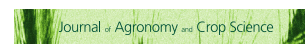


ORIGINAL ARTICLE

DROUGHT STRESS



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Warm-season turfgrass species genotype-by-environment interaction for turfgrass quality under drought

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Funding information

National Institute of Food and Agriculture, Grant/Award Number: 2015- 51181-24291; U.S. Department of Agriculture

Abstract

One of the biggest challenges the turfgrass industry is currently facing is limitations of available water for irrigation of turfgrass areas. Efforts on breeding for drought resistance have increased over the past several years across the United States. Thus, the objectives of this study were to evaluate the performance of bermudagrass (*Cynodon* spp. Rich.), St. Augustinegrass (*Stenotaphrum secundatum* (Walter) Kuntze), seashore paspalum (*Paspalum vaginatum* Swartz) and zoysiagrass (*Zoysia* spp. Willd.) breeding lines from five different breeding programs under drought and estimate genetic parameters in order to increase selection efficiency for drought resistance improvement in these breeding programs. The germplasm sources were bermudagrass from Oklahoma State University and University of Georgia (UGA); St. Augustinegrass from North Carolina State University, Texas A&M University System (TAMUS) and University of Florida (UF); zoysiagrass from UF and TAMUS; seashore paspalum from UGA. Field trials were conducted from 2016 to 2019 at research facilities in Citra, FL and Dallas, TX. The response variables evaluated were per cent living ground cover (%GC), and turfgrass quality under normal or non-drought (TQND) and drought conditions (TQD). The genetic variance was significant for TQND and TQD in bermudagrass, TQD in St. Augustinegrass and all traits in zoysiagrass. The heritability estimates were higher for TQD than for TQND in bermudagrass and St. Augustinegrass. Genetic correlation estimates showed that indirect selection can be effective to select drought-resistant genotypes. Several genotypes performed better than all commercial cultivars in both St. Augustinegrass and zoysiagrass.

KEYWORDS

bermudagrass, drought stress, seashore paspalum, St. Augustinegrass, zoysiagrass

Key points

- Genetic variability was observed for turfgrass quality under drought in all species, except seashore paspalum.
- Indirect selection might be effective to select drought-resistant genotypes.

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- Per cent living ground cover was not a good predictor of turfgrass quality under drought and non-drought.

1 | INTRODUCTION

The turfgrass industry impacts the US economy by providing hundreds of thousands of jobs in activities such as the development of new cultivars, production and supply of turfgrass products, and intermediate and final consumption of turf products and services (Haydu et al., 2006). In addition, turfgrasses positively affect the environment by moderating temperatures, reducing noise, absorbing radiation, reducing runoff and increasing infiltration, purifying water from sediments and pollutants, controlling erosion and improving soil quality (Monteiro, 2017). Furthermore, turfgrasses also provide aesthetic and health benefits to humans because they are surfaces for recreational sports/activities (Beard & Green, 1994; Monteiro, 2017).

Bermudagrass [*Cynodon* spp. Rich.], St. Augustinegrass [*Stenotaphrum secundatum* (Walter) Kuntze], seashore paspalum [*Paspalum vaginatum* Swartz] and zoysiagrass [*Zoysia* spp. Willd.] are the most commonly grown warm-season turfgrass species in the United States, being widely used in the southern and transitional climatic zones of the country (Gelernter et al., 2017; Patton et al., 2017). These species are used for home lawns, public parks, roadsides and athletic and golf fields, with the exception of St. Augustinegrass, which is not preferred for athletic or golf settings because of its coarse leaf texture and low tolerance to traffic (Gelernter et al., 2017; Hanna et al., 2013). Bermudagrass is known for its superior heat and drought tolerance (Zhang et al., 2018; Zhang, Kenworthy, et al., 2017), wear tolerance and recovery ability (Hanna et al., 2013). Breeding programs of this species have focused on producing F_1 sterile interspecific hybrids ($2n = 3x = 27$ [*C. dactylon* (L.) Pers. ($2n = 4x = 36$) $\times$ *C. transvaalensis* Burt Davy ($2n = 2x = 18$)] or exploring the *C. dactylon* gene pool to produce superior cultivars (Baxter & Schwartz, 2018; Wu et al., 2009). St. Augustinegrass exhibits good performance under shade relative to other warm-season grasses (Zhang, Glenn, et al., 2017), and diploids ($2n = 2x = 18$) are mainly used in breeding programs, whereas the use of polyploids is still limited because of the low success rates and the need for embryo rescue technology in the development of interploid hybrids (Meeks & Chandra, 2020; Milla-Lewis et al., 2013). Diploid ($2n = 2x = 20$) germplasm has been used in seashore paspalum breeding programs, and this species is known for tolerance to abiotic stresses, such as salinity (Chavarria et al., 2019, 2021; Marcum & Murdoch, 1994) and waterlogging (Hanna et al., 2013). Zoysiagrasses are popularly known for their low fertility requirements (Meeks et al., 2021) and resistance to weed colonization (Patton et al., 2017). In zoysiagrass, production of either intra or interspecific hybrids, especially among the species *Z. japonica* Steud., *Z. pacifica* (Goudsw.) M. Hotta & S. Kuroki and *Z. matrella* (L.) Merr., has been a commonly used strategy in breeding programs (Kimball et al., 2013; Meeks et al., 2021).

Limited water for irrigating turfgrass areas is the biggest challenge the turfgrass industry currently faces. Drought events are becoming more common in the United States and elsewhere around the world (Otkin et al., 2018; Zhang et al., 2021) and, under limited availability of water, ornamental plants are often the first to be placed under water use restrictions (National Turfgrass Federation, 2022; UMass Extension Turf Program, 2011). Therefore, drought-resistant genotypes that can sustain growth and maintain active metabolic activities during periods of drought stress, either through strategies of avoidance (maintenance of favourable water status either by increasing the capacity for water uptake of the root systems and/or reducing water loss from leaves) and/or tolerance (maintain growth and metabolic activity under water deficits), are highly desirable (Levitt, 1980; Huang et al., 2014). For these reasons, a collaborative project was started in 2010 among North Carolina State University (NCSU), Oklahoma State University (OSU), University of Florida (UF), University of Georgia (UGA) and Texas A&M University System (TAMUS) to breed for drought resistance in four economically important warm-season turfgrass species in the southern US: bermudagrass, St. Augustinegrass, seashore paspalum and zoysiagrass (Gouveia, Rios, et al., 2021). As part of this collaboration, breeding lines from the above-mentioned universities' breeding programs are initially screened for drought response in multi-location nurseries (Gouveia et al., 2020; Gouveia, Rios, et al., 2021; Wang et al., 2022). Then, the best-performing lines are advanced to replicated trials, where they are evaluated for other traits of agronomic and commercial importance such as turfgrass quality (TQ), establishment rate, fall colour, spring green up, inflorescence abundance, drought, shade and salinity resistances as well as sod production traits (Gouveia, Raymer, et al., 2021; Katuwal et al., 2022; Pirtle et al., 2022).

Some parameters help plant breeders decide the best strategies to improve selection efficiency in their breeding programs. Heritability helps quantify the influence of the genetic effects on the expression of a trait (Falconer & Mackay, 2005). In turfgrass species, heritability estimates for TQ ranging from null to high have been reported: broad-sense heritabilities of 0.00 and 0.31 in *C. dactylon* (L.) Pers. (Stefaniak et al., 2009) and *Paspalum notatum* Flügge (Rios et al., 2017), respectively; genotype-mean broad-sense heritability estimates from 0.70 to 0.76 in *Zoysia* spp. (Schwartz et al., 2009), and 0.74 in *C. transvaalensis* Burt Davy (Kenworthy et al., 2006), and generalized measures of heritability from 0.00 to 0.93 in *Cynodon* spp. (Gouveia et al., 2020; Gouveia, Rios, et al., 2021), 0.00–0.92 in *Stenotaphrum secundatum* (Gouveia, Rios, et al., 2021; Graham et al., 2022), 0.00–0.66 in *Paspalum vaginatum* (Gouveia, Raymer, et al., 2021; Gouveia, Rios, et al., 2021) and 0.36–0.93 in *Zoysia* spp. (Gouveia, Rios, et al., 2021).

Another critical parameter for plant breeders is the genotype-by-environment interaction (GEI) as it allows them to assess the

stability of genotypes across target environments. Whereas GEI across locations can be estimated by type-B genetic correlations (Yamada, 1962), in perennial crops, the type-A genetic correlation (correlation between traits) can be used to estimate GEI in contrasting conditions on the same trial, such as drought and non-drought (Gouveia et al., 2020). Gouveia et al. (2020) estimated genetic correlations between TQ under drought and non-drought ranging from 0 to 1 in bermudagrass. However, genetic correlation estimates are unknown in St. Augustinegrass, seashore paspalum and zoysiagrass. In addition, correlations among traits can indicate the possibility of success in performing indirect selection. A high correlation between TQ under drought (TQD) and per cent living ground cover (%GC) evaluated in the establishment year would allow the early selection for drought resistance. Low positive correlation has been reported among those traits (Graham et al., 2022). Therefore, the objectives of this study were to (1) quantify levels of GEI of four warm-season turfgrass species for turfgrass quality evaluated under drought and non-drought conditions at the target locations in the Southern US, (2) estimate the correlation between all evaluated traits and (3) identify superior breeding lines across traits for the target environments.

2 | MATERIALS AND METHODS

2.1 | Field trials and crop management

Field trials were conducted from 2016 to 2019 at two locations: Citra, FL (UF) and Dallas, TX (TAMUS). The soil was characterized as Chipley sand soil (Thermic coated Aquic Quartzipsamments) at Citra and Austin silty clay (fine-silty, carbonatic, thermic Udorthentic Haplustolls) at Dallas (<http://websoilsurvey.nrcs.usda.gov/>). Temperature and precipitation data for the duration of the study are available in Figure S1 (<https://fawn.ifas.ufl.edu>, <https://texaset.tamu.edu/>). Each trial was arranged as a randomized complete block design with three replications. The trials were established in the spring of 2016 by transplanting six 10.2 cm × 10.2 cm plugs into 1.5 m × 1.5 m plots with 0.46 m alleys between plots for all species except zoysiagrass for which twenty-four 4.7 cm × 4.7 cm plugs were planted per plot. Management practices varied slightly between the locations based on recommended management practices for each species in each state, as described by Gouveia, Rios, et al. (2021). Plots were mowed weekly at 7.6 cm and 8.9 cm for St. Augustinegrass, and 3.8 cm and 5 cm for all other species in Dallas and Citra, respectively. The nitrogen (N) rates applied were 145 and 196 kg N ha⁻¹ per year in Dallas and Citra, respectively, split into several applications per year. Other nutrients were applied as needed based on soil sampling at each location and following fertility management recommendations for each state. At both locations, plots were irrigated weekly (more frequently if needed) only during the establishment year. Weed management was performed using chemical and mechanical control as needed at both locations. In Citra, weed management was performed using oxadiazon 2.2 kg a.i. ha⁻¹ in spring and proflaminate {2,4-dinitro-3-N,3-N-dipropyl-6-(trifluoromethyl)benzene-1,3-diamine} 0.61 L a.i. ha⁻¹ in fall. In Dallas, oxadiazon 3.30 kg a.i. ha⁻¹ was applied after planting, and proflaminate {2,4-dinitro-3-N,3-N-dipropyl-6-(trifluoromethyl)benzene-1,3-diamine} twice a year, in the spring and fall. For the alley maintenance, glyphosate [N-(phosphonomethyl) glycine] was applied every 30 days between March and November at Citra and every 2 weeks at Dallas.

2.2 | Germplasm

The breeding lines evaluated in this study were developed by five different breeding programs. Bermudagrass lines evaluated included 20 breeding lines each from the OSU and UGA-Tifton breeding programs, and four commercial cultivars ('Riley's Super Sport' [Celebration®; Riley, 2000], 'Latitude 36 Turf Bermudagrass' [Latitude 36®; Wu et al., 2012], 'DT-1' [TifTuf®; Schwartz et al., 2018] and 'Tifway' [Burton, 1966]). St. Augustinegrass lines evaluated included 17, 20 and three breeding lines from the NCSU, TAMUS and UF breeding programs, respectively, and four commercial cultivars ('Floratum' [Alderson & Sharp, 1994], 'SS-100' [Palmetto®; Kirkland & Wagner, 1995], 'Raleigh' [Alderson & Sharp, 1994] and 'DALSA 0605' [TamStar™; Chandra et al., 2015]). Twenty breeding lines from the UGA-Griffin breeding program and two commercial cultivars ('SDX-1' [SeaDwarf™; DePew et al., 2002], and 'UGA-31' [SeaStar®; Raymer et al., 2015]) were evaluated for seashore paspalum. Finally, 20 breeding lines each from the TAMUS and UF breeding programs, and three commercial cultivars ('Palisades' [Engelke et al., 2002], 'SS-500' [Empire®; Ito & Gurgel, 2000], and 'Zeon' [Doguet, 2002]) were included for zoysiagrass. All breeding lines were selected based on their superior drought resistance in previous multi-environment nurseries performed at eight locations in the Southeastern United States (Gouveia, Rios, et al., 2021).

2.3 | Phenotypic data

The response variables evaluated were per cent living ground cover (%GC) and TQ. At the end of the planting year, %GC was evaluated visually from 0% to 100% as a measure of establishment rate. Meanwhile, TQ was rated visually using a 1–9 scale, as described by the National Turfgrass Evaluation Program (Morris, 2004), for 3 years after the establishment year (Tables S1 and S2). For TQ, a rating of 9 indicated outstanding or ideal turfgrass quality, and 1 reflected very poor or dead turf. A TQ rating equal to or greater than 6 was generally considered as acceptable TQ. Conversely, a rating of less than 6 was considered unacceptable. The TQ ratings consider aesthetic and functional aspects of the turfgrass, and it is based on a combination of five traits: colour, density, uniformity, texture and disease or stress environment (Morris, 2004). The data collection was performed for 3 years at both locations (Tables S1 and S2). Turfgrass quality was collected under two specific environmental conditions: TQ under normal or non-drought conditions (TQND) and TQ under drought conditions (TQD). At both locations, TQND was

collected in the summer of 2017, 2018 and 2019, except for seashore paspalum and zoysiagrass in 2019 when TQND was evaluated in late spring. Meanwhile, TQD was evaluated under natural prevalence of drought due to the lack of rainout shelters. Plots were evaluated for TQD when at least 50% of plots showed ratings below 5. Due to differences in soil texture and soil water content across locations, data collection for this trait occurred on different dates at the different locations in both 2018 and 2019 (Tables S1 and S2). Thus, for statistical purposes, the TQD average of individual ratings across drought periods was calculated for each plot.

2.4 | Statistical analysis

Data were analysed using the ASReml-R package v.4 (Butler et al., 2017) in the R environment (R Core Team, 2021). The mixed model approach was performed to estimate variance components using the residual maximum likelihood (REML), tests of random effects variances by likelihood ratio test (LRT) and fixed effects by Wald test (Gilmour et al., 1995).

The modelling of the residual (R) variance/covariance matrix was performed for all Eqs., except Equation 2., and the best structure for R was indicated by the lower Bayesian information criterion (BIC) as proposed by Schwarz (1978). Then, the LRT test was also used to verify the significance of the most complex structure for R in the fitted model. Generalized measures of heritability, proposed by Cullis et al. (2006), were estimated for all equations using the standard estimator $H^2 = 1 - \frac{\bar{v}_{\Delta}^{BLUP}}{2\sigma_g^2}$, where $\bar{v}_{\Delta}^{BLUP}$ is the mean variance of a

difference between pairs of Best Linear Unbiased Predictions (BLUPs) for the genotypic effect, and σ_g^2 is the variance component of the entries.

The single-environment data analysis was performed using a repeated measures model (Equation 1) for TQND and TQD, whereas for %GC the analysis was performed using the model in Equation 2. The multi-environment analysis was performed using Equation 3 for TQND and TQD and Equation 4 for %GC:

$$y = \mu 1 + X_1 b(p) + X_2 p + Z_1 g + Z_2 gp + e \quad (\text{Eq 1})$$

$$y = \mu 1 + X_1 b + Z_1 g + e \quad (\text{Eq 2})$$

$$y = \mu 1 + X_1 l + X_2 p + X_3 r + X_4 b(p)(l) + Z_1 g + Z_2 gp + Z_3 gl + Z_4 glp + e \quad (\text{Eq 3})$$

$$y = \mu 1 + X_1 l + X_2 b(l) + Z_1 g + Z_2 gl + e \quad (\text{Eq 4})$$

where, y is the vector of phenotypic values; μ is the overall mean; X and Z are the incidence matrices for fixed and random effects, respectively; b is the fixed vector of block effects; p is the fixed vector of year effects; l is the fixed vector of location effects; r is the fixed vector of the effects of interaction between location and year; $b(p)(l)$, $b(p)$ and $b(l)$ are the fixed vector of block effects nested within locations and years, years and location, respectively; g is the random vector of entry

effects with $g \sim \text{MVN}(0, \sigma_g^2 I)$, where σ_g^2 is the variance component of the entries; gp is the random vector of effects of interaction between entry and year with $gp \sim \text{MVN}(0, \sigma_{gp}^2 I)$, where σ_{gp}^2 is the variance component of interaction between entry and year; gl is the random vector of effects of interaction between entry and location with $gl \sim \text{MVN}(0, \sigma_{gl}^2 I)$, where σ_{gl}^2 is the variance component of interaction between entry and location; glp is the random vector of effects of interaction between entry, location and year with $glp \sim \text{MVN}(0, \sigma_{glp}^2 I)$, where σ_{glp}^2 is the variance component of interaction between entry, location and year, and e is the random vector of errors with $e \sim \text{NMV}(0, R \otimes I)$ in the Equations 1, 3 and 4, and e is the random vector of residual effects with $e \sim \text{MVN}(0, \sigma_e^2 I)$, where σ_e^2 is the variance component of the residuals in Equation 2. R is the covariance matrix of residuals and in Equation 3 it was structured considering locations and years and thus $R = R_l \otimes R_t$, being R_l the covariance matrix for locations, and R_t the covariance matrix for years. 1 is a vector of ones and I is an identity matrix of its proper size. The Kronecker product is denoted by $\otimes$.

Type-B genetic correlations between locations and years were estimated for Equation 3 and Equation 4 using the estimator $r_g = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_i^2}$, where σ_g^2 is the variance component of the entries and σ_i^2 is the variance component of interaction between entries and locations or entries and years. Principal component analyses were carried out using predicted values of entries for each trait in Equations 3 and 4, followed by the construction of biplots of the first two principal components. The R package *stats* (R Core Team, 2021) was used to perform these analyses, and the packages *ggfortify* (Tang et al., 2016) and *ggplot2* (Wickham, 2016) were used to construct biplots.

Genetic correlation among contrasting environmental conditions was quantified by the type-A genetic correlations between TQD and TQND, and it was estimated for each location (Equation 5) and for multi-environment (Equation 6) using the bivariate models:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = X_1 t + X_2 p(t) + Z_1 r(p)(t) + Z_2 g(t) + Z_3 gp(t) + e \quad (\text{Eq 5})$$

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = X_1 t + X_2 l(t) + X_3 p(t) + X_4 pl(t) + Z_1 r(p)(l)(t) + Z_2 g(t) + Z_3 gl(t) + Z_4 glp(t) + e \quad (\text{Eq 6})$$

where, y_1 and y_2 are the data vectors for the two traits of interest; t is the fixed vector of main trait effects; $p(t)$ is the fixed vector of years effects within trait; $l(t)$ is the fixed vector of location effects within trait; $pl(t)$ is the fixed vector of effects of interaction between locations and years within trait; $r(p)(t)$ is the random vector of block effects within years and trait, with $r(p)(t) \sim \text{MVN}(0, I \otimes D)$, and $r(p)(l)(t)$ is the random vector of block effects within locations, years and trait, with $r(p)(l)(t) \sim \text{MVN}(0, I \otimes E)$; $g(t)$ is the random vector of genotypes effects within traits, with $g(t) \sim \text{MVN}(0, I \otimes G)$; $gp(t)$ is the random vector of genotype $\times$ year interaction effects within traits, with $gp(t) \sim \text{MVN}(0, I \otimes P)$; $gl(t)$ is the random

vector of genotype $\times$ location interaction effects within traits, with $gl(t) \sim \text{MVN}(0, I \otimes L)$; $glp(t)$ is the random vector of genotype $\times$ location $\times$ year interaction effects within traits, with $glp(t) \sim \text{MVN}(0, I \otimes T)$, and e is the random vector of errors, with $e \sim \text{MVN}(0, I \otimes R)$. D and E are 2×2 diagonal variance matrixes with unique j^{th} variance term for each trait and null covariances. G , P , L and T are compound symmetry heterogeneous 2×2 variance-covariance matrix between traits, which is defined by a single trait-to-trait (type-A genetic correlation term in G matrix, r_A), and a unique j^{th} variance term for each trait. R is an unstructured 2×2 residual variance-covariance matrices with different variance for each trait ($\sigma_{e_j}^2$) and covariance between traits ($\sigma_{e_{ij}}$). I is an identity matrix of its proper size, and the Kronecker product is denoted by $\otimes$. In Equation 6, the interaction between genotype and year was not explicit in the model because it did not converge due to unbalanced data.

3 | RESULTS

3.1 | Heritability and genotype-by-environment interaction

The residual matrix that provided the lowest BIC varied across traits in both the single and multi-environment models (Tables S3 and S4). In the single-environment analysis, the entry variance was not significant (<0.05) by LRT for %GC in seashore paspalum in Dallas, for TQD in seashore paspalum and zoysiagrass in both locations

and for TQND in seashore paspalum and St. Augustinegrass in Citra (Table S5). In the multi-environment analysis, the year effect was significant (<0.05) by Wald statistic for TQND and TQD in all species, whereas the location effect was significant for all traits and species, except for TQND in bermudagrass and TQD in St. Augustinegrass (Table S6). The entry variance was significant (<0.05) by LRT for TQND and TQD in bermudagrass, TQD in St. Augustinegrass and all traits in zoysiagrass (Figure 1, Table S6). The heritability estimate was high for TQD in bermudagrass, and moderate for all traits in zoysiagrass, TQD in St. Augustinegrass and TQND in bermudagrass and null for all others (Figure 1).

The variance of the entry $\times$ location interaction was significant (<0.05) for all traits in St. Augustinegrass and for %GC in bermudagrass, seashore paspalum and zoysiagrass (Table S6). The type-B genetic correlation across locations varied across traits: for %GC, it was lower than 0.5 for all species, except zoysiagrass (0.52); for TQD, it was lower than 0.5 in seashore paspalum and St. Augustinegrass and 1 for the other two species; and for TQND, it was 1 for all species except St. Augustinegrass (Figure 2). The entry $\times$ year interaction variance was non-null (<0.05) for TQND in bermudagrass and zoysiagrass, and TQD in St. Augustinegrass (Table S6). The type-B genetic correlation across years was higher than .5 for both TQD and TQND in all species except for TQD in seashore paspalum (0.00) (Figure 2). Except for seashore paspalum, estimates of type-B genetic correlation across years were higher (above 0.75) under TQD as compared to TQND (Figure 2).

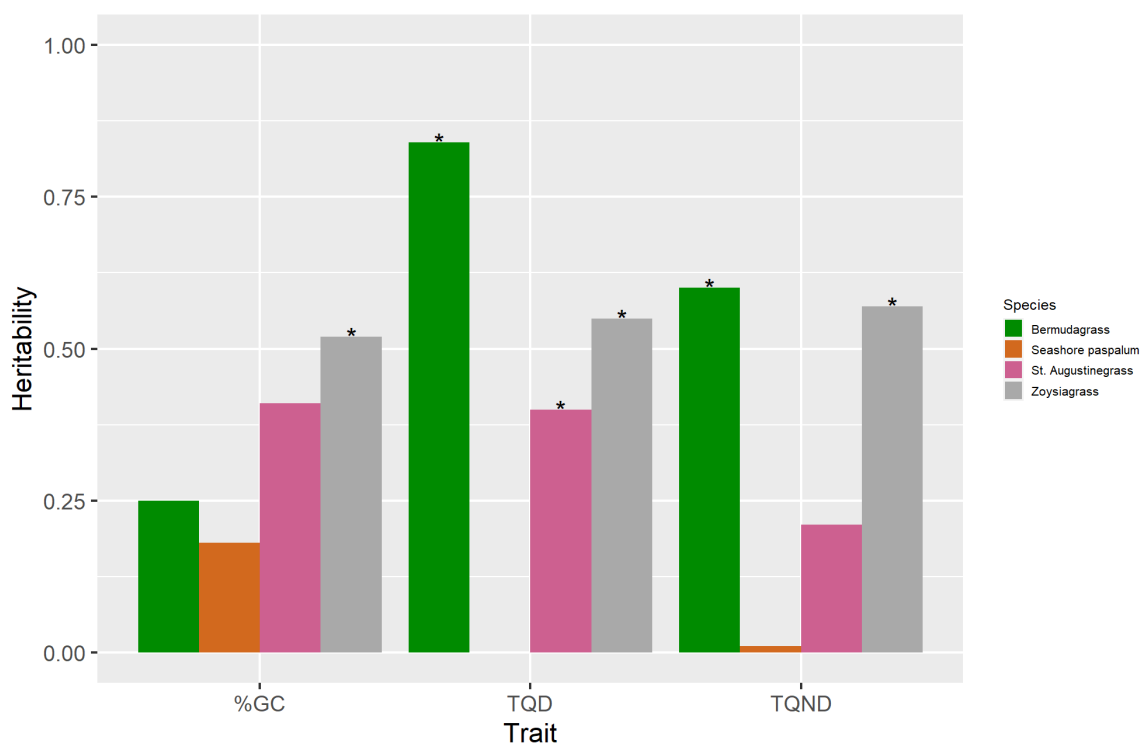


FIGURE 1 Generalized measures of heritability (H^2) for bermudagrass, St. Augustinegrass, seashore paspalum, and zoysiagrass field trials evaluated for per cent living ground cover (%GC), and turfgrass quality under drought (TQD) and non-drought (TQND) conditions in Citra, FL and Dallas, TX. *Entry variance significant by LRT at 0.05 probability level.

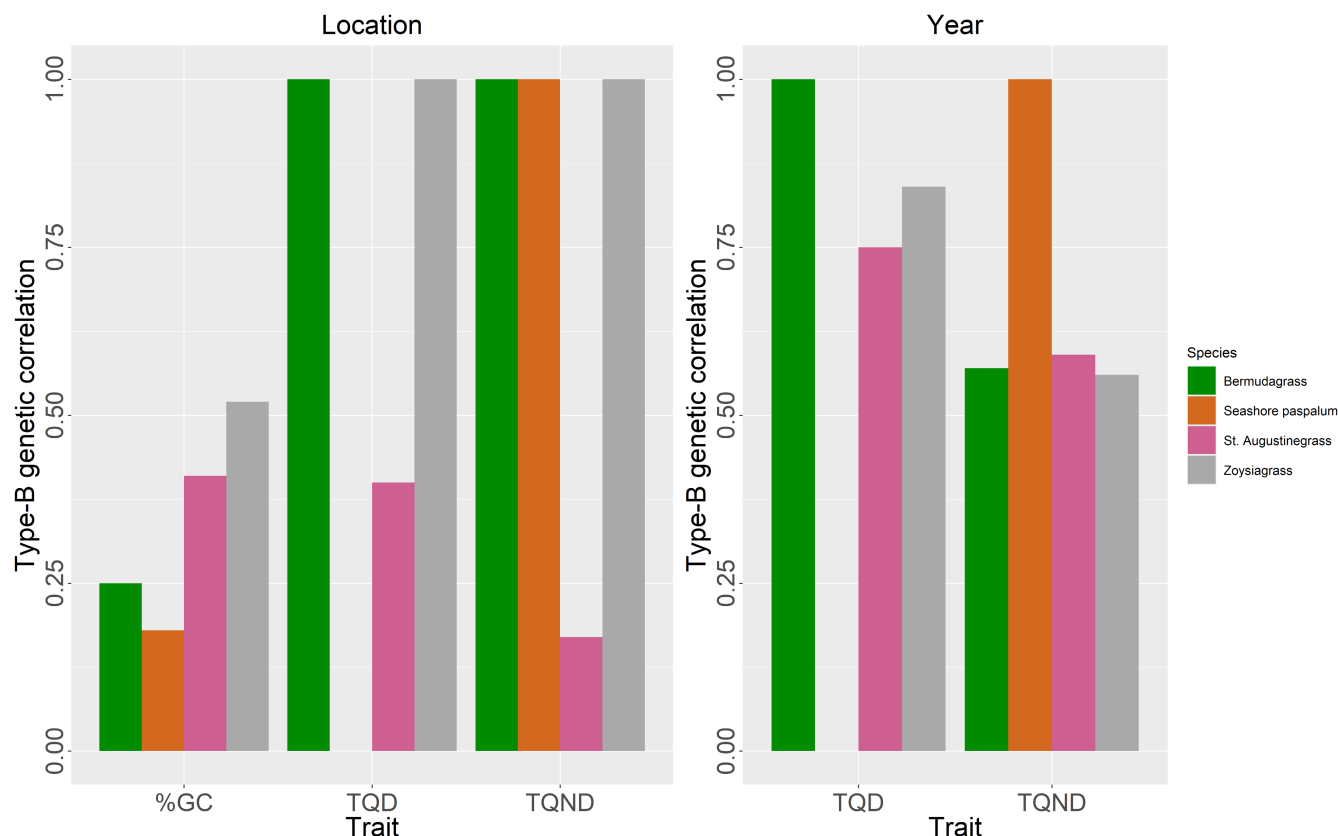


FIGURE 2 Type-B genetic correlation (r_g) across locations and years for bermudagrass, St. Augustinegrass, seashore paspalum and zoysiagrass field trials evaluated for per cent living ground cover (%GC) and turfgrass quality under drought (TQD) and non-drought (TQND) conditions in Citra, FL and Dallas, TX.

3.2 | Type-A genetic correlation between contrasting environments and genotype performance

In the single-environment analysis, the type-A genetic correlations between TQND and TQD were 0.62 for zoysiagrass and 0.86 for St. Augustinegrass at Citra, 0.70 for bermudagrass and 0.89 for seashore paspalum at Dallas, and 1 for all others. In the multi-location analysis, the estimate of this parameter was 1 for all species, except for St. Augustinegrass (0.91). For TQD, the commercial cultivar TifTuf was the top-ranked genotype for bermudagrass, whereas breeding lines DALSA1618 (Cobalt™) and DALZ1615 from TAMUS were the top-ranked genotypes for St. Augustinegrass and zoysiagrass, respectively (Figure 3). For TQND, TifB16112, TifB16118 and TifB16117 were the top-ranked bermudagrass genotypes, whereas DALZ1601, DALZ1603, DALZ1311 and DALZ1606 were the top-ranked lines for zoysiagrass (Figure 3). The bermudagrass breeding lines from UGA and St. Augustinegrass breeding lines from TAMUS had better performance for both TQND and TQD across locations. However, as mentioned above, the entry variance for TQND in St. Augustinegrass was null. Meanwhile, there was not a clear separation among zoysiagrass breeding lines from TAMUS and UF (Figure 3).

As mentioned above, the entry $\times$ location interaction was significant (<0.05) for %GC in bermudagrass, seashore paspalum and zoysiagrass (Table S6). The top-ranked genotypes were for bermudagrass, TifTuf and TifB16116 at Citra and OSU1337 at Dallas; for seashore paspalum, SeaStar at Citra and UGP228 at Dallas, and for zoysiagrass DALZ1606 at Citra and DALZ1601 at Dallas (Figure 4). Meanwhile, the entry $\times$ location variance component was significant (<0.05) for all traits in St. Augustinegrass. For %GC, the top-ranked lines were XSA11168 at Citra and XSA11231 at Dallas; for TQD, DALSA1618 (Cobalt™) and DALSA 1404 at Citra and Dallas, respectively, and for TQND, DALSA1618 (Cobalt™) and DALSA1623 at Citra and Dallas, respectively (Figure 4 and Figure 5). St. Augustinegrass breeding lines from TAMUS performed better than NCSU breeding lines for TQD and TQND at Dallas, whereas bermudagrass breeding lines from UGA performed better than OSU for %GC at Citra. There was not a clear difference between sources for other species by trait combinations.

In the multi-trait principal component analysis, the first two principal components explained 96, 92, 95 and 95% of the variation in bermudagrass, seashore paspalum, St. Augustinegrass and zoysiagrass, respectively (Figure 6). The correlation between traits can be visualized by the angle between two vectors (0°, high positive correlation; 90°, no correlation and 180° high negative correlation).



Therefore, TQD was highly correlated with TQND for all species, except seashore paspalum where these traits showed moderate correlation. However, both TQD and TQND were poorly correlated with %GC in all species. TifTuf and DALZ1601 performed better for all traits in bermudagrass and zoysiagrass, respectively. In seashore paspalum, UGP288 had superior performance for %GC, UGP113 for TQND and SeaDwarf for TQD. In St. Augustinegrass, DALSA1618 (Cobalt™) performed better for both TQD and TQND, whereas XSA11231 performed better for %GC.

The heritability and genetic variances varied between drought and non-drought conditions for TQ in bermudagrass, St. Augustinegrass and zoysiagrass, which indicated the presence of genetic variability among the evaluated genotypes. However, the estimates for those parameters were higher under drought in bermudagrass and St. Augustinegrass, whereas they were higher under non-drought in zoysiagrass. Given that some adaptive traits will be expressed

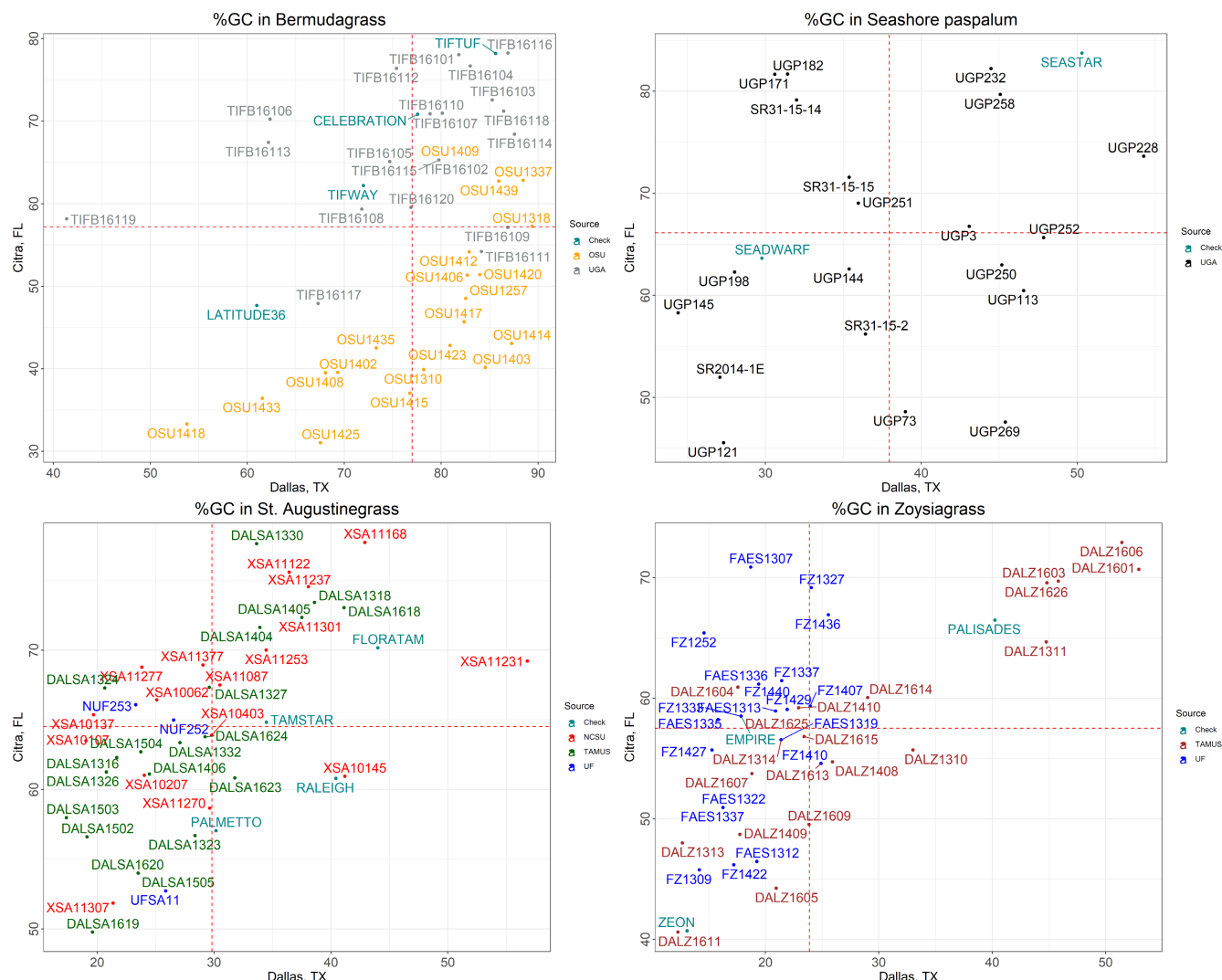


FIGURE 4 Predicted values of significant interaction between entry by location for per cent green ground cover (%GC) from bermudagrass, St. Augustinegrass, seashore paspalum and zoysiagrass genotypes evaluated in multi-environment field trials. The genotype sources were the North Carolina State University (NCSU), Oklahoma State University (OSU), University of Florida (UF), University of Georgia (UGA) and Texas A&M University System (TAMUS) breeding programs and commercial cultivars (check). The dashed line indicates the average for the trait.

only when exposed to a given environment (stress or non-stress), the magnitude of the heritability varies more as a function of the genetic variability of the population for the evaluated traits under a specific environment than as a function of the environment itself (Ceccarelli, 1989). In wheat, eight of 17 evaluated traits had higher heritability under drought stress compared to well-irrigated conditions, whereas four traits showed relatively similar heritability estimates in both environments (Sobhaninan et al., 2019). In a historical yield study in rice, eight trials out of 17 showed lower heritability values under drought conditions as compared to non-stress trials (Khanna et al., 2022). In *Urochloa* spp., Matias et al. (2016) found smaller heritability estimates for the majority of forage production traits during the dry season in interspecific *Urochloa* hybrids. However, in maize (*Zea mays* L.) hybrids, the mean generalized heritability was lower under well-watered conditions when compared with drought conditions for several traits including

grain yield (Dias et al., 2018). In general, smaller heritability estimates were observed under drought conditions in bermudagrass in earlier stages of the breeding process (Gouveia et al., 2020). In that study, while a higher residual variance was observed under drought, there was not a clear tendency for lower or higher genetic variance under those same conditions. The experimental lines evaluated in this study were among those evaluated in the bermudagrass study by Gouveia et al. (2020). Despite the lower number of entries in the present study, which directly influences the genetic variance, the higher number of replicates and larger plot size might have contributed to obtaining better estimates of those parameters.

In seashore paspalum, significant genetic variability was observed only for %GC in our study. Narrow genetic diversity, assessed with Amplified Fragment Length Polymorphism (AFLP) markers, was observed among commercial cultivars for this species (Chen

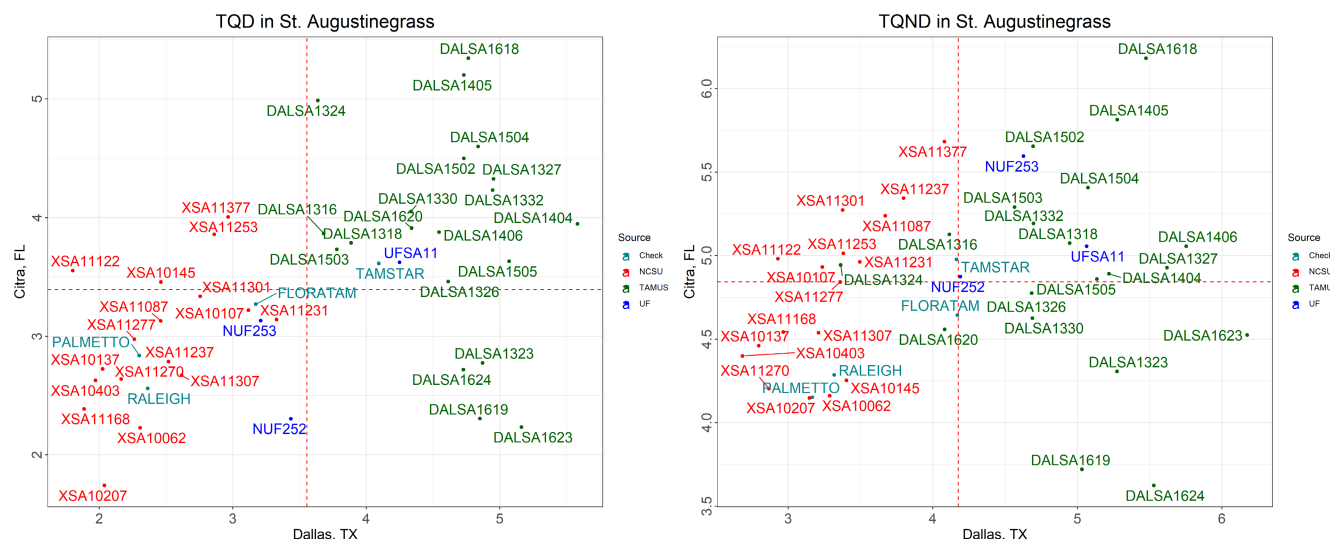


FIGURE 5 Predicted values of significant interaction between entry by location for turfgrass quality under drought (TQD) and turfgrass quality under non-drought (TQND) from St. Augustinegrass genotypes evaluated in multi-environment field trials. The genotype sources were the North Carolina State University (NCSU) and Texas A&M University System (TAMUS) breeding programs and commercial cultivars (check). The dashed line indicates the average for the trait.

et al., 2009). Low genetic variation was also observed in breeding lines evaluated for TQ (Gouveia, Rios, et al., 2021). However, Katuwal et al. (2022) observed differences in performance for drought resistance in seashore paspalum genotypes. In our study, evaluations were conducted under natural occurrence of drought, whereas that study was performed under a rainout shelter. Furthermore, in our study, the traits were evaluated using visual ratings, while the Katuwal et al. (2022) study used digital image analysis, which may have contributed to obtaining more accurate phenotypes. Therefore, integrating the use of high-throughput phenotyping technologies in breeding programs will be helpful for improving phenotyping accuracy and consequently increase the selection efficiency for drought resistance in turfgrass breeding (Rockstad et al., 2022; Wang et al., 2022; Zhang et al., 2019).

The level of GEI impacts breeders' decisions on the number of locations to evaluate their genotypes in the target environments. High entry $\times$ location interaction was observed for %GC in all species. Additionally, GEI was also high for TQD and TQND in St. Augustinegrass. Graham et al. (2022) also found high GEI for %GC in St. Augustinegrass at target environments in North Carolina, whereas no genotype $\times$ location interaction was observed for other evaluated traits, including TQ, in that study. Unlike our study, Gouveia, Rios, et al. (2021) found that the GEI was lower for TQ in St. Augustinegrass than in bermudagrass, seashore paspalum and zoysiagrass at eight locations across the Southern US. A different study at target environments in Florida, showed that GEI was slightly more pronounced for TQ than for %GC in St. Augustinegrass. However, all locations were grouped in the same mega-environment for TQ, whereas three mega-environments were formed for %GC (Pereira et al., 2022). Time influences the gain from selection (Eberhart, 1970) and it is the most powerful parameter for increasing genetic gains in a breeding program

(Cobb et al., 2019). This is especially true for perennial crops, for which the cycle of selection can take several years. In our study, lower entry $\times$ year interaction (type-B genetic correlation above 0.75) was observed for TQD than for TQND in bermudagrass, St. Augustinegrass and zoysiagrass, suggesting that only 1 year of evaluation under drought might be sufficient to identify superior genotypes. If corroborated, this approach would increase genetic gains and save time and resources for breeding programs. Therefore, studies to quantify rank changes between single-year and combined analyses, and repeatability coefficients (Figueiredo et al., 2019) in turfgrasses will help to verify the efficiency of a one-year evaluation strategy.

High correlation between traits or between stress and non-stress environments is desirable for indirect selection. In our study, low GEI between drought and non-drought (i.e. high type-A genetic correlation) was observed for TQ across species indicating that it is possible to perform indirect selection for these traits. Gouveia et al. (2020) found the type-A genetic correlation to range from low (0.17) to high (1) across bermudagrass nurseries in a single-location, but similarly to our study, the estimates were high in multi-location trials. A faster establishment rate may lead to superior TQD if it is highly correlated with fast root development and deeper roots, which showed to be important to maintain turfgrass quality later during drought stress (Boeri et al., 2020). A high correlation between %GC and TQD would be desirable as it would enable early selection of drought-resistant genotypes in a breeding program. However, in our study, %GC was not a good predictor of TQD and TQND performance across all species because their correlation was low. Conversely, %GC was positively correlated (0.30) with TQD in St. Augustinegrass (Graham et al., 2022). Additionally, high genetic correlations between drought resistance and traits evaluated before the drought stress (TQ (0.62), Digital

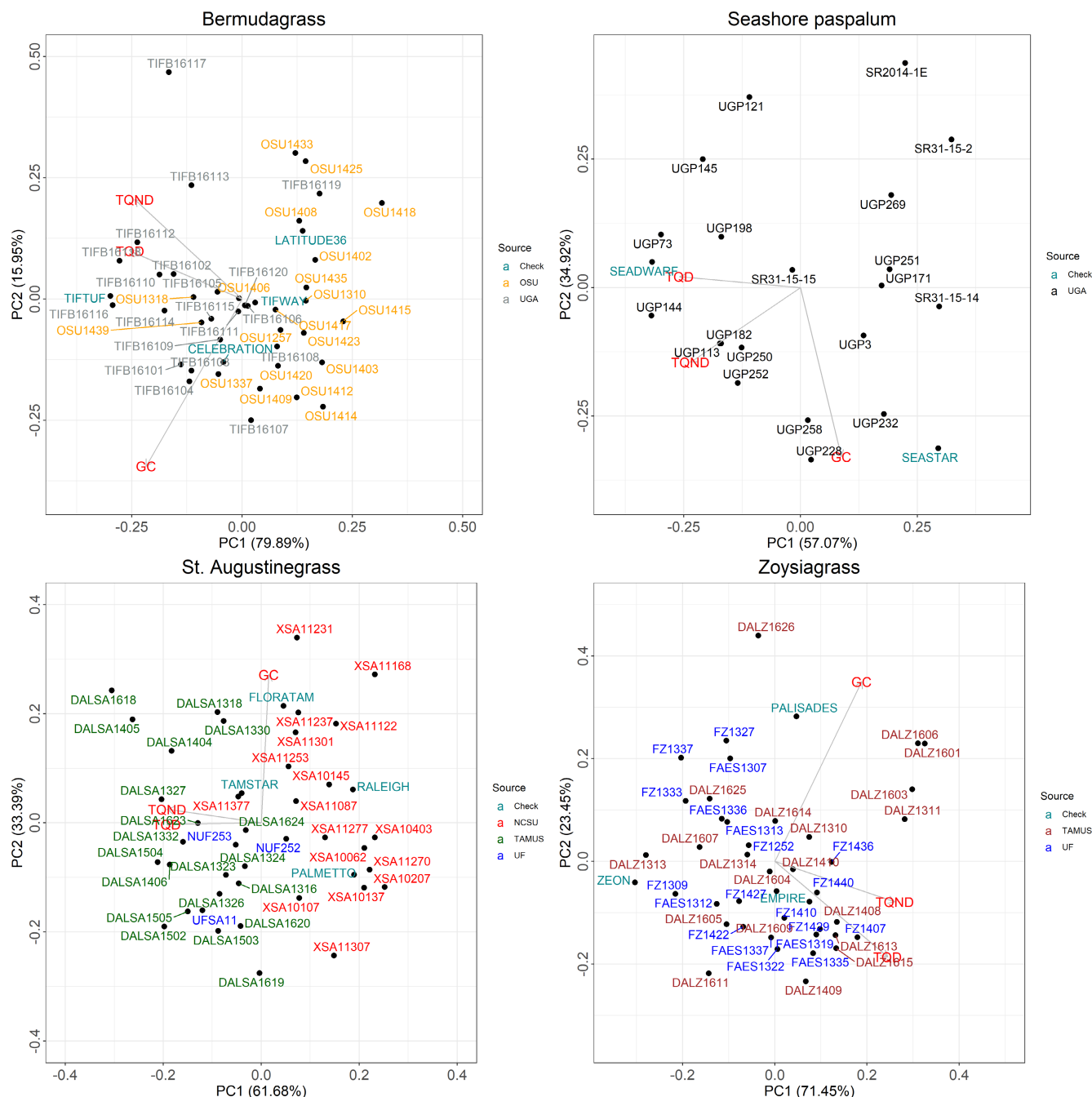


FIGURE 6 Multi-trait principal component analysis using the predicted values of entry for per cent living ground cover (%GC) and turfgrass quality under drought (TQD) and non-drought (TQND) conditions from bermudagrass, St. Augustinegrass, seashore paspalum and zoysiagrass genotypes evaluated in multi-environment field trials. The genotype sources were the North Carolina State University (NCSU), Oklahoma State University (OSU), University of Florida (UF), University of Georgia (UGA) and Texas A&M University System (TAMUS) breeding programs and commercial cultivars (check).

Green Colour Index (0.65), %GC (0.77) and Normalized Difference Vegetation Index (0.76)) were observed in the same four species under a rainout shelter (Katuwal et al., 2022). Currently, there are few studies in turfgrass that have evaluated the correlation between %GC, TQ under drought and non-drought. Thus, more studies are needed to confirm the relationships among them.

Plant breeding is a continuous process to develop superior cultivars for target traits (Bhargava & Srivastava, 2019). In our study,

there were breeding lines that performed better than the commercial cultivars in all species with the exception of bermudagrass, for which the commercial cultivar TifTuf was the top-ranked genotype for all traits across locations. Bermudagrass breeding lines from UGA and St. Augustinegrass breeding lines from TAMUS performed better across locations for both TQND and TQD, whereas there was not a clear separation between sources for all traits in zoysiagrass and for %GC in St. Augustinegrass. The

NCSU and OSU breeding programs are located in the turfgrass transition zone in the United States and thus a heavy emphasis of those programs is developing freeze-tolerant turfgrass cultivars (Dunne et al., 2019; Fontanier et al., 2020; Graham et al., 2022; Kimball et al., 2016). In a previous study, no specific adaptability was observed for TQ among OSU and NCSU breeding lines for the locations where these breeding programs are based at (Gouveia, Rios, et al., 2021). Additionally, there was superior performance of OSU breeding lines at Texas and Florida, and NCSU breeding lines at Florida in some nurseries, which suggests these programs can successfully develop superior cultivars for other locations in the southeastern US. In our study, there was not a clear separation of performance between sources for TQD and TQND in St. Augustinegrass at Citra and for %GC in bermudagrass at Dallas (Figure 5), which also indicates that the NCSU and OSU breeding program's efforts to continue to improve these species are important to get superior drought-resistant cultivars for some target environments in the southern US.

Our results showed that because of the high correlation identified between TQD and TQND, and the low GEI between these contrasting periods, indirect selection for TQD might be possible under non-drought conditions for bermudagrass, St. Augustinegrass and zoysiagrass. However, the correlation between TQD and TQND with %GC showed that the latter trait is not a good predictor of drought resistance or TQ. Across locations, the GEI was high for all traits in St. Augustinegrass and for %GC in the other species. However, GEI was lower for TQD in bermudagrass, St. Augustinegrass and zoysiagrass across years. Therefore, our results indicate that only 1 year of drought evaluations is effective to select drought-resistant genotypes for those species in multi-location trials, which can save resources in a breeding program. In addition, several zoysiagrass breeding lines (including DALZ1615, FZ1429, FZ1407 and DALZ1311) and St. Augustinegrass breeding lines (including DALSA1618 (Cobalt™), DALSA1405, DALSA1404 and DALSA1504) performed better (Figure S2) than all commercial cultivars for TQD, which demonstrates the importance and efficiency of the partnership between NCSU, OSU, UF, UGA and TAMUS to develop drought-resistant warm-season turfgrass cultivars for the southern US.

AUTHOR CONTRIBUTIONS

Beatriz Tome Gouveia: Writing – original draft; formal analysis; data curation; software; methodology; visualization; writing – review and editing; investigation. **Ambika Chandra:** Writing – review and editing; funding acquisition; resources. **Kevin Kenworthy:** Writing – review and editing; funding acquisition; resources; project administration. **Paul L. Raymer:** Writing – review and editing; funding acquisition; resources. **Brian M. Schwartz:** Writing – review and editing; funding acquisition; resources. **Yanqi Q. Wu:** Writing – review and editing; funding acquisition; resources. **Susana Milla-Lewis:** Writing – review and editing; funding acquisition; resources; supervision; conceptualization; project administration; validation.

ACKNOWLEDGEMENTS

Funding for this project was provided by a Specialty Crop Research Initiative grant [2015-51181-24291] from the USDA National Institute for Food and Agriculture.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data sets generated during the current study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Tome Gouveia, B., Chandra, A., Kenworthy, K. E., Raymer, P. L., Schwartz, B. M., Wu, Y. Q., & Milla-Lewis, S. R. (2024). Warm-season turfgrass species genotype-by-environment interaction for turfgrass quality under drought. *Journal of Agronomy and Crop Science*, 210, e12681. <https://doi.org/10.1111/jac.12681>