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Exploring genotypic diversity in sorghum breeding lines for water-saving traits to enhance drought adaptation during the post-rainy season

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Abstract

Sorghum [*Sorghum bicolor* (L.) Moench], a crucial staple crop in South Asia and sub-Saharan Africa, faces challenges amid increasing climate variability. Post-rainy sorghum serves as a dominant food and fodder crop in India. Aligned with International Crops Research Institute for the Semi-Arid Tropics's post-rainy sorghum product profile, this research extensively characterizes sorghum lines, emphasizing the traits vital for post-rainy drought adaptation in hybrid parents. We examined genotypic differences and trait correlations in 25 sorghum hybrid parents and varieties (B line for seed parent, R line for restorer, and check for varieties) through atmospheric and soil drought experiments. Results from atmospheric drought experiments revealed significant variation in transpiration rate (TR) under high vapor pressure deficit (VPD), with certain lines showing limited TR (BTX623 and ICSR 21002), while others exhibited high TR. In soil drought experiments, transpiration decline occurred at fractions of transpirable soil water ranging between 0.38 (ICSR 174) and 0.65 (40162 and ICSR 21005). R lines consistently displayed superior plant growth, water use, and biomass compared to B lines. Transpiration efficiency (TE) and total biomass showed positive correlations (r^2 = 0.69) in well-watered and (r^2 = 0.45) in water-stressed conditions. Most R lines displayed higher biomass and TE. Genotypes exhibiting enhanced vigor and limited TR in high VPD conditions and

Abbreviations: DAS, days after sowing; FTSW, fraction of transpirable soil water; NTR, normalized transpiration ratio; TE, transpiration efficiency; TR, transpiration rate; VPD, vapor pressure deficit; WS, water stressed; WW, well watered.

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high TE hold potential for enhancing drought adaptation in post-rainy sorghum. Notably, genotypes with higher biomass, lower TR, and increased TE within both R and B line groups represent valuable genetic resources for enhancing sorghum crops, post-rainy sorghum adaptation to water deficit.

1 | INTRODUCTION

Sorghum [*Sorghum bicolor* (L.) Moench] plays a vital role as both a staple food and fodder crop, particularly in semiarid regions, where it meets the dietary and agricultural needs of millions in South Asia and sub-Saharan Africa. In addition to providing grains and forage, sorghum yields fermentable sugars and cellulosic fibers, supporting a diverse range of applications from food to bio-industrial uses (Boatwright et al., 2021). As of 2021, global sorghum production has reached 60.10 million tonnes, cultivated across 45.90 million ha, with an average productivity of 1309 kg/ha (FAO, 2021).

Sorghum holds the position of the fourth most significant food crop in India, cultivated across two distinct seasons: the rainy season (June–October) and the post-rainy season (October–January). Traditionally, post-rainy sorghum has been instrumental in ensuring food and fodder security for millions of rural families in India (Upadhaya et al., 2017), while rainy season sorghum primarily serves feed and fodder purposes. During the post-rainy season, approximately 3 million tonnes of sorghum are harvested from 5.7 million ha, with notably low productivity averaging about 600–700 kg/ha (Anisha et al., 2022; Kholova et al., 2013). Rainy season sorghum, due to a higher incidence of grain mold infections and leaf diseases, is predominantly used for feed and fodder. In contrast, the clean, lustrous, and bold sorghum grains harvested during the post-rainy season dominate food consumption in India, underscoring the pivotal role of post-rainy sorghum cultivation in sustaining both human and livestock populations.

The area devoted to post-rainy sorghum cultivation in India has experienced a significant decline, dropping from 10.25 million ha in 1999–2000 to 5.82 million ha in 2014–2015. As a result, total production has also decreased from 8.68 million metric tons to 5.39 million metric tons. However, sorghum productivity has shown an upward trend in both seasons, increasing from 847 kg/ha to 907 kg/ha during the same period. This increase can be attributed to farmers adopting improved varieties and production technologies (Chapke et al., 2017).

Post-rainy sorghum cultivation in the Deccan Plateau, India, which spans an extensive area of 5.7 million ha, relies on stored-receding soil moisture following the cessation of rains, particularly on shallow- and medium-deep soils (Kholová et al., 2013; Patil et al., 2014). As a result of insufficient or absent in-season rains, sorghum cultivation often encounters progressively severe water deficits as the season advances and the crop approaches maturity (Kholová et al., 2013). It is noteworthy that sorghum productivity in India lags significantly behind the global average, with yields reaching only 864 kg/ha compared to the global average of 1481 kg/ha (Sandeep et al., 2018). Given that sorghum is primarily a rainfed crop, its productivity is greatly influenced by climatic factors. Predictions indicate that climate change could result in a decline in post-rainy sorghum yields by up to 7% by 2020, 11% by 2050, and 32% by 2080 (Srivastava et al., 2010). Hence, there is an urgent need to focus on improving yields in these regions through the implementation of various physiological and breeding strategies.

Breeding efforts aimed at developing improved varieties and top-cross hybrids tailored for water-limited environments have been slow, particularly in developing countries, primarily due to the unpredictable nature of drought environments. In order to address the environmental variations observed from season to season, a sorghum crop model integrated within the APSIM (The Agricultural Production Systems sIMulator) software platform was utilized to categorize and quantify five distinct stress scenarios across the post-rainy sorghum cultivation region (Hammer et al., 2010; Keating et al., 2003). These stress scenarios encompass a spectrum ranging from very severe stress (with an average grain yield of approximately 100 kg/ha) to no stress conditions (with an average grain yield of approximately 1500 kg/ha), thereby delineating the post-rainy sorghum tract into four zones: Central (accounting for 40% of the annual rabi-belt sorghum grain production), Southern (30%), Northern (20%), and Far South (10%) (Kholová et al., 2013).

Enhancing drought adaptation through breeding can benefit from an integrated physiological approach, focusing on plant features that contribute to adaptation in water-limited

environments (Cooper et al., 2014; Kholova et al., 2013; Messina et al., 2015). Successful breeding for drought adaptation necessitates a thorough understanding of the constraints and the plant traits that facilitate adaptation (Hammer et al., 1996; Sheshashee et al., 2003; Vadez et al., 2012).

The sorghum breeding product profile at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) is specifically tailored to target traits for post-flowering drought adaptation, with the goal of developing hybrids/varieties suitable for the rabi-belt regions of India and sub-Saharan Africa. To expedite post-rainy sorghum improvement, the identification and incorporation of physiological traits into breeding programs are crucial (ICRISAT Sorghum Target Product profiles, https://www.icrisat.org/crops/sorghum/overview; Crops Overview, https://genebank.icrisat.org/). Recent emphasis has been placed on traits related to water use, which can enhance crop yield and adaptation to drought. It is hypothesized that there are two major water-saving mechanisms: (1) restricting or limiting transpiration under high evaporative demand and (2) controlling water use when plants are exposed to progressive water stress, reducing transpiration even at high soil moisture levels (expressed as the fraction of transpirable soil water [FTSW] remaining in the soil). These water conservation strategies may enable the crop to maintain water availability during the critical phase of grain filling (Gholipoor et al., 2012; Vadez et al., 2013).

The restriction or limitation of transpiration rate (TR) under increasing atmospheric vapor pressure deficit (VPD) involves a partial closure of stomata under high VPD conditions, contributing to water conservation. Genotypic variation in traits that restrict TR has been documented in sorghum by Gholipoor et al. (2010), Choudhary et al. (2013, 2020), and Shekoofa et al. (2014). Similar genotypic variation for limited transpiration response has been reported in various other species, including pearl millet (*Pennisetum glaucum* L.; Kholová et al., 2010), maize (*Zea mays* L.; Choudhary et al., 2020; Gholipoor et al., 2013; Yang et al., 2012), chickpea (*Cicer arietinum* L.; Sivasakthi et al., 2019; Zaman-Allah et al., 2011), peanut (*Arachis hypogaea* L.; Devi et al., 2010), cowpea (*Vigna unguiculata* L.; Belko et al., 2012), and soybean (*Glycine max* (L.) Merr; Fletcher et al., 2007; Gilbert et al., 2011).

Managing water loss under water-deficit conditions includes decreasing transpiration when FTSW is higher in the root zone. Genetic variation in sorghum crops regarding the FTSW threshold, where a decrease in transpiration and biomass begins, has been observed by Gholipoor et al. (2013), Choudhary et al. (2020), and Karthika et al. (2019). This genotypic variation for FTSW thresholds is also reported in various other species, including pearl millet (*P. glaucum* L.; Kholová et al., 2010), maize (*Z. mays* L.; Gholipoor et al., 2013; Yang et al., 2012; Choudhary et al., 2020), chickpea (*C. arietinum* L.; Sivasakthi et al., 2019; Zaman-Allah et al., 2011), peanut (*A. hypogaea* L.; Devi et al., 2010), and cowpea (*V. unguiculata* L.; Belko et al., 2012). This water conservation strategy is directly linked to increased crop production under water-limited conditions (Kholova et al., 2013; Messina et al., 2015; Sinclair et al., 2005).

Simulation studies conducted across various crops, such as sorghum in Australia (Sinclair et al., 2005), post-rainy sorghum in India (Kholova et al., 2013), soybean [*G. max* (L.) Merr.] in the United States (Sinclair et al., 2010), and maize (*Z. mays* L.) in the United States (Messina et al., 2015), consistently indicate that limiting maximum TR under high evaporative demand generally leads to enhanced grain yield in regions prone to post-anthesis drought stress. However, restricting maximum TR, which results from reduced stomatal conductance, may constrain CO_2 uptake and, consequently, photosynthetic rates, potentially explaining the yield penalty observed under well-watered (WW) conditions (Kholova et al., 2013; Messina et al., 2015; Sinclair et al., 2005).

Over the span of 50 years, ICRISAT has made significant progress in developing and disseminating 1600 hybrid parents, advanced breeding lines, and germplasm, collaborating with various partners, including the National Agricultural Research System. However, a pivotal aspect in introducing high-yielding hybrids and broadening the existing gene pool based on Maldandi is the breeding and selection process for post-rainy adaptation. Enhancing ICRISAT's post-rainy sorghum breeding product profiles requires a comprehensive examination of the physiological traits linked to sorghum's capacity to thrive in arid environments with limited water resources.

Therefore, this study sought to assess different traits related to plant water usage in sorghum breeding lines and varieties designed for post-rainy adaptation through agronomic and phenotyping selection. The specific objectives included evaluating the plant's transpiration response to: (1) atmospheric

Core Ideas

- Post-rainy sorghum cultivation in India is vital and aligns with ICRISAT's product profile.
- Water conservation traits (e.g., limited transpiration rate [TR]) optimize yield under water deficit by maximizing water capture and use.
- We observed significant variation in TR, NTR-FTSW (normalized transpiration ratio-fraction of transpirable soil water) thresholds, and transpiration efficiency (TE), crucial for drought adaptation.
- R lines consistently showed better plant growth, higher biomass, and TE, compared to B lines.
- Promising sorghum genotypes, with enhanced vigor and improved TE, offer for post-rainy drought adaptation.

drought, (2) progressive soil drought, and (3) investigating potential correlations between the traits associated with plant growth and water conservation.

2 | MATERIALS AND METHODS

2.1 | Sorghum genetic materials

ICRISAT serves as a significant repository of sorghum germplasm, featuring over 41,000 accessions collected from 90 countries (http://genebank.icrisat.org; B. V. S. Reddy et al., 2008). This extensive collection represents approximately 80% of the global sorghum variability (Eberhart et al., 1997). Since its establishment in 1972, ICRISAT has leveraged these germplasm sources to develop high-yielding male-sterile lines and restorers (B. V. Reddy et al., 2010). Over the years, sorghum improvement research at ICRISAT, Patancheru, has yielded more than 680 A-/B-pairs and over 880 R lines, carefully selected for various traits including high yield, large grain size, resistance to biotic stress (such as shoot fly, midge, and grain mold), tolerance to abiotic stress (drought and salinity), enhanced grain micronutrient density (Fe and Zn), and desirable sweet stalk characteristics (B. V. Reddy et al., 2010).

The present study utilized 25 genotypes, consisting of 10 B lines and 11 R lines, along with four checks (BT x 623, B35, M35-1, and R16) selected randomly, with variation in plant height and maturity. Furthermore, most of the genotypes were sourced from the ICRISAT sorghum breeding unit and are typically used for post-rainy sorghum cultivation, aiming to investigate drought adaptive mechanisms. Table 1 provides detailed information on the genotypes, their pedigrees, and specific trait adaptations. Additionally, Table S1 presents agronomic data for most of the lines, enhancing the comprehensive understanding of the study.

2.2 | Plant growth conditions

The experiments were conducted at ICRISAT-India (17.30° N, 78.16° E, 549 m a.s.l.) from February to March 2021, and the plants were grown in controlled glasshouse environments. Experiment 1, aimed at measuring the plant TR response to natural changes in atmospheric VPD, was conducted outdoors on a clear sunny day (Figure S1 provides weather data). Experiment 2, designed to assess plant transpiration in response to progressive soil drying, was carried out under controlled glasshouse conditions.

In both experiments, plants were cultivated in 10-in. plastic pots filled with a mixture of 7 kg Alfisol and sand (in a 3:2 ratio) sourced from the ICRISAT farm. The soil received supplementation with di-ammonium phosphate at a rate of 0.3 g/kg of soil, and 0.3 g of carbofuran was incorporated into the topsoil of each pot 1 day prior to sowing to mitigate soil-borne pests. Four hills were prepared during seed sowing, with two seeds planted in each hill. A week post-sowing, primary thinning was conducted to maintain four plants per pot. Subsequently, 2 weeks later, final thinning was carried out to ensure two plants per pot. The experiments followed a completely randomized design, with each experiment comprising five replications.

In experiment 1, focusing on atmospheric drought conditions, 25 genotypes were replicated five times, resulting in a total of 125 pots. In experiment 2, which addressed soil drought, each of the 25 genotypes was replicated five times under both WW (125 pots) and water-stressed (WS; 125 pots) conditions, totaling 250 pots. Under WW conditions, plants were cultivated up to 30 days after sowing (DAS). Air temperature and relative humidity within the glasshouse were regularly recorded by a data logger (Lascar Electronics Inc.) positioned at the level corresponding to the plant canopy during the measurement period. The average day and night temperatures were maintained at 28/22°C, with relative humidity fluctuating between 70% and 90%, mimicking natural daylight oscillations.

2.2.1 | Experiment 1: Atmospheric drought

The VPD experiment aimed to evaluate the genotype's ability to regulate transpiration under drying atmospheric conditions (natural changes in atmospheric VPD). The assessment was conducted during the vegetative growth stage under WW conditions, following the methodology outlined by Kholova et al. (2010). Thirty-day-old plants in pots were irrigated to approximately 90% field capacity. Direct soil evaporation was minimized using plastic sheets and beads (Karthika et al., 2019). Plant transpiration response to atmospheric drought was measured outdoor on a clear sunny day aligning with the natural circadian cycle, with weather data details available in Figure S1. Transpiration was measured using the gravimetric method, which involved recording weight losses from the pots between consecutive weighings. Pots were weighed using a precision scale (KERN 24100, Kern & Sohn GmbH) every hour from 6:00 a.m. to 6:00 p.m. At the end of the experiment, plants were harvested, and leaf area was measured using an LI-3100 instrument (Licor). Transpiration and leaf area data were then used to calculate the TR, representing the amount of water lost per unit of leaf area (TR, mg H_2O cm^{-2} min^{-1}). The harvested plant parts were subsequently dried in an oven at 60°C for 3 days, and dry weights were recorded.

2.2.2 | Experiment 2: Soil drought

The primary objective of "dry-down" experiment is to assess the genotypic capacity to regulate transpiration during decline

TABLE 1 Overview of pedigree information or genotype descriptions for the 25 tested genotypes, including both B and R lines, along with the reference checks utilized in the experiments.

S. No	Genotype	Pedigree or genotype description	B line/R line/checks	Adaptations/ cultivation
1	40157/18PR	(ICSB 101 x SF 152-2-1-1-1-1-1-1-1-1)−1-1-1-1	B	Post-rainy
2	40154/18PR	((Giddi Maldandi x 296B)−8-8-1-2-1-3-1 x ((SFB 111) x (ICSB 444))12-1-3-1-1-1-1-2-1)−1-1-1-1	B	Post-rainy
3	40158/18PR	(ICSB 101 x 30921-2-1-1-1-2-1-1-1-1)−1-1-1-1	B	Post-rainy
4	40160/18PR	(ICSB 238 x 30921-2-1-1-1-1-2-2-1-1)−1-1-1-1	B	Post-rainy
5	40162/18PR	(ICSB 675 x 30921-2-1-1-1-1-2-2-1-1)−1-1-1-1	B	Post-rainy
6	40165/18PR	(22438 B x ((SFB 111) x (ICSB 444))12-1-2-1-1-2-1-2-1)−1-1-1-1	B	Post-rainy
7	40172/18PR	((M 35-1-Bulk-3-15-1-1 x ICSB 93)−3-2-3-1-2-1-2-2-1 x ((SFB 111) x (ICSB 444))12-1-2-1-1-2-1-2-1)−1-1-1-1	B	Post-rainy
8	104 B	Reference variety	B	Post-rainy
9	ICSB 684	((Ind. Syn. 89-2) x PM 1861) 4-1-2-2	B	Stay-green
10	ICSB 685	((Diallal 346-8556-2-1) x ((GPR 148 x 555)−29-3-2-1-1))44-3-2-2-3	B	Stay-green
11	B 35	B35, a three-gene dwarf genotype, originates from Ethiopian germplasm (IS12555) with slower senescence. It is a BC1 selection, derived from the converted version of the Ethiopian landrace IS12555 durra sorghum, known for dwarf height and early flowering traits (PI534133/SC35-6/BTx642).	Check	Stay-green donor parent
12	BTx 623	BTx623' (PI 659985 MAP) is an elite, white-seeded, inbred line with the pedigree BTx3197/SC170−6-4. It is a short-stature, early maturing genotype primarily utilized to produce grain sorghum hybrids.	Check	Cold sensitive/inbred, early maturing, short stature & high biomass yield
13	ICSR 174	[9-13 x (SC 108-3 x CSV 4) x (D 181 x SPV 104)]−1-1	R	Drought tolerance
14	ICSR 21002	(([9-13 x (SC 108-3 xCSV 4) x (B.Y xD181 xSPV 104)]−1-1-1-1) x S 53-1 x ICSP2B/R MFR-S2 Bulk 7} x ([(BTx 623 x UChV2)B lines bulk]−3-1-4-3)}1-1-1	R	Stay-green
15	ICSR 21005	(((IS 5622 x CS 3541)−20-1-2-1-1-1-1-1-1) x SPV 386)−1-3-2-2-1	R	Stay-green
16	ICSR 91020	(([(IS 12622C x 555) x ((IS 3612C x 2219 B)−5-1 x E 35-1)]−5-2) x ([(M 35-1 x (SC 108-3 x CS 3541) derivative)−3-2-1 x F5s-6]−5-2-3-1-2))−1	R	Drought tolerance
17	ICSV 15012	IS 29025-1	R	Postrainy; high iron (Fe) and zinc (Zn)
18	ICSV 15013	IS 30310-1	R	Postrainy and rainy; High Fe and Zn
19	IS 23525	IS 23525	R	Traditional cultivar/landrace
20	ICSV 100291 (REVT 18PR #10)	(([{[SPV 462 x (ICSB 102 x PS 28060-3)−4-2-2-2-1-2] x 296 B}−5 x SP 46545]−1-1-1-1-1 x ICSB 101)−3-2 x ICSP-B-98R Sel-17-2-3-1-1-1-1-1-1-1-1-1)−1-2-1-2-4-3-1	R	Stay green
21	ICSV 15014 (REVT 18PR #14)	(IS 33844-5 x M 35-1-Bulk-3-15-1-3-4-1-1)−1-1-1-2-2	R	Stay green; high Fe and Zn; post-rainy
22	REVT 18PR #24	(Giddi Maldandi x (M 35-1xSPV 1359)−3-1(Tan)−1-1)−2-1-1	R	Stay green
23	SPV 1411	IS 33844-1-1	R	Post-rainy
24	M 35-1	M35-1: Popular, tall, single-gene dwarf sorghum with bold, lustrous grains and excellent stover. Land race selection from local maldandi bulk.	Check	Terminal drought tolerance
25	R 16	Post-rainy sorghum cultivars in India and highly senescent type.	Check	Drought susceptible

in soil moisture content, which is important for adaptation in water-limited environments. The experiments were done according to the guidelines outlined by Kholova et al. (2010). Before the experiment, pots were thoroughly irrigated and left to drain overnight to achieve field capacity. The next morning, a plastic sheet was placed over the soil, and a 2 cm layer of plastic beads was added to minimize water evaporation. Around 9:00 a.m., initial pot weights were recorded, with subsequent weighings conducted daily around the same time to calculate daily transpiration. To maintain WW conditions, plants were kept at approximately 80% of field capacity by regular watering. For the WS treatment, available water to the plant was gradually reduced by allowing a maximum daily water loss of 70 g. Any transpiration exceeding 70 g was replenished back into the pots. The experiment concluded when transpiration in all WS plants dropped below 10% of their WW counterparts. For more details, please refer to Belko et al. (2012), Karthika et al. (2019), Kholova et al. (2010), Sivasakthi et al. (2019), and Zaman-Allah et al. (2011).

To facilitate comparison, transpiration data were normalized following the methodology described by Kholová et al. (2010). The daily transpiration ratio for each plant was determined by dividing the TR of an individual WS plant by the average TR of WW plants of the same genotype. Subsequently, the daily TR was divided by the mean TR of that particular plant during the initial 3 days of the experiment, characterized by high soil moisture content. This normalization process yielded the normalized transpiration ratio (NTR), effectively accounting for plant-to-plant variation in transpiration within each genotype. For more detailed information, refer to Belko et al. (2012), Devi and Sinclair (2011), Kholova et al. (2010), and Sivasakthi et al. (2019).

Comparison of genotypes was further enhanced by representing the available soil water as FTSW for each pot in the drought-stressed treatment on a daily basis. FTSW, expressed as the volumetric water content of the soil, was calculated using the following formula: (daily weight − final weight)/(initial weight − daily weight). To visualize the data plotted as NTR against FTSW, a two-segment linear regression was applied. The slope and FTSW threshold obtained from the regression were then compared between genotypes. For additional details, refer to Devi and Sinclair (2011), Kholova et al. (2010), and Sivasakthi et al. (2019).

2.3 | Data analysis

In experiments 1 and 2, variations among the examined genotypes were evaluated using one-way analysis of variance (ANOVA), followed by the Tukey–Kramer test to establish the significance of genotypic differences (Statistical program package CoStat version 6.204, Cohort Software). Furthermore, two-way ANOVA was utilized to analyze plant biomass component traits, exploring disparities among genotypes (G), treatments (T) (WW and WS), and their interactions (G × E) using Cohort software. Line graphs (experiment 1), bar graphs (experiments 1 and 2), and simple linear regressions were created using Microsoft Excel 2017 (Microsoft Corp.). The relationship between NTR and FTSW was analyzed using GraphPad Prism version 6 (GraphPad Software Inc.). This software determined the breakpoint for the two-segment linear regression model, and the FTSW value at the intersection of the two linear segments served as the critical statistic for genotype comparison. To assess trait correlations for selected phenotypic traits, simple Pearson correlation analysis was conducted using R software (version 2.11.1).

3 | RESULTS

3.1 | Atmospheric drought experiment

3.1.1 | Genotypic variation for plant growth under WW condition at 30 DAS

Significant variations were observed in growth parameters among the genotypes assessed at 30 DAS (Table 2). SPV 1411 exhibited the highest total biomass (TBM), followed by REVT 18PR#24 and ICSV15012 (Table 2). The highest root dry weight was observed in ICSR 91020, M35-1, and SPV 1411, while the lowest was in 40154, 40157, and 40158. Notably, most of the B lines showed significantly lower plant biomass (leaf dry weight [LDW], stem dry weight [StDW], root dry weight [RDW], shoot dry weight [ShootDW], and TBM) compared to R lines (Table 2). The B line checks (B35 and BT x 623) had lower TBM than the R line checks (M35 and R16). Additionally, many of the B lines exhibited lower leaf area than the R lines (Figure 1). Several R lines, including REVT 18PR#24, REVT 18PR#14, SPV1411, ICSV 15012, and ICSV 15013, showed significantly higher TBM than B lines (40154, 40157, 40158, 40160, 40162, and 40172; Table 1). In summary, the majority of the R lines demonstrated higher plant growth and biomass (leaf area [LA], LDW, StDW, Shoot DW, RDW, and TBM) compared to the tested B lines.

3.1.2 | Response of plant TR to changing atmospheric VPD

Transpiration rate (TR) was measured under naturally increasing atmospheric VPD in outdoor conditions, ranging between 1.15 and 4.70 kPa (Figure 2a,b). TR closely followed the diurnal pattern, with the highest atmospheric VPD recorded around 3:00 p.m. (Figure 2a,b). At the lowest VPD (1.15 kPa),

TABLE 2 Means and one-way analysis of variance (ANOVA) for biomass-related traits measured in R and B lines under well-watered (WW) conditions.

Genotype	Genotype number	Group	LDW	StDW	RDW	Shoot DW	TBM	R/S
40154	**G1**	**B**	3.07 ± 0.29e	1.98 ± 0.14f	2.91 ± 0.04f	5.04 ± 0.15g	07.95 ± 0.12i	0.58 ± 0.03a
40157	**G2**	**B**	5.86 ± 0.72cde	3.56 ± 0.65ef	3.56 ± 0.18ef	9.42 ± 1.35fg	12.97 ± 1.53ghi	0.39 ± 0.05ab
40158	**G3**	**B**	5.25 ± 0.36de	3.72 ± 0.23def	3.95 ± 0.44def	8.97 ± 0.48fg	12.92 ± 0.65hi	0.45 ± 0.06ab
40160	**G4**	**B**	7.17 ± 1.07bcd	4.85 ± 0.76bcdef	4.68 ± 0.54cdef	12.0 ± 1.82cdef	16.69 ± 2.29fgh	0.40 ± 0.04ab
40162	**G5**	**B**	7.06 ± 0.91bcd	4.84 ± 0.74bcdef	4.53 ± 0.54cdef	11.9 ± 1.57cdef	16.42 ± 2.09fgh	0.39 ± 0.02ab
40165	**G6**	**B**	8.30 ± 0.23abcd	5.57 ± 0.47bcde	5.68 ± 0.31abcdef	13.9 ± 0.62bcdef	19.55 ± 0.9bcdefgh	0.41 ± 0.02ab
40172	**G7**	**B**	6.68 ± 0.75bcd	3.79 ± 0.17def	5.77 ± 0.28abcdef	10.5 ± 0.78efg	16.23 ± 0.74fgh	0.56 ± 0.06ab
104 B	**G8**	**B**	7.23 ± 0.17bcd	5.85 ± 0.54bcde	5.24 ± 0.35bcdef	13.1 ± 0.62bcdef	18.31 ± 0.7cdefgh	0.41 ± 0.04ab
B 35	**G9**	**Check**	7.18 ± 0.53bcd	4.77 ± 0.64cdef	5.12 ± 0.33bcdef	11.9 ± 1.13cdef	17.07 ± 1.24efgh	0.44 ± 0.05ab
BTx 623	**G10**	**Check**	7.58 ± 0.29bcd	4.30 ± 0.33cdef	5.86 ± 0.21abcde	11.9 ± 0.61def	17.73 ± 0.55defgh	0.5 ± 0.04ab
ICSB 684	**G11**	**B**	7.32 ± 0.34bcd	5.45 ± 0.18bcde	5.05 ± 0.37cdef	12.8 ± 0.5bcdef	17.82 ± 0.23cdefgh	0.41 ± 0.05ab
ICSB 685	**G12**	**B**	8.22 ± 0.85abcd	5.94 ± 0.59bcde	5.82 ± 0.46abcde	14.2 ± 0.34abcdef	19.98 ± 0.68abcdef	0.42 ± 0.03ab
ICSR 174	**G13**	**R**	8.05 ± 0.27abcd	5.49 ± 0.2bcde	6.08 ± 0.81abcde	13.5 ± 0.38bcdef	19.61 ± 1.08abcdefg	0.45 ± 0.06ab
ICSR 21002	**G14**	**R**	9.32 ± 0.41ab	6.72 ± 0.7abcd	6.34 ± 0.49abcd	16.0 ± 1.05abcd	22.37 ± 1.46abcdef	0.40 ± 0.03ab
ICSR 21005	**G15**	**R**	8.73 ± 0.71abc	5.46 ± 0.44bcde	5.76 ± 0.89abcdef	14.2 ± 0.74abcdef	19.95 ± 0.68abcdef	0.42 ± 0.08ab
ICSR 91020	**G16**	**R**	9.78 ± 0.58ab	5.58 ± 0.27bcdef	7.89 ± 0.63a	15.3 ± 0.55abcde	23.24 ± 0.55abcde	0.52 ± 0.06ab
ICSV 15012	**G17**	**R**	9.34 ± 0.76ab	7.68 ± 0.89ab	7.21 ± 0.6abc	17.0 ± 1.41abc	24.22 ± 2ab	0.43 ± 0.01ab
ICSV 15013	**G18**	**R**	8.28 ± 0.64abcd	9.22 ± 0.56a	6.47 ± 0.29abcd	17.5 ± 1.13ab	23.97 ± 1.31abc	0.38 ± 0.02ab
IS 23525	**G19**	**R**	7.97 ± 0.68abcd	7.42 ± 1.12abc	6.24 ± 0.13abcde	15.4 ± 1.63abcde	21.63 ± 1.72abcdef	0.42 ± 0.04ab
M 35-1	**G20**	**Check**	8.98 ± 0.71abc	7.15 ± 0.68abc	7.72 ± 0.38ab	16.1 ± 1.2abcd	23.85 ± 1.51abcd	0.49 ± 0.03ab
R 16	**G21**	**Check**	9.43 ± 0.31ab	6.47 ± 0.45bcde	6.55 ± 0.35abcd	15.9 ± 0.68abcd	22.44 ± 0.53abcdef	0.42 ± 0.04ab
REVT 18PR # 10	**G22**	**R**	7.93 ± 0.25abcd	5.17 ± 0.36bcdef	6.48 ± 0.97abcd	13.1 ± 0.35bcdef	19.57 ± 1.16abcdefgh	0.50 ± 0.07ab
REVT 18PR # 14	**G23**	**R**	9.62 ± 0.51ab	7.63 ± 0.3ab	6.83 ± 0.29abc	17.2 ± 0.78ab	24.07 ± 0.93ab	0.40 ± 0.02ab
REVT 18PR # 24	**G24**	**R**	9.77 ± 0.6ab	9.06 ± 0.75a	6.57 ± 0.33abcd	18.8 ± 1.06a	25.39 ± 1.17a	0.36 ± 0.03b
SPV 1411	**G25**	**R**	10.82 ± 0.52a	7.80 ± 0.32ab	6.83 ± 0.67abc	18.6 ± 0.84a	25.44 ± 0.83a	0.38 ± 0.05ab
		B mean	06.74 ± 0.42B	04.55 ± 0.33B	04.85 ± 0.28B	11.29 ± 0.73B	16.14 ± 0.97B	0.45 ± 0.02A
		R mean	09.08 ± 0.24A	06.99 ± 0.37A	06.69 ± 0.17A	16.06 ± 0.50A	22.75 ± 0.57A	0.43 ± 0.01A

Note: The traits include leaf dry weight (LDW; g), stem dry weight (StDW; g), root dry weight (RDW; g), shoot dry weight (Shoot DW; g), total biomass (TBM; g), and root-to-shoot ratio (R/S). Values are presented as means (± SE) of five replicated plants per genotype. Lowercase letters following means distinguish genotypes for each trait using Tukey's method at $p < 0.05$.

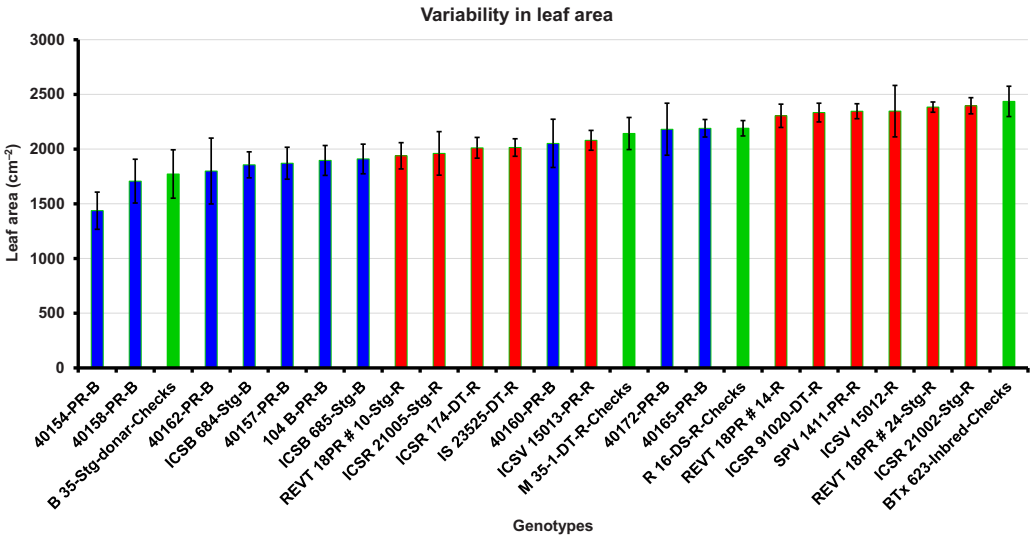

FIGURE 1 Genotypic variation in leaf area at 25 days after sowing (DAS) under well-watered conditions. The bars filled with red color represent R lines, blue color represents B lines, and green color represents checks. The data presented in the bar graphs are mean values with standard error (± SE).

no significant differences in TR were observed among genotypes (Table 3). However, at the highest VPD (4.66 kPa), the range of variation in TR was from 0.55 mg H_2O cm^{-2} min^{-1} for ICSR 21002 (Figure 2a) to 0.73 mg H_2O cm^{-2} min^{-1} for 40162 (Figure 2b). The B line check, BTx 623, exhibited the lowest TR, followed by ICSR 21002, REVT 18PR#14, and ICSV15012 (Table 3). Under high VPD conditions, the TR was lower in 50% of the R lines (5/10 lines) than in B lines (Table 3). Within R lines, TR varied from 0.50 to 0.58 mg H_2O cm^{-2} min^{-1}, with low TR found in ICSV 21002 and high TR in REVT 18PR#10. Similarly, within B lines, TR varied from 0.56 to 0.62 mg H_2O cm^{-2} min^{-1}, with low TR found in 40160 and high TR in 40162. The TR responses of both B and R group checks are detailed in Table 3. The TR response to increasing time and rising VPD in selected contrasting low and high TR lines of B and R groups, along with their respective checks, is illustrated in Figure 2a,b.

3.1.3 | Relationship between leaf area, transpiration, and biomass

A significant positive correlation was identified between leaf area and transpiration ($r^2 = 0.81$; $p < 0.001$), indicating that most of the R lines exhibited higher leaf area with increased transpiration (Figure 3a). However, the leaf area did not show a correlation with the slope of TR (Figure 3b). Moreover, leaf area demonstrated a significant correlation with root dry weight ($r^2 = 0.61$; $p < 0.001$; Figure 3c) and TBM ($r^2 = 0.60$; $p < 0.001$; Figure 3d). In summary, most of the R lines displayed higher leaf area, transpiration, root dry weight, and TBM, compared to the B lines.

3.2 | Soil drought experiment

3.2.1 | Effect of soil water deficit on plant growth

Variation in plant growth and biomass traits at the end of the dry-down experiment (45 DAS) under both WW and WS conditions is presented in Table 4. Under WW conditions, R lines exhibited higher plant growth, water use, and biomass-related traits such as LDW, StDW, RDW, ShootDW, TBM, and PH compared to B lines (Table 4). The interaction between genotype and environment (G × E) significantly influenced plant growth, water use, and biomass-related parameters (Table 4). R line genotypes ICSV 15012 and REVT 18 PR# 24 showed higher TBM and RDW (Table 4). TOT-T was highest in M35-1 (R line check) and REVT 18 PR# 24 (R lines), and lowest in 40157 (B lines; Table 4). The highest transpiration efficiency (TE) was recorded in ICSR 21005, followed by ICSV 15012, while the lowest was observed in 40157, followed by ICSB 684 (Table 4). PH was highest in ICSV 15013 (R line), followed by M35-1 (R line check) and REVT 18 PR# 24 (R line), with the lowest found in ICSB 684 and ICSB 685 (B lines; Table 4). R line checks (M35-1 and R16) exhibited higher PH, TBM, RDW, TOT-T, and TE than B line checks (B35 and BT x 623).

Under WS conditions, plant growth, water use, and biomass-related traits, including LDW, StDW, RDW, ShootDW, TBM, PH, and TOT-T, were higher in R lines compared to B lines (Table 4). A significant interaction between genotype (G) and environment (E) (G × E) influenced the variation in plant growth, water use, and biomass-related parameters (Table 4). TBM was highest in

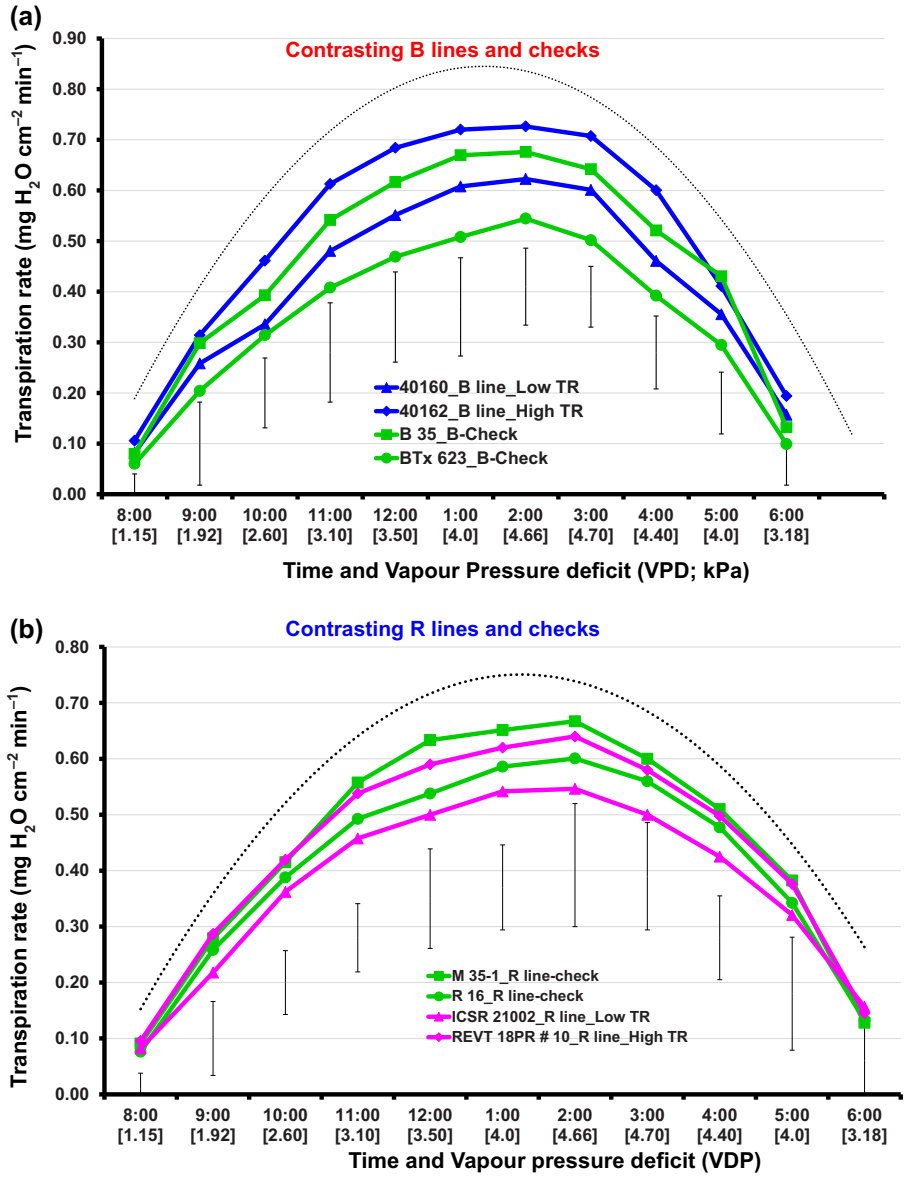

FIGURE 2 (a) Transpiration rate response of selected B lines (low transpiration rate [TR; 40160; triangle with blue line] and high TR [40162; diamond with blue line]) checks (B35 [square with green line] and BT x 623 [round with green line]) in response to natural changing atmospheric vapor pressure deficit (VPD) cycle and time. Plants were grown under well-watered condition in the glasshouse and temporarily transferred to outdoor conditions during experimentation exposing them to naturally changing atmospheric VPD. Bars at each measurement time indicate the least significant difference (LSD) for genotypes means ($n = 5$). The dotted line represents the fitting of VPD over the course of the day. (b) Transpiration rate response of selected R lines (low transpiration rate[TR; ICSR 21002; triangle with pink line] and high TR [REVT18PR#10; diamond with pink line]) and their checks (M35 [square with green line] and R16 [round with green line]) in response to natural variations in the atmospheric vapor pressure deficit (VPD) cycle and time. Transpiration rates were measured on well-watered plants initially grown in the glasshouse, which were then temporarily transferred to outdoor conditions, exposing them to the natural variations in atmospheric VPD. Each data point represents the means (± SE) of five replicates per genotype. Bars at each measurement time represent the least significant difference (LSD) for genotype means ($n = 5$). The dotted line represents the fitting of VPD over the course of the day.

SPV 1411, followed by ICSV 15012 and REVT 18 PR# 24 (R lines), and lowest in 40154 and ICSB 684 (B lines; Table 4). RDW was higher in SPV 1411 and ICSV 15012, and lower in 40154 and ICSB 684. Genotypes ICSV 15012 and ICSV 15013 had higher TOT-T, whereas 40154 and ICSB 684 had lower TOT-T (Table 4). TE was highest in SPV 1411 and REVT 18 PR# 14, and lowest in 40157. PH was highest in ICSV 15013 (R line), followed by REVT 18 PR# 24 (R line), and lowest in ICSB 684 (B line) and B 35 (B check; Table 4). R line checks (M35-1 and R16) exhibited higher PH, TBM, RDW, TOT-T, and TE than B line checks (B35 and BT x 623). In summary, most of the R lines demonstrated

TABLE 3 Results of regression analysis for the transpiration response of 25-day-old sorghum genotypes to naturally changing atmospheric vapor pressure deficit (VPD) outdoors under well-watered conditions.

Genotypes	Groups	Mean of high VPD transpiration rate (2.6–4.7 kPa)	Mean of low VPD transpiration rate (1.1–1.92 kPa)
BTx 623	B-check	0.46 ± 0.02 c	0.10 ± 0.01a
40160	B	0.56 ± 0.02abc	0.13 ± 0.01a
40172	B	0.56 ± 0.01abc	0.13 ± 0.01a
40165	B	0.56 ± 0.02abc	0.15 ± 0.02a
ICSB 684	B	0.57 ± 0.02abc	0.14 ± 0.01a
ICSB 685	B	0.57 ± 0.02abc	0.14 ± 0.02a
104B	B	0.59 ± 0.04ab	0.14 ± 0.01a
B 35	B-check	0.59 ± 0.03ab	0.14 ± 0.02a
40158	B	0.60 ± 0.04ab	0.15 ± 0.02a
40157	B	0.61 ± 0.03ab	0.14 ± 0.02a
40154	B	0.61 ± 0.05ab	0.15 ± 0.02a
40162	B	0.62 ± 0.04a	0.13 ± 0.03a
ICSR 21002	R	0.50 ± 0.02 bc	0.11 ± 0.01a
REVT 18PR # 14	R	0.53 ± 0.02abc	0.13 ± 0.01a
ICSV 15012	R	0.53 ± 0.03abc	0.14 ± 0.02a
R 16	R-check	0.53 ± 0.01abc	0.13 ± 0.01a
SPV 1411	R	0.54 ± 0.02abc	0.13 ± 0.02a
ICSR 91020	R	0.54 ± 0.02abc	0.13 ± 0.02a
ICSR 21005	R	0.56 ± 0.03abc	0.14 ± 0.02a
ICSV 15013	R	0.56 ± 0.01abc	0.14 ± 0.01a
IS 23525	R	0.56 ± 0.02abc	0.13 ± 0.01a
ICSR 174	R	0.57 ± 0.03abc	0.15 ± 0.02a
M 35-1	R-check	0.58 ± 0.03abc	0.14 ± 0.02a
REVT 18PR # 24	R	0.58 ± 0.02ab	0.15 ± 0.02a
REVT 18PR # 10	R	0.58 ± 0.03ab	0.15 ± 0.02a
	B lines mean	0.57 ± 0.01	0.131 ± 0.004
	R lines mean	0.55 ± 0.01	0.132 ± 0.002

Note: The mean values of transpiration rate (TR) at high vapor pressure deficit (VPD) were calculated as the average of TR values corresponding to 2.6–4.70 kPa, while the mean values at low VPD were obtained by averaging TR values corresponding to 1.12–1.92 kPa. These mean values were derived from five replications per genotype. Transpiration rates at high and low VPD identified with the same letter are not statistically different from each other based on Tukey's test ($p > 0.05$).

higher plant growth, water use, and biomass than the B lines in both WW and WS conditions, with significant G × E interactions.

3.2.2 | Response of plant transpiration to progressive soil drying

The sensitivity of plants to soil moisture deficit can be assessed by the soil moisture threshold, denoted as FTSW, at which there is a significant decrease in plant transpiration compared to WW plants. In this experiment, transpiration started declining at FTSW values ranging between 0.38 and 0.65 (Table 5; Figure 4). The lowest FTSW was recorded in ICSR 174 (0.38), followed by ICSR 91020, and the highest was recorded in 40162 (0.65), followed by ICSR 21005 (0.65; Table 4). A substantial range of variation was observed for both R and B lines (Table 5; Figure 4).

Among the R lines, the lowest NTR-FTSW threshold value (0.38) was observed in ICSR 174 (Figure 4a), while the highest NTR-FTSW threshold value (0.65) was seen in ICSR 21005 (Figure 4b). Both R line checks (M35-1 and R16) exhibited NTR-FTSW threshold values of 0.50 (further details in Table 5; Figure 4c). Significant variations in NTR values among the R lines and checks were observed at 0.50 and 0.25 FTSW (Figure 5c,d). At 0.50 FTSW, the highest NTR values were recorded in M35-1 and R16 (R line checks), followed by ICSV 15013 and ICSR 174 (R lines), with the lowest observed in ICSR 21005 and REVT 18PR#10 (Figure 5c). At 0.25 FTSW, ICSR 174 and

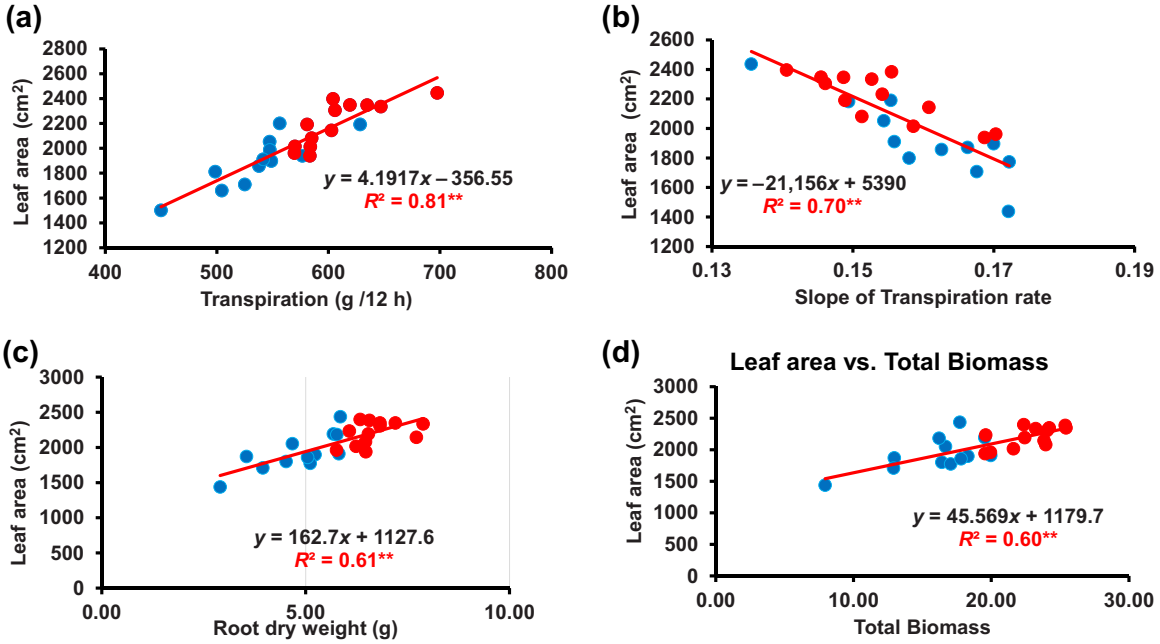

FIGURE 3 Relationships between leaf area and: (a) transpiration; (b) slope of transpiration rate; (c) root dry weight; and (d) total biomass under well-watered (WW) conditions. The dataset employed for these regression analyses consists of mean values, with each genotype mean derived from five replicates. Data points for R lines are illustrated in red, while those for B lines are in blue. The figures present the slopes and R2 values of the regressions, with ** denoting significance at $p < 0.001$.

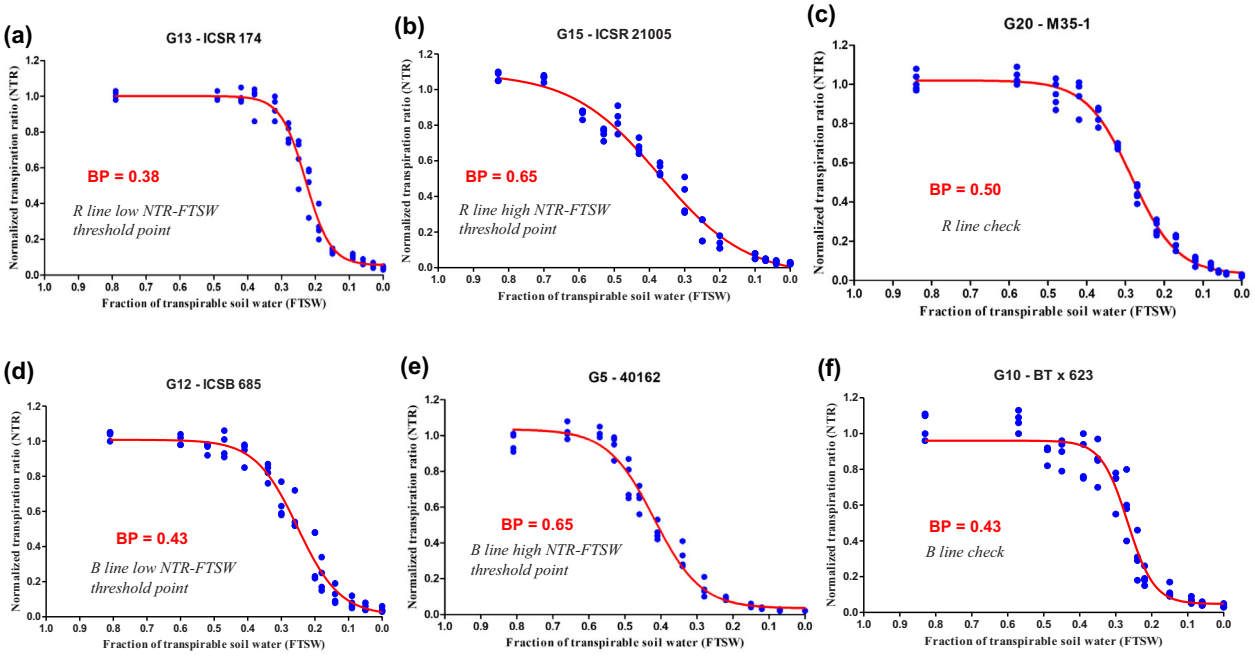

FIGURE 4 Comparison of normalized transpiration ratio (NTR) and fraction of transpirable soil water (FTSW) for selected R lines (a) ICSR 174, (b) ICSR 21005, and (c) M35-1 and B lines (d) ICSB 685, (e) 40162, and (f) BT x 623 genotypes subjected to progressive soil drying under glasshouse conditions. Transpiration data for each genotype at different FTSW conditions were collected from five replicated plants. FTSW thresholds indicating the initiation of transpiration decline were determined using a segmental linear regression procedure in GraphPad Prism. The regression lines illustrating the relationship between NTR and FTSW were fitted using GraphPad Prism, with the FTSW breakpoint (BP) of regressions presented in the figures.

TABLE 4 Summary of means and two-way analysis of variance (ANOVA) for biomass-related traits measured in R and B lines under well-watered (WW) conditions and progressive soil drying in the glasshouse environment.

			Leaf dry weight (g)		Stem dry weights (g)		Root dry weights (g)		Shoot dry weights (g)		Total biomass (g)		Root/Shoot Ratio		Stem girth (mm)		Plant height (cm)		Total transpiration (kg)		Transpiration efficiency (g/kg)	
Geno	Group	Genotype	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
1	B	40154	12.50 ± 0.29fgh	08.63 ± 0.84e	10.50 ± 0.87hi	6.35 ± 0.58de	06.92 ± 0.53fgh	4.23 ± 0.43d	23.00 ± 1.16gh	07.49 ± 0.43e	29.92 ± 1.68hi	19.20 ± 1.19h	0.30 ± 0.01abcd	0.57 ± 0.05a	14.14 ± 0.79ab	9.12 ± 0.68abc	99.50 ± 2.60hij	74.67 ± 2.91hij	3.15 ± 0.06hi	1.19 ± 0.03j	9.53 ± 0.68fg	16.20 ± 1.23abc
2	B	40157	10.38 ± 0.88gh	11.51 ± 0.72bcde	08.05 ± 0.44i	7.61 ± 0.83de	05.35 ± 0.25h	4.92 ± 0.67d	18.44 ± 1.25h	09.57 ± 0.76cde	23.78 ± 1.46i	24.04 ± 2.13gh	0.29 ± 0.01abcd	0.51 ± 0.05a	13.19 ± 0.70abc	7.69 ± 0.38bc	105.5 ± 4.91ghij	101.2 ± 6.01cdefgh	2.88 ± 0.13i	2.01 ± 0.09defgh	8.28 ± 0.36g	11.91 ± 0.66c
3	B	40158	19.94 ± 1.13ab	13.69 ± 0.52abcd	18.95 ± 0.71defgh	8.98 ± 0.63cde	10.57 ± 0.36cdef	6.32 ± 0.72bcd	38.89 ± 1.06cde	11.34 ± 0.55bcd	49.46 ± 1.27def	28.99 ± 1.76cdefg	0.27 ± 0.01abcd	0.56 ± 0.05a	14.09 ± 1.12ab	7.84 ± 0.72bc	98.00 ± 1.77j	93.60 ± 3.7fghij	4.71 ± 0.16abcd	1.84 ± 0.07fghi	10.5 ± 0.27defg	15.89 ± 1.14abc
4	B	40160	12.64 ± 0.21fgh	11.69 ± 1.02bcde	16.73 ± 1.95fghi	8.99 ± 0.48cde	07.91 ± 0.62efgh	5.24 ± 0.45cd	29.37 ± 1.94efgh	10.34 ± 0.52cde	37.28 ± 2.33fghi	25.92 ± 1.34efgh	0.27 ± 0.02abcd	0.51 ± 0.04a	11.00 ± 0.73abcde	8.87 ± 0.23abc	105.6 ± 6.8ghij	92.30 ± 4.44fghij	3.70 ± 0.22fghi	1.81 ± 0.04ghi	10.1 ± 0.47fg	14.33 ± 0.56abc
5	B	40162	15.16 ± 0.35abcdefg	15.52 ± 0.87abc	12.82 ± 0.35hi	10.8 ± 0.48bcd	06.06 ± 0.30gh	6.90 ± 0.69abcd	27.99 ± 0.47efgh	13.19 ± 0.54abc	34.04 ± 0.57ghi	33.27 ± 1.59abcdef	0.22 ± 0.01d	0.53 ± 0.05a	14.27 ± 0.74ab	8.30 ± 0.6abc	148.6 ± 5.39bcdef	99.00 ± 3.07defghi	3.58 ± 0.18ghi	2.37 ± 0.06abcd	9.58 ± 0.33fg	14.11 ± 0.72abc
6	B	40165	13.49 ± 0.62efgh	12.47 ± 0.84abcde	17.14 ± 0.93fghi	7.76 ± 0.96de	10.58 ± 0.28cdef	5.42 ± 0.54cd	30.63 ± 1.23efg	10.12 ± 0.81cde	41.21 ± 1.38efgh	25.65 ± 2.16fgh	0.35 ± 0.01ab	0.54 ± 0.02a	11.79 ± 1.27abcd	8.40 ± 0.28abc	142.1 ± 9.55cdef	90.38 ± 7.72fghij	4.75 ± 0.19abcd	1.82 ± 0.03fghi	8.76 ± 0.51g	14.15 ± 1.14abc
7	B	40172	13.81 ± 1.46defgh	14.39 ± 0.65abc	18.60 ± 2.27efghi	7.69 ± 0.5de	09.74 ± 0.25cdefg	6.72 ± 0.22abcd	32.41 ± 2.86defg	11.04 ± 0.45cde	42.14 ± 2.98efgh	28.80 ± 0.99cdefg	0.31 ± 0.02abcd	0.62 ± 0.03a	12.32 ± 0.34abcd	8.20 ± 0.4abc	132.7 ± 9.35defghi	92.30 ± 3.18fghij	5.01 ± 0.23abc	1.91 ± 0.07fghi	8.55 ± 0.94g	15.17 ± 0.5abc
8	B	104 B	15.58 ± 0.99abcdef	13.40 ± 0.59abcde	22.64 ± 2.28cdefg	10.1 ± 0.79bcde	09.90 ± 1.11cdef	6.75 ± 0.38abcd	38.23 ± 2.93cde	11.74 ± 0.19bc	48.12 ± 3.48def	30.23 ± 0.6bcdefg	0.26 ± 0.03abcd	0.58 ± 0.03a	10.39 ± 0.43bcde	8.79 ± 0.45abc	161.8 ± 7.89bcd	108.6 ± 5.81cdefg	4.87 ± 0.2abc	1.98 ± 0.03efgh	9.85 ± 0.38fg	15.35 ± 0.32abc
9	B	ICSB 684	08.88 ± 0.45h	10.05 ± 0.44de	16.25 ± 0.95ghi	6.29 ± 0.61e	05.87 ± 0.41gh	4.36 ± 0.13d	31.23 ± 1.92fgh	08.17 ± 0.45de	31.00 ± 0.91hi	20.70 ± 0.98h	0.23 ± 0.01cd	0.54 ± 0.03a	12.13 ± 0.34abcd	8.69 ± 0.22abc	91.90 ± 4.2j	66.50 ± 2.74j	3.74 ± 0.09efghi	1.60 ± 0.04i	8.33 ± 0.36g	13.05 ± 0.71abc
10	B	ICSB 685	12.41 ± 0.99fgh	11.34 ± 0.19cde	16.81 ± 1.53fghi	8.32 ± 0.81de	07.08 ± 0.77fgh	5.64 ± 0.56cd	37.66 ± 0.88efgh	09.83 ± 0.45cde	36.30 ± 1.66fghi	25.30 ± 1.39fgh	0.25 ± 0.04bcd	0.57 ± 0.04a	10.28 ± 0.84bcde	8.69 ± 0.54abc	91.25 ± 5.54j	85.20 ± 3.84ghij	3.63 ± 0.22ghi	1.68 ± 0.04hi	9.54 ± 0.32fg	15.09 ± 0.85abc
11	B-check	B 35	13.85 ± 0.85defg	13.15 ± 0.65abcde	17.37 ± 1.19fghi	7.96 ± 0.76de	09.20 ± 0.62defgh	5.27 ± 0.56cd	25.13 ± 0.63efg	10.56 ± 0.59cde	40.43 ± 2.21fgh	26.37 ± 1.63efgh	0.3 ± 0.02abcd	0.50 ± 0.04a	13.33 ± 0.41ab	7.26 ± 0.25c	106.5 ± 7.01ghij	71.50 ± 6.25ij	4.20 ± 0.24cdefg	2.03 ± 0.07defg	9.71 ± 0.56fg	13.05 ± 0.73abc
12	B-check	BTx 623	14.39 ± 0.37cdefg	13.04 ± 0.92abcde	23.26 ± 0.67cdefg	9.47 ± 1.24bcde	09.29 ± 0.35defgh	5.58 ± 0.43cd	29.22 ± 1.79cde	11.26 ± 0.65bcd	46.95 ± 0.65defg	28.09 ± 1.6defgh	0.25 ± 0.01bcd	0.50 ± 0.04a	13.07 ± 0.66abc	7.78 ± 0.31bc	99.00 ± 3.56ij	82.20 ± 5.37ghij	4.62 ± 0.22abcde	2.09 ± 0.08defg	10.2 ± 0.52efg	13.48 ± 0.76abc
13	R	ICSR 174	17.55 ± 0.93abcdef	11.84 ± 0.86abcde	17.91 ± 1.80fghi	8.60 ± 0.72de	11.09 ± 0.43cdef	6.44 ± 0.59abcd	35.47 ± 2.31cdefg	10.23 ± 0.19cde	46.55 ± 2.46defg	26.89 ± 0.48efgh	0.32 ± 0.02abcd	0.64 ± 0.07a	12.47 ± 0.73abc	7.83 ± 0.18bc	124.1 ± 5.3efghij	90.40 ± 3.33fghij	4.48 ± 0.19bcdef	2.14 ± 0.06cdef	10.4 ± 0.22efg	12.61 ± 0.42bc
14	R	ICSR 21002	20.53 ± 0.67abcd	15.55 ± 0.73abc	25.90 ± 1.08cdefg	10.4 ± 1.12bcde	11.51 ± 0.87cde	7.31 ± 0.44abcd	46.44 ± 1.31bcd	13.00 ± 0.64abc	57.95 ± 2.07cde	33.29 ± 1.17bcdefg	0.25 ± 0.01abcd	0.57 ± 0.06a	12.69 ± 0.10abc	8.54 ± 0.31abc	136.9 ± 5.93defgh	103.5 ± 2.33cdefgh	4.72 ± 0.18bcde	2.03 ± 0.04defg	12.0 ± 0.18bcdef	16.47 ± 0.52abc
14	R	ICSR 21005	14.14 ± 0.95abcdefg	13.45 ± 1.17abcde	17.75 ± 1.31defghi	7.37 ± 0.53de	12.25 ± 0.85bcd	5.43 ± 0.49cd	31.90 ± 2.06cdefg	10.41 ± 0.82cde	44.14 ± 2.66defg	26.25 ± 2.02efgh	0.39 ± 0.02a	0.53 ± 0.04a	14.91 ± 0.93a	9.40 ± 0.22abc	110.0 ± 6.2ghij	85.38 ± 5.61ghij	3.22 ± 0.14hi	1.88 ± 0.06fghi	13.9 ± 1.26a	14.01 ± 0.9abc
16	R	ICSR 91020	19.67 ± 1.93abc	14.83 ± 0.69abc	17.11 ± 1.50fghi	9.57 ± 0.66bcde	11.95 ± 1.89cd	6.46 ± 0.35abcd	36.78 ± 3.35cdef	12.20 ± 0.67bc	48.73 ± 5.11def	30.85 ± 1.64bcdefg	0.32 ± 0.03abcd	0.54 ± 0.02a	14.38 ± 1.46ab	9.63 ± 0.52ab	100.1 ± 7.04hij	91.30 ± 3.23fghij	3.98 ± 0.15defgh	2.31 ± 0.07abcd	12.3 ± 1.25abcdef	13.40 ± 0.7abc
17	R	ICSV 15012	20.76 ± 0.56a	15.50 ± 0.68abc	30.76 ± 2.52abc	13.2 ± 1.08ab	17.25 ± 1.11ab	8.95 ± 0.77a	51.52 ± 1.97ab	14.34 ± 0.63ab	68.77 ± 2.38ab	37.62 ± 1.74ab	0.34 ± 0.02abc	0.63 ± 0.05a	11.51 ± 0.60abcde	8.47 ± 0.43abc	161.2 ± 6.23bcd	128.1 ± 2.61abc	5.09 ± 0.11ab	2.55 ± 0.1a	13.6 ± 0.44ab	14.84 ± 0.62abc
18	R	ICSV 15013	14.32 ± 0.43defg	13.21 ± 0.62abcde	39.03 ± 1.46a	16.1 ± 0.89a	11.87 ± 0.77cd	7.21 ± 0.27abcd	53.35 ± 1.73ab	14.65 ± 0.59ab	65.22 ± 2.04abc	36.49 ± 1.19abcd	0.22 ± 0.01cd	0.50 ± 0.03a	07.61 ± 0.20e	8.40 ± 0.31abc	198.4 ± 6.99a	151.7 ± 3.93a	5.01 ± 0.17abc	2.50 ± 0.1ab	13.1 ± 0.22abc	14.66 ± 0.7abc
19	R	IS 23525	20.14 ± 0.92a	13.57 ± 0.98abcde	25.52 ± 3.38bcdef	10.3 ± 0.5bcde	11.96 ± 0.28cd	5.91 ± 0.51bcd	45.67 ± 3.03abc	11.93 ± 0.63bc	57.62 ± 3.01bcd	29.76 ± 1.52bcdefg	0.27 ± 0.02abcd	0.50 ± 0.05a	09.26 ± 1.11cde	8.28 ± 0.22abc	158.4 ± 3.39bcd	130.0 ± 7.74abc	5.12 ± 0.14ab	2.11 ± 0.02cdefg	11.2 ± 0.35bcdef	14.17 ± 0.86abc
20	R	REVT 18PR # 10	14.96 ± 0.67bcdefg	12.71 ± 1.75abcde	20.75 ± 1.49defgh	8.11 ± 0.93de	11.50 ± 0.65cde	6.83 ± 0.49abcd	53.81 ± 1.69cdefg	10.41 ± 1.33cde	47.21 ± 1.29defg	27.64 ± 2.72defgh	0.32 ± 0.02abcd	0.70 ± 0.13a	13.38 ± 1.24ab	10.1 ± 0.6a	120.4 ± 9.41fghij	96.75 ± 5.3efghi	4.40 ± 0.08bcdefg	2.18 ± 0.17bcdef	10.9 ± 0.14bcdefg	12.68 ± 0.75bc
21	R	REVT 18PR # 14 (ICSV 15014)	18.61 ± 0.97abcde	15.57 ± 1.18ab	24.91 ± 1.72bcdefg	13.2 ± 0.55ab	11.19 ± 0.17cdef	7.76 ± 0.12abc	45.69 ± 0.88abcd	14.41 ± 0.84ab	54.71 ± 2.26bcde	36.58 ± 1.72abc	0.26 ± 0.02abcd	0.55 ± 0.04a	10.46 ± 0.39bcde	9.00 ± 0.37abc	147.2 ± 5.35bcdef	124.0 ± 7.36abcde	5.11 ± 0.12ab	2.25 ± 0.08abcde	10.7 ± 0.25cdefg	16.31 ± 0.75ab

(Continues)

TABLE 4 (Continued)

Geno	Group	Genotype	Leaf dry weight (g)		Stem dry weights (g)		Root dry weights (g)		Shoot dry weights (g)		Total biomass (g)		Root/Shoot Ratio		Stem girth (mm)		Plant height (cm)		Total transpiration (kg)		Transpiration efficiency (g/kg)	
			WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
22	R	REVT 18PR # 24	18.94 ± 1.01abcd	15.63 ± 0.44ab	31.40 ± 1.21abc	13.0 ± 1.29abc	17.10 ± 0.87ab	8.51 ± 0.46ab	35.71 ± 1.3ab	14.34 ± 0.72ab	67.44 ± 2.58ab	37.18 ± 1.74ab	0.34 ± 0.01ab	0.60 ± 0.03a	10.26 ± 0.42bcde	9.17 ± 0.35abc	173.6 ± 6.08abc	136.6 ± 10.37ab	5.23 ± 0.05ab	2.43 ± 0.05abc	12.9 ± 0.42abcd	15.34 ± 0.62abc
23	R	SPV 1411	17.66 ± 1.52abcdef	15.99 ± 0.95a	28.03 ± 3.36bcde	15.6 ± 0.69a	13.51 ± 0.64abc	8.96 ± 0.48a	43.52 ± 2.29abc	15.81 ± 0.79a	59.20 ± 4.81abcd	40.57 ± 1.86a	0.3 ± 0.03abcd	0.57 ± 0.03a	07.95 ± 0.88de	9.36 ± 0.28abc	157.2 ± 3.87bcde	127.4 ± 4.21abcd	4.71 ± 0.16abcd	2.43 ± 0.06abc	12.8 ± 0.84abcde	16.79 ± 0.76a
24	R-check	M 35-1	19.47 ± 0.75abc	12.92 ± 0.35bcde	34.33 ± 1.69ab	12.8 ± 0.38abc	17.38 ± 0.66a	8.93 ± 0.65a	50.34 ± 1.94a	12.87 ± 0.18abc	71.19 ± 1.72a	34.65 ± 0.81abcde	0.32 ± 0.02abc	0.70 ± 0.05a	11.78 ± 0.23abcd	8.98 ± 0.33abc	178.3 ± 6.98ab	124.9 ± 4.19abcde	5.50 ± 0.14a	2.28 ± 0.04abcde	13.0 ± 0.44abcd	15.25 ± 0.49abc
25	R-check	R 16	16.73 ± 0.53abcdef	11.73 ± 0.82bcde	28.95 ± 1.09bcd	12.8 ± 0.96abc	12.95 ± 1.13cd	7.19 ± 0.26abcd	45.70 ± 4.45abc	12.27 ± 0.6bc	58.64 ± 0.67abcd	31.71 ± 1.13bcdefg	0.29 ± 0.03abcd	0.60 ± 0.05a	12.41 ± 0.63abc	9.16 ± 0.54abc	139.5 ± 7.03cdefg	112.9 ± 7.24bcdef	5.02 ± 0.11abc	2.31 ± 0.08abcd	11.7 ± 0.33bcdef	13.76 ± 0.43abc
		B mean	13.59 ± 0.8B	12.41 ± 0.55B	16.59 ± 1.28B	8.36 ± 0.4B	08.21 ± 0.55B	5.61 ± 0.27B	30.18 ± 1.8B	10.39 ± 0.45B	38.39 ± 2.27B	26.38 ± 1.14B	0.27 ± 0.01B	0.54 ± 0.02A	12.50 ± 0.41A	8.3 ± 0.17	115.21 ± 7.02B	88.13 ± 3.64B	4.07 ± 0.21B	1.86 ± 0.09B	9.42 ± 0.23B	14.32 ± 0.38A
		R mean	17.96 ± 0.64A	14.04 ± 0.42A	26.33 ± 1.87A	11.6 ± 0.78A	13.19 ± 0.67A	7.38 ± 0.33A	44.3 ± 2.02A	12.84 ± 0.51A	57.49 ± 2.49A	33.04 ± 1.28A	0.3 ± 0.01A	0.59 ± 0.02A	11.47 ± 0.64A	8.95 ± 0.18	146.58 ± 7.9A	115.6 ± 5.7A	4.74 ± 0.17A	2.26 ± 0.06A	12.2 ± 0.32A	14.64 ± 0.38A

Two-way-ANOVA		LDW	StDW	RDW	Shoot DW	TBM	Root/shoot ratio	Stgirth (mm)	Plant height; PH (cm)	Total transpiration; TOT-T (kg)	TE (g/kg)
Genotype (G)	*F* value	13.47	2.46	26.21	24.31	33.77	2.91	4.98	38.32	25.83	7.62
	p value	<0.00001	<.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001
Treatment (T)	*F* value	101.89	882.69	587.37	3156.08	961.26	744.41	357.94	303.54	4239.47	401.32
	p value	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001	<0.00001
G × T interaction	*F* value	3.71	7.51	7.29	12.37	8.9	1.17	5.74	3.31	108.69	4.16
	p value	<0.00001	<.00001	<0.00001	<0.00001	<0.00001	0.2775	<0.00001	<0.00001	<0.00001	<0.00001

Note: The mean values (± SE) are derived from five replications per genotype. Mean values followed by the same lowercase letter indicate the absence of genotypic differences. Outputs from the analysis of genotype, environment, and genotype × environment interaction effects on various growth and water use-related traits are presented at the bottom of the table. Uppercase letters following mean values distinguish between B and R line groups for each trait based on Tukey's test ($p > 0.05$).

Abbreviations: LDW, leaf dry weight; PH, plant height; RDW, root dry weight; Shoot DW, shoot dry weight; StDW, stem dry weight; TBM, total biomass; TE, transpiration efficiency; TOT-T, total transpiration; WS, water-stressed.

TABLE 5 NTR-FTSW (normalized transpiration ratio-fraction of transpirable soil water) threshold values for the 25 sorghum genotypes cultivated under progressive soil drying conditions in the glasshouse.

Genotypes	Lines	NTR-FTSW threshold point (break point)	Standard error	95% Confidence intervals
G12-ICSB 685	B	0.43	0.024	0.3864–0.4723
G10-BT x 623	B-check	0.43	0.032	0.3621–0.4890
G7-40172	B	0.46	0.030	0.3984–0.5191
G9-B 35	B-check	0.50	0.031	0.4670–0.5810
G11-ICSB 684	B	0.53	0.023	0.4837–0.5763
G8-104B	B	0.54	0.044	0.4513–0.6287
G1-40154	B	0.60	0.032	0.5600–0.6203
G6-40165	B	0.60	0.021	0.5670–0.6810
G4-40160	B	0.63	0.036	0.5652–0.7204
G3-40158	B	0.64	0.035	0.5952–0.7003
G2-40157	B	0.64	0.034	0.5752–0.7103
G5-40162	B	0.65	0.033	0.5870–0.7209
G13-ICSR 174	R	0.38	0.021	0.3403–0.4233
G16-ICSR 91020	R	0.41	0.023	0.3586–0.4517
G17-ICSV 15012	R	0.44	0.022	0.3984–0.4843
G18-ICSV 15013	R	0.44	0.020	0.4042–0.4827
G25-SPV1411	R	0.48	0.021	0.4621–0.5131
G19-IS 23525	R	0.49	0.018	0.4521–0.5231
G20-M35-1	R-check	0.50	0.024	0.4505–0.5463
G21-RI6	R-check	0.50	0.029	0.4423–0.5577
G14-ICSR 21002	R	0.53	0.030	0.4737–0.5663
G22-REVT-18PR≠10	R	0.57	0.032	0.5052–0.6322
G24-REVT-18PR≠24	R	0.58	0.040	0.4951–0.6570
G23-REVT-18PR≠14	R	0.62	0.037	0.5552–0.7104
G15-ICSR 21005	R	0.65	0.035	0.5776–0.7019

Note: The FTSW thresholds were calculated using the segmental regression procedure, incorporating standard error and confidence intervals. The presented data represent the means obtained from five replicates per genotype.

ICSR 21005 exhibited the highest NTR value, while lower NTR values were found in SPV 1411 and REVT 18PR#10 (Figure 5d).

Among the B lines, ICSB 685 demonstrated the lowest NTR-FTSW threshold value at 0.43 (Figure 4d), whereas 40162 exhibited the highest at 0.65 (Figure 4e). The NTR-FTSW threshold values for the B line checks, BT x 623 and B 35, were recorded as 0.43 and 0.50, respectively (as detailed in Table 5; Figure 4f). Notably, there was considerable variation in NTR values among the B lines and their checks at both 0.50 and 0.25 FTSW (Figure 5a,b). At 0.50 FTSW, the highest NTR values were observed in BT x 623 (B line check), followed by ICSB 685 (R lines), while the lowest values were found in 40160 and 40162 (Figure 5a). At 0.25 FTSW, R line genotypes 40154 and BT x 623 (B line check) exhibited higher NTR values, whereas lower NTR values were evident in 40162 and 40158 (Figure 5b). In summary, most of the R lines displayed higher NTR values compared to the B lines at both 0.50 and 0.25 FTSW.

3.2.3 | Relationship between plant water use and biomass traits

Under both WW and WS conditions, a strong positive correlation was observed between TE and TBM ($r^2 = 0.69$; $p < 0.001$ in WW and $r^2 = 0.45$; $p < 0.001$ in WS). Most of the R lines exhibited higher biomass along with higher TE (Figure 6b). Leaf area, measured in both the VPD and dry-down experiments, showed a negative correlation ($r^2 = 0.31$; $p < 0.001$) with most R lines having higher leaf area associated with lower NTR-FTSW threshold values (Figure 6a). The NTR-FTSW threshold value demonstrated a negative correlation with the slope of TR, LA, RDW, and TBM from the VPD

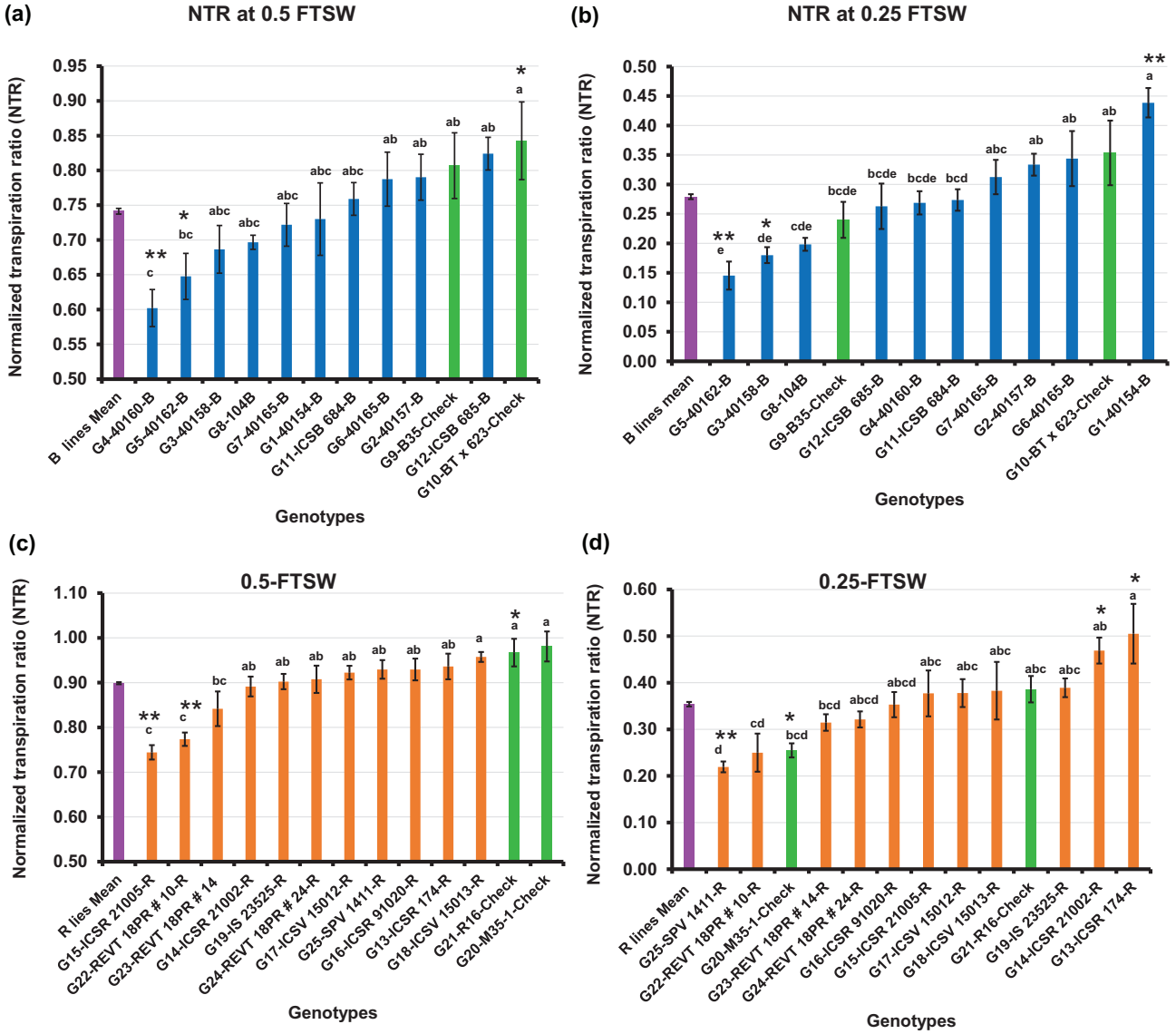

FIGURE 5 Variation in normalized transpiration ratio (NTR) for R lines (a) 0.5 FTSW (fraction of transpirable soil water) and (b) 0.25 FTSW, and B lines (c) 0.5 FTSW and (d) 0.25 FTSWat different FTSW conditions. Blue-filled bars represent B lines, and brown-filled bars represent R lines. Additionally, checks of both B and R lines are depicted in green, and the mean of both B and R lines is represented by pink bars. The bar graph is based on mean data obtained from water stress of NTR data, using data points from five replications for each genotype. Bars with different alphabet letters are significantly different ($p < 0.05$), while identical letters denote nonsignificance. Bars marked with * indicate genotypes that are significantly different ($p < 0.05$) from the mean data of B or R lines (pink bars data).

experiment (details in Table 6). Additionally, TE from WW and WS conditions exhibited a significant positive correlation with biomass (Table 6).

4 | DISCUSSION

In controlled glasshouse conditions, significant differences in biomass at 25 DAS were noted among sorghum genotypes under WW conditions. Notably, several R lines demonstrated higher biomass production compared to B lines, aligning with findings from prior studies (Chaudhary et al., 2020). This suggests a trend where R lines exhibit enhanced photosynthetic assimilate production and increased biomass yields, attributes previously associated with higher grain yields in post-rainy cultivation (B. V. Reddy et al., 2007, 2012).

Moreover, R lines demonstrated greater leaf area, a trait strongly associated with high transpiration. Similar relationships between leaf area and transpiration have been reported in earlier studies on pearl millet and chickpea (Kholova et al., 2010; Sivasakthi et al., 2017, 2020). Additionally, significant differences in plant heights were observed between B and R lines, with B lines averaging between 91 and 162 cm (mean 115 cm) and R lines between 100 and 198 cm

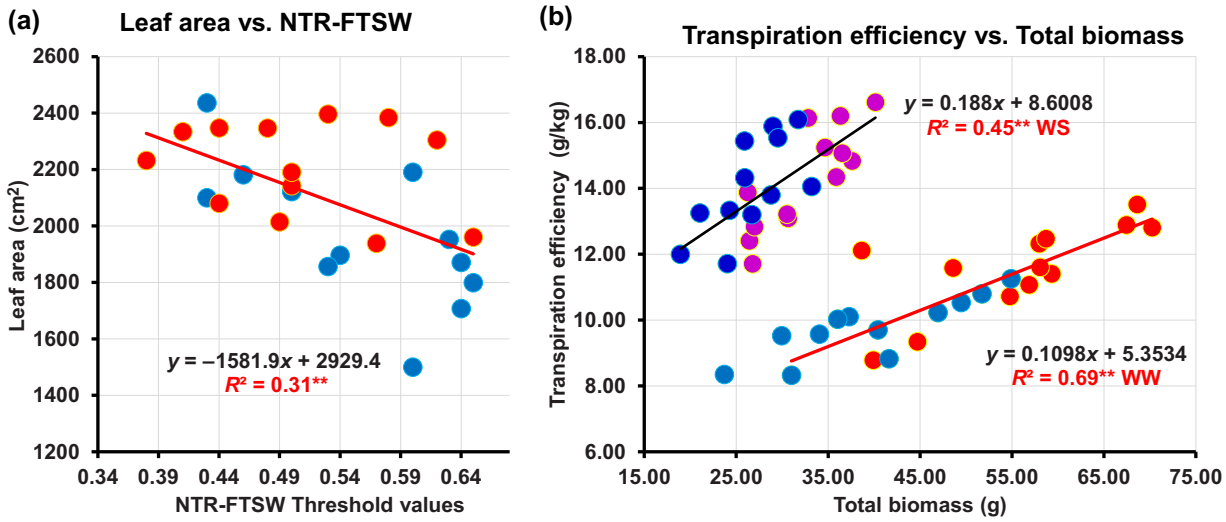

FIGURE 6 (a) Exploring the correlations between leaf area and the NTR-FTSW (normalized transpiration ratio-fraction of transpirable soil water) threshold point or break point (BP); (b) Investigating the relationships between transpiration efficiency and total biomass under well-watered (WW) and water-stressed (WS) conditions. The regression analyses utilize mean data, with each genotype mean derived from five replicates. Data points of R lines are denoted in red, while B lines are represented in blue. The figures showcase the R2 values of the regressions, with ** indicating significance at $p < 0.001$.

(mean 145 cm). This difference in height may contribute to the observed disparities in biomass traits between the two distinct gene pools.

In experiment 2, notable limitations in growth and biomass accumulation were observed among B lines compared to R line genotypes. R line genotypes showed better adaptation to available soil moisture under WW conditions, with the onset of transpiration decline in response to soil drying being delayed in most R lines compared to B lines. Similar findings were reported in studies on pearl millet (Kholova et al., 2010) and chickpea (Sivasakthi et al., 2017), where high-vigor genotypes exhibited higher growth and biomass under water-limited conditions.

Under WW conditions, notable variation in TE, defined as the ratio between TBM and water use, was evident between B and R line genotypes. This corresponds with the previous findings in sorghum (Hammer et al., 1998; Xin et al., 2009; Choudhary et al., 2020; Vadez et al., 2021), where TE variation under WW conditions has been documented. Intriguingly, under WS conditions, no significant difference in TE was observed between the R and B line groups. Within the R line groups, certain lines (SPV1411, ICSR 174, and REVT18#PR10) exhibited a notable range of variation in TE, whereas in the B line group, the variation in TE was insignificant. This observation is in line with earlier findings in sorghum (Vadez et al., 2011), where lines introgressed with stay-green quantitative trait loci (QTLs) showed higher TE in the R16 background but not in the S35 background, highlighting the dependency of TE expression on the genetic background.

TR plays a crucial role in regulating plant water loss, particularly for crops encountering drought conditions. Remarkably, certain R lines, including ICSR 21002, REVT 18PR # 14, ICSV 15012, R 16, SPV 1411, and ICSR 91020, exhibited lower TR during the vegetative stage under WW conditions compared to all genotypes in the B line group (excluding BT x 623) (Table 3). These findings are consistent with previous research on sorghum (Gholipoor et al., 2010), pearl millet (Kholova et al., 2010), and chickpea (Sivasakthi et al., 2017), where genotypes displaying lower canopy conductance at low VPD and further restriction of canopy conductance at high VPD were associated with reduced TR and increased biomass. Hence, genotypes that restrict TR, particularly under high VPD, have the potential for water conservation, which is crucial during the grain-filling stage (Sivasakthi et al., 2017, 2020; Vadez et al., 2013).

The concept of a limited TR holds particular significance in water-limited crop production environments. This notion finds support in studies such as Sinclair et al. (2005), which demonstrated a 65%–78% increase in sorghum yield in arid regions attributed to a limited TR, resulting in water conservation and improved TE. Similar results were reported by Kholova et al. (2014) in sorghum, highlighting the beneficial effect of constraining maximum TR on crop productivity under water-limited conditions.

Therefore, the capacity of crops to mitigate water loss under conditions of high evaporative demand, particularly through the regulation of TR, can lead to increased TE. Although this may result in a reduction in yield under WW conditions, it proves beneficial in arid environments typical

TABLE 6 Results of simple Pearson correlation analysis for 25 sorghum genotypes with selected traits.

Traits	*r* coefficient
BP_NTR_FTSW—LA_VPD	−0.54**
BP_NTR_FTSW—RDW_VPD	−0.56**
BP_NTR_FTSW—TBM_VPD	−0.41*
BP_NTR_FTSW—TOT-T_WW	−0.42*
BP_NTR_FTSW—TR_Slope_VPD	−0.46*
TE_WS—RDW_WS	0.51**
TE_WS—TBM_WS	0.43*
TE_WS—TBM_WW	0.67***
TE_WW - 0.50 FTSW	0.51**
TE_WW—LA_VPD	0.54**
TE_WW—RDW_VPD	0.63***
TE_WW—TBM_VPD	0.66***
TE_WW—TBM_WW	0.85***
TE_WW—RDW_WW	0.77***
TE_WW—TOT_WW	0.54**
TE_WW—TBM_WS	0.76***
TE_WW—RDW_WS	0.73***
TE_WW—TOT_WS	0.52**

Note: The data utilized for these correlation analyses represent mean values obtained from atmospheric and soil drought experiments. Each mean value is derived from five replications per genotype.
The correlation coefficient (r) values annotated with *, **, and *** symbols indicate significance at $p < 0.05$, $p < 0.001$, and $p < 0.0001$, respectively.

of post-rainy sorghum production as explained in Sinclair et al. (2010), Kholova et al. (2014), and Messina et al. (2015). Consequently, the trait of limited TR under high VPD assumes critical importance in breeding programs aimed at enhancing terminal drought tolerance, especially in regions characterized by high VPD and low soil moisture during the post-rainy crop season. This strategy underscores the significance of optimizing water use efficiency in water-limited environments to ensure sustainable crop production.

The observed variability in FTSW thresholds among different sorghum genotypes underscores the genetic diversity in their response to soil moisture deficit. In this study, R lines such as ICSR 174, ICSR 91020, ICSV 15012, ICSV 15013, SPV1411, and IS 23525 exhibited lower FTSW thresholds, indicating a delayed decline in transpiration during progressive soil drying. Conversely, B lines like ICSB 685 and 40172 demonstrated higher FTSW values, suggesting a comparatively faster reduction in transpiration under soil drought conditions. This trend is consistent with findings in sorghum (Gholipoor et al., 2012) and pearl millet (Kholova et al., 2010).

The slower decline in transpiration observed in certain R lines during soil drying may indicate a genotype-specific water conservation strategy. This strategy enables these sorghum varieties and hybrids to utilize available soil moisture for an extended duration, potentially enhancing their ability to withstand drought conditions. Such prolonged access to water could be particularly advantageous during the critical grain-filling phase in post-rainy seasons. Studies have highlighted genetic variability for NTR-FTSW thresholds in sorghum, underscoring the significance of comprehending and leveraging such traits in breeding programs (Choudhary et al., 2013; Gholipoor et al., 2012, 2019; Karthika et al., 2019).

4.1 | Strategies for post-rainy drought stress adaptation

An optimal sorghum ideotype for post-rainy cultivation would exhibit significant biomass and yield while efficiently utilizing available soil moisture by minimizing water loss during periods of high evaporative demand. This targeted breeding strategy has the potential to establish sorghum pipelines characterized by high water-use efficiency, leading to water conservation and ultimately successful post-rainy sorghum production. It is important to note that the selection of measurable physiological traits for drought adaptation is highly context-dependent, as highlighted by Tardieu et al. (2012). While acknowledging the context-specific impact of various drought-adaptive traits on yield (Varshney et al., 2021), we explore some essential traits suitable for water-limited or drought adaptations below.

1. Early vigor, defined as the extent of leaf area developed during the initial growth stage (25 DAS), significantly influences genotype-specific water use under drought conditions, ultimately determining crop production success. In this study, R line genotypes, specifically ICSR 21002, REVT18PR#24, ICSV 15012, and SPV1411, demonstrated notably high leaf area (>2300 cm^2) and biomass (>24 g), making them well-suited for the post-rainy season. This observation aligns with previous research indicating a 16% increase in wheat yield by selecting doubled early leaf sizes (Zhao et al., 2019). Simulation modeling has also suggested that a combination of traits, such as increased depth of water extraction and faster leaf area development, could enhance chickpea yield by 14% (Vadez et al., 2012). However, the significance of early vigor is context-dependent (Tardieu et al., 2012). In regions with limited water resources, such as the Mediterranean facing late-season droughts, the potential of early vigor in plants to enhance water-use efficiency has been recognized (Botwright et al., 2002; Rebetzke et al., 2009; Richards et al., 1987; Vukasovic et al., 2022). However,

it is crucial to consider the interplay of early vigor with variables like soil type, environmental factors, and the availability of sufficient nitrogen in fertilizers. This consideration is essential as it can result in either positive or negative impacts on yield based on the interaction, ultimately preventing adverse effects on crop production (Asseng & van Herwaarden, 2003).

2. The plant's ability to restrict transpiration under high VPD conditions may contribute to water conservation before flowering, ensuring water availability for grain filling during drought. However, the most significant impact of the limited-transpiration trait on yield is likely to be seen through an increased shift in water use from the vegetative to the reproductive stages of crop development (Cooper et al., 2014; Kholova et al., 2014; Messina et al., 2015; Sinclair, 2012; Vadez et al., 2013). Genotypes like ICSR 21002, REVT18PR#14, ICSV 15012, and SPV1411 in our study exhibited limited transpiration under high VPD and an early decline in transpiration even under well-irrigated conditions, which may favor improved yields under drought. A sorghum modeling study by Kholova et al. (2014) demonstrated that limiting the maximum TR under severe water stress scenarios restored yield by enhancing water use after anthesis. This trait did not involve trade-offs between grain and stover production but increased overall water productivity. Similarly, a simulation study in maize by Messina et al. (2015) revealed that the limited-transpiration trait could enhance yield of 135 g m^{-2} in drought-prone environments, while a small yield penalty was simulated for environments where water was not limiting (-33 g m^{-2}).
3. Enhancing TE is considered a crucial strategy for increasing crop yields in arid environments, where limited water availability constrains biomass and yield (Christy et al., 2018; Craufurd et al., 1991; Ehdaie et al., 1991; Martin & Thorstenson, 1988; Passioura, 1977). Genotypes such as SPV1411, M35-1, REVT18PR#24, and ICSV15012 from the R line group exhibited high TE in both WW and WS conditions, indicating their possession of drought-adaptive traits that could make them well-suited for post-rainy sorghum cultivation. A trial across the Australian wheat belt, using a high-TE cultivar and its low-TE parent (Rebetzke et al., 2009), demonstrated a significant crop yield advantage for high-TE lines in various environments. Similarly, a simulation study by Christy et al. (2018) underscored a substantial yield benefit from the high-TE genetic trait in rainfed wheat crops across much of Australia under current climate conditions. Although an increase in grain productivity was often offset by a decrease in stover productivity and vice versa in many scenarios, the concurrent improvement of both grain and stover productivity was achievable through enhanced plant water productivity (TE) resulting from a restricted TR under high VPD conditions (Kholova et al., 2014).

This study identified crucial component traits (refer to Table S2) contributing to post-rainy drought adaptation in both R and B line groups. Overall, specific genotypes from the R line, namely REVT 18PR # 24 and ICSV 15012, and from the B line, namely 40172 and 104 B, exhibit traits such as high biomass, limited TR, and high TE, making them potentially well-suited for post-rainy drought adaptation. Moreover, these identified genotypes could serve as donors for the development of hybrids and varieties aimed at enhancing drought adaptation in post-rainy sorghum production zones. Furthermore, Mace et al. (2019) reported numerous QTLs in diverse sorghum populations, encompassing traits such as leaf area (24 QTLs), root dry weight (16 QTLs), TBM (64 QTLs), plant height (350 QTLs), early vigor (2 QTLs), transpiration (3 QTLs), TR (225 QTLs), and water use efficiency (1 QTL), as detailed in Table S3. The identification of genetic regions linked to drought adaptive traits, including leaf area, TR, and TE, presents an opportunity to manipulate these loci, facilitating the development of recombinants characterized by lower TR and enhanced plant vigor, thereby rendering them suitable for water-limited environments.

5 | CONCLUSION

In conclusion, this study offers valuable insights into the variations in sorghum plant growth, water use, and biomass traits among the hybrid parents (R and B lines) under different water regimes. The significant genotypic variation in biomass production, leaf area, and plant height underscore how these lines adapt to varying water availability. Certain R lines (e.g., REVT 18PR # 24 and ICSV 15012) demonstrated enhanced biomass, increased leaf area, and a delayed decline in transpiration under WS conditions, suggesting their suitability for post-rainy sorghum breeding and variety development.

Moreover, the study highlights the importance of a limited TR and its role in water conservation, particularly under high VPD conditions. R lines (e.g., REVT18PR#14) exhibited lower TR during the vegetative stage, indicating their potential for improved water-use efficiency. The observed genetic diversity in FTSW thresholds further underscores the significance of genotype-specific water conservation strategies, contributing to prolonged water availability during soil drying.

Strategies for post-rainy drought stress adaptation are proposed based on key but measurable physiological traits. Therefore, an ideal sorghum ideotype for post-rainy cultivation would possess substantial plant biomass and yield while effectively minimizing water loss under high

evaporative demand. However, it is crucial to recognize the context-specific nature of these traits for drought adaptation, as highlighted by Tardieu et al. (2012). The research identified early vigor, restricted TR under high VPD, and high TE as crucial traits. It also pinpointed hybrid parents (see Table S2) suitable for integrating these traits into new breeding pipelines, varieties, and hybrids aimed at enhancing terminal drought adaptation in post-rainy sorghum production in India. These strategies prioritize water conservation and efficient water use, offering promising avenues for selection in sorghum testing and promotion for sustainable crop production in water-limited environments.

AUTHOR CONTRIBUTIONS

Kaliamoorthy Sivasakthi: Conceptualization; data curation; formal analysis; investigation; methodology; supervision; visualization; writing—original draft. **Anil Gaddameedi**: Data curation; formal analysis; investigation; methodology; writing—original draft. **Murugesan Tharanya**: Data curation; formal analysis; methodology; writing—original draft. **Sunita Gorthy**: Data curation; investigation. **Boddupalli Sravani**: Investigation. **Nagalakshmi Neelam**: Investigation. **Jaganathan Jayakumar**: Project administration; resources. **Sunita Choudhary**: Writing—review and editing. **Jana Kholovà**: Writing—review and editing. **Mahalingham Govindaraj**: Conceptualization; funding acquisition; investigation; project administration; resources; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data supporting the conclusions of this study can be obtained from the corresponding author, Mahalingham Govindaraj, upon 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.

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