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Genetic gains and genotype-by-environment interaction in turf bermudagrass drought resistance improvement in the southern United States

Shuhao Yu[1] | **Beatriz Tome Gouveia**[2] | **Jing Zhang**[3] | **Yanqi Wu**[4] | **Brian R. Schwartz**[5] | **Susana R. Milla-Lewis**[2] | **Kevin E. Kenworthy**[6] | **Bryan J. Unruh**[7] | **Ambika Chandra**[8] | **Paul L. Raymer**[9] | **Marta T. Pudzianowska**[10] | **James H. Baird**[11] | **Esdras Melgar Carbajal**[2] | **Mingying Xiang**[1] | **Justin Q. Moss**[1] | **Ryan Earp**[4]

[1]Department of Horticulture and Landscape Architecture, Oklahoma State University, Stillwater, Oklahoma, USA

[2]Department of Crop and Soil Sciences, North Carolina State University, Raleigh, North Carolina, USA

[3]Department of Horticultural Science, North Carolina State University, Raleigh, North Carolina, USA

[4]Department of Plant and Soil Sciences, Oklahoma State University, Stillwater, Oklahoma, USA

[5]Department of Crop and Soil Sciences, University of Georgia, Tifton, Georgia, USA

[6]Agronomy Department, University of Florida, Gainesville, Florida, USA

[7]Environmental Horticulture Department, University of Florida, West Florida Research and Education Center, Jay, Florida, USA

[8]Department of Soil and Crop Sciences, Texas A&M AgriLife Research-Dallas, Dallas, Texas, USA

[9]Department of Crop and Soil Sciences, University of Georgia, Griffin Campus, Griffin, Georgia, USA

[10]Department of Plant and Soil Sciences, Mississippi State University, Mississippi State, Mississippi, USA

[11]Department of Botany and Plant Sciences, University of California Riverside, Riverside, California, USA

Correspondence

Shuhao Yu, Department of Horticulture and Landscape Architecture, Oklahoma State University, 320G Ag Hall, Stillwater, OK 74078, USA.

Email: shuhao.yu@okstate.edu

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Abstract

Breeding bermudagrass (*Cynodon* spp.) involves creating progeny combining multiple desired traits from hybridization and ensuring their adaptation and performance to various environments through rigorous testing. Turfgrass breeding programs in the southern United States collaborated to breed new bermudagrass lines for drought resistance. Thus, the objectives of this study were to evaluate advanced bermudagrass lines and to characterize their genetic gain in performance traits, reliability, genotype-by-environment interaction (GEI), and stability. The study, encompassing 34 advanced lines and three standard cultivars planted in randomized complete block designs with three replications, was carried out at eight locations across the

Abbreviations: BLUP, best unbiased linear prediction; ER, establishment rate; FCR, fall color retention; GEI, genotype-by-environment interaction; GGE, genotype plus genotype-by-environment interaction; GLI, green leaf index; IP, inflorescence prolificacy; ME, mega-environment; NCSU, North Carolina State University; NDVI, normalized difference vegetation index; NTEP, National Turfgrass Evaluation Program; OSU, Oklahoma State University; PGC, percent green cover; RGB, red, green, and blue; RP, recovery potential; SG, spring green-up; TPI, turf performance index; TQ, turfgrass quality; UAS, unmanned aircraft system; UF, University of Florida; UGA, University of Georgia.

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southern United States from 2020 to 2023. Experimental lines OSU2073, OSU2081, OSU2082, TifB20201, and TifB20205 showed improved drought response relative to the drought resistant cultivar TifTuf with significant genetic gain in the mega-environment (a group of locations that share similar environment conditions in which a crop has consistent performance across them) of Dallas, TX, and Stillwater, OK. Substantial GEIs were observed under drought stress across the southern United States. This study highlights the continuous genetic gain made in breeding efforts to improve drought resistance of bermudagrass and identifies new cultivar candidates for conserving irrigation water to the turf industry.

Plain Language Summary

Breeding and selecting drought-resistant bermudagrass is essential due to the increasing scarcity of water for irrigation. This study evaluated 34 advanced bermudagrass breeding lines and three standard cultivars across eight locations from 2020 to 2023 to assess drought resistance and performance. Five experimental lines—OSU2073, OSU2081, OSU2082, TifB20201, and TifB20205—showed better drought resistance than the widely used TifTuf, a leading drought resistant cultivar. These lines also performed reliably in key locations like Dallas, TX, and Stillwater, OK, showing progress in breeding efforts. This research highlights ongoing improvements in bermudagrass drought resistance, offering new bermudagrass options for water-efficient turf management in lawns, sports fields, and landscapes.

1 | INTRODUCTION

Bermudagrasses (*Cynodon* spp.) are warm-season perennial sod-forming grass species widely distributed in tropical and subtropical regions in the world (Beard, 1973; Taliaferro et al., 2004). There is enormous morphological variation within and among bermudagrass species, ranging from small, fine-textured plants to large, leafy robust plants that suit different purposes, such as turf, pastures, and soil stabilization, etc. (Harlan & de Wet, 1969; Taliaferro et al., 2004). Common bermudagrass [*Cynodon dactylon* (L.) Pers.] and interspecific hybrid bermudagrass [*Cynodon dactylon* (L.) Pers. × *Cynodon transvaalensis* Burtt-Davy] are known for their high turfgrass quality (TQ), fast establishment rate (ER), quick recovery from wear damage, and tolerance to heat and drought stresses (Beard, 1973). These attributes make them highly sought after as turfgrass on residential lawns, golf courses, and athletic fields in the southern and transitional climatic regions of the United States. For example, bermudagrass is the dominant species used on golf courses in the United States (Shaddox et al., 2023). It was estimated that bermudagrass is grown on ~20–25 million ha (for turf, forage, pasture, and soil erosion control uses), providing substantial economic impact and ecological service (Taliaferro et al., 2004).

The wide use of bermudagrass has been achieved primarily through its genetic improvement and associated management practices. Programmatic turf bermudagrass breeding started in 1946 at the U.S. Department of Agriculture Agricultural Research Service (USDA-ARS) Coastal Plain Experiment Station in Tifton, GA (Burton, 1974). Since then, breeding programs have released a number of cultivars (Baxter & Schwartz, 2018; Wu et al., 2013, 2014, 2020). With rapid urbanization and frequent drought conditions compounded with warming climates in recent decades, previously non-irrigated lands have been converted to irrigated lawns and landscapes, which has exacerbated water scarcity in many locations, especially in the southwestern United States. Turfgrass drought resistance is one of the most valued traits for homeowners in Texas, Florida, Georgia, Oklahoma, and North Carolina (Ghimire et al., 2016). With full adoption, drought resistant turfgrass cultivars would conserve freshwater and generate up to $142.4 million of total economic output, triggering the development of drought resistant bermudagrass cultivars (Chung et al., 2018).

In the past decade, the turfgrass breeding programs at six universities, including Oklahoma State University (OSU), University of Georgia (UGA), North Carolina State University (NCSU), Texas A&M University System, University of Florida (UF), and University of California–Riverside collaborated to develop new bermudagrass cultivars with improved drought resistance and turf performance. In 2014, UGA and the USDA-ARS released 'DT-1' (commercial name TifTuf), which exhibited improved drought resistance and high TQ compared to Tifway (Schwartz et al., 2018). Later, OSU released 'OKC1131' (Tahoma 31) due to its improved water use efficiency, freeze tolerance, and high TQ (Amgain et al., 2018; Wu et al., 2020). These breeding programs continued their collaborative efforts with the major aim to further improve drought resistance. In addition, breeders also strive to combine multiple favorable traits into new bermudagrass cultivars. Freeze tolerance, a major factor contributing to winter survivability, is critical for bermudagrass to adapt to transitional climatic regions (Anderson & Martin, 2002). Chilling temperature (2˚C–10˚C) tolerance (evaluated as fall color retention [FCR]) is an important trait for bermudagrass use in the southern United States, where an extended green period is desirable (Fontanier et al., 2020). Fast ER is a critical trait for sod production since fast growing cultivars can shorten the interval between two harvests and recover faster from damages. Turfgrass users, especially golf course superintendents prefer cultivars with few or no seedheads (Kane & Miller, 2003). Seedheads diminish aesthetic turf qualities and playability and divert energy from vegetative growth to reproductive development (Kane & Miller, 2003). Frequent mowing is needed to remove seedheads, which increases management costs.

Unlike major food crops, bermudagrass is a perennial crop and its cultivars tend to be marketed and produced across a much larger geographic area. Therefore, characterization of genotype-by-environment interaction (GEI) plays a critical role in the identification of testing environments and the selection of germplasm for varietal release (de Leon et al., 2016). It would be ideal if new cultivars have both high turf performance traits and stability across the target environments (Gouveia et al., 2020, 2021, 2024; Windhausen et al., 2012; Yan, 2015; Yan & Tinker, 2006; Yan et al., 2000). In this study, we evaluated drought response and turf performance of new advanced lines from OSU, UGA, UF, and NCSU at eight locations in six southern states. Accordingly, the objectives of this study were to (1) quantify the genetic variability and GEI of drought response and performance traits and (2) identify high performing genotypes under drought and estimate genetic gains achieved by the bermudagrass breeding programs.

Core Ideas

- New breeding lines exhibited improved drought resistance, high turfgrass quality, and stable performance.
- Genotype-by-environment interaction was significant for drought performance in the southern United States.
- The south-central United States is a unique region for evaluating drought resistance.

2 | MATERIALS AND METHODS

2.1 | Plant materials and field experiments

Thirty-four bermudagrass experimental lines (Table 1) from OSU, UGA, UF, and NCSU and three standard cultivars DT-1 (marketed as TifTuf), Tifway, and OKC1131 (Tahoma 31) were planted at eight locations, including Stillwater, OK; Dallas, TX; Riverside, CA; Jackson Springs, NC; Griffin and Tifton, GA; and Jay and Citra, FL, in the summer of 2020 (Table S1). Weather data (average monthly maximum and minimum temperatures, monthly accumulated precipitation, and average monthly relative humidity) from 2020 to 2023 are presented in Figures S1 and S2. Weather data were obtained using the R packages "nasapower" (Sparks, 2018) modified from Gouveia et al. (2025). The experimental design for each location was a randomized complete block design with three replications. Six plugs (10.2 cm × 10.2 cm × 5.0 cm) cultivated in greenhouse media (BM2, Berger) were transplanted into an approximately 1.5 m by 1.5 m plot with 0.2 m alleys between neighboring plots. Detailed management information for fertilization, mowing, weed management, and irrigation is reported in Table S1. From 2021 to 2023, plots were subjected to slightly varied management practices according to the bermudagrass management recommendation in each state (Table S1). No supplementary irrigation was provided during summer to induce drought periods. In fall, irrigation was resumed to foster injury recovery post drought conditions.

2.2 | Data collection

One month after transplanting, percent green plot cover was used to evaluate ER. This trait was evaluated once from unmanned aircraft systems (UAS) imagery at all locations, except for Riverside, CA, where it was assessed visually due to the absence of UAS and Stillwater, OK, where it was quantified using the smartphone application Canopeo (Patrignani & Ochsner, 2015). In the spring of 2021, 2022, and 2023, spring green-up (SG) was visually rated monthly on a 1–9 scale according to the National Turfgrass Evaluation Program (NTEP) protocol (Morris & Shearman, 2000). Inflorescence prolificacy (IP) was visually rated once a year before drought on a 1–9 scale, where 9 = *most abundant seedheads* and

TABLE 1 Bermudagrass entries evaluated at eight locations from 2020 to 2023.

Entry	Source	Entry	Source	Entry	Source	Entry	Source
FB1628	UF	OSU2026	OSU	OSU2081	OSU	TifB20204	UGA
FB1630	UF	OSU2034	OSU	OSU2082	OSU	TifB20205	UGA
FB1633	UF	OSU2035	OSU	OSU2088	OSU	TifB20206	UGA
FB2001	UF	OSU2037	OSU	OSU2094	OSU	TifB20207	UGA
FB2002	UF	OSU2039	OSU	OSU2101	OSU	TifB20208	UGA
NCWIN10F	NCSU	OSU2043	OSU	OSU2102	OSU	TifTuf	Standard
OSU2015	OSU	OSU2066	OSU	Tahoma 31	Standard	Tifway	Standard
OSU2018	OSU	OSU2073	OSU	TifB20201	UGA		
OSU2021	OSU	OSU2074	OSU	TifB20202	UGA		
OSU2022	OSU	OSU2075	OSU	TifB20203	UGA		

Abbreviations: NCSU, North Carolina State University; OSU, Oklahoma State University; UF, University of Florida; UGA, University of Georgia.

1 = *no seedheads*. TQ (1 to 9 scale, 1 = *completely dead or dormant turf*, 9 = *outstanding turf*, and 6 = *acceptable quality turf*) was collected monthly under non-drought conditions and weekly under drought conditions. During the drought recovery phase, recovery potential (RP) was visually rated on a 1–9 scale, where 9 = *full recovery* and 1 = *dead or dormant*. FCR was visually rated monthly before dormant on a 1–9 scale (1 = *brown color* and 9 = *full green*) in the fall of 2021 and 2022. All visual evaluations were performed according to the NTEP protocols (Morris & Shearman, 2000). Detailed measurement dates for all traits assessed at each location are provided in Table S2.

To evaluate turf performance under drought and non-drought conditions, UAS were used to collect RGB (red, green, and blue) and multispectral images. The UAS flights were conducted at 75% side and front overlap with a flight altitude of 40 m. The flight times were 2 h within solar noon. The cameras, UAS platforms, and flight software for each location are listed in Table S3. Images from each location were uploaded to a server located at the UGA-Tifton campus. The workflow for image processing was adapted from a previous study of turfgrass field trials (Zhang et al., 2019). Briefly, RGB images were processed and stitched in Pix4Dmapper Pro 4.2.27 (Pix4D SA) to generate an RGB orthomosaic using the standard template of “Ag RGB.” Multispectral images were processed using the same software and template of “Ag Multispectral,” resulting in maps of red and NIR bands. These georeferenced orthomosaics were exported in a TIFF format for further analysis. From RGB orthomosaic, green leaf index (GLI) was computed with normalized values for red (R), green (G), and blue (B) bands from the digital image using Equation (1). Normalized difference vegetation index (NDVI) was computed from red and near infrared (NIR) bands using Equation 2.

$$\mathrm{GLI} = (2g - b - r) / (2g + b + r)\,, \tag{1}$$

where $g = \mathrm{G}/(\mathrm{R} + \mathrm{G} + \mathrm{B})$, $b = \mathrm{B}/(\mathrm{R} + \mathrm{G} + \mathrm{B})$, and $r = \mathrm{R}/(\mathrm{R} + \mathrm{G} + \mathrm{B})$,

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{red}) / (\mathrm{NIR} + \mathrm{red})\,. \tag{2}$$

Shape files for each location were created in ArcMap version 10.4.1 (Esri), outlining individual plot boundaries with polygons. The size of the polygons varied slightly in each location to capture the majority of the established plot while excluding a margin (Table S3). Averages of GLI and NDVI for each plot were extracted within each polygon in a Python script with packages *rasterio* (Gillies, 2019), *geopandas*, and *gdal*. The percent green cover (PGC) was calculated as the number of pixels with values larger than the threshold value of GLI divided by the total number of pixels within a plot. The GLI threshold value was determined and adjusted through trial and error in each location due to the different sensors used.

2.3 | Statistical analyses

Analysis of variance (ANOVA) for all traits was conducted using the MIXED procedure within SAS 9.4 (SAS Institute). The analysis was conducted separately for each trait under drought and non-drought conditions. The annual mean value of all data collected for each trait under conditions without drought was used for data analysis. Under drought conditions, means of the last two TQ, PGC, and NDVI (showing more drought symptoms; Figure S3) in each year were used for data analysis at each location for better drought response separations. Variance components were estimated using Type III method of moments estimation. Entry, location, and year were considered random effects because the information on trait performance of this bermudagrass set in each location was unknown and year and rating date were not chosen based on expected environmental conditions (Yu et al., 2022). The reliability (i^2) (Bernardo, 2002) for each trait was calculated by the Equation (3) adopted from Hallauer (1970).

$$i^2 = \sigma^2{}_G / \left(\sigma^2{}_G + \sigma^2{}_{GY}/Y + \sigma^2{}_{GL}/L + \sigma^2{}_{GLY}/LY + \sigma^2{}_E/RLY \right), \quad (3)$$

where $\sigma^2{}_G$ is the variance of genotype, $\sigma^2{}_{GY}$ is the variance of interaction between genotype and year, $\sigma^2{}_{GL}$ is the variance of interaction between genotype and location, $\sigma^2{}_{GLY}$ is the variance of interaction between genotype, location and year, $\sigma^2{}_E$ is the error variance, R is the number of replications, Y is the number of years, and L is the number of locations. To summarize line performance, the turf performance index (TPI) was calculated as the number of times each entry appeared in the top statistical group for each trait in each location and year once significant genotype-by-location and genotype-by-year interactions were identified (Engelke et al., 1995). The identification of mega-environment (MEs) and the ranking of genotypes based on mean and stability was realized through genotype plus genotype-by-environment interaction (GGE) biplot analysis and the biplots were created using the R package *metan* (Olivoto & Lucio, 2020). Under drought conditions, mean values of the traits collected on the last one to two dates were used for data analysis due to varying weather conditions (Figures S1 and S2), duration of drought, and number of evaluations across locations. For traits collected without drought stress, the mean value of all collected data for a trait was used for analysis. The best linear unbiased prediction (BLUP) values were estimated for all phenotypic data using the linear mixed model described in Equation (4):

$$\mathbf{y} = \mu\mathbf{1} + \mathbf{Z1u} + \mathbf{e}, \quad (4)$$

where $\mathbf{y}$ is the vector of phenotypic values; μ is the overall mean; $\mathbf{1}$ is the vector of ones; $\mathbf{Z}$ is the incidence matrices for random effects; $\mathbf{u}$ is the vector of random effects of location, entry, year, blocks nested within location, interaction between location and year, interaction between entry and location, interaction between entry and year, and interaction between entry, location, and year; and $\mathbf{e}$ is the random vector of errors. The percentage relative genetic gain was calculated by dividing the difference between the BLUP mean of the selected top 10% entries and BLUP mean of the checks, by the genotypic predicted value of the checks. The genetic gain bar chart was created using the R package *ggplot2* (Wickham, 2016) following the format of chart generated by Gouveia et al. (2025). Pearson correlation coefficients for measurements were visualized in R (v 4.3.1) using the package *metan* (Olivoto & Lucio, 2020).

3 | RESULTS

3.1 | ANOVA and reliability

The ANOVA and variance components for each trait under drought and non-drought conditions are given in Table 2 and Table S4, respectively. Under drought conditions, highly significant ($p < 0.0001$) genotype effects existed for all traits. All interactions involved with genotype were highly significant ($p < 0.0001$) for all traits except for the genotype-by-year interaction for TQ and PGC. The reliability estimates for traits collected under drought ranged from $i^2 = 0.84$ (PGC) to $i^2 = 0.90$ (TQ). For traits collected without drought, significant ($p < 0.05$) genotype effects were found for all traits. Except for SG, IP, and RP, significant genotype-by-year interactions were found for all traits. The genotype-by-location interaction was not significant for ER, but significant for all other traits. The reliability estimates for the traits without drought ranged from $i^2 = 0.50$ (NDVI) to $i^2 = 0.89$ (PGC).

3.2 | Genotype-by-environment interactions

For traits collected under drought conditions, the GEI for TQ was visualized in Figure 1a. Two MEs were observed. Dallas and Stillwater were in one ME and the rest locations were in another. The first two components explained 84.0% of the total phenotypic variance. Experimental line OSU2073 was the top performer in Dallas and Stillwater ME, followed by OSU2081. TifB20201 was the top performer in another ME, followed by TifTuf. The GEI for PGC showed three MEs (Figure 1b). Griffin was a separate ME while Dallas and Stillwater were grouped in one ME and the rest locations in another. The first two components of PGC explained 84.3% of the total phenotypic variance. The best performer for the ME of Dallas and Stillwater was OSU2073. TifTuf performed well in the ME of Citra, Tifton, and Jackson Springs. The best performer for the Griffin ME was FB1628. Two MEs were observed for NDVI (Figure 1c). Like TQ, Dallas and Stillwater were grouped in an ME while the rest locations were in another. OSU2082 was the best performer for the ME of Dallas and Stillwater while TifTuf was the best performer for another ME. Consistent for all traits collected under drought conditions, Stillwater was the location that showed the largest variation among genotypes.

For turfgrass performance under non-drought conditions, the GEI was identified for all traits except for PGC (Figure S4), which resulted in the separation of the target environments into two or more MEs. For TQ, the first two components explained 81.1% of the phenotypic variance (Figure S4A). Besides Stillwater, all locations were grouped in one ME. Tahoma 31 and TifB20208 were best performers

TABLE 2 Analysis of variance and variance component estimates of turfgrass quality (TQ), percent green cover (PGC), and normalized difference vegetation index (NDVI) under drought conditions.

	TQ[a]		PGC[b]		NDVI[c]	
	Drought		Drought		Drought	
Source of variation	*p* > *F*	Variance component	*p* > *F*	Variance component	*p* > *F*	Variance component
Loc	0.4482		0.1667		<.0001	
Year	0.3007		0.6387		NA	
Loc(Rep)	<0.0001		<0.0001		<.0001	
Loc × Year	<0.0001		<0.0001		NA	
Genotype	<0.0001	0.6232	<0.0001	288.4000	<.0001	0.0060
Genotype × Year	0.0011	0.0411	0.048	34.6184	NA	NA
Genotype × Loc	<0.0001	0.3133	<0.0001	193.9600	<.0001	0.0045
Genotype × Loc × Year	<0.0001	0.1265	<0.0001	120.7800	NA	NA
Residual		0.5590		197.4900		0.0029
Reliability (i^2)		0.90		0.84		0.85

Abbreviation Loc, location.

[a]TQ was visually rated on a scale of 1–9, where 1 = *lowest quality* and 9 = *excellent quality*.

[b]PGC measured by unmanned aircraft systems (UAS) red, green, and blue (RGB) images calculating the percent live cover on a scale of 0–100 where 0 = *no green cover* and 100 = *all the leaves are green*.

[c]NDVI measured by UAS multispectral images on a scale of 0–1, where 0 = *no green cover* and 1 = *complete green cover*.

in the Stillwater ME, and TifB20205 and TifTuf were best performers in the other ME. The GEI for SG can be visualized in Figure S4B. Three MEs were formed. Riverside was classified in a distinct ME. Citra, Stillwater, and Jackson Springs formed an ME and the rest locations formed the third ME. The best performer of Citra, Stillwater, and Jackson Springs ME was Tahoma 31. TifB20205 was the best performer at the Riverside ME. The best performer of the Jay, Dallas, Griffin, and Tifton ME was TifTuf. The GEI for ER can be visualized in Figure S4C. The first two components explained 81.2% of the phenotypic variation. Griffin was included in a separate ME in which the fastest establishing genotype was TifB20205. The other seven locations formed an ME and TifTuf was the genotype with the fastest ER. For FCR, the first two components explained 79.9% of the phenotypic variation and three MEs were observed (Figure S4D). The first ME included Riverside, Dallas, and Citra, where TifTuf was the best performer. The second one included Tifton, Jay, and Jackson Springs, where the best performer was TifB20205. Stillwater was in its own ME where TifB20208 was the best performer. Three MEs were observed for IP and OSU2034 was the best-performing genotype in the ME of Riverside, Dallas, Jay, and Tifton (Figure S4E). Stillwater and Griffin were in two distinct MEs, where the best performer was OSU2039 at Stillwater and the best performer for Griffin was OSU2034. GEI for RP from drought injuries can be visualized in Figure S4F. Jay, Citra, and Jackson Springs were in distinct MEs. Riverside, Dallas, and Stillwater were grouped into an ME where TifB20201 and TifTuf were best performers. For PGC and NDVI collected from UAS, GEIs were visualized in Figure S4G,H.

3.3 | Turf performance index, stability, and genetic gain

Due to the significant (p < 0.0001) genotype-by-location interaction, Dallas and Stillwater formed a unique ME for all traits under drought conditions. Therefore, we analyzed the TPI across locations and separated them by ME. When pooled all locations, OSU2081, TifB20201, and TifTuf all had a TPI of 8 (Table 3). For the ME (ME1) formed by Jay, Citra, Tifton, Griffin, Jackson Springs, and Riverside, TifTuf had the highest TPI with 8, followed by experimental lines TifB20201 and TifB20205 (TPI = 6) (Table 3). In the Dallas and Stillwater ME (ME2), OSU2073, OSU2081, OSU2082, TifB20201, and TifB20205 had higher TPI than TifTuf (TPI = 5). Due to significant (p < 0.05) genotype-by-year and genotype-by-location interactions, the TPI for each genotype without drought is summarized by trait and location in Tables S5 and S6. For ER, TifTuf and experimental line TifB20207 were top performers. For RP from drought, TifB20201 and TifB20205 were top performers. For SG, experimental lines OSU2037, OSU2018, and Tahoma 31 were top performers. The best performers for FCR, IP, PGC, TQ, and NDVI were TifB20205, OSU2034, TifB20207, TifB20205, and TifTuf, respectively (Table S5). When summarized by locations (Table S6), TifB20205 was the top performer in Citra, Dallas, Griffin, Jay, and Riverside. The top performers for Jackson Springs and Tifton were FB1628 and TifB20207, respectively. Both TifB20206 and TifB20208 performed well in Stillwater.

To evaluate the performance and stability of genotypes across years, the mean versus stability GGE biplots for traits

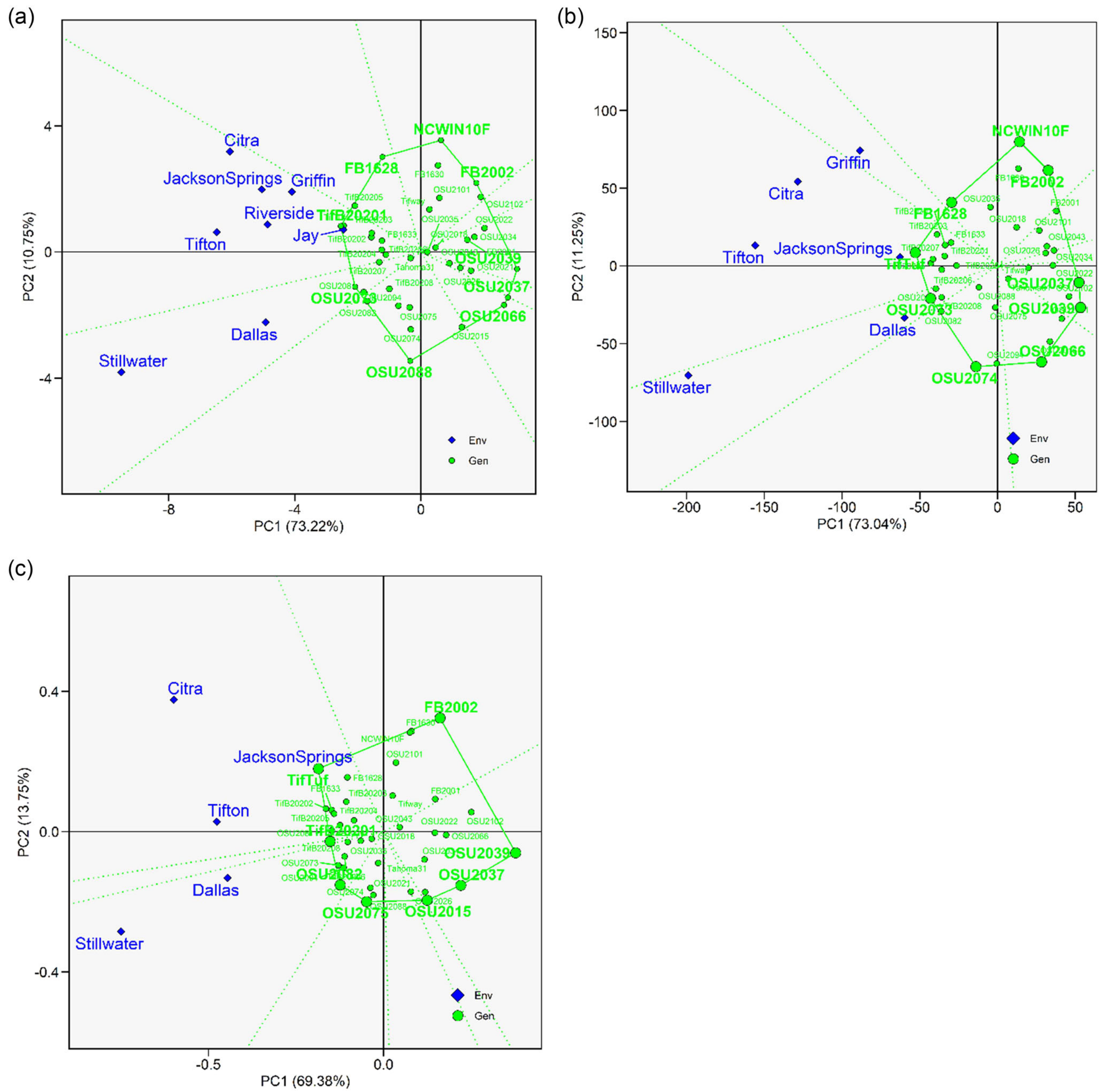

FIGURE 1 Which-won-where genotype plus genotype-by-environment interaction (GGE) biplots for turfgrass quality (a), percent green cover (b), and normalized difference vegetation index (c) in bermudagrass experimental lines and standards evaluated under drought conditions across eight locations: Citra, FL; Dallas, TX; Griffin, GA; Jay, FL; Tifton, GA; Jackson Springs, NC; Stillwater, OK; and Riverside, CA from 2020 to 2023. The sectors delineated by dotted lines represent distinct mega-environments, with locations grouped into the same mega-environment when they fall within the same sector. The bolded genotypes positioned at the vertices of the polygon indicate the highest performing genotype(s) for each corresponding mega-environment. PC1 and PC2 represent the first and second principal components, respectively. The values on the axes indicate the proportion of the total variance explained by each component.

under drought conditions are presented in Figure 2. The top-performing genotype is the farthest from the origin on the *x*-axis on the left. The most stable genotype has the shortest green dashed line on the *y*-axis. For TQ, the genotypes TifB20201, TifB20202, TifB20203, TifB20205, FB1633, and TifTuf showed high stability. In addition, the experimental line TifB20201 showed an excellent performance under drought conditions. The top three most stable genotypes for PGC were FB1633, TifB20202, and TifB20203. For NDVI, the top stable performing genotypes were TifB20202, FB1633, TifB20205, and TifB20204.

Since interspecific hybrid bermudagrasses are triploids, they cannot be used as parents for further crossing. Genetic gains in hybrid bermudagrass were calculated as the

TABLE 3 Turf performance index (TPI) of percent green cover (PGC), turfgrass quality (TQ), and normalized difference vegetation index (NDVI) under drought conditions from across all locations, Jay, Citra, Tifton, Griffin, Jackson Springs, and Riverside mega-environment (ME1) and Dallas and Stillwater ME (ME2).

Entry	All locations				ME1				ME2			
	TQ	PGC	NDVI	Total	TQ	PGC	NDVI	Total	TQ	PGC	NDVI	Total
FB1628	0	2	2	4	2	3	0	5	0	1	0	1
FB1630	0	1	0	1	1	2	0	3	0	0	0	0
FB1633	1	2	2	5	1	3	0	4	1	1	2	4
FB2001	0	1	0	1	0	1	0	1	1	0	0	1
FB2002	0	1	0	1	0	1	0	1	0	0	0	0
NCWIN10F	0	1	0	1	1	2	0	3	0	0	0	0
OSU2015	0	1	0	1	0	1	0	1	1	0	0	1
OSU2018	0	1	1	2	0	1	0	1	0	0	1	1
OSU2021	0	1	1	2	0	1	0	1	0	0	1	1
OSU2022	0	0	0	0	0	0	0	0	0	0	0	0
OSU2026	0	1	0	1	0	1	0	1	0	0	0	0
OSU2034	0	1	0	1	0	1	0	1	0	0	0	0
OSU2035	0	1	1	2	0	1	1	2	0	0	1	1
OSU2037	0	0	0	0	0	0	0	0	0	0	0	0
OSU2039	0	0	0	0	0	0	0	0	0	0	0	0
OSU2043	0	1	1	2	0	1	0	1	1	0	1	2
OSU2066	0	1	0	1	0	1	0	1	0	0	0	0
OSU2073	3	3	1	7	2	3	0	5	3	2	2	7
OSU2074	0	2	1	3	0	1	0	1	0	1	0	1
OSU2075	0	2	1	3	0	1	0	1	1	1	1	3
OSU2081	3	3	2	8	2	3	0	5	3	2	2	7
OSU2082	2	3	1	6	1	2	0	3	2	2	2	6
OSU2088	0	1	0	1	0	1	0	1	2	1	1	4
OSU2094	0	2	1	3	0	1	0	1	1	1	2	4
OSU2101	0	1	1	2	0	2	0	2	0	0	0	0
OSU2102	0	1	0	1	0	1	0	1	0	0	0	0
Tahoma 31	0	1	1	2	0	1	0	1	0	1	0	1
TifB20201	3	3	2	8	3	3	0	6	3	1	2	6
TifB20202	1	2	2	5	1	3	1	5	2	1	2	5
TifB20203	0	3	1	4	2	3	0	5	1	1	0	2
TifB20204	0	2	1	3	1	2	0	3	2	1	1	4
TifB20205	2	3	2	7	3	3	0	6	2	2	2	6
TifB20206	0	3	1	4	1	2	0	3	0	1	1	2
TifB20207	0	3	1	4	1	3	0	4	1	1	1	3
TifB20208	0	3	1	4	0	3	0	3	1	2	1	4
TifTuf	3	3	2	8	3	3	2	8	2	2	1	5
Tifway	0	1	0	1	0	2	0	2	0	0	1	1

Note: The number in each column indicates the number of times each genotype ranked in the top statistical group. Darker green color indicates higher TPI value.

difference between check cultivar performance and the mean of the top 10% genotypes, with results visualized in Figure 3. For traits collected under drought conditions, when separated by ME, positive genetic gains were observed as compared to all commercial cultivars, including the most drought resistance cultivar TifTuf in the industry, in the Dallas–Stillwater ME. However, genetic gains, ranging from −2% to 30% for TQ, from −6% to 51% for PGC, and from −6% to 12% for NDVI were observed in the ME grouped by Jay, Citra, Tifton, Griffin, Jackson Springs, and Riverside. Consistent

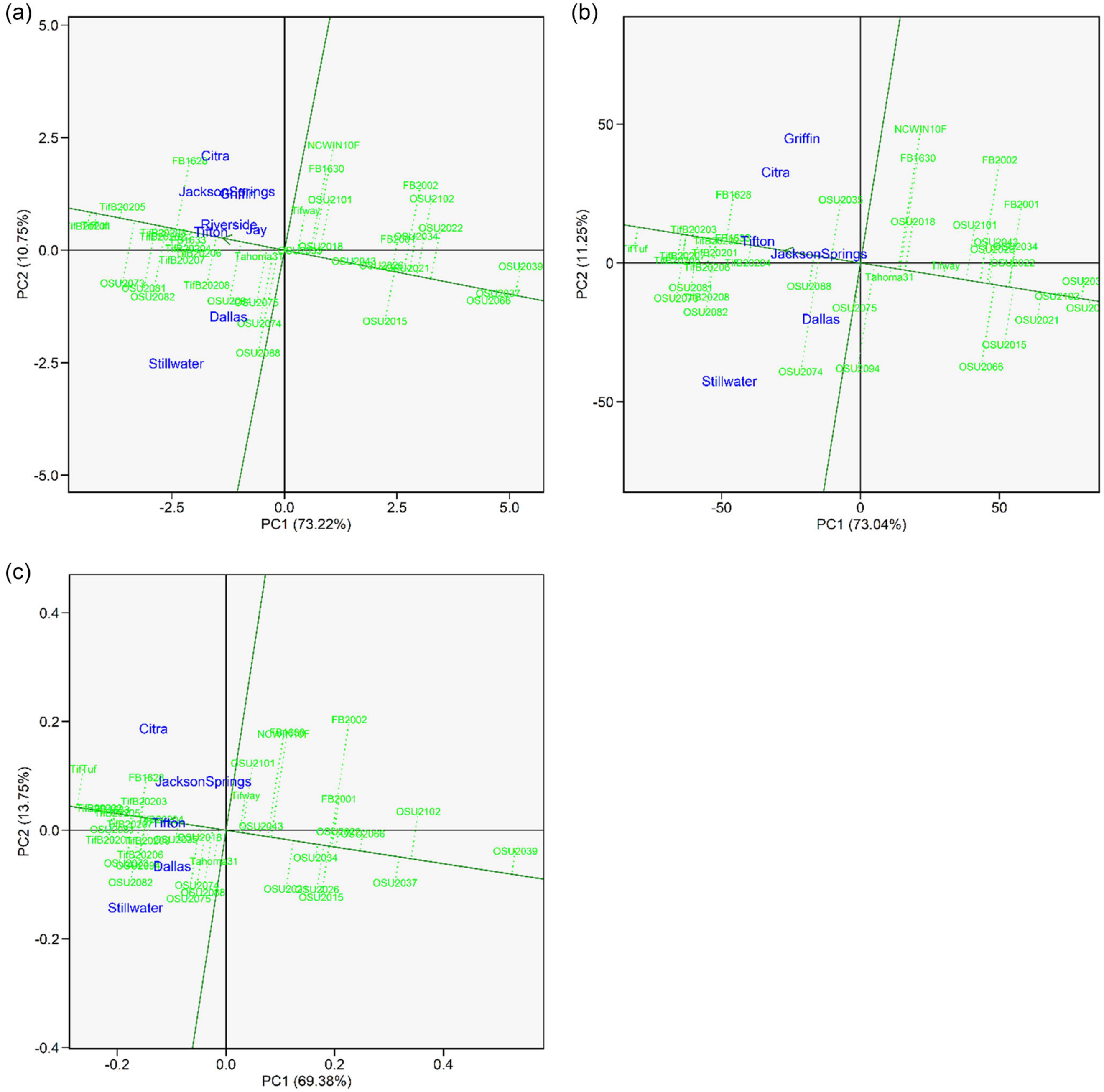

FIGURE 2 The mean versus stability genotype plus genotype-by-environment interaction biplots of bermudagrass genotypes for turfgrass quality (a), percent green cover (b), and normalized difference vegetation index (c) under drought conditions across eight locations: Citra, FL; Dallas, TX; Griffin, GA; Jay, FL; Tifton, GA; Jackson Springs, NC; Stillwater, OK; and Riverside, CA from 2020 to 2023. PC1 and PC2 represent the first and second principal components, respectively. The values on the axes indicate the proportion of the total variance explained by each component.

genetic gains were observed as compared to the long-term industry standard Tifway, showing decades of breeding efforts made significant improvement in drought resistance in turf bermudagrass. Without drought conditions, solid improvement was observed in IP. Breeding lines had more than 38% improvement as compared to the best-performing cultivar Tifway for seedhead reduction. The top 10% of experimental lines showed more than 10% improvement as compared to all three standards in recovery post drought. We observed positive genetic gains in other traits under non-drought as compared to all commercial cultivars, except TifTuf.

4 | DISCUSSION

This study reports the improvement in drought resistance and performance-related traits of advanced breeding lines recently developed by four breeding programs as compared

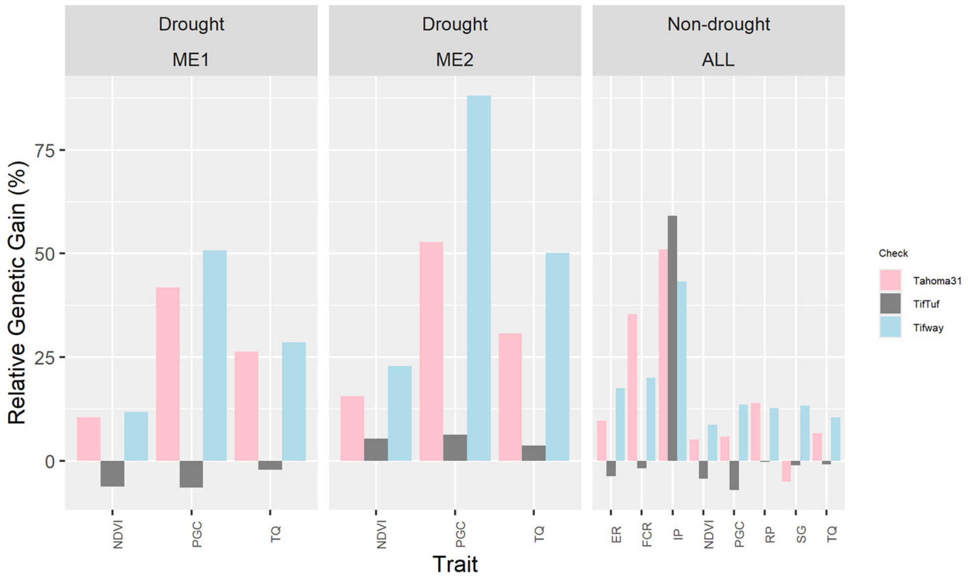

FIGURE 3 Genetic gains of turfgrass quality (TQ), spring green-up (SG), establishment rate (ER), fall color retention (FCR), inflorescence prolificacy (IP), recovery potential (RP), percent green cover (PGC), and normalized difference vegetation index (NDVI) in advanced bermudagrass lines under and without drought stress as compared to standard cultivars Tifway, Tahoma 31, and TifTuf. The genetic gains under drought conditions are separated by mega-environments (ME). The ME1 includes Jay, Citra, Tifton, Griffin, Jackson Springs, and Riverside. The ME2 includes Dallas and Stillwater. The genetic gains under non-drought conditions are presented all together

to three commercial standard cultivars, Tahoma 31, TifTuf, and Tifway. In the study, both PGC and NDVI derived from high-throughput phenotyping (HTP) were incorporated into data analysis with visual ratings. Different from traditional digital measurements collected on the ground, HTP using drone-mounted RGB and multispectral sensors is a proven method in turfgrass research, especially for breeding programs to evaluate many experimental lines frequently and rapidly (Vines & Zhang, 2022; Zhang et al., 2019). Interestingly, PGC measured by an RGB sensor had higher reliability estimates compared to traits measured by multispectral sensors, suggesting that RGB sensors are a more reliable option to quantify turfgrass performance than multispectral sensors. The reliability estimates for most adaptive traits, especially drought resistance was greater than 0.8 (Table 2; Table S4), suggesting that the expression of these traits in the tested lines is less influenced by environments and that the trials were carried out with less errors. The reliability estimates of an early-stage selection trial and a mapping population were slightly lower for adaptive traits, such as SG (Gouveia et al., 2020; Yu et al., 2022; Yu, Fontanier, et al., 2023).

Due to the relatively large number of locations for testing the experimental lines, we were able to investigate GEI to identify MEs. For traits collected under drought conditions, we observed that Dallas and Stillwater were grouped into an ME for all traits (Figure 1). Dallas and Stillwater are both located in the south-central United States, showing similar climates and rainfall patterns (Figure S1). It was expected that the drought performance of bermudagrass genotypes at Riverside would be more similar to Stillwater and Dallas than other locations as these three locations received less rainfall than the other locations. However, Riverside grouped with the eastern locations (Figure 1). Based on MEs observed in this study, two locations, one in south-central and one in southeastern United States, are needed to evaluate drought resistance of bermudagrass. In addition, the larger phenotypical variations (Figure S3) among the experimental lines evaluated in the south-central region than the south-eastern region indicated that the south-central region provides better environments to test drought resistance. The prolonged drought season in the south-central region allows fuller expression of drought resistance in the field.

For traits without drought stress, GEI existed for ER, FCR, RP, SG, and TQ. The other traits, such as IP, NDVI, and PGC, did not show GEI since the genotype effect explained much of the phenotypic variance while GEI explained less than 1%. For FCR, Riverside and Stillwater were in the same ME in which Riverside was the most discriminative location to separate FCR performance (Figure S4D). Riverside would be an ideal location compared to the others to select elite genotypes if the goal is focused on FCR improvement. Meanwhile, breeding programs like OSU and NCSU have focused on improving freeze tolerance, which is negatively associated with chilling temperature tolerance in bermudagrass (Fontanier et al., 2020). Some genotypes from OSU exhibited poor FCR performance, while multiple genotypes from the breeding programs in the South showed better FCR. For SG, we observed a greater GEI at Stillwater and Jackson

Springs, which were in the same ME (Figure S4B). It is not surprising that these higher latitude locations can differentiate winter hardiness of the experimental entries better than other warmer locations. For TQ, Stillwater was a single unique ME and the similar finding has been reported by Gouveia et al. (2020).

Higher genetic gains in drought resistance were found compared to Tifway and Tahoma 31. Tifway was released in the 1960s but is still a popular cultivar worldwide. The higher genetic gain summarized 60 years' progress in drought resistance improvement. In this study, Tahoma 31 showed improvement in drought resistance as compared to Tifway. But Tahoma 31 was selected and released primarily for improved winter hardiness (Wu et al., 2020). TifTuf released in 2014 was selected for drought resistance (Schwartz et al., 2018). Therefore, the relatively low genetic gains as compared to TifTuf suggested the slow improvement in the recent years, consistent with the conclusion by Hall and Richards (2013). Genetic gain in turf-type bermudagrass is often limited by its long breeding cycle, the sterility of interspecific offspring which cannot be backcrossed to enrich favorable traits, and research resources to evaluate more germplasm. However, this study clearly indicated that significant genetic improvement has been achieved in drought resistance of turf-type bermudagrass by the breeding programs (Figure 3). Under drought conditions, we calculated the TPI across all locations and separated them by MEs. OSU2081 and TifB20201 were comparable to the drought resistance standard cultivar, TifTuf across all locations and years. However, in the Dallas and Stillwater ME, OSU2081, OSU2082, TifB20201, and TifB20205 showed improved drought response over TifTuf (Table 3). It has been predicted that climate change and global warming will increase the evapotranspiration rate of turfgrass, leading to a quick onset of drought stress, highlighting the need for greater efforts in improving drought resistance (Kerr, 2007). Recently, several quantitative trait loci (QTL) have been identified in bermudagrass drought resistance (Yu et al., 2022, 2025). Once these QTL are verified and converted to breeder friendly molecular markers, the integration of marker-assisted selection and HTP could increase the selection accuracy. Thus, more genetic gain could be achieved in improving bermudagrass drought resistance in the future.

Since the first recorded introduction of bermudagrass to Savannah, GA, in 1751, bermudagrass has been grown and become the major turfgrass in the southern and transitional climatic regions of the United States (Juska & Hanson, 1964). The early breeding efforts led by Dr. Glenn Burton at USDA-ARS Coastal Plain Experiment Station focused on improving TQ and adaptation to different turf use purposes. Later bermudagrass breeding efforts were targeted towards improving stress resistance/tolerance while maintaining high quality. For instance, Tahoma 31 has improved winter hardiness and decreased evapotranspiration rate, and TifTuf has improved drought resistance, while both produce high TQ (Amgain et al., 2018; Yu, Martin, et al., 2023). Different drought tolerant mechanisms, including synthesis of phytohormone ABA and various amino acids exists in bermudagrass (Seelam & Jespersen, 2025). Drought avoidance mechanisms, such as deep and extensive root structures, affect the overall drought resistance of bermudagrass (Gopinath et al., 2022). Various avoidance and tolerance mechanisms enable breeders to use different strategies in selecting drought resistance of bermudagrass genotypes. Breeders should also integrate drought resistance, high TQ, and performance stability in cultivar development programs. The observed reduction in IP among these breeding lines as compared to commercial cultivars TifTuf and Tahoma 31 in this study demonstrated significant genetic improvement for this trait (Figure 3). This progress is particularly notable as IP showed minimal correlations with other key traits targeted for enhancement in the breeding programs (Figure S5). Fewer seedheads not only benefit TQ, but also reduce energy lost for inflorescence production, and decrease the mowing requirement, resulting in management cost reduction. The large GEI for turf performance under drought conditions implied that developing regionally adapted cultivars is a more realistic target than cultivars with stable performance across multiple geographic regions (i.e., the southeast, southwest, and transition zone in the United States) (Figure 1). Similarly, major food crops like wheat (*Triticum aestivum* L.) and rice (*Oryza Sativa* L.) showed strong GEI, so locally adapted cultivars are developed and used (Coast et al., 2022; Liang et al., 2015). Several experimental lines in this study showed significant drought resistance improvement in the south-central region. These elite breeding lines, if released for commercial production, would provide better choices than the existing cultivars for water conservation in the region.

5 | CONCLUSIONS

In this study, we evaluated the performance of advanced breeding materials in eight locations under both drought and no-drought conditions over 4 years. Under drought conditions, Dallas and Stillwater constituted a unique ME and six other locations formed another ME for turf bermudagrass performance. In the six-location ME, experimental lines TifB20201 and TifB20205 showed similar performance to TifTuf. In the Dallas and Stillwater ME, OSU2073, OSU2081, OSU2082, TifB20201, and TifB20205 exhibited superior drought resistance to TifTuf, Tahoma 31, and Tifway, highlighting positive genetic gains. Several top-performing experimental lines produced much fewer seedheads than the standard cultivars.

AUTHOR CONTRIBUTIONS

Shuhao Yu: Data curation; formal analysis; software; validation; visualization; writing—original draft. **Beatriz Tome Gouveia**: Data curation; formal analysis; software; validation; visualization; writing—review and editing. **Jing Zhang**: Formal analysis; investigation; methodology; software; validation; writing—review and editing. **Yanqi Wu**: Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing—review and editing. **Brian R. Schwartz**: Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing—review and editing. **Susana R. Milla-Lewis**: Conceptualization; funding acquisition; methodology; project administration; supervision; writing—review and editing. **Kevin E. Kenworthy**: Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing—review and editing. **Bryan J. Unruh**: Conceptualization; investigation; methodology; writing—review and editing. **Ambika Chandra**: Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing—review and editing. **Paul L. Raymer**: Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing—review and editing. **Marta T. Pudzianowska**: Data curation; investigation; methodology; writing—review and editing. **James H. Baird**: Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing—review and editing. **Esdras Carbajal Melgar**: Data curation; investigation; methodology; writing—review and editing. **Mingying Xiang**: Investigation; writing—review and editing. **Justin Q. Moss**: Conceptualization; investigation; methodology; writing—review and editing. **Ryan Earp**: Data curation; investigation; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Shuhao Yu https://orcid.org/0000-0003-2955-1503
Beatriz Tome Gouveia https://orcid.org/0000-0002-2455-373X
Yanqi Wu https://orcid.org/0000-0003-0802-6881
Brian R. Schwartz https://orcid.org/0000-0002-9509-8797
Kevin E. Kenworthy https://orcid.org/0000-0001-8944-7543
Ambika Chandra https://orcid.org/0000-0002-4996-4383
Paul L. Raymer https://orcid.org/0000-0001-6396-7276
Marta T. Pudzianowska https://orcid.org/0000-0001-8941-3562
James H. Baird https://orcid.org/0000-0001-8412-5836
Mingying Xiang https://orcid.org/0000-0002-9826-8157
Justin Q. Moss https://orcid.org/0000-0002-6758-3488

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SUPPORTING INFORMATION

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

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