

Drought Tolerance Responses of Purple Lovegrass and ‘Adagio’ Maiden Grass

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Abstract. Nonnative *Miscanthus sinensis* Anderss ‘Adagio’ and native *Eragrostis spectabilis* (Pursh) Steud. were evaluated for drought tolerance in a rain-excluded landscape setting in sandy soil in response to irrigation application volumes of 0 L, 0.25 L, 0.5 L, or 0.75 L. As irrigation rates increased, plant mass, canopy size, and shoot-to-root ratios increased for both species, being greatest at the 0.75-L rate. Shoot dry weight, root dry weight, total biomass, and shoot-to-root ratios were greater for *E. spectabilis* than *M. sinensis*. Cumulative water stress integral was also greater for *E. spectabilis*. Greater growth in conjunction with higher cumulative water stress indicates the native *E. spectabilis* is anisohydric and more drought-tolerant than the isohydric nonnative *M. sinensis*.

Drought and corresponding water restrictions are forcing landscapers and consumers to seek alternative irrigation practices and plants that require minimal irrigation for survival (Knox, 1990). Ornamental grasses are generally regarded as problem-free, low-maintenance plants (Dana, 2002) and recommended for their putative low-water requirements. Relationships between ornamental grasses and water use have been reported (Blicker et al., 2003; Bolger et al., 2005; Greco and Cavagnaro, 2002; Guenni et al., 2002; Mohsenzadeh et al., 2006), yet research quantifying water requirements of ornamental grasses for establishment or maintenance in a residential landscape is limited (Zollinger et al., 2006). Many Florida water management districts have recommended native plants to their consumers (Southwest Florida Water Management District (SFWMD), 2001, 2003) under the premise that Florida native plants use less water than nonnative plants (Haehle, 2004; Hostetler et al., 2003; SFWMD, 2001).

Limited research has been done to substantiate the assumption that native plants use less water than nonnative plants. Kissel et al. (1987) examined water relations of four exotic and three native New Zealand species and found no overall difference existed

between adaptation mechanisms of native and exotic species. Glenn et al. (1998) found no difference in water use efficiency between two native and two invasive riparian species from the Colorado River delta. However, Blicker et al. (2003) found that native *Pseudoroegneria spicata* (Scribn. and Smith) and *Pascopyrum smithii* (Rybd.) produced more biomass under drought conditions than invasive *Centaurea maculosa* (Lam). A study in Australia of seven native and three introduced perennial grass species subjected grasses to continuous drought and found mixed results among performance of native and exotic species (Bolger et al., 2005). Drought resistance may be less a function of a plant’s status as native or nonnative, and more that of its individual physiology and natural range (Chapman and Auge, 1994).

In addition, ecology of cultivated landscapes is not the same as natural environments. Plant selection should take into account individual site criteria and plants’ cultural requirements in addition to their native or nonnative status (Anella, 2000; Knox, 1990). The objective of this study was to quantify water stress and growth of nonnative *Miscanthus sinensis* ‘Adagio’, a 1.5-m tall fine-textured C4 grass native to Asia, and the Florida native *Eragrostis spectabilis*, a 0.5-m medium-textured C4 grass, in response to different irrigation volumes.

Materials and Methods

On 25 April 2005, 0.72-L containers of *E. spectabilis* and *M. sinensis* ‘Adagio’ were planted in native soil (Apopka fine sand series) in an open-sided clear polyethylene covered shelter ≈4 m tall at the University of

Florida Mid-Florida Research and Education Center in Apopka, FL (lat. 28°41’N, long. 81°31’W). Thirty-two plants of each species for a total of 64 plants were planted to original container depth in six rows oriented north–south on 0.6-m centers in 1.5-m wide strips. Planting rows were covered with 7.5- to 10-cm screened pine bark nuggets to a depth of 7.6 cm (Sunrise Landscape Supply, Orlando, FL.). Areas between strips were covered with 0.9-m wide strips of polypropylene ground cloth (BWI Companies, Apopka, FL) to inhibit weed growth. Before transplant, soil under the shelter was saturated to a depth of 0.9 m.

The experiment was conducted as a randomized complete block design with two species and four treatments with four replications per treatment × species combination. There were 32 experimental units (i.e., each species × treatment combination replicated four times) with each unit containing two plants of the same species for a total of 64 plants. One plant of each species was used for water potential measurements and the other plant of each species was used for growth measurements. Blocks were spatially L-shaped across rows to account for variations in the environment of the rainout shelter. One of four irrigation volumes was applied to each plant within an experimental unit: 0 L, 0.25 L, 0.50 L, and 0.75 L. Irrigation volumes were applied as one event on alternate days for a 90-d period beginning at transplant through 25-mm polyethylene pipe and 90° gray spray stakes (Roberts Irrigation Products, San Marcos, CA). Pressure compensators (Bowsmith Super-Drip N.D., Exeter, CA) were placed inline for each emitter to regulate water flow at 1.9 L-h. Two spray stakes were placed 0.46 m apart in the northwest and southeast directions to cover a 0.21-m² area around each plant. The Christiansen Coefficient of Uniformity was a minimum of 0.77 before planting (Haman et al., 2005). Irrigation of each experimental unit was controlled as a separate zone using an automated irrigation time clock (model Sterling 12; Superior Controls Co., Valencia, CA). Irrigations began at 0500 HR and were completed by 0600 HR each day. Flow meters (model C700TP, ABS, Ocala, FL) were installed for each zone to record irrigation volumes Monday through Friday.

Weather data. Weather data were obtained from a weather station site at the research site. Reference evapotranspiration (ET₀) was calculated daily by a CR10X data logger (Campbell Scientific, Logan, UT) using a program supplied in Campbell’s Application Note 4D. This program calculates ET₀ on an hourly basis using the ASCE Penman-Monteith equation with resistances (Allen et al., 1989). Input for ET₀ calculations was measured with a pyranometer (Li-190; LI-COR, Lincoln, NE), anemometer (014; Met-One Instruments, Meford, OR), and temperature/humidity sensor (HMP45C-L; Campbell Scientific). Rainfall was recorded with a tipping bucket rain gauge (TE525; Texas Instruments, Dallas, TX).

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Each midnight, the data logger calculated daily ET_0 .

Growth indices and biomass. At planting, six additional plants of each species were partitioned into roots and shoots, washed to remove substrate, then dried at 70 °C until a constant mass was obtained for initial shoot and root dry weight values. Plant height, widest canopy width (width 1), and width perpendicular to the widest width (width 2) were recorded to calculate growth indices (growth index = height × width 1 × width 2) at transplant and every 14 d after planting. On 27 July 2005, the southernmost plant of each species in each experimental unit, the plant not used for water potential readings, was destructively harvested. Shoots were removed to the crown. To obtain root biomass gain, one-fourth segments of the soil volume outside of the original root ball and extending beyond the longest root to the depth of the deepest root in each quadrant were removed from the northeast and southwest sides of each plant. Soil was removed from roots, and shoots and roots were processed as described previously. Dry weights of northeast and southeast segments were summed and multiplied by two to obtain total root biomass gain. Average initial root dry weight in the root ball and total root biomass gain were summed to obtain an estimated total root dry weight for calculation of shoot-to-root ratios. Shoot biomass gain was calculated as the difference between total shoot dry weight at final harvest and initial shoot dry weight. Total biomass gain was calculated as described for shoot biomass gain. Shoot-to-root ratios were calculated by dividing total shoot dry weight by total root dry weight.

Leaf water potential measurements. Beginning 1 month after transplant (MAT), on 23 May 2005, leaf water potential (Ψ_T) was measured monthly. Measurements were made at predawn, midday, and dusk on the nonirrigated day (stressed) and irrigation day (unstressed). Leaf water potential was determined with a pressure chamber (model 3000; Soil Moisture Equipment Corp., Santa Barbara, CA) using compressed nitrogen with pressure increasing at a rate of 25 kPa·s. Measurements were made on individual grass blades (≈ 10 cm long) taken from the northernmost plant of each replication. As described by Schulze et al. (1980) and Beeson (1992), cumulative daily water stress integrals ($S\psi$) were calculated as the integrated area over the water potential curve and absolute value taken for each replication on each sampling date.

Data analysis. The experiment was conducted as a randomized complete block design with four blocks of single plant replicates. Plants that died during the experiment were included in the analysis as opposed to being represented as missing data. Regression equations were calculated for shoot dry weight gain, root dry weight gain, biomass gain, and shoot-to-root ratios as a function of irrigation volume for each species. For these variables, in which at least one of the regression lines was quadratic, data

were analyzed as a two × four factorial with two species and four irrigation volumes. Comparisons were made between species to determine effects of both species and irrigation volume on dry weight gain. Regression equations were also calculated for growth indices over time at each irrigation volume. Growth indices were analyzed separately by species. Comparisons were only made within a species to determine effects of irrigation volume on growth rate. Where at least one of the regression lines was quadratic, data were additionally analyzed as repeated measures

separately by species. Analysis was by split plot with irrigation volume as the main plot and month after transplanting as the subplot. Cumulative water stress integral values, predawn Ψ_T , midday Ψ_T , and dusk Ψ_T , were analyzed as repeated measures using a split plot design with irrigation volume as the main plot, species as a subplot, and stress day as a subsubplot (Snedecor and Cochran, 1980). Each sampling date was analyzed separately. Where significant differences were indicated, mean separation was by Fisher's protected least significant differences

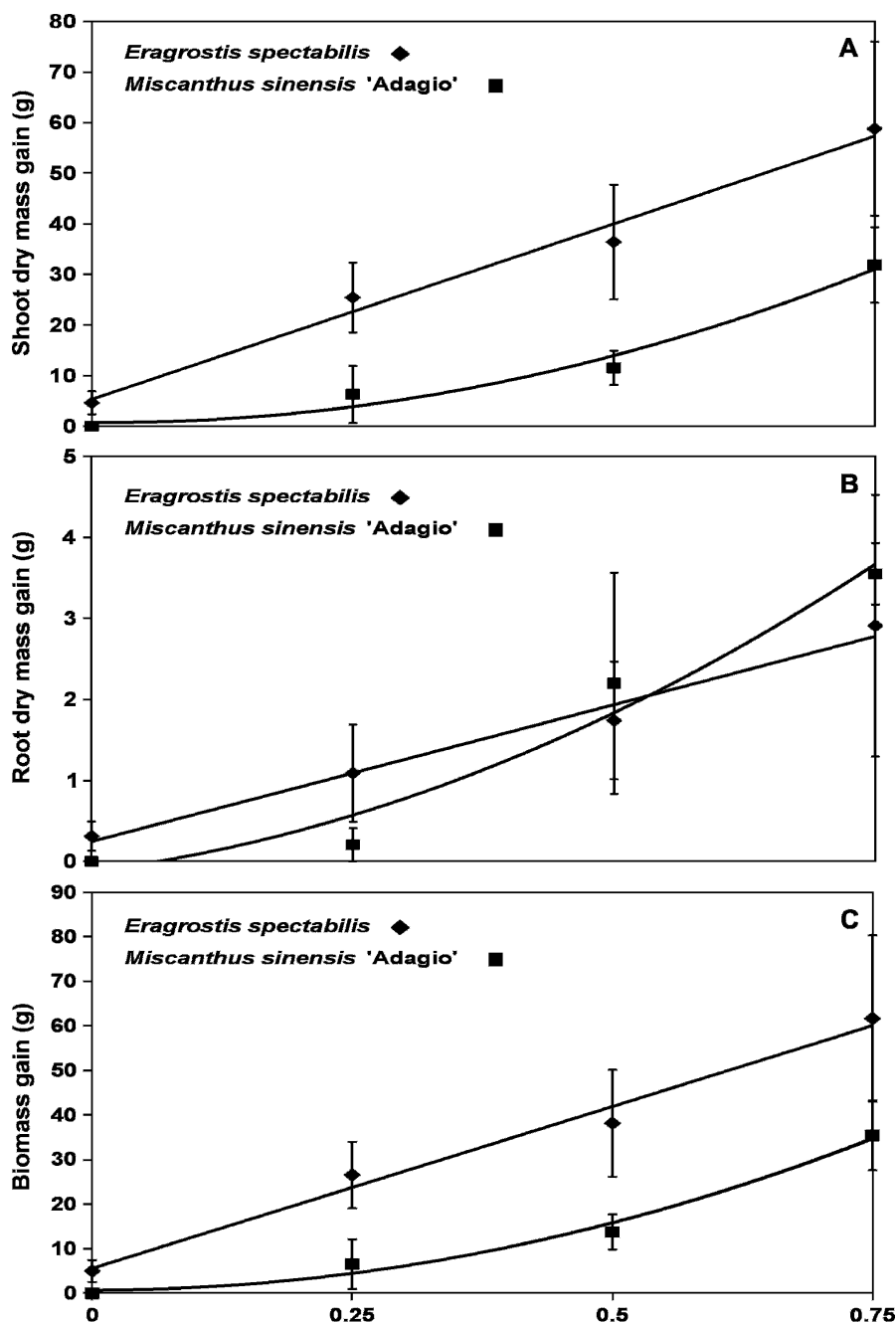


Fig. 1. (A) Shoot biomass gain of *Eragrostis spectabilis* (♦) $y = 69.344x + 5.326$, $r^2 = 0.98$ and *Miscanthus sinensis* 'Adagio' (■) $y = 56x^2 - 1.648x + 0.808$, $r^2 = 0.98$; (B) root biomass gain of (♦) $y = 3.3764x + 0.2471$, $r^2 = 0.98$ and (■) $y = 4.572x^2 + 1.6282x - 0.1215$, $r^2 = 0.97$; and (C) total biomass gain of (♦) $y = 72.716x + 5.569$, $r^2 = 0.99$ and (■) $y = 60.64x^2 - 0.072x + 0.687$, $r^2 = 0.99$. Plants were grown for 90 d and irrigated every other day with 0 L, 0.25 L, 0.50 L, or 0.75 L water. Each point represents the means \pm SE indicated by standard error bars ($n = 4$).

(F-protected LSD; Snedecor and Cochran, 1980). All analysis was conducted using SAS (version 9.1.3; SAS Institute, Cary, NC).

Results and Discussion

Mortality. By 3 MAT, 75% and 25% of nonirrigated *M. sinensis* and *E. spectabilis* plants, respectively, were dead. *E. spectabilis* plants receiving 0.25 L per event had a 50% mortality rate.

Biomass. Biomass gain of both *M. sinensis* and *E. spectabilis* increased with increasing irrigation volumes (Fig. 1A–C). Shoot, root, and total biomass gain of *M. sinensis* increased quadratically, whereas shoot, root, and total biomass gain of *E. spectabilis* increased linearly (Fig. 1A–C). Shoot biomass gain was greatest at 0.75-L treatments and lowest for nonirrigated plants. Shoot biomass gain of *E. spectabilis* was greater ($P < 0.01$) than *M. sinensis* (Fig. 1A). The 0.75-L treatment increased shoot biomass gain of *E. spectabilis* and *M. sinensis* by 12.6- and 32-fold, respectively, relative to nonirrigated plants.

Root biomass gain increased with increasing irrigation volumes with greater root gain for *E. spectabilis* than *M. sinensis* ($P < 0.05$). At the 0-L and 0.25-L treatments, root biomass gain of *E. spectabilis* was higher than *M. sinensis*, although mean values included dead plants (Fig. 1B). *Miscanthus sinensis* irrigated at 0.75 L per event had the greatest root biomass gains.

Irrigation rates of 0.75 L resulted in greater ($P < 0.0001$) total biomass gain than the 0-L treatment. Other treatment comparisons were similar ($P > 0.05$). Total biomass gain of *E. spectabilis* was greater ($P < 0.01$) than *M. sinensis* (Fig. 1C). Average total biomass gain of *E. spectabilis* was greater than *M. sinensis* by 74%, 178%, and 307% for the 0.75-L, 0.50-L, and 0.25-L treatments, respectively (Fig. 1C).

Observed decreases in biomass with decreased irrigation quantities are well documented. Guenni et al. (2002) recorded a reduction in dry weight for *Brachiaria brizantha* (A. Rich.) when subjected to moderate drought stress. Dry weight of drought-stressed *Gaillardia aristata* Pursh was reduced by 50% and 84%, and dry weight of *Leucanthemum × superbum* (Bergmans ex J.Ingram) Soreng & E.A.Cope was reduced by 47% and 99%, respectively, when exposed to 2- and 4-week intervals in irrigation (Zollinger et al., 2006). *Trichloris crinita* (Laq.) Parodi also showed reduced dry weight under drought conditions (Greco and Cavagnaro, 2002) as did drought-stressed *Bouteloua eriopoda* Torr. and *Eragrostis lehmanniana* Nees (Fernandez et al., 2002).

Shoot-to-root ratio. Shoot-to-root ratios increased linearly with irrigation volume (data not shown) with larger ($P < 0.01$) ratios for *E. spectabilis* (32.19 ± 28.75) than *M. sinensis* (4.97 ± 5.80). Ratios within a species were similar ($P > 0.05$) among all treatments. Low shoot-to-root ratios of *M. sinensis* at low irrigation volumes were the result of high mortality and exclusion of dead material.

This is consistent with Greco and Cavagnaro (2002), who found no significant difference in shoot-to-root ratio between levels of drought-stressed *T. crinita*.

Growth indices. Mean growth indices for both species at 0.25-L, 0.50-L, and 0.75-L irrigation treatments generally increased over time. Mean growth indices for the nonirrigated plants decreased over time (Fig. 2A–B). For *E. spectabilis*, growth indices for 0.25-L, 0.50-L, and 0.75-L treatments increased by 40%, 170%, and 230%, respectively. Growth indices of *M. sinensis* receiving 0.25 L, 0.50 L, and 0.75 L increased by 7%, 29%, and 585%, respectively. However, at 0-L and 0.25-L treat-

ment volumes, mean growth indices of both species decreased between 2 MAT and 3 MAT (Fig. 2A–B). Reduced shoot growth and decreased cell elongation are common effects of drought stress, having been observed in multiple experiments (Kalapos et al., 1996; Kramer and Boyer, 1996; Neumann et al., 1988; Sadras and Milroy, 1996; Sakurai and Kuraishi, 1988). In addition, significant leaf necrosis was observed with low irrigation levels. Zollinger et al. (2006) observed leaf death and senescence as a drought avoidance mechanism in herbaceous perennials.

Trends in growth indices were similar ($P < 0.05$) to biomass gains with greater canopy

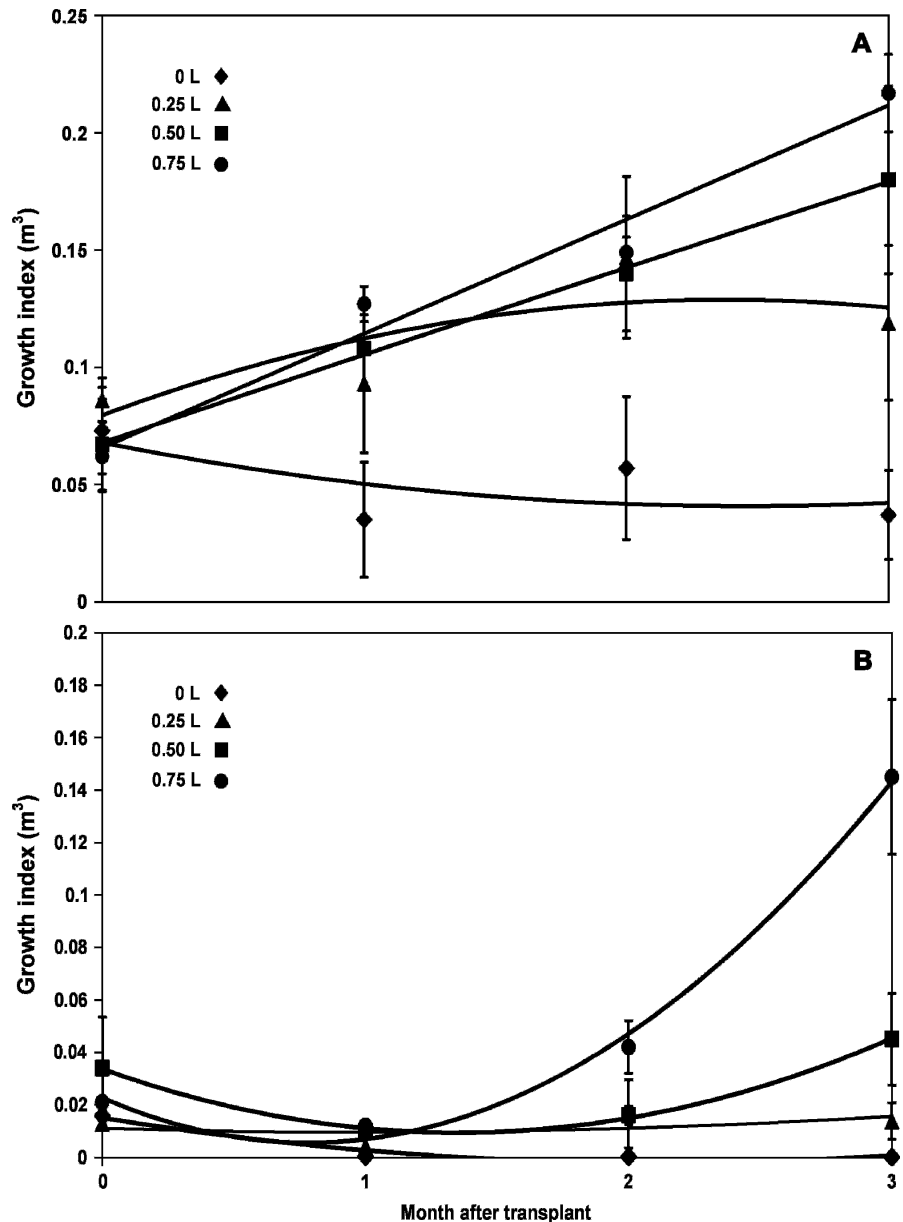


Fig. 2. Mean growth indices for (A) *Eragrostis spectabilis* irrigated at 0 L (\blacklozenge) $y = 0.0045x^2 - 0.0221x + 0.0679$, $r^2 = 0.46$; 0.25 L (\blacktriangle) $y = -0.0088x^2 + 0.0416x + 0.0795$, $r^2 = 0.64$; 0.5 L (\blacktriangledown) $y = 0.0371x + 0.0681$, $r^2 = 1.00$; or 0.75 L (\bullet) $y = 0.0487x + 0.0657$, $r^2 = 0.97$ and (B) *Miscanthus sinensis* 'Adagio' irrigated at (\blacklozenge) $y = 0.0038x^2 - 0.0162x + 0.015$, $r^2 = 0.93$; (\blacktriangle) $y = 0.0015x^2 - 0.0031x + 0.0111$, $r^2 = 0.24$; (\blacktriangledown) $y = 0.0133x^2 - 0.0359x + 0.0336$, $r^2 = 1.00$, or 0.75 L (\bullet) $y = 0.028x^2 - 0.0438x + 0.0227$, $r^2 = 1.00$ per event over a 3-month period during summer in central Florida. Each point represents the means \pm SE indicated by standard error bars ($n = 4$).

size at higher application rates (Figs. 1A–C and 2A–B). For both species, canopy size was greatest ($P < 0.05$) at 0.75-L and smallest within the 0-L treatment. At 3 MAT, the 0.75-L treatment increased the mean growth index of *E. spectabilis* by 3.75 times relative to the 0-L treatment and *M. sinensis* by 7.5 times relative to the 0.25-L treatment.

Water potentials. Irrigation treatment effects only occurred twice during the experiment. An irrigation effect was observed at 2 MAT for the midday Ψ_T , in which 0-L (–1.7 MPa) and 0.25-L (–1.6 MPa) treatments were similar ($P > 0.05$) yet more negative ($P < 0.05$) than 0.50-L (–1.2 MPa) and 0.75-L (–1.2 MPa) treatments. At 3 MAT, $S\psi$ was greater ($P < 0.05$) for nonirrigated plants (24.0 MPa·h) compared with grasses receiving 0.25, 0.50, and 0.75 L (19.3, 16.7, and 16.1 MPa, respectively). Cumulative water stress was comparable ($P < 0.05$) between 0.75-L and 0.50-L treatments. For both sampling periods, Ψ_T became more negative as the irrigation amount decreased, indicating higher stress levels occurred as less water was applied to plants.

Species effects, however, were seen at 2 and 3 MAT for predawn, midday, and dusk readings; each time, Ψ_T was more negative for *E. spectabilis* than for *M. sinensis* except for 2 MAT predawn (Table 1). Cumulative water stress was also greater ($P < 0.05$) for *E. spectabilis* at 2 MAT than *M. sinensis* (Table 1). Higher shoot-to-root ratios of *E. spectabilis* account for increased water stress resulting from the inability of the root system to compensate for transpirational water losses (Gilman et al., 1998; Montague et al., 2000).

A stress day \times species interaction was observed in $S\psi$ at 1 and 3 MAT (Fig. 3). At 1 MAT, $S\psi$ was highest for *E. spectabilis* on the nonirrigated day (stress day) and lowest for *E. spectabilis* on the irrigation day (unstressed day). Cumulative water stress results were intermediate for *M. sinensis* with comparable values between stressed and unstressed days. Results were similar for *M. sinensis* at 3 MAT except regardless of stress day; $S\psi$ was higher for *E. spectabilis* compared with *M. sinensis* ($P < 0.05$). For *E. spectabilis*, $S\psi$ was higher on the unstressed day (19.7 MPa·h) than on the stressed day (19.7 MPa·h) ($P < 0.01$) (Fig. 3). Weather effects likely influenced these results. Regardless of whether *E. spectabilis* plants were irrigated, $S\psi$ (Fig. 3) was always highest on days with the highest the ET_0 , which also occurred on days with the greatest incident solar radiation (Fig. 2). This suggests *E. spectabilis* transpiration and therefore g_S were coupled to microclimate and less sensitive to water stress. These responses are consistent with anisohydric behavior in which stomata remain open independent of water potentials (Tardieu and Simonneau, 1998). Conversely, there was little change in $S\psi$ of *M. sinensis* whether or not plants were irrigated the day of measurement. This suggests these plants were decoupled from the microclimate and their transpiration was limited by water stress-inducing stomatal

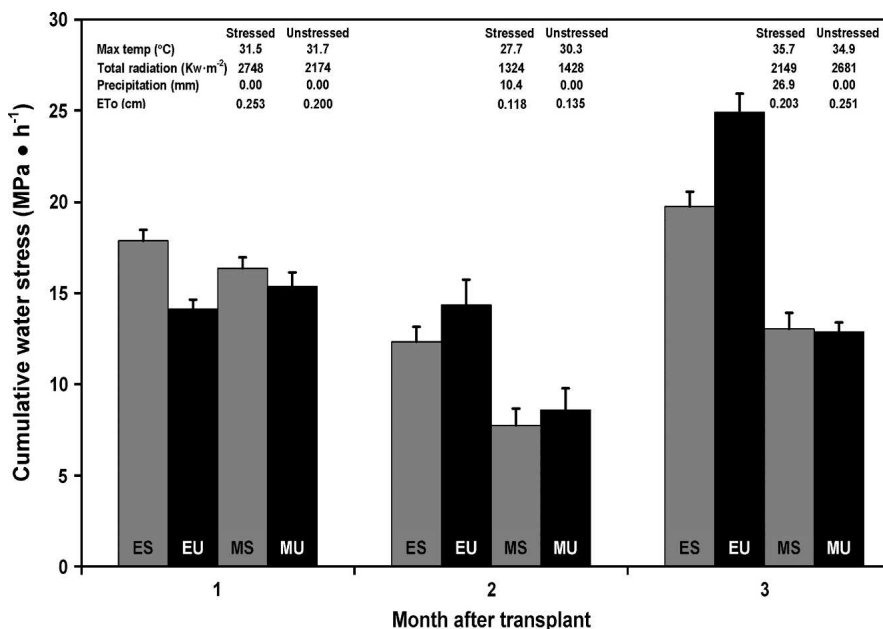


Fig. 3. Cumulative daily water stress integrals ($S\psi$) calculated monthly on the day before irrigation (stressed) and irrigation day (unstressed) for *Eragrostis spectabilis* and *Miscanthus sinensis* ‘Adagio’ irrigated with four irrigation rates (0, 0.25, 0.50, or 0.75 L) over a 3-month period during summer in central Florida. ES = *Eragrostis spectabilis*—nonirrigated day (stressed); EU = *Eragrostis spectabilis*—irrigation day (unstressed); MS = *Miscanthus sinensis*—nonirrigated day (stressed); MU = *Miscanthus sinensis*—irrigation day (unstressed). Each point represents the means \pm SE indicated by standard error bars ($n = 4$).

Table 1. Predawn water potential, midday water potential, dusk water potential, and cumulative daily water stress integrals ($S\psi$) calculated monthly for ornamental grass species irrigated with 0, 0.25, 0.50, or 0.75 L per irrigation event over a 3-month period during summer in central Florida.

MAT ²	Species	Predawn Ψ_T (MPa)	Midday Ψ_T (MPa)	Dusk Ψ_T (MPa)	Cumulative water stress, $S\psi$ (MPa·h)
2	<i>E. spectabilis</i>	–0.131 a ^x	–1.67 a	–0.35 a	13.34 a
	<i>M. sinensis</i>	–0.105 a	–1.02 b	–0.19 b	8.17 b
	<i>P</i> value	>0.05	<0.0151	<0.0305	<0.0149
3	<i>E. spectabilis</i>	–0.216 a	–2.61 a	–1.13 a ^w	22.33 a ^v
	<i>M. sinensis</i>	–0.129 b	–1.69 b	–0.28 b	12.92 b
	<i>P</i> value	<0.0357	<0.0005	<0.05	<0.05

²Months after transplant.

^xMeans calculated from four single plant replicates.

^wMean separations within columns and species ($P < 0.05$).

^vValues represent pooled dusk water potential means; however, species effect cannot be clearly identified as a result of a significant species \times stress day interaction ($P < 0.05$).

^wValues represent pooled $S\psi$ species means; however, species effect cannot be clearly identified as a result of a significant species \times stress day interaction ($P < 0.05$).

closure indicating these are isohydric (Tardieu and Simonneau, 1998). This interpretation of the water relations data is consistent with the higher biomass gains of *E. spectabilis* despite generally lower Ψ_T measurements recorded the last 2 months after transplanting. Similar results were seen for sunflower and barley, anisohydric species, and maize and poplar, isohydric species (Tardieu and Simonneau, 1998).

Conclusions

Across treatments, both grasses had similar trends with increased biomass gain and canopy size with increasing irrigation rates. The greatest portion of biomass gain for both species was shoot biomass, with little species effect seen for root biomass gain.

Miscanthus sinensis has a larger mature size than *E. spectabilis* (Darke, 1999). However, overall growth of *E. spectabilis* was normally greater ($P < 0.05$) than *M. sinensis* across all treatments. For *M. sinensis*, low biomass gain and low water stress integrals indicate stomata were closed most of the time under low irrigation volumes. Isohydric plants strive to maintain constant water potentials in response to drought conditions at the expense of biomass gain (Tardieu and Simonneau, 1998). In contrast, greater biomass gain and higher water stress integrals of *E. spectabilis* indicate stomata remained open for photosynthesis and subsequent biomass gain. Anisohydric plants seek biomass gain by tolerating low water potentials under drought conditions (Tardieu and Simonneau, 1998).

Although *E. spectabilis* is a native plant, its higher tolerance to moderate water stress than *M. sinensis* does not necessarily imply that native grasses outperform nonnatives in drought situations. Water use and drought tolerance vary greatly from species to species, even varying by genotype within species. Careful evaluation of individual grass species and sites should always be performed when selecting plants for low water-use landscapes.

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