the low and 0.14 ± 0.04 cm^3 cm^{-3} for the high strength soil. For the medium strength soil, the calculated water-filled pore space was equal to or greater than the calculated total porosity, with a soil water content of 0.45 ± 0.02 cm^3 cm^{-3} at −10 kPa. Therefore, the air-filled porosity was essentially zero, well below the 10% considered necessary for uninhibited root growth (da Silva et al., 1994). Because of low levels of organic matter in Tatum B-horizon soil, it is unlikely that there were anoxic conditions in medium soil strength treatments.

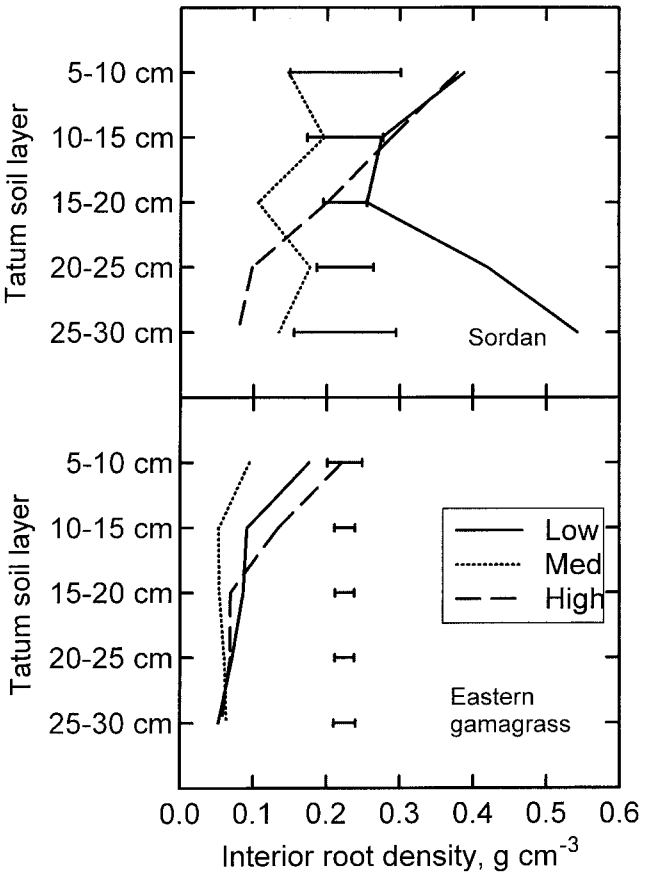

Fig. 4. Soil-strength effect on interior root density of eastern gamagrass and sordan. Bars denote 1 standard error.

Contrary to the expected responses, changes in the soil strength of clayey subsoil layers had no significant effect on EG mean interior root density and interior root density at different depths in the Tatum soil (Tables 3 and 4, Fig. 4). However, soil strength did affect total interior root weight and total root weight per column (Table 3). Total root weight per column was highest for EG in high soil strength treatments. Eastern gamagrass roots in high soil strength did not show stubby growth and lack of fine root hairs, morphological features associated with mechanical impedance.

Certain characteristics of EG roots may be responsible for the lack of a significant effect of soil strength treatments on EG interior root density because of the soil strength treatments. Eastern gamagrass may have responded to the relatively low soil water available in high soil strength treatments by increasing root growth, just as drought-avoidant species of turfgrass show greater root growth under drier conditions (Marcum et al., 1995; Qian et al., 1997). Another possibility is that EG roots penetrate high soil strength layers because of their root morphology, which includes strong fibers surrounding the young nodal roots (Zobel, 2000).

The absence of the expected increase in interior root density in medium versus high soil strength treatments may have been because of the low air-filled porosity of medium soil strength treatments. This suggests that even with the constitutive expression of aerenchyma seen by Drew et al. (2000), EG root growth may be stunted under nearly saturated conditions at this early stage of development. Other studies presently in progress (D. T. Krizek, personal communication, 2000) confirm this likelihood.

In general, sordan responded to soil strength differently than did EG. Sordan total root weight per column was not significantly affected by soil strength because of compensatory root growth in the top and bottom sections (Tables 3 and 4). Sordan average interior root density (Table 2) was lowest in medium soil strength treatments and highest in low soil strength treatments. This may have been because of the low air-filled porosity in the medium soil strength treatments. However, for the 20- to 30-cm depths of Tatum, sordan interior root density followed the order, low > medium > high soil strength (Fig. 4). The interior root density at the 20- to 30- cm depths in Tatum soil agreed with results reported for other species, namely, that increased soil strength is inversely related to root growth (Bengough, 1991; Bengough, 1997; Ehlers et al., 1983).

CONCLUSIONS

Eastern gamagrass root growth, based on root weight, was not inhibited by acid Al-toxic conditions; in contrast, sordan root growth was greatly inhibited under these conditions. Neither low pH nor high soil strength treatments adversely affected EG root growth. Eastern gamagrass root weight was lower in the saturated conditions of the medium soil strength treatments than in the better aerated high soil strength treatments, even though EG roots produce aerenchyma constitutively. The inhibited root growth in the absence of adequate (>10%) air-filled porosity did not support our expectation that EG is able to penetrate claypans and compacted soil layers when the soils are saturated and soil strength is lower. Instead, the presence of aerenchyma in EG roots and other structural properties (e.g., a fibrous sheath) may have enabled the roots to penetrate the restrictive high soil strength Tatum soil.

The characteristics of tolerance to acid and Al and to high soil strength conditions may make EG valuable in establishing grassed buffers, vegetative conservation barriers, and pastures. These characteristics of EG may allow EG to form root channels, which, in turn, may ameliorate subsoils for the growth of less tolerant crops, allowing land now considered unproductive to be used more profitably after the growth of EG.

ACKNOWLEDGMENTS

This research was partially funded by the USDA CSREES Competitive Grant No. 97-36200-5235 awarded to DTK as Principal Investigator. Thanks to Charles D. Foy, Robert L. Hill, William G. Harris, Paul E. Balsley Jr., Miguel L. Mc Cloud, and David Starner for their help in the technical preparations for this experiment.

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