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Growth and Physiological Factors Involved in Interspecific Variations in Drought Tolerance and Postdrought Recovery in Warm- and Cool-season Turfgrass Species

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Abstract. **Drought stress is one of the most important abiotic stresses limiting plant growth, while high recuperative capacity of plants from drought damages is critical for plant survival in periods of drought stress and rewatering. The objective of our study was to determine physiological and growth factors in association with drought tolerance and recuperative capacity of cool-season kentucky bluegrass (*Poa pratensis* cv. Excursion II) and warm-season zoysigrass (*Zoysia matrella* cv. Diomand), which were grown in controlled environment chambers and maintained well watered (control) or subjected to drought stress and subsequently rewatering. Compared with kentucky bluegrass, zoysiagrass maintained higher leaf hydration level during drought stress, as shown by greater relative water content (RWC), improved osmotic adjustment (OA), increased leaf thickness, and more extensive root system at deeper soil layers. Turf quality (TQ) and photosynthesis recovered to a greater level and sooner in response to rewatering for zoysiagrass, compared with kentucky bluegrass, which could be due to more rapid reopening of stomata [higher stomatal conductance (g_S)] and leaf rehydration (higher RWC). The aforementioned physiological factors associated with leaf dehydration tolerance during drought and rapid resumption in turf growth and photosynthesis in zoysiagrass could be useful traits for improving drought tolerance in turfgrasses.**

Drought stress is one of the most important abiotic stresses limiting plant growth in many arid areas. Drought tolerance and recuperative ability differ inter- and intraspecifically for turfgrass species (Carrow, 1996; Du et al., 2008; Pessarakli, 2007; Qian and Fry, 1997). It is generally known that warm-season turfgrass species have better drought tolerance than cool-season species (Fry and Huang, 2004; Pessarakli, 2007; Turgeon, 2011). For example, warm-season species, such as zoysiagrass, seashore paspalum (*Paspalum vaginatum*), buffalograss (*Buchloe dactyloides*), and bermudagrass (*Cynodon dactylon*) were reported to exhibit better TQ and leaf hydration levels or lower level of leaf wilting than cool-season species, such as tall fescue (*Festuca arundinacea*) during drought stress (Jiang and Carrow, 2005; Qian and Fry, 1997). Various physiological factors could be associated with the interspecific variations in drought tolerance across different turfgrass species (Fry and Huang, 2004; Pessarakli, 2007).

Physiological responses to drought stress vary between warm- and cool-season grass species, as reported in different studies. Some cool-season turfgrass species were reported to exhibit earlier leaf rolling and lower level of OA (Qian and Fry, 1997), more rapid decline in membrane stability and photochemical efficiency (Du et al., 2008), and higher water demand or lower water use efficiency (Fu et al., 2007) during drought stress, compared with warm-season species. Despite the general recognition of superior drought tolerance for warm-season turfgrass species relative to cool-season species as a group collectively (Fry and Huang, 2004; Pessarakli, 2007; Turgeon, 2011), the interspecific species variations between individual species within each group, and associated traits accounting for differential drought tolerance are not well documented. In addition, rapid rehydration and regrowth of shoots and roots on water available is critically important for perennial plant species that are often exposed to cyclic periods of drought and rewatering. But few studies examined physiological and morphological traits associated with differential postdrought recuperative ability between warm- and cool-season turfgrass species. Studies with different cultivars within a plant species found that resumption of leaf hydration level, cell membrane stability, and photosynthesis, as well as root production play important roles for plants to recover from drought damages, such as in kentucky bluegrass (Chai et al., 2010; Hu et al., 2010a; Wang and Huang, 2004). Selecting for traits that enable plants to rapidly resume growth and physiological activities from drought stress on rewatering is important for water conservation and can be economical in areas with limited water resources (Norris and Thomas, 1982).

Therefore, the objective of our study was to examine growth and physiological factors in association with drought tolerance and recuperative capacity of a warm-season zoysiagrass and a cool-season kentucky bluegrass. Growth and physiological traits examined in this study during drought stress and rewatering for both turfgrass species including TQ, leaf RWC, OA, leaf

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membrane stability, photosynthetic rate, rate of water loss, specific leaf area (SLA), and leaf wax content (LWC), as well as root length.

Materials and Methods

Plant material and growth conditions. Sods of zoysiagrass (cv. Diomand) and kentucky bluegrass (cv. Excursion II) were obtained from the research farm at Nanjing Agricultural University in Jiangsu province, China, and transplanted into plastic tubes (10 cm diameter, 60 cm deep) filled with a mixture of fine sand and soil (1:1, v/v). Plants were maintained in a greenhouse for 2 months with an average temperature of 30/26 °C (day/night) and natural sun light to establish the canopy and roots. During the period of establishment, plants in each pot in the greenhouse were irrigated twice a week until water draining from the bottom of the pot to maintain soil water content (SWC) at the field capacity level, and fertilized once a week with 400 mL of half-strength Hoagland's nutrient solution (Hoagland and Arnon, 1950). Grass was maintained at $\approx$10 cm height by trimming weekly. After establishment, plants were moved to growth chambers (XBQH-1; Jinan Xubang, Jinan, China) set at 70% relative humidity, 650 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation and a 12-h photoperiod. The temperature for zoysiagrass and kentucky bluegrass in growth chamber was 30/25 °C and 25/20 °C (day/night), respectively.

Treatment and experimental design. After 2 weeks of acclimation to growth chamber conditions, three treatments were conducted in plants: 1) for well-watered control, plants were watered every other day until drops of water started to drain from the bottom of the pots (22% SWC), 2) for drought treatment, irrigation was withheld until permanent leaf wilting occurred, and 3) for rewatering, plants initially exposed to drought stress by withholding irrigation were irrigated every other day to allow for recovery from drought stress.

Treatments and species were arranged as a split-plot design with species as main plots and water treatments as subplots. Each water treatment was replicated four times in four pots randomly placed in four growth chambers for each grass species (four chambers set at temperature of 30/25 °C for zoysiagrass and for kentucky bluegrass due to warm- and cool-season turfgrass species with different optimal temperature requirement).

Measurements of soil, plant growth, and physiological indices. SWC in a 0–20 cm deep soil layer of each pot was measured as an indication of the level of soil water deficit using time domain reflectometry (Mini Trase Kit 6050X3; Soil Moisture Equipment Corp., Santa Barbara, CA) by inserting the 20-cm-long wave guide vertically in the top 20-cm soil profile.

Turf quality is a widely used parameter evaluating overall plant performance (Turgeon, 2011). Turf quality was visually rated based on turfgrass texture, density, uniformity, and color on a scale from 1 (completely dead plants) to 9 (green and dense canopy).

Leaf RWC of fully expanded leaves were determined by leaf water status based on fresh (FW), turgid (TW), and dry weight (DW) using the following formula: RWC (%) = [(FW – DW)/(TW – DW)] × 100. Fully expanded leaves were immediately weighed for FW after being excised from the plants, and then placed into tubes filled with deionized water for 12 h in dark at 4 °C. Leaf samples were then blotted dry and immediately weighed for TW. Samples were then dried in an oven at 80 °C for at least 72 h to get DW (Barrs and Weatherley, 1962).

Leaf membrane stability was evaluated by measuring electrolyte leakage (EL) of leaves (Blum and Ebercon, 1981). Fresh fully expanded leaves (0.1–0.2 g) were collected, rinsed, and immersed in 30 mL deionized water and placed on a shaker for 24 h. The initial conductivity of the solution (C_{initial}) was then measured using a conductivity meter (Orion Star A212; Thermo Scientific, Waltham, MA). Leaves were then killed by autoclaving at 120 °C for 20 min and placed back on the shaker for 12 h. The final conductivity of killed tissues (C_{max}) was then measured and EL calculated as ($C_{\text{initial}}/C_{\text{max}}$) × 100.

To determine differences in rate of water loss and leaf water status during the course of dehydration between the two grass species, relative water leakage (RWL) and RWC of detached leaves were measured (Hu et al., 2010b). Fresh fully expanded leaves were detached and weighed immediately for initial FW, and then placed in petri dishes in a growth chamber with controlled temperature (25 °C), light intensity (150 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and relative humidity (50%). RWL was determined as the difference of leaf weight (Wt) at a specific time (T) of dehydration (20, 40, 60, 90, 120, 150, 180, 210, 240, 300, 360, and 420 min) from the initial FW relative to the DW: RWL (milligrams per gram DW per minute) = {[(FW–Wt)/DW/T]}. During rehydration, detached leaves after 240 min dehydration were immersed in water in petri dishes and measured for RWC at 20, 40, 60, 90, 120, 150, 180, and 210 min of rewatering to determine water hydration status of detached leaves at a given time of the dehydration process.

Osmotic adjustment was determined by Ψ_S of leaf sap at full turgor. Leaf samples were collected and soaked in deionized water for 4 h, blotted dry, placed into microcentrifuge tubes, frozen in liquid nitrogen, and stored at –20 °C until further analysis. Leaf sap was pressed out and added to the chamber in an osmometer (Vapro 5600; Wescor, Logan, UT) for the determination of the osmolality (C, value in millimoles per kilogram). Osmolarity of leaf sap was converted from millimoles per kilogram to megapascals using the formula: megapascals = $-C \times 2.58 \times 10^{-3}$. Then, OA was calculated as the difference between the Ψ_S of well-watered control leaves at full turgor and drought-treated leaves at full turgor (Qian and Fry, 1997).

Leaf net photosynthetic rate (P_n), transpiration rate (T_r), and g_S were measured at 0, 5, 10, 15, and 20 d under drought stress and 2 and 6 d of rewatering on leaves (second fully expanded from the top) from each pot (Yu et al., 2015). Intact leaves were enclosed in a 6-cm^2 cuvette with a portable infrared gas analyzer (LI-6400; LI-COR, Lincoln, NE). Leaves were placed in a leaf chamber with a built-in red and blue light source of the LI-6400 with the light intensity of 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The area of leaves enclosed in the leaf chamber was determined on a scanner, which was used to calculate P_n, g_S, and T_r.

LWC was determined by the method of Zhang et al. (2007). In brief, fresh sample pieces were weighed (FW_0) and immersed in 30 mL chloroform for 15 s. The extract was evaporated on a boiling water bath and weighed again to get final weight (FW_1). Then, leaves were dried in an oven at 80 °C for at least 72 h and weighed for DW. LWC was calculated as ($FW_0 - FW_1$)/DW (milligrams per gram DW).

The SLA as an indicator of leaf thinness was measured at 0, 5, 10, 15, and 20 d under drought stress and 2, 4, and 6 d of rewatering. For SLA, 20 s-fully expanded leaves from each tube were trimmed off and scanned for fresh leaf area using a scanner (Epson version 2.94A; Seiko Epson Corp., Suwa, Japan) with Digimizer software (version 3.6.0.0; MedCalc Software, Mariakerke, Belgium) to analyze digital images. Then, leaves were dried in an oven at 80 °C for at least 72 h and weighed for DW. SLA was calculated as leaf area per unit leaf DW.

All plants were sampled at 20 d of drought stress and 6 d of rewatering treatment for an analysis of the root length. The 60-cm soil profile in the 60-cm deep tube was divided into two segments (upper 0–20 cm and lower 20–60 cm). Roots from each segment were then washed free of growth medium and stained in 1% crystal violet solution. Roots were scanned with a scanner (Epson version 2.94A) to generate root images. The images were then analyzed with Digimizer software (version 3.6.0.0) for their total root length.

Statistical analysis. Data analysis was performed with SPSS (version 13.0 for Windows; IBM Corp., Armonk, NY). Analysis of variance with a fixed model was used to determine effects of treatment and interaction of treatment and species. When a particular F test was significant, the means were separated with least significance difference test at a probability level of 0.05.

Results and Discussion

Soil water status during drought and postdrought rewatering. Soil water content in pots for both turfgrass species was maintained at ≈20% under well-watered conditions, but exhibited rapid decline during drought stress, to ≈5% at 20 d of drought stress, and increased to prestress level after rewatering (Fig. 1). SWC content did not differ in pots planted with zoysiagrass from those with kentucky bluegrass, indicating that both zoysiagrass and kentucky bluegrass were exposed to the same level of water deficit during drought stress and rewatering.

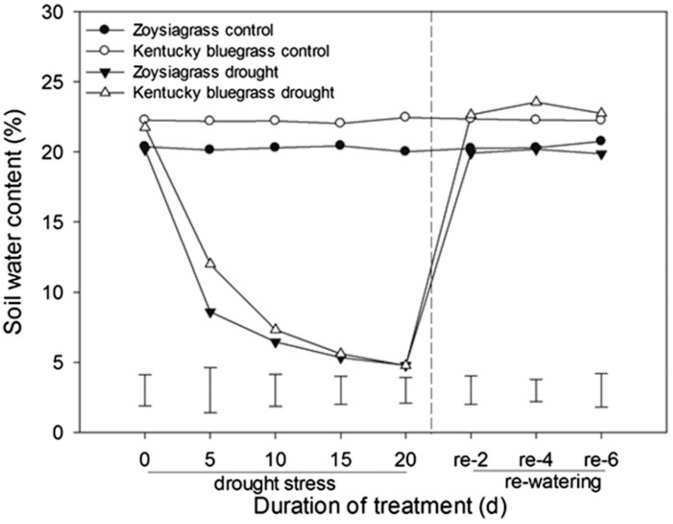

Fig. 1. Changes in soil water content (SWC) in zoysiagrass and kentucky bluegrass exposed to 20-d drought stress and 6-d rewatering. Vertical bars indicate least significant difference values ($P \leq 0.05$) for the comparison among treatments at a given sampling day.

Interspecific variations in physiological responses to drought and rewatering. Turf quality rapidly declined after 15 d of drought stress in both species, and kentucky bluegrass had a lower TQ of 3.46 than zoysiagrass of 5.0 at 20 d of treatment (Fig. 2A). Turf quality recovered to prestress level in zoysiagrass, but not in kentucky bluegrass on rewatering for 6 d. These results suggested that zoysiagrass had better drought tolerance and recuperative potential from drought injury compared with kentucky bluegrass. The difference in turf performance in response to drought stress and postdrought rewatering might be associated with physiological changes discussed in this study.

Leaf cell membrane stability has been extensively used as an indicator of cellular damages induced by various stresses, including drought (Blum and Ebercon, 1981). Kentucky bluegrass exhibited rapid increase in EL during 20 d of drought stress whereas no significant increase in EL was observed in zoysiagrass during the experimental period (Fig. 2B). These results suggested that leaves of zoysiagrass maintained greater membrane stability during drought stress than those of kentucky bluegrass. Du et al. (2008) compared zoysiagrass to another cool-season grass species, tall fescue, and reported that zoysiagrass leaves had a lower drought-induced EL and higher TQ during drought stress. On rewatering, EL declined rapidly to the level of well-watered control in kentucky bluegrass, which was not significantly different from that of zoysiagrass. The differential EL responses to drought between the two species and the lack of significant differences in EL on rewatering suggested that loss of cellular membrane stability was associated with the greater extent of TQ decline for kentucky bluegrass under drought stress, while other physiological factors rather than EL could play more critical roles in regulating the differential TQ responses to rewatering.

Drought tolerance is closely related to photosynthesis and water loss through transpiration. In this study, P_n, g_S, and T_r declined rapidly during drought stress in both species. No significant difference was found in P_n between two species during drought stress, but on postdrought rewatering, leaf P_n was significantly higher in zoysiagrass than that in kentucky bluegrass, which was 68.9% and 39.4% of respective well-watered control at 2 d of rewatering and increased to 93.9% and 51.5% of respective well-watered control after 6 d of rewatering (Fig. 3A). These results suggested that leaves of both species suffered the same level of photosynthetic damages during drought stress, but zoysiagrass leaves had greater recovery potential for rapid resumption of photosynthesis on rewatering. Zoysiagrass leaves exhibited significantly higher g_S and T_r at 10 and 15 d of drought stress than kentucky bluegrass, which could lead to more water loss, but reflect less damages of stomata by drought stress. On rewatering, stomata of zoysiagrass resumed g_S rapidly, which could contribute to the recovery in photosynthetic activities under rewatering compared with that in kentucky bluegrass. The lesser cellular damages in zoysiagrass leaves during drought stress reflected by lower EL and higher g_S was associated with the maintenance of higher leaf hydration status, as manifested by higher RWC in zoysiagrass than kentucky bluegrass during drought stress.

Whole-plant leaf RWC is an extensively used parameter to indicate leaf water status and the level of drought tolerance (Flexas and Medrano, 2002). In this study, no significant difference was observed in RWC between two turfgrass species

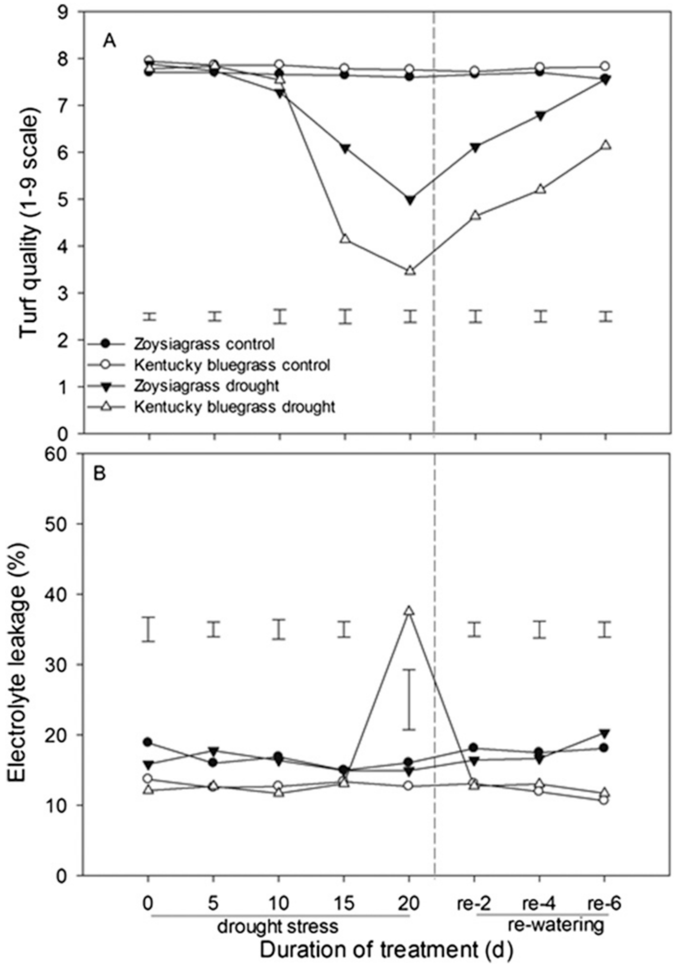

Fig. 2. (**A**) Changes in turf quality (TQ) and (**B**) electrolyte leakage (EL) in zoysiagrass and kentucky bluegrass exposed to 20-d drought stress and 6-d rewatering. TQ was rated based on the scale of 1–9, with 9 being the best. Vertical bars indicate least significant difference values ($P \leq 0.05$) for the comparison among treatments at a given sampling day.

under well-watered conditions (Fig. 4). Drought caused rapid decrease in RWC after 10 d of treatment in both species, and kentucky bluegrass maintained lower water status than zoysiagrass, to 23.4% and 43.7% at the end of drought stress, respectively. In perennial kentucky bluegrass, 25% of leaf RWC was reported to be a critical point for whole plant to survive (Xu et al., 2011a, 2011b, 2013). On rewatering, RWC was sharply increased to 97.1% in zoysiagrass, reaching the same level of the well-watered control after only 2 d of water rehydration. However, kentucky bluegrass did not fully recover to the level of control even with 6 d of rewatering, only to 80.3% of well-watered control. These results suggested that zoysiagrass developed a stronger adaptation strategy for leaf water maintenance during drought stress and rehydration during postdrought rewatering. Leaf cellular water status during drought stress is in association with OA and morphological indexes, which is discussed below.

Zoysiagrass leaves had lower RWL than kentucky bluegrass, which was 30.8% lower at the first 20 min of dehydration (Fig. 5A). The significant difference maintained until 300 min of dehydration. The above results indicated that zoysiagrass had better water retention ability compared with kentucky bluegrass during the beginning and mild water deficit conditions, which was consistent with the result of whole-plant response to drought stress. On rehydration, detached leaves of both turfgrass species absorbed water rapidly, and zoysiagrass showed significantly higher RWC than kentucky bluegrass after 40 min of rewatering, from 43.4% and 44.4% to 98.2% and 91.4% of well-watered control, respectively (Fig. 5B). Results from

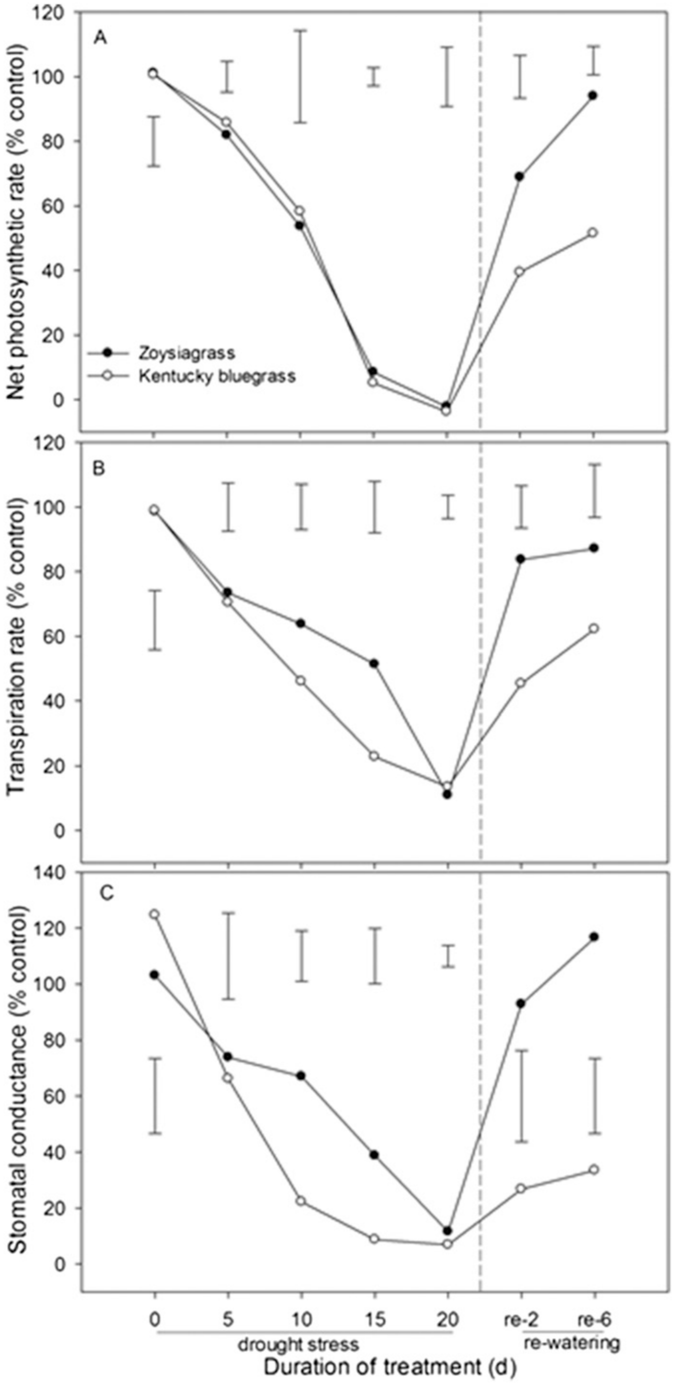

Fig. 3. (**A**) Changes in net photosynthetic rate (P_n), (**B**) transpiration rate (T_r), and (**C**) stomatal conductance (g_S) in zoysiagrass and kentucky bluegrass exposed to 20-d drought stress and 6-d rewatering. Vertical bars indicate least significant difference values ($P \leq 0.05$) for the comparison among treatments at a given sampling day.

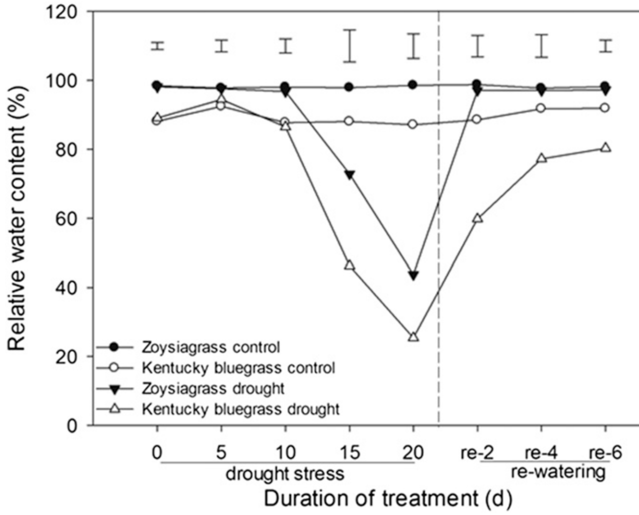

Fig. 4. Changes in leaf relative water content (RWC) in zoysiagrass and kentucky bluegrass exposed to 20-d drought stress and 6-d rewatering. Vertical bars indicate least significant difference (LSD) values ($P \leq 0.05$) for the comparison among treatments at a given sampling day.

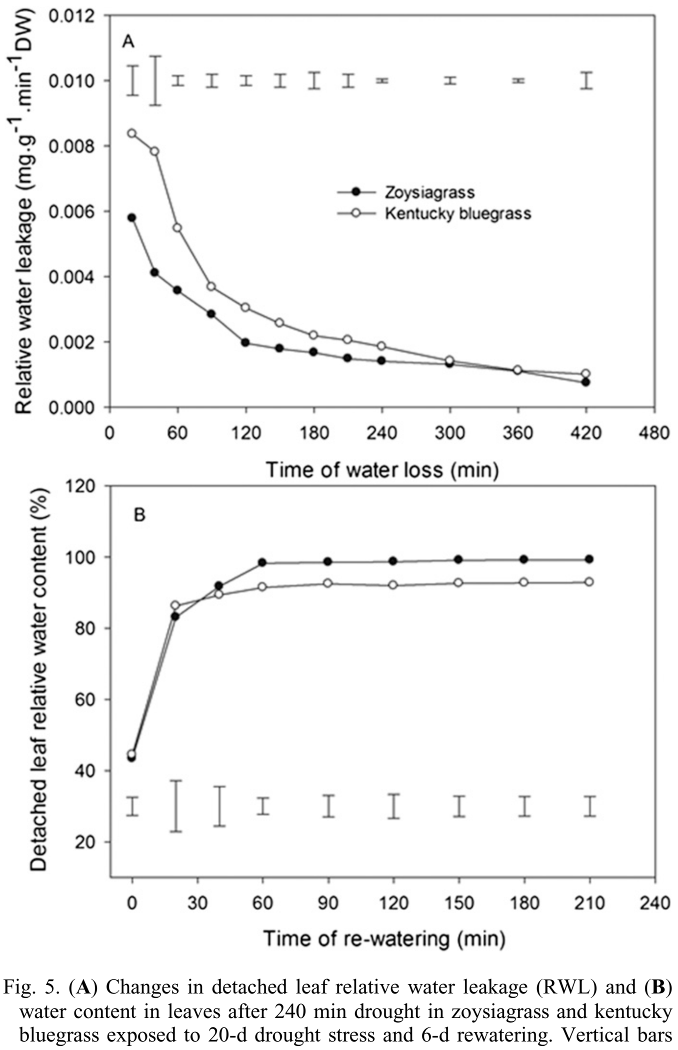

Fig. 5. (**A**) Changes in detached leaf relative water leakage (RWL) and (**B**) water content in leaves after 240 min drought in zoysiagrass and kentucky bluegrass exposed to 20-d drought stress and 6-d rewatering. Vertical bars indicate least significant difference values ($P \leq 0.05$) for the comparison among treatments at a given sampling day.

detached leaves that underwent dehydration and rehydration suggested that zoysiagrass could maintain more leaf water through slow water loss and fast water absorption, compared with kentucky bluegrass.

OA plays important roles in cellular water retention and turgor maintenance among many physiological factors when water deficit occurs in plants (Farooq et al., 2009; Huang, 2008; Kramer and Boyer, 1995). In this study, OA of zoysiagrass increased from 0.02 to 0.67 MPa during drought treatment, but from 0.04 to 0.52 MPa for that of kentucky bluegrass (Fig. 6A). A significantly higher OA in zoysiagrass was found at 15 and 20 d of drought stress, compared with that in kentucky bluegrass. On 2 d of rewatering, OA of both turfgrass species declined rapidly and zoysiagrass was observed with significant higher OA during postdrought rewatering, except that at 6 d of rewatering. These results indicated that zoysiagrass retained greater RWC using OA capacity during drought stressed period and postdrought rewatering, compared with that of kentucky bluegrass. Previous studies also observed warm-season zoysiagrass (0.77 MPa) had higher OA than cool-season tall fescue (0.34 MPa) during drought stress (Qian and Fry, 1997), the same as Barker et al. (1993). The enhanced OA was attributed to the accumulation of some compatible solutes, such as water-soluble sugars, proline and glycine betaine during various abiotic stresses (Geissler et al., 2009; Pérez-López et al., 2010; Wang et al., 2004; Yu et al., 2015). The specific mechanism for the higher OA in zoysiagrass compared with kentucky bluegrass needs to be further measured and confirmed in future studies.

Specific leaf area as an indicator of leaf thickness has often been observed to decline under water deficit conditions and drought tolerant plants exhibit lower SLA than drought sensitive ones (Liu and Stutzel, 2004; Marron et al., 2003). In this study, SLA in zoysiagrass and kentucky bluegrass showed a significant decline with the duration of drought stress, to 37.5% and 49.1% of respective well-watered control at 20 d of drought treatment (Fig. 6B). However, on 6 d of rewatering, SLA in zoysiagrass rose more rapidly to 94.5% of well-watered control than that in kentucky bluegrass (81.3%). Decline in SLA was an adaptive strategy for plants to limit leaf water loss through reduced leaf area and transpiration rate under drought conditions (Craufurd et al., 1999; Marron et al., 2003). Results from this study indicated that SLA could be involved in leaf water maintenance in zoysiagrass in response to postdrought rewatering.

Leaf wax content is another indicator of drought resistance used in various plant species (Chen et al., 2015; Haque et al., 1992; Seo et al., 2011). Leaf rolling and LWC exhibited a positive effect on leaf water maintenance in weeping lovegrass (*Eragrostis curvula*) plants (Colom and Vazzana, 2003). Zoysiagrass exhibited significant higher LWC in plants grown under either well-watered control or drought stress conditions compared with kentucky bluegrass (Fig. 6C), indicating that LWC, along with other leaf physiological and morphological traits, played important roles in the maintenance of higher leaf water status in zoysiagrass.

The higher leaf water status during drought stress can be attributable to active growing and extensive root system (Henry et al., 2011). Plants with a deeper root system usually had higher drought avoidance capacity than plants with shallow root systems (Carrow, 1996; Huang and Gao, 1999; Su et al., 2008), but few studies examined root regrowth after rewatering for different plant species. In this study, no significant differ-

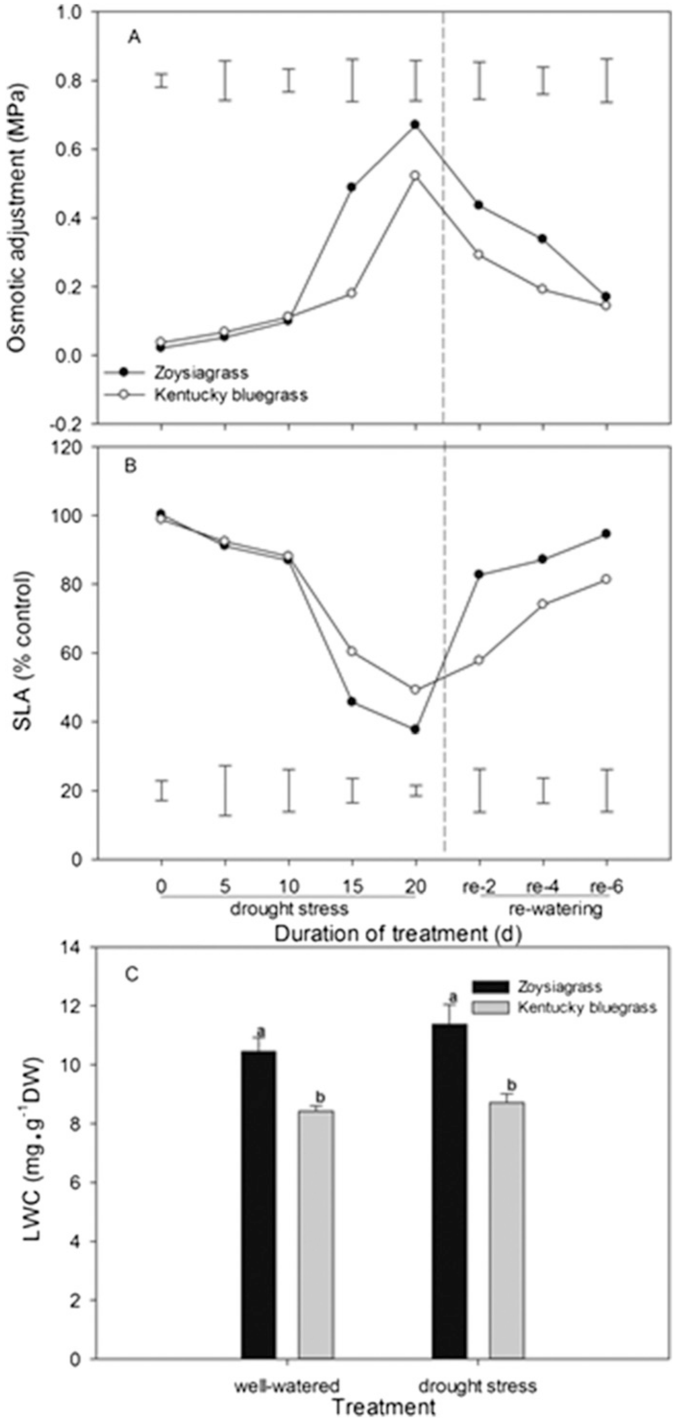

Fig. 6. (**A**) Changes in leaf osmotic adjustment (OA), (**B**) specific leaf area (SLA) in zoysiagrass and kentucky bluegrass exposed to 20-d drought stress and 6-d rewatering, and (**C**) leaf wax content (LWC) at 6 d of rewatering. Vertical bars indicate least significant difference values [LSD ($P \leq 0.05$)] for the comparison among treatments at a given sampling day in **A** and **B**. Different letters indicate significant differences based on LSD test ($P \leq 0.05$) between the same treatment in **C**. The vertical bar over each column was SE for four replicates in **C**.

ence in total root length was found between zoysiagrass and kentucky bluegrass in the upper soil layers of 0–20 cm at the 20 d of drought treatment (Fig. 7A). However, zoysiagrass developed more root in the deeper soil layers of 20–50 cm compared with kentucky bluegrass that could transport and provide water from deeper soil to aboveground plants. On 6 d of rewatering, kentucky bluegrass developed more roots in upper soil layers of 0–20 cm, but fewer roots in the deeper soil layers of 20–50 cm (Fig. 7B) compared with zoysiagrass under drought stress. The more extensive roots in the deeper soil profile in zoysiagrass during drought stress and rewatering could facilitate water uptake from deeper soil profile, which is vital for plants to avoid drought stress and the resumption of growth after rewatering.

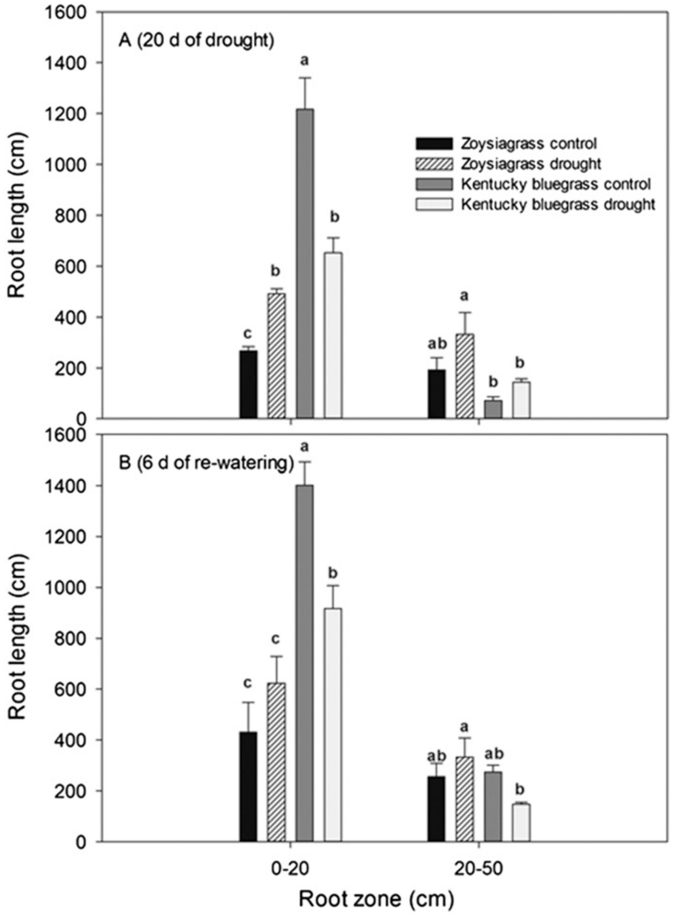

Fig. 7. (**A**) Changes in root length in zoysiagrass and kentucky bluegrass at 20-d drought stress and (**B**) 6-d rewatering. Different letters indicate significant differences based on least significant difference test ($P \leq 0.05$) among the same soil layer. The vertical bar over each column was SE for four replicates.

In summary, warm-season zoysiagrass had superior drought tolerance and postdrought recovery compared with cool-season kentucky bluegrass as shown by better turf performance (TQ) and RWC. Leaves of zoysiagrass maintained higher leaf hydration level during drought stress, as shown by greater RWC, which could be associated with higher leaf cellular membrane stability, improved OA, increased leaf thickness (lower SLA), and more extensive root system at deeper soil profile. The rapid resumption of TQ and photosynthesis could be due to rapid reopening of stomata (higher g_S) and leaf rehydration (higher RWC). Those abovementioned growth and physiological traits could be used as screening parameter to select for drought-tolerant turfgrass germplasm that can tolerate prolonged periods of drought stress and recuperate from drought stress quickly on rewatering.

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