Physiological Responses in C₃ and C₄ Turfgrasses under Soil Water Deficit

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Abstract. Lawns must be managed increasingly under less frequent or deficit irrigation. Deficit irrigation can reduce gas exchange, carbon assimilation, and physiological function in both warm- (C₄) and cool- (C₃) season turfgrasses, yet limited research has compared the physiological response to increasing levels of soil water deficit. The objectives of this greenhouse study were to compare three commonly used transition-zone turfgrasses—bermudagrass [*Cynodon dactylon* (L.) Pers.] (C₄), buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.] (C₄), and tall fescue (*Festuca arundinacea* Schreb.) (C₃)—and their ability to maintain quality and physiological function under water deficit stress. Visual turf quality, normalized difference vegetation index (NDVI), reflective canopy temperature, and gross photosynthesis were evaluated initially near field capacity (FC), and subsequent soil water deficit [48% (moderate) and 33% (severe) of plant-available water] conditions. Bermudagrass and tall fescue had similar quality ratings near FC, although the photosynthetic rate was greater for bermudagrass. Compared with other turfgrasses, bermudagrass maintained greater turf quality, NDVI, and photosynthetic rates further into water deficit stress. Tall fescue quality and photosynthetic rates declined most rapidly in both experiments as a result of the combined heat and drought stress. Buffalograss used less water compared with other species, and maintained consistent turf quality, NDVI, and photosynthetic rates under moderate and severe water deficit. These results support the notion that buffalograss and bermudagrass are better adapted than tall fescue at maintaining functional and ecosystem services with shallow soil depths in landscape situations under imposed summertime water restrictions.

Shifts in population dynamics from rural to urban have placed increased pressures on potable water supplies in many areas (Alig et al., 2003; Vörösmarty et al., 2000). Property values increase with aesthetically pleasing landscapes (Council of Tree and Landscape Appraisers, 2003), but supplemental irrigation is often necessary for maintaining outdoor landscapes in semiarid to arid climates (St. Hilaire et al., 2008). It is estimated that in some hydrological regions, as much as 30% to 50% of all urban water is applied to landscapes, with the majority applied during the summer months (Gerston et al., 2002; Nouri et al., 2013). A major component of urban landscapes is turfgrass (Milesi et al., 2005). Benefits of turfgrass and green urban spaces include reducing air temperature, mitigating environmental pol-

lutants, and soil stability, as well as improved human mental and physical health, social cohesion, and lower crime levels (Beard and Green, 1994; Fam et al., 2008; Stier et al., 2013).

As the potable water demand increases, local municipalities often develop ordinances to regulate water use in urban residential areas. Municipal water conservation ordinances typically regulate landscape irrigation as opposed to indoor water use (Devitt et al., 1995). Because water availability is decreased during dry periods, irrigation may be permitted only as often as one to two times per month, or prohibited indefinitely in response to long-term drought conditions (City of Lubbock, 2010). Turfgrasses may express drought symptoms initially as chlorosis at the leaf tip, extending down the leaf blade as dry conditions persist (Carrow, 1996; Colmer and Barton, 2017; Kim et al., 2009). C₄ turfgrass species use drought-induced dormancy as a coping mechanism during extended periods of water deficit stress (Zhang et al., 2019). Recovery and regrowth from drought-induced dormancy would be ex-

pected as rainfall or irrigation returned, as long as soil conditions did not restrict root production (Steinke et al., 2011).

A number of C₃ and C₄ turfgrasses are adapted to the transition zone region of the United States, including bermudagrass [*Cynodon dactylon* (L.) Pers.] (C₄), buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.] (C₄), and tall fescue (*Festuca arundinacea* Schreb.) (C₃). However, in recent years, a growing number of municipalities in the southwestern United States have incentivized removal of or completely banned use of C₃ turf species such as tall fescue in landscapes as a result of their perceived lack of heat and drought resistance (Schiavon et al., 2013). Where water restriction periods occur routinely, maximal ecosystem services (i.e., continued CO₂ fixation, O₂ production, and heat dissipation) may be provided by turfgrasses capable of maintaining green cover, photosynthetic production, and reduced canopy temperatures under combined heat and soil water deficit resulting from summertime landscape irrigation restrictions.

Physiological adaptation and response to heat and soil water deficit conditions differ between C₃ and C₄ grasses, yet few studies have sought to evaluate comparative physiological responses to combined heat and soil water stress. The ability of turfgrasses to maintain quality and physiological function under soil water stress can be influenced by rooting characteristics or osmotic adjustments (Fu et al., 2004; Qian and Fry, 1997; Stier et al., 2013). Therefore, research is needed to understand more fully how water deficit stress in restricted root zones affects the physiological function of turfgrasses. The objectives of this greenhouse study were to compare three commonly used C₃ and C₄ transition zone turfgrass species and their ability to maintain quality and physiological function (as measured through NDVI, reflective canopy temperature, and gross photosynthetic rates) under water deficit stress.

Materials and Methods

Two independent, sequential greenhouse trials were conducted between March and May 2017 at the Plant and Soil Science Research Greenhouse on the Texas Tech campus in Lubbock, TX. Turfgrass cores [diameter, 2.5 inch (6.4 cm)] were obtained from established ‘ATF-1434’ tall fescue, ‘Legacy’ buffalograss, and ‘Celebration’ bermudagrass field research plots in Sept. 2016 with a Turf-Tec Turf Plugger (Turf-Tec International, Tallahassee, FL). Turfgrass species were grown in 7-inch (17.8 cm) (height) by 4-inch (10.2 cm) (i.d.) polyvinyl chloride pots with weed fabric (Vigoro Weed Barrier Landscape Fabric with PowerGrid; Vigoro Corp., Chicago, IL) secured to the bottom of the container to retain soil but allow drainage. The soil substrate consisted of a 4:1 (sand: calcareous clay) ratio using greens-grade profile mix (Profile Products, LLC, Buffalo Grove, IL) to ensure effective drainage and root growth while enhancing water deficit

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Fig. 1. Daily maximum incoming shortwave radiation (A), maximum air temperature (B), and maximum vapor pressure deficit (C) for turf species grown inside a greenhouse at Texas Tech University. Trial 1 was conducted from day of year (DOY) 62 to 94 and Trial 2 was conducted from DOY 107 to 138.

Table 1. Analysis of variance for response variables measured from turfgrass species maintained near field capacity at initiation of replicated greenhouse experiment.

Factor	Turf quality	NDVI	Canopy temp	CO ₂ fixed
Trial (T)	***	***	***	***
Species (S)	***	***	***	***
T × S	*	NS	NS	NS

NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.
 NDVI = normalized difference vegetation index.

stress. Additional sand plus calcareous clay mix was added around the turfgrass core to bring the soil level up to 1 cm below the top of the container. Samples of each species ($n = 36$) were established in the greenhouse over a 6-month period before initiating the study. During establishment, containers were maintained under well-watered (three times per week to saturation) greenhouse conditions and fertilized monthly with 18.5 kg N/ha of 24N-3.5P-14.1K plus micronutrients (Plant Food; Scotts Miracle-Gro Products, Inc., Marysville, OH).

An evaporative cooling system and fans were engaged to maintain more stable greenhouse conditions when the internal temperature reached 90 °F (32.2 °C). A CR1000 data

logger (Campbell Scientific, Logan, UT) recorded greenhouse environmental data. Solar radiation was monitored using a pyranometer (LI200X; LI-COR Biosciences, Lincoln, NE) placed 6.6 ft (2 m) above the greenhouse bench surface. Supplemental lighting was not provided to plants during either trial. An additional temperature and humidity sensor (HMP60; Vaisala, Helsinki, Finland) was placed at greenhouse bench level throughout each experiment. Each sensor recorded measurements every 60 s, and hourly means were calculated and stored by the data logger. Evaporative demand was estimated through hourly mean vapor pressure deficit (VPD), calculated using saturated vapor pressure and ambient vapor pressure of

hourly mean air temperature and relative humidity (Jones, 1992).

Containers were arranged as a randomized complete block design with four replications of each treatment. Blocks were oriented linearly away from the evaporative cooling system to reduce the potential for temperature as a confounding variable. The first and second trials were initiated in 2017 on 7 Mar. and 18 Apr., respectively. All treatments were irrigated to saturation and allowed to drain for 24 h to reach FC. An initial set of turf quality and physiological measurements were collected from all containers near FC. Containers were irrigated three times per week with 90 or 180 mL water to provide 1.6 or 3.3 cm water/week. Gravimetric measurements of containers before initiating the experiment and each irrigation event were used to determine plant-available water (PAW). Subsequent measurements of turf parameters were initiated on day 8 of both trials after experimental units had reached consistent water deficit stress.

Visual turf quality was assessed by three researchers two days per week. The three

Table 2. Analysis of variance for interactions or main treatment effects of three turfgrass species maintained under two levels of water deficit stress under greenhouse conditions.

Trial	Factor	PAW (%)	Turf quality	NDVI	Canopy temp	CO ₂ fixed
Trial 1	Day (D)	***	NS	***	***	***
	Species (S)	*	***	***	NS	***
	D × S	NS	*	**	NS	***
	Irrigation (I)	***	***	***	***	*
	D × I	NS	***	NS	NS	NS
	S × I	***	***	**	NS	NS
	D × S × I	NS	NS	NS	NS	NS
Trial 2	D	***	***	***	***	***
	S	***	***	***	***	***
	D × S	***	*	NS	***	***
	I	***	***	***	***	***
	D × I	*	***	NS	NS	***
	S × I	***	**	NS	NS	*
	D × S × I	NS	NS	NS	*	NS

NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.
PAW = plant-available water; NDVI = normalized difference vegetation index.

Fig. 2. Mean turf quality for species near field capacity at the initiation of Trials 1 and 2. Data were analyzed separately for trials as a result of an interaction with trial and species. Bars sharing the same letter are the same statistically at $\alpha = 0.05$.

independent ratings were averaged for each experimental unit. Turf quality ratings were based on the National Turfgrass Evaluation Program 1- to 9-point scale, with 1 being poorest, 9 being highest quality, and 6 as minimal acceptability (Morris and Shearman, 1998).

Spectral analyses were conducted with a Holland Scientific RapidScan CS-45 meter (Holland Scientific Inc., Lincoln, NE) to estimate objectively the drought response of species experiencing water deficit stress. The RapidScan measured light centered on 670 nm [red (R)], 730 nm (red edge), and 780 nm [near infrared (NIR)]. Two pieces of black felt fabric were used; one piece of fabric measuring 15 inches × 15 inches (38 cm × 38 cm) square was used as a background black color with no reflectance; the second piece of fabric was identical in size, with a 4-inch- (10-cm)-diameter hole in the center. This was draped over the container to eliminate all white surface and expose turf and soil only. The instrument was held ≈60 cm

over the sample for measurement. Data were obtained twice weekly and uploaded to the TurfScout, LLC (Greensboro, NC) website for all calculations. The resulting analysis included the following spectral vegetation indices: ratio vegetation index, NDVI, and a color index. All indices and specific light band reflectance values were evaluated, but results for each were comparable. Therefore, NDVI was chosen because it represents a ratio of $(\text{NIR} - \text{R})/(\text{NIR} + \text{R})$ and is used frequently in agricultural situations (Blackburn, 1998; Bowman, 1989). The ratio vegetation index (NIR/R) is often more effective for full turf canopy measurements. However, drought-induced dormancy reduced the reliability of the ratio vegetation index in our study (Huete and Jackson, 1987).

Reflective canopy temperatures (Infrared Thermometer model 8872; Spectrum Technologies Inc., Aurora, IL) were collected with a single measurement from the center of each pot 2 d each week. Data were obtained between 1100 and 1400 HR. The meter was

held ≈10 cm from the turf canopy, with an 8:1 distance-to-target ratio and ±2 °C accuracy.

A Li-COR LI 6400 XT portable photosynthesis system with 6400-19 Custom Chamber Kit PPS-234 (LI-COR Biosciences) was used to obtain photosynthetic measurements. The chamber was constructed from plexiglass (Regal Plastics, Dallas, TX) with dimensions of 4 inches (10 cm) tall, an i.d. of 3.3 inches (8.3 cm), and a wall thickness of 0.13 inch (0.32 cm). The top of the chamber was sealed with thin, translucent plastic secured to the top of the chamber with clear tape. The base area of the chamber was 12.6 in² (54 cm²) and was included as leaf area for each measurement. The LI-COR 6400 XT captured net ecosystem exchange of CO₂ during measurements conducted under full sun between 1100 and 1400 HR once each week (Bremer and Ham, 2005). Dark respiration measurements to account for soil and canopy respiration were obtained by covering the chamber and container with black felt material used during NDVI measurements. Gross photosynthesis was calculated as the sum of light measurements and absolute value of dark measurements (Bremer and Ham, 2005; Su et al., 2008).

All data were analyzed using SAS software (version 9.4; SAS Institute, Cary, NC) using the glimmix procedure. Analysis of variance (ANOVA) was conducted separately for response variables measured near FC and water deficit stress periods (day 8 to conclusion) of both trials. Initial data analyses included trial in the model to determine whether data should be pooled or analyzed separately. All response variables in the water deficit phase contained a trial-by-main treatment factor interaction, so each trial was analyzed separately for all response variables. Trial day from the water deficit stress period was included in the model, with species and irrigation as main treatment factors. Block was the random factor in the model. Fisher's least significant difference was used to calculate values for mean separation of all significant effects at $\alpha = 0.05$.

Results and Discussion

Greenhouse conditions. Based on PAW estimated before each irrigation event, it was determined that deficit irrigation resulted in soil moisture levels of $52 \pm 0.13\%$ (SD) and $35 \pm 0.14\%$ of PAW (moderate and severe, respectively) during Trial 1, and between $44 \pm 0.11\%$ and $31 \pm 0.09\%$ of PAW during Trial 2. Daily maximum shortwave radiation, air temperature, and VPD were recorded during both trials (Fig. 1). For Trial 1, maximum daily shortwave radiation averaged $665 \pm 224 \text{ W}\cdot\text{m}^{-2}$, whereas maximum daily shortwave radiation for Trial 2 averaged $846 \pm 112 \text{ W}\cdot\text{m}^{-2}$. Maximum and minimum daily greenhouse air temperatures for Trial 1 averaged 36.7 ± 3.5 and 22.8 ± 0.5 °C, respectively. Maximum and minimum daily air temperatures for Trial 2 averaged 38.3 ± 2.1 and 28.0 ± 2.8 °C, respectively. In addition,

Fig. 3. Mean normalized difference vegetation index (A) and canopy temperature (B) for species near field capacity at initiation of the experiments. Data were pooled for Trials 1 and 2 because of a lack of significant interaction with trial and species. Bars sharing the same letter are the same statistically at $\alpha = 0.05$.

daily maximum VPD within the greenhouse averaged 5.4 ± 1.2 kPa for Trial 1 and 5.6 ± 1.0 kPa for Trial 2. The somewhat elevated radiation, temperature, and evaporative demand experienced during Trial 2 likely contributed to trial main effects detected through ANOVA (Tables 1 and 2).

FC conditions. Species main effects were observed for all parameters when soil moisture was near FC (Table 1). A trial $\times$ species interaction occurred for turf quality with soil water near FC, so each trial was analyzed separately. Turf quality was numerically lower for all species at the beginning of Trial 1 compared with Trial 2 (Fig. 2). Buffalograss had lower turf quality (5 of 9) in Trial 1 than other species based on reduced foliar density achieved during the 6 months of greenhouse acclimation and growth. Reduced greenhouse light levels (Baldwin

et al., 2009), greater soil moisture (Qian and Engelke, 1999), or both may have contributed to reduced buffalograss quality during acclimation. Although somewhat reduced relative to Trial 2, both tall fescue and bermudagrass had acceptable levels of turf quality (6 and 7, respectively) at FC in Trial 1. In Trial 2, all species had acceptable turf quality, with tall fescue and bermudagrass showing similar visual quality (7.5 of 9) near FC, and buffalograss also having greater turf quality than in Trial 1 (7 of 9) (Fig. 2).

There were no trial $\times$ species interactions for NDVI or canopy temperature near FC, so data were pooled across trials for each parameter (Table 1). Similar to turf quality, reduced buffalograss coverage lowered NDVI compared with bermudagrass and tall fescue (Fig. 3A). Tall fescue exhibited lower canopy temperatures than both C_4 grasses at

FC (Fig. 3B). This was likely associated with greater transpirational water loss, which would reduce canopy temperature during optimum water availability (Sun et al., 2013). Differences observed among species near FC highlight natural variation in C_3 and C_4 turfgrasses not related to water deficit stress.

Water deficit stress conditions. Soil moisture levels from two irrigation treatments were less in Trial 2 compared with Trial 1 as a result of greater evaporative demand during Trial 2. The only difference observed at moderate water deficit stress was a decreased percentage of PAW for tall fescue relative to the C_4 grasses in Trial 2 (Fig. 4B), which is consistent with previous research demonstrating greater water use rates and reduced moisture in tall fescue relative to C_4 turfgrass (Huang et al., 1998). In contrast, bermudagrass PAW percentage was lowest at severe water deficit stress when compared with other species in both trials (Fig. 4). These results demonstrate variations in water usage by the three species under water deficit stress consistent with previous research (Beard and Beard, 2004; Fu et al., 2004; Huang, 2008; Qian and Fry, 1997). Interestingly, there were no differences in water usage among species when greater than 50% PAW was maintained, but reducing water availability to less than 50% led to differences in water usage among the species. Results may demonstrate the ability of buffalograss to reduce overall water usage in drier conditions through osmotic adjustment compared with bermudagrass using more available water before leaf firing and dormancy (Hsiao, 1973; Ludlow et al., 1985; Qian and Fry, 1997). These mechanisms indicate differences in water use and drought symptom expression between the two C_4 turfgrasses.

Visual turf quality and NDVI measurements provided evidence of changes in canopy appearance during water deficit stress. ANOVA revealed both day $\times$ species and species $\times$ irrigation interactions on turf quality for both trials (Table 2). Buffalograss had the lowest turf quality at the start of the water deficit phase, but improved as the trial progressed; tall fescue quality declined through day 15 in Trial 1 (Fig. 5A). Bermudagrass maintained acceptable turf quality throughout Trial 1 except for day 22. Bermudagrass had the best visual quality at moderate water deficit stress, but buffalograss had the highest turf quality at severe water deficit stress in Trial 1 (Fig. 5B). Buffalograss was able to maintain acceptable and similar turf quality ratings at both water deficit levels when combining all dates, whereas bermudagrass and tall fescue had lower turf quality at severe water deficit stress in Trial 1 (Fig. 5B). Warmer temperatures in Trial 2 affected tall fescue more extensively than C_4 species under water deficit stress (Fig. 5C). Bermudagrass and buffalograss maintained similar turf quality throughout most of Trial 2, but both C_4 grasses experienced significant decline in turf quality between days 11 and 15.

Fig. 4. Percent of plant-available water for species $\times$ irrigation interaction in Trials 1 (A) and 2 (B). Pot weights during water deficit stress were subtracted from initial pot weight near field capacity to determine the percentage of plant-available water for each pot after each measurement. All measurements dates were averaged. Bars sharing the same letter are the same statistically at $\alpha = 0.05$.

Fig. 5. Mean turf quality for day $\times$ species (A and C) and species $\times$ irrigation (B and D) interactions during Trials 1 (A and B) and 2 (C and D). Each figure represents treatments averaged over water deficit level (A and C) or day (B and D). Turf quality was measured by three researchers on a 1- to 9-point scale with 1 = poorest, 9 = best, and 6 = minimum acceptability. The error bars represent the least significant difference (LSD) value at $\alpha = 0.05$ for the day $\times$ species interaction (A and C). Bars sharing the same letter in the species $\times$ irrigation interaction (B and D) are the same statistically at $\alpha = 0.05$.

At the conclusion of Trial 2, bermudagrass declined below acceptable turf quality levels and below that of buffalograss. This obser-

vation is consistent with previous research that showed buffalograss maintained acceptable quality further into water stress than

other species (Qian and Engelke, 1999; Sifers et al., 1990). Buffalograss continued to outperform other species under severe water

Fig. 6. Mean normalized difference vegetation index (NDVI) for day $\times$ species (A) and species $\times$ irrigation (B) interactions during Trial 1. Each view represents treatments averaged over a water deficit level (A) or day (B). A RapidScan CS-45 was used for reflectance measurements and NDVI was calculated as (Near infrared - Red)/(Near infrared + Red) with red centered at 670 nm and near infrared centered at 780 nm. The error bar represents the least significant difference (LSD) value at $\alpha = 0.05$ for the day $\times$ species interaction (B). Bars sharing the same letter in the species $\times$ irrigation interaction (B) are the same statistically at $\alpha = 0.05$.

Fig. 7. Mean canopy temperature for the day $\times$ species $\times$ irrigation interaction in Trial 2. The error bar represents the least significant difference (LSD) value at $\alpha = 0.05$ for this interaction.

deficit stress, but both C₄ grasses had better visual quality when compared with tall fescue at moderate water deficits in Trial 2 (Fig. 5D). Increased light quantity and air temperatures in Trial 2 affected visual quality positively of C₄ species, but combined drought and heat stress reduced visual quality of tall fescue.

There was a day $\times$ species interaction on NDVI in Trial 1 (Table 2). Limited lateral growth of buffalograss reduced NDVI when compared with other turfgrasses (Fig. 6).

However, buffalograss NDVI did not decrease under severe water deficit stress as observed with bermudagrass and tall fescue (Fig. 6B). All species had significant increases in NDVI from days 8 to 11, but bermudagrass and tall fescue declined from day 12 to 15 (Fig. 6A). All species stabilized through the remainder of Trial 1. Main treatment effects occurred for day, species, and irrigation on NDVI in Trial 2 (Table 2). As such, bermudagrass (0.452) and tall fescue (0.442) each had greater NDVIs than

buffalograss (0.356), and moderate water deficit stress (0.415) resulted in a greater NDVI than severe water deficit stress (0.383) when combining all other factors.

Canopy temperature measurements during the study provided additional evidence of plant water use and stomatal regulation through transpirational cooling. There were significant day and irrigation main effects on canopy temperature during the water deficit phase for Trial 1 (Table 2). Turfgrasses maintained under severe water deficit had increased canopy temperature relative to those grown under moderate water deficit (30.3 vs. 28.0 °C, respectively) when combining species and measurement dates. In contrast, there was a three-way interaction for day $\times$ species $\times$ irrigation in Trial 2 (Table 2). Initially, tall fescue had higher canopy temperatures when compared with C₄ species at the start of water deficit stress (Fig. 7). The peak canopy temperature was reached for all species on day 15, followed by reduction of canopy temperatures through the remainder of Trial 2. Peak canopy temperatures corresponded to turf quality reductions in both C₄ species noted previously (Fig. 5C). Buffalograss was the only species with similar canopy temperatures at both water deficit stress levels on all dates (Fig. 7). Buffalograss canopy temperatures did not fluctuate as greatly as other species between dates. Previous research suggests high pubescence and the glaucous nature of buffalograss may allow for minimal transpiration while still maintaining reduced canopy temperature (Jefferson et al., 1989; Stewart et al., 2004). Tall fescue maintained a similar canopy temperature regardless of water deficit level until the final two rating dates, at which time

the severe water deficit stress treatment experienced increased canopy temperature compared with moderate water deficit stress (Fig. 7). Bermudagrass at severe water deficit stress exhibited greater canopy temperatures than moderate water deficit stress between days 15 and 18. As temperatures decreased

through day 22 and the remainder of Trial 2, both water deficit treatments maintained similar canopy temperatures. Lack of difference in canopy temperature for buffalograss at two water deficit stress levels demonstrates improved drought tolerance and limited water use characteristics compared with bermudagrass and tall fescue (Colmer and Barton, 2017). In contrast, severe water deficit stress led to rapidly increasing canopy temperatures in tall fescue and, to some extent, in bermudagrass.

There was a species main effect on gross photosynthesis measured near FC in both trials (Table 1). As such, bermudagrass exhibited the greatest gross photosynthesis, with tall fescue being intermediate and buffalograss lowest in Trial 1 (Fig. 8A). Tall fescue and buffalograss showed similar rates of gross photosynthesis at the beginning of Trial 2, but less than that of bermudagrass (Fig. 8B). A day $\times$ species interaction in both trials resulted in similar results for species as water deficit stress increased (Table 2). Gross photosynthesis of tall fescue diminished rapidly as soils reached water deficit stress (Fig. 8). Water deficit stress likely altered leaf water content in tall fescue, which increased photorespiration potential and altered biochemical reactions that reduced photosynthesis (Hu et al., 2010; Huang et al., 1998; Sun et al., 2013). As tall fescue entered into water deficit stress, gross photosynthesis decreased to the lowest levels of all species, approaching 2 and 3 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ for Trials 1 and 2, respectively. Bermudagrass gross photosynthesis gradually declined to similar levels as that of tall fescue as water deficit stress progressed in Trial 1. In Trial 2, bermudagrass again declined, but stabilized at levels of 8 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ (Fig. 8B). Interestingly, although buffalograss showed a trend toward lowest gross photosynthesis near FC, buffalograss main-

tained moderate rates of gas exchange relative to other species as water deficit stress ensued. There was also a day $\times$ irrigation interaction for gross photosynthesis in Trial 2 (Table 2). When combining across species, moderate water deficit stress produced relatively consistent gross photosynthesis levels over the trial duration. However, under severe water deficit stress, gross photosynthesis declined from 8 to 4 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$ through the trial period (Fig. 9A). Under moderate water deficit stress, bermudagrass had the greatest gross photosynthesis (10 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$), buffalograss was intermediate (8 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$), and tall fescue was the lowest (4.5 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$) (Fig. 9B). Under severe water deficit stress, bermudagrass and buffalograss showed similar gross photosynthesis (7 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$), both of which were greater than tall fescue (3 $\mu\text{mol CO}_2/\text{m}^2/\text{s}$) (Fig. 9B). These results demonstrate the benefits of the C_4 vs. C_3 photosynthetic pathway under combined water deficit and heat stress conditions (Su et al., 2008). However, it should be noted that rooting may have been restricted in this study, which may have prevented grasses from extending roots to access greater available water. This may have affected tall fescue negatively to a greater extent than other species as a result of its well-documented drought avoidance characteristics (Bremer et al., 2006; Qian and Fry, 1997; Su et al., 2008; Younger, 1985).

Conclusions

This greenhouse research evaluated physiological responses of commonly used transition-zone turf species to soil water deficit stress. Although restricting rooting depth could have contributed to results that may differ somewhat from field situations, some notable differences were demonstrated

Fig. 8. Mean gross photosynthesis for species near field capacity (FC) (day 2) and day $\times$ species interaction in Trials 1 (A) and 2 (B) under water deficit stress. Each figure represents the treatments averaged over water deficit levels. Gross photosynthesis was determined as the sum of a full sunlit measure and absolute value of dark respiration measure to account for soil and plant respiration. Error bars represent the least significant difference (LSD) values at $\alpha = 0.05$ for species near FC or day $\times$ species interaction during water deficit conditions for Trial 1 (A) or 2 (B) above the final collection date.

Fig. 9. Mean gross photosynthesis for day $\times$ irrigation (A) and species $\times$ irrigation (B) interactions during Trial 2. Each figure represents treatments averaged over water deficit level (A) or day (B). Gross photosynthesis was determined as the sum of a full sunlit measure and absolute value of dark respiration measure to account for soil and plant respiration. The error bar represents the least significant difference (LSD) value at $\alpha = 0.05$ for the day $\times$ irrigation interaction (A). Bars sharing the same letter within the species $\times$ irrigation interaction (B) are the same statistically at $\alpha = 0.05$.

among species. Buffalograss maintained the lowest canopy temperatures during water deficit stress, and had the least notable reductions in turf quality, NDVI, and gross photosynthetic rate as water deficit stress progressed. Although bermudagrass showed greater gross photosynthetic rate and NDVI compared with buffalograss near FC, both response variables declined to levels at or less than that of buffalograss as water deficit stress progressed. Tall fescue exhibited the greatest stress when combining heat and water deficit stress, sustaining only 50% of the gross photosynthesis levels measured in bermudagrass and buffalograss in Trial 2. Although a variety of adaptive and functional attributes should be considered when making appropriate species selection, these data support use of C_4 species as opposed to tall fescue for maximizing ecosystem services in landscapes routinely experiencing heat and soil water deficit stress throughout the summer months. These results demonstrate more explicitly the limited physiological adaptation of tall fescue on restricted root zones (<7 inches), which may occur in rockier soil profiles or following home construction practices.

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