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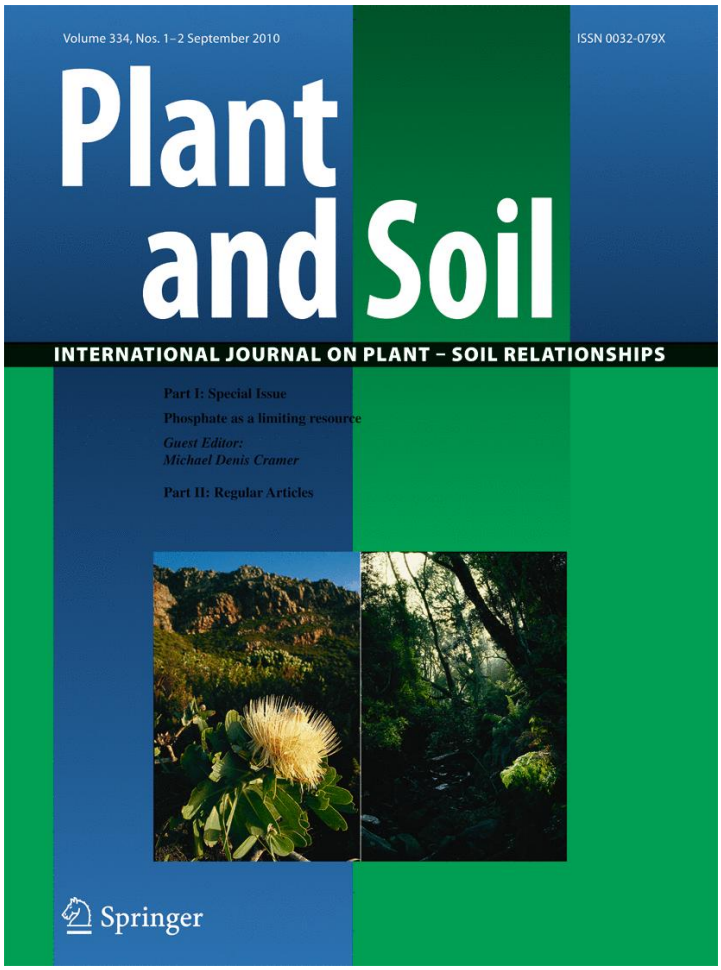

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REGULAR ARTICLE

Potential root depth development and nitrogen uptake by tetraploid bahiagrass hybrids

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Abstract The objectives were to develop a screening technique to evaluate the tetraploid germplasm of *Paspalum notatum* Flüggé (bahiagrass) for potential rate of root depth development (RRDD), estimate the variability for RRDD among hybrids, and analyze the association between RRDD and nitrogen (N) uptake. First, a screening technique was developed based on the evaluation of two clones grown in clear acrylic columns of different sizes, filled with mineral or organic substrates. The RRDD response was determined to be constant across substrates, and tube sizes. Second, differences in RRDD among thirteen clones were compared by growing plants in acrylic columns filled with mineral substrate. Genetic variability was identified among the bahiagrass germplasm for RRDD. Greater RRDD values resulted in greater root and shoot mass, indicating that RRDD was related to early vigor. Finally, to evaluate the relation between RRDD and N uptake, labeled N (^{15}N) was injected either at the depth of the deepest root of each clone or at the maximum depth of all clones. Rapid root depth development was a determining factor for rapid access and uptake of nitrogen present in deep soil layers. This relationship might explain why clones exhibiting rapid root penetration also showed greater early vigor.

Keywords Apomictic hybrids · Nitrogen uptake · ^{15}N · Root development · Root growth

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Introduction

Most physiological processes contributing to crop yield are quantitatively dependent on plant nitrogen (N) availability (Sinclair and Vadez 2002). Therefore, addition of organic or inorganic sources of N is essential for crop production in most environments. The highly weathered soils of the U.S. Southern Coastal Plain require high N inputs for adequate crop production. However, application of N fertilizer raises

concerns that in this region's subtropical environment (warm temperatures and heavy rains) there can be significant N contamination of surface and groundwaters (Hubbard et al. 2004). Several studies have shown that deep-rooted crops can mitigate N leaching losses by capturing N from deep soil or subsoil horizons (Peterson et al. 1979; Huang et al. 1996; Thorup-Kristensen 2001; Kristensen and Thorup-Kristensen 2004). Bahiagrass, *Paspalum notatum* Flüggé, may be a good candidate for mitigating excess soil N since it has been reported to have a large and a deep fibrous root system (Burton 1943).

Deep rooting has also been associated with plant ability for recovering water from deep soil layers and thereby expression of drought tolerance. Burton (1943) observed that root systems of subtropical grasses varied greatly in terms of root growth and penetration. This pioneer study was carried out by cutting out a prism of soil where *P. notatum* Flüggé, *P. malachophyllum* Trin., *P. urvillei* Steud., *P. dilatatum* Poir., *Digitaria eriantha* Steud., *Axonopus affinis* Chace, and *Cynodon dactilon* (L.) Pers. were growing after a year of being sown. It was also observed in another experiment that root penetration of warm-season grasses, studied by analyzing the uptake of labeled phosphorus (^{32}P) applied at different soil depths, was correlated with drought tolerance (Burton et al. 1954). In contrast, total root dry mass was not correlated with drought tolerance. In a more recent experiment, Marcum et al. (1995) compared maximum root depth of 25 Zoysiagrass (*Zoysia* sp.) cultivars, by studying root growth of plants grown in flexible polyethylene tubes, and found that cultivar rooting depth correlated with the drought tolerance of these cultivars. Genotypic variation for rooting depth was also found within grain crops, such as rice (*Oryza sativa* L.) (Shen et al. 2001), sunflower (*Helianthus annus* L.) and soybean (*Glycine max* (L.) Merr.) (Dardanelli et al. 1997). Rapid vertical root development is expected to result in deeper rooting, and has been recognized by Ludlow and Muchow (1990) as one determinant characteristic to optimize productivity under water-limited conditions. In addition, Lehman and Engelke (1991) found that narrow-sense heritability was relatively high for root extension, when plants of *Agrostis stolonifera* L. were grown in flexible root tubes, indicating that progress could be made in breeding for this characteristic.

Bahiagrass is a warm-season grass cultivated in the southeastern USA for forage and for use as utility turf. It is also used in crop rotations, particularly with row crops and various vegetable crops (Blount and Acuña 2009). Short-term rotations of bahiagrass with peanut (*Arachis hypogea* L.), cotton (*Gossypium hirsutum* L.) and soybean have been linked to increased crop yields and decreased insect, nematode, and disease problems. While genetic variability for several agronomically important traits has been reported for this species (Gates et al. 2004; Acuña et al. 2007, 2009), there is no information on the genetic variability for root depth and associated plant growth performance. Initial evaluation of the bahiagrass germplasm for potential rate of root depth development (RRDD) may indentify genotypes that have the capability to reach deep soil layers, thereby allowing greater access to water and N.

A screening technique would be advantageous to quickly evaluate a large number of genotypes in less space. If genetic variability for RRDD is present in the bahiagrass germplasm, it will be a good opportunity to evaluate the potential advantage of rapid RRDD for nutrient uptake from deep soil layers. Additionally, bahiagrass has several ploidy types: diploid germplasm, which reproduces sexually, and tetraploid germplasm, which typically reproduces asexually by apomixis. In the tetraploid germplasm, apomixis could be manipulated to allow for the perpetuation of superior hybrids. If tetraploid hybrids with rapid root development could be identified, then apomixis could be useful in ensuring that genotype's superior root architecture is a fixed trait.

The objectives of this research were (1) to generate a screening technique, which can be readily used to detect potential genotypic variation for RRDD, (2) to apply the technique to estimate the genetic variability for RRDD among tetraploid cultivars and novel hybrids, and (3) to evaluate the association between RRDD and N uptake.

Material and methods

Development of a screening technique

Two tetraploid bahiagrass clones were selected for use in developing a screening technique. One clone was the cultivar "Argentine" (PI 148996), and the other one was

the unreleased germplasm Tifton 7 (obtained from Dr. G. W. Burton, USDA-ARS, Tifton, GA). These two genotypes were chosen because they were considered well-adapted clones to southeastern USA (Blount and Acuña 2009), and because they were classified as highly apomictic, based on embryo sac observations and field progeny tests (Acuña et al. 2007).

RRDD was calculated from the linear increase in depth of the deepest root as a function of time. The depth of the roots was measured by growing plants in two column sizes (3.5-cm or 10-cm diameter) to evaluate the effect of soil volume and plant competition on RRDD. The columns were clear, acrylic tubes cut to 100-cm length. All columns were filled with a sandy soil collected at Live Oak, Florida, or with commercial potting mix (Jungle Growth, Professional Grower Mix, Piedmont Pacific Inc., Statham, GA). Therefore, the two substrates represented examples of low and high organic matter growing medium, as well as two different bulk densities. The field soil (Thermic, coated Typic Quartzipsamments) was collected from three successive 31-cm depth increments, which included the A and upper B horizons. The bulk density of each layer was determined (0 to 30-cm layer: 1.55 g cm^{-1}; 31 to 62-cm layer: 1.49 g cm^{-1}; 63 to 94-cm layer: 1.59 g cm^{-1}), and columns were filled with the three consecutive soil layers, while maintaining respective layer depth and bulk density. This was accomplished by marking the column's surface with the limits of the three consecutive 31-cm layers, and by filling each section with a mass of soil corresponding to the delimited volume and bulk density for each layer. A single bulk density (0.77 g cm^{-3}) was used for all depths in the columns filled with potting mix.

Seeds from Argentine and Tifton 7 were scarified using concentrated sulfuric acid for 10 min, washed, and sown on the substrate surface of each column. A single plant was grown in 3.5-cm diameter columns, while five plants were grown in the 10-cm diameter columns. To prevent exposure of the rhizosphere to light, the 3.5-cm diameter columns were maintained in vertical position inside 4-cm diameter PVC tubes, while the 10-cm diameter columns were placed inside a wooden box leaving only the upper 3 cm exposed to light. The cut surface and upper 5 cm wall of each column was painted white to prevent intercepted light from being transmitted down the clear acrylic wall into the soil portion of the column. Ten columns (replicates) of each size for each clone were established. The columns were placed outdoors at Gainesville, FL (29°7′59″N, 82°21′18″W). The experiment was undertaken in 2006 both in the beginning (from 16 May to 17 July) and middle (from 7 August to 7 October) of the bahiagrass growing season. The substrates were maintained at field capacity by watering every other day. The depth of the deepest visible root in each column was recorded three times per week.

Genotypic variation for rate of root depth development

Thirteen bahiagrass tetraploid clones were selected for this study. Three important cultivars were studied: Argentine, Tifton 7, and Common (an ecotype collected near Batatais, in Sao Paulo, Brazil). The other ten clones were novel hybrids generated by crossing sexual-induced autotetraploid clones as female parents and apomictic clones as pollen donors. Seven of these hybrids (FL-3, FL-3B, FL-13, FL-14, FL-21, FL-93 and FL-122) were developed at the University of Florida, and selected for this study because of their extended growing season, cold tolerance, and high apomictic expression (Acuña et al. 2009). The other three hybrids (C-49, C-65, and C-92) were generated at Universidad Nacional del Nordeste, Argentina, where they were selected for high forage yields (Dr. C. L. Quarin, personal communication).

All thirteen clones were grown from 21 May to 5 July 2007, as described above, in 3.5-cm diameter columns filled with sandy soil. Columns were filled with the three consecutive soil layers as previously described. Eight replications of each clone were used in this trial. From previous experiments, it was known that seed from all clones germinate at the same time after acid scarification. The depth of the deepest visible root was recorded three times per week. At the end of the trial, plants along with the soil column on which they were growing were placed on a 2-mm mesh and washed with a stream of water. Roots and shoots (rhizomes+leaves) were separated by cutting the roots at the base of the rhizomes, dried at 60°C for 48 h, and dry weights were determined.

^{15}N uptake and partitioning between roots and shoots

Argentine, FL-3, FL-122 and C-65 were used in this experiment because variation for RRDD was

observed among these genotypes in the earlier comparison. These clones were grown in clear acrylic columns (3.5-cm diameter) filled with mineral growing media as previously explained. Columns were filled with the three consecutive soil layers as described above. The experiment was conducted twice during 2009: spring (2 May to 7 June) and summer (31 July to 16 September). In each trial, one column of each clone was positioned in each of eight blocks. The RRDD response was measured twice a week during each trial. Shoot and root mass were determined at the end of each trial.

To determine N uptake capacity with soil depth, ^{15}N label was applied at defined depths in the soil 3 d before harvest. A solution containing ^{15}N was prepared by dissolving 1,444 mg of 10% enriched ^{15}N as KNO3 in 200 mL of distilled water. A 2-mm diameter hole was drilled through the column wall where ^{15}N was to be applied and 5 mL of labeled solution was injected into the soil using a 5-mL syringe. Application of the solution was done when at least one clone within each replicate had observable roots deeper than 60 cm.

There were two treatments of ^{15}N based on rooting depth. The first treatment was designed to measure the N uptake capacity in the immediate vicinity of the roots. Therefore, in four blocks ^{15}N was injected at the maximum depth observed for the roots in each column. That is, ^{15}N was placed at the root tips of each plant for all clones. The second treatment on the remaining four replicate blocks was done by injecting ^{15}N at the depth equivalent to the depth observed for clone FL-122 root, which proved to have the fastest vertical root development within each replicate block. Injection of ^{15}N at a common depth for all clones was designed to offer insight about the possible advantage of greater RRDD in N recovery from the soil.

Dried root and shoot were ground with a cyclone mill to 1-mm particle size. Determinations of ^{15}N atom abundance were conducted on these samples at the Soil and Water Science Department Stable Isotope Mass Spectrometry Laboratory at the University of Florida. The atom % $^{15}N/^{14}N$ ratios were determined using a Costech model 4010 elemental analyzer (Costech Analytical Industries, Valencia, CA) coupled to a Finnigan MAT DeltaPlusXL mass spectrometer (continuous flow isotope ratio mass spectrometry; Thermo Finnigan, San Jose, CA) via a Finnigan Conflo III interface. Results were standardized using NH4SO4 at 0.5, 1.0, 1.5, 2.0 and 5.0 atom percent ^{15}N.

Statistical analyses

Regression analysis was used to estimate RRDD from the slope of a linear function between observations of the depth of the deepest visible root and time. Data were analyzed using PROC GLM (SAS version 9.2, SAS Institute, Cary NC) as a randomized complete block design. When significant differences were detected, the Duncan's Multiple Range Test was used for mean separations. Unless otherwise stated in the text, all differences refer to significance at $P<0.05$.

Results

Development of a screening technique

A linear relationship between root depth and time was observed when Argentine and Tifton 7 were grown in clear acrylic columns (Fig. 1). The increasing root depth proved to be highly linear regardless of treatment ($r^2>0.99$) over the entire observation period. The RRDD values, (i.e., slope) were similar between genotypes. There were no interactions between genotypes and the growing medium or column size. The RRDD of plants grown in potting mix or soil were similar, indicating that bulk density and other soil attributes tested had no measurable effect on potential RRDD in these columns. These results demonstrated that, either medium can be used to screen a larger number of bahiagrass genotypes. The RRDD response was similar when plants were grown in small or large column diameters, indicating that small columns could be used effectively to test a large number of genotypes.

Genotypic variation for rate of root depth development

Since there were no appreciable differences among growing medium, column size or date during the growing season, the novel apomictic hybrids were grown in small columns filled with soil and were grown at the end of the spring 2008. Hybrid FL-122 had a greater RRDD than the other 12 apomictic hybrids in this study (Fig. 2) including its male parent,

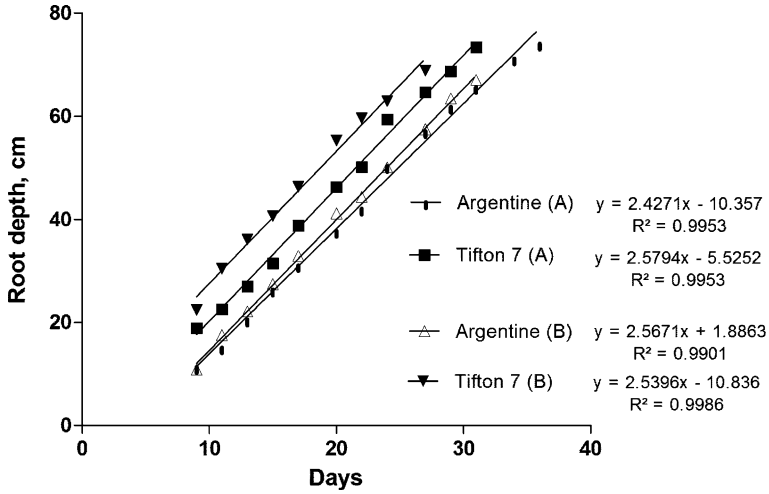

Fig. 1 Rate of root depth development for two clones of bahiagrass (Argentine and Tifton 7) growing in (*A*) clear acrylic columns (10-cm diameter) filled with potting mix, and (*B*) clear acrylic columns (3.5-cm diameter) filled with soil (n=10)

Argentine, or other hybrids sharing this same male parent. Unfortunately, there were not any other hybrids sharing the same female parent (Q-4188). The superiority of FL-122 for potential RRDD might be related to genes present in Q-4188 or it could also be related to heterosis resulting from this combination of parents. No differences were observed among the other 12 hybrids for RRDD. The low variation among the eight replications included in this experiment indicates the consistency of these results. Hybrid FL-122 also produced more above and below ground dry mass compared with the other hybrids (Fig. 2).

^{15}N uptake and partitioning between roots and shoots

The test for ^{15}N uptake was performed in the 3.5-cm acrylic columns filled with mineral soil. Among the four clones in this test, FL-122 again exhibited faster RRDD compared with the other three clones during the spring and summer 2008 (Fig. 3).

When ^{15}N-enriched KNO3 was applied at the position of the deepest visible root of each plant, atom % ^{15}N abundance in roots and shoots was not significantly different among clones (Fig. 4). Results were similar in spring and summer. Also, the ratio of % ^{15}N in roots to that in shoots was not different among clones in either spring or summer (Fig. 5). In addition, there was not a significant season effect on this ratio. In all cases, the atom % ^{15}N abundance was significantly greater in shoots than in roots, i.e. the ratio between root and shoot was less than 1.0.

Atom % ^{15}N abundance in roots and shoots was significantly different among clones when ^{15}N-enriched KNO3 was applied to all clones at the point of the deepest visible root of FL-122 within each block (Fig. 6). Greater atom % ^{15}N abundance was detected in FL-122 three days after the injection than it was in the other three test clones. Clone C-65 had greater ^{15}N abundance than FL-3 and Argentine for the spring trial. The shoots of FL-122 had greater ^{15}N abundance than roots. However, there were no differences for ^{15}N abundance between roots and shoots of C-65, FL-3 or Argentine. Correlations between ^{15}N abundance in roots and RRDD were high for the spring (r=0.91) and summer (r=0.80). The correlations between ^{15}N abundance in shoots and RRDD were similarly high for both spring (r=0.90) and summer (r=0.80).

Discussion

These experiments demonstrated that clear acrylic columns can be effectively used to screen bahiagrass germplasm for genetic potential in RRDD. Of particular interest was the lack of variation resulting from the use of two contrasting growing media, indicating that either mineral or organic growing media can be used to screen bahiagrass genotypes for potential RRDD. These findings also indicated that bahiagrass plants were able to penetrate the soil at a constant rate independently of the soil bulk density, between the tested range (from 0.8 to 1.60 g cm^{-3}). This plasticity might contribute to the bahiagrass large and heterogeneous area of adaptation. The results also indicated that small columns (3.5-cm diameter) can be

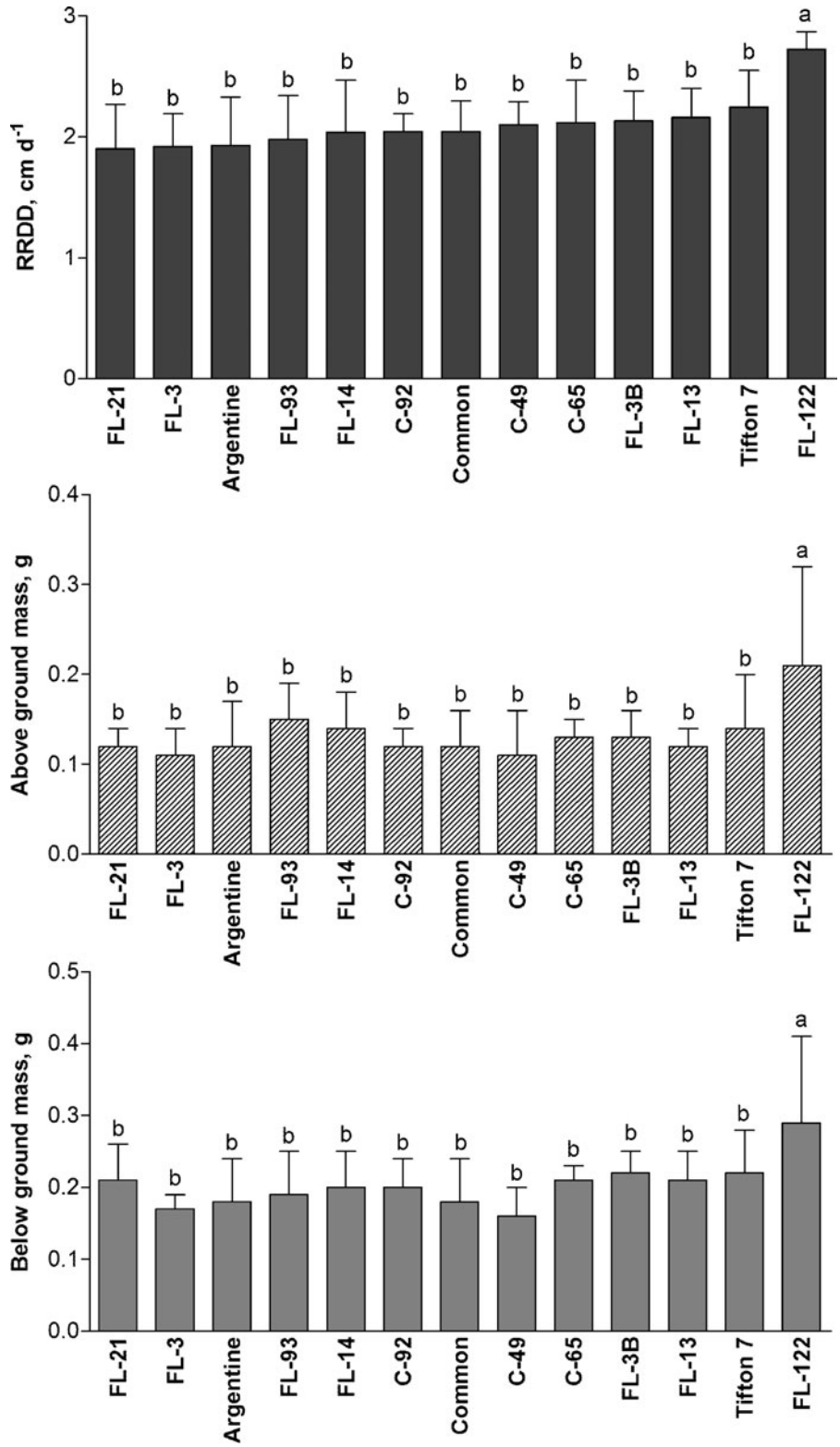

Fig. 2 Rate of root depth development (*RRDD*), above and below ground mass for 13 novel apomictic bahiagrass hybrids grown in clear plastic columns during spring 2007. *Error bars* represent standard deviations. *Different letters* indicate significant differences between treatments (n=8)

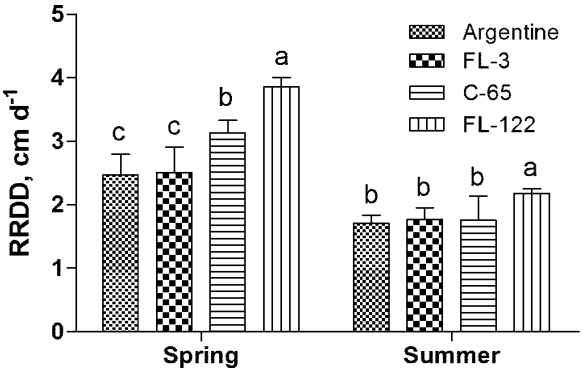

Fig. 3 Rate of root depth development (*RRDD*) for four bahiagrass clones (Argentine, FL-3, C-65 and FL-122) grown in clear acrylic columns filled with soil during the spring and summer 2008. *Different letters* indicate significant differences between means within each season. *Error bars* represent standard deviations (n=8)

used as effectively as large columns (10-cm diameter) to screen genotypes for RRDD differences during early growth. These results are important because small columns are lighter, use less growing medium, and require less space, allowing for the screening of a larger number of genotypes.

Rooting depth increased linearly (Fig. 1) over time for all treatments during the first 6 weeks after germination. These results indicated that bahiagrass roots develop at a constant rate during establishment when no soil physical limitations are present. This linear response was also observed for annual crops. Thorup-Kristensen (1998) working with green pea (*Pisum sativum* L.) also found a linear increase of rooting depth, after a short lag phase during germination, that ended a few days after the onset of flowering. A linear increase in rooting depth was also observed for early root development of wheat cultivars (Bai et al. 1997).

Kramer and Boyer (1995) stated that a RRDD of 10 to 12 mm per day was considered typical among grasses. In our experiment, the average potential RRDD was 18 mm per day. Of course, expression of genetic potential in the field could be affected by environmental variables, such as temperature, soil available water, and nutrient concentration in the growing medium.

Genotypic variability for potential RRDD was limited among this group of novel apomictic bahiagrass hybrids with different genetic backgrounds. Only one genotype (FL-122) was different from the others with a RRDD of 27 mm d^{-1}. This hybrid may be useful as pollen donor in subsequent cycles of hybridization between sexual and apomictic tetraploid clones to introgress this characteristic into novel hybrids. Further studies are needed to evaluate the RRDD response under different environmental conditions.

It is difficult to compare the current results on RRDD with past root studies with perennial grasses since previous studies have relied on measurements of root mass and maximum root depth instead of RRDD. However, some indirect comparisons can be made with studies involving maximum root depth. Genotypic variation for maximum root depth was reported

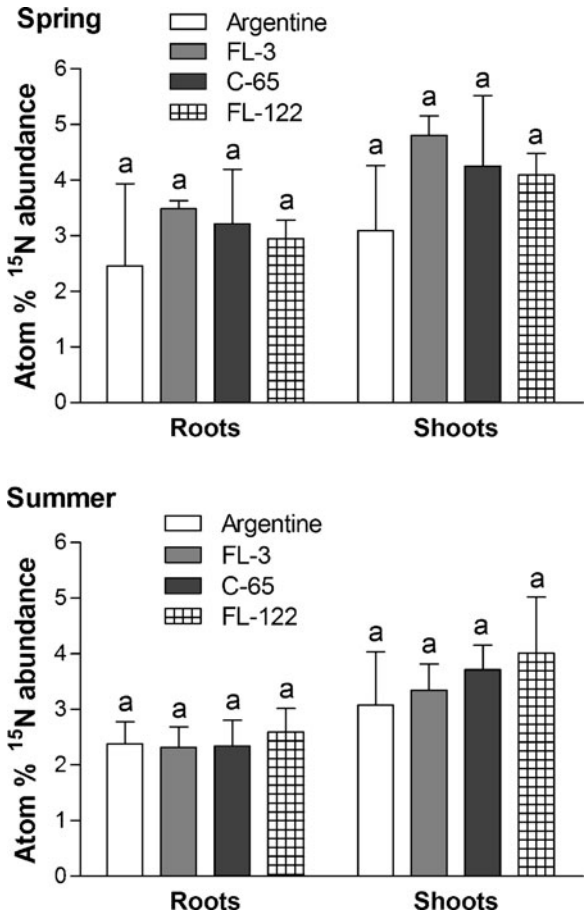

Fig. 4 Atom % ^{15}N abundance in roots and shoots of four bahiagrass clones (Argentine, FL-3, C-65 and FL-122) grown in acrylic columns during the spring and summer 2008. ^{15}N-enriched KNO_3 was injected at the depth of the deepest root in each column. *Different letters* represent significant differences among clones. The *error bars* represent standard deviations (n=4)

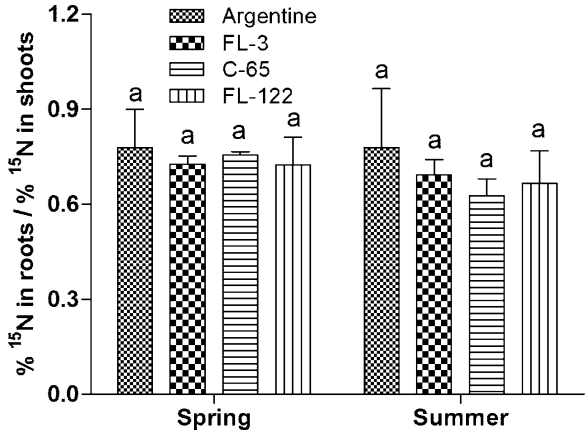

Fig. 5 Ratio of atom % ^{15}N abundance in the root to that in the shoot of four bahiagrass clones (Argentine, FL-3, C-65 and FL-122) grown in acrylic columns during the spring and summer 2008. *Different letters* represent significant differences among clones within each seson. The *error bars* represent standard deviations (n=4)

for zoysiagrass (Marcum et al. 1995), fescue and perennial ryegrass (Bonos et al. 2004). Subsequent studies have shown that selection for maximum rooting depth can result in drought-tolerant plants, and that selection based on root characteristics can be more effective than selection based on field screening (Karcher et al. 2008). In our experiment in soil columns, hybrid FL-122 not only showed greater potential RRDD but also greater above and below ground mass. This might be the result of its ability for exploring deeper soil layers, particularly for nutrients in the well-watered environment of these columns.

The ^{15}N technique was successful in evaluating the genetic variability for N uptake capacity among bahiagrass clones. No genotypic differences were observed for ^{15}N abundance in shoots or roots when ^{15}N was injected at maximum rooting depth for each clone (Fig. 4). These results indicate that the nitrogen uptake capacity of actively growing roots was not different among the four tested genotypes. These results also indicate that once N is taken up by bahiagrass plants, it is mobilized to shoots resulting in a stable partitioning between root and shoot (Fig. 5). Since the N uptake capacity of roots is consistent among clones, the amount of N that a bahiagrass clone can accumulate at establishment appears mainly to be dependent on soil exploration by actively growing roots.

The ^{15}N technique was also used effectively to evaluate the relationship between RRDD and the uptake of N present in deep soil layers. Our results showed that rapid deep root penetration was the major determinant in explaining clonal differences in rapid access and uptake of N present in deep soil layers (Fig. 6). That is, the deep rooting of FL-122 conferred potential for it to recover more N than the other three clones with shallower root penetration in the soil. Bahiagrass is typically characterized as having slow establishment due, in part, to weak seedlings that may be outcompeted by weeds (Gates et al. 2004). Early rapid root penetration could result in a faster establishment due to rapid access to soil N and soil water. It will be interesting to analyze this association between rapid root penetration and early vigor in

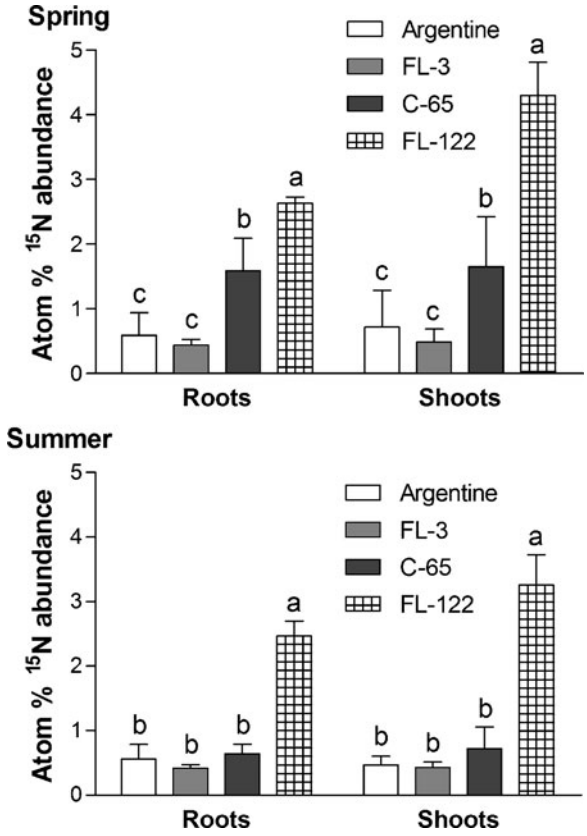

Fig. 6 Atom % ^{15}N abundance in roots and shoots of four bahiagrass clones (Argentine, FL-3, C-65 and FL-122) grown in acrylic columns during the spring and summer 2008. ^{15}N-enriched KNO_3 was injected where the deepest root of FL-122 was observed in each block. *Different letters* represent significant differences among clones. The *error bars* represent standard deviations (n=4)

other warm-season grasses to see if this relation can be generalized. Utilization of bahiagrass cultivars with rapid root penetration in crop rotations would lead to better use of soil N and likely minimize the leaching of N from the overall cropping system. Although selection for genotypes exhibiting rapid RRDD could also lead to the indirect modification of other plant characteristics, there is no evidence indicating that it could affect the nutritive value of forage, more specifically digestibility and nutrient concentration.

When ^{15}N was injected at the rooting depth of each clone, higher ^{15}N abundance was observed in shoots of bahiagrass plants compared to roots. This result indicates that nitrogen is preferentially mobilized to shoots after it is taken up by bahiagrass plants. Shoots are the predominant site of nitrate reduction in grasses (Scheurwater et al. 2002). The observed rapid accumulation of ^{15}N in bahiagrass shoots could be the result of absorbed nitrate being preferentially translocated to shoots for reduction and incorporation in organic forms. This hypothesis might be tested by analyzing xylem sap after nitrate absorption, or by measuring the activity of nitrogen reductase in roots and shoots.

Based on both the RRDD and ^{15}N uptake results, it is concluded that clone FL-122 is a good candidate for use in a bahiagrass breeding program with the objective of improving early vigor. Progeny of FL-122 could lead to genotypes with better drought tolerance and more N uptake due to deeper early rooting. Since apomictic tetraploid plants produce normally reduced pollen, favorable genes present in FL-122 may be transferred to other lines or populations by using FL-122 as pollen donor.

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