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Original Article

Preventing canopy mortality during drought is essential for efficient recovery in cotton

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ABSTRACT

This study aimed to identify the underlying traits associated with drought avoidance, tolerance, and recovery capacity in high-yielding cotton, as well as to contribute to the selection of the best-fit variety for water-limited environments. Six commercial varieties utilized for cotton production in the USA were selected. Despite the large variability within each variety, differences in drought avoidance and tolerance were observed among varieties. The variety DP2127, which achieves the greatest lint production in the field, exhibited both low avoidance and low tolerance. The variety ST4990, which efficiently sustains lint production in the absence of irrigation in semi-arid sites, exhibited both high avoidance and high tolerance. Differences in drought avoidance across varieties could not be explained by leaf hydraulic traits or early declines in transpiration during drought. Differences in drought tolerance across varieties could not be explained by leaf embolism resistance. By analyzing the response of individual plants, rather than varieties, we could establish that (1) plants with lower canopy transpiration during well-watered conditions delayed dehydration and physiological dysfunction during drought and (2) lower canopy mortality during drought resulted in more efficient recovery post-drought. Our findings suggest that selecting cotton varieties that limit transpiration per leaf area, instead of varieties that trigger leaf shedding during drought, might result in greater avoidance and recovery in combination. Field-based studies are warranted to confirm the avoidance, tolerance, and recovery capacity for these six varieties and to determine how these strategies contribute to yield stability in cotton under water limitation.

1. Introduction

Soil drought, caused by declining water levels in the plant rhizosphere, results in several plant physiological alterations that can lead to declines in growth and productivity (Vadez et al., 2024), and even organ and plant mortality in severe cases (Cardoso et al., 2020; Choat et al., 2018; Tonet et al., 2023). These physiological impairments represent a threat to the production of plant-derived goods, even for relatively drought-resistant crops, such as cotton (*Gossypium hirsutum* L.) (Chastain et al., 2014; Constable and Bange, 2015; Ray et al., 2018; Turner et al., 1986). Cotton is a perennial shrub cultivated as an annual crop primarily for fiber; seeds can also be the target of production in some fields. Cotton is produced across a broad climatic gradient, including humid, semi-arid, and arid regions, with or without irrigation (Constable and Bange, 2015; Ray et al., 2018; Tang et al., 2010). In all these environments and conditions, drought threatens the economic sustainability of cotton production.

In non-irrigated fields, the cotton production relies solely on rainfall, and severe yield losses can occur in dry years, particularly in arid and semi-arid regions (Ray et al., 2018). Even in humid regions, where average precipitation is typically sufficient to satisfy the demand of cotton plants, production losses can occur when rainfall distribution does not align with the plant water requirements throughout the growing season (Lacerda et al., 2022). Cotton production losses due to water limitation also occur in irrigated fields of arid and semi-arid regions when prolonged and severe droughts limit the employment of irrigation via shortage in the water source (e.g. water bodies or aquifers), field water requirements surpass the pumping capacity, and

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irrigation is restricted to ensure water availability for human consumption (Elliott et al., 2014).

During drought, losses in cotton production occur because of declines in carbohydrate assimilation (Chastain et al., 2014; Pettigrew, 2004) and increases in the abscission of flowers and fruits (referred to as bolls in cotton) (Hu et al., 2018; Turner et al., 1986). Cotton production is strongly determined by the ability of plants to accumulate carbohydrates and allocate them to the bolls (as long as they are present), where they will contribute to the production of lint and seeds (Mauney et al., 1994; Yang et al., 2019). Leaves are the main source of carbohydrates to developing bolls, with subtending leaves adjacent to bolls providing up to 60% of the total assimilates translocated to bolls (Wullschleger and Oosterhuis, 1990). Limitations to carbohydrate accumulation during drought occur because of declines in leaf gas exchange per leaf area (which reduces not only canopy transpiration but also photosynthesis) (Chastain et al., 2014), as well as declines in canopy leaf area associated with reductions in leaf expansion (Pettigrew, 2004) and increases in leaf abscission (Li et al., 2020). Finally, increased abscission of flowers and developing bolls also reduces the final number of mature bolls with lint and seeds, which directly impacts yield (Hu et al., 2018; Turner et al., 1986). Interestingly, the abscission of flowers and developing bolls during drought has been suggested to be actively triggered by plants because of their inability to allocate sufficient carbohydrates to a large number of bolls (Pilon et al., 2019; Turner et al., 1986).

As soil water declines, several mechanisms minimize the plant water loss to the atmosphere, delaying plant dehydration and dysfunction (Cardoso et al., 2025; Vadez et al., 2024; Volaire, 2018). Altogether, these mechanisms contribute to a drought resistance strategy named drought avoidance (Cardoso et al., 2025; Volaire, 2018). In cotton, the main mechanism described in the literature as contributing to drought avoidance is stomatal closure (Chastain et al., 2014; Li et al., 2020). Other mechanisms at the leaf level to avoid dehydration, such as increased leaf capacitance (Blackman and Brodribb, 2011) and reduced leaf residual conductance (Duursma et al., 2019), have not been explored in cotton. At the plant level, canopy transpiration and capacity to delay dehydration also remain to be explored.

Although stomatal closure limits photosynthesis, its importance for cotton production in water-limited environments has been recently demonstrated. Cotton varieties that close their stomata at higher leaf water potentials (LWP) (shown by their higher leaf osmotic potential) were shown to produce greater amounts of lint with better-quality under non-irrigated conditions in Texas, USA (Dong et al., 2023). Greater yield might be achieved for plants closing the stomata early during drought because the water conserved in the soils during the vegetative stages can be used later in the season during the critical reproductive stage (Vadez et al., 2024), when water deficit limits the lint production more strongly (Snowden et al., 2014). Conversely, varieties closing the stomata at lower LWP to sustain photosynthesis need to actively accumulate osmolytes in their leaves (i.e. osmotic adjustment) to maintain leaf turgor and stomatal aperture (Pilon et al., 2019). This approach potentially comes at a high carbon cost, as carbohydrates are used for leaf osmotic adjustment instead of being stored for subsequent boll development. This strategy also entails a greater risk of exacerbating soil drought, as soil water consumption is maintained at high levels during periods of limited availability. In this study, we hypothesized that a higher leaf turgor loss point would translate into earlier declines in whole-plant transpiration during drought, thus resulting in greater avoidance. Higher leaf capacitance and lower leaf residual conductance would also contribute to greater avoidance.

Increases in leaf abscission have also been suggested to prevent excessive plant dehydration by reducing canopy transpiration (Li et al., 2020), but its importance to sustain cotton production in water-limited environments is implausible. This is because stomatal closure and declines in photosynthesis at the leaf level can be relatively quickly reverted at the end of the drought, but leaf shedding has a more lasting effect, potentially delaying the recovery of photosynthesis at the canopy level. For canopy photosynthesis to resume to pre-drought levels, new leaves need to develop, furthering the use of carbohydrates that could otherwise be used for boll development. Therefore, while one study had suggested that leaf shedding is an effective way to delay plant dehydration and prevent more permanent damage to stems (Li et al., 2020), we hypothesized that leaf mortality and shedding rather represent drought-induced damage that impairs the ability of cotton plants to rapidly recover from drought.

A different drought resistance strategy is tolerance, through which plants tolerate high levels of tissue dehydration (Cardoso et al., 2025; Volaire, 2018). To tolerate dehydration, plants display mechanisms such as efficient antioxidant systems that maintain cellular integrity and resistant xylem that prevent hydraulic dysfunction due to embolism (Choat et al., 2018). One variety of cotton was recently demonstrated to exhibit high resistance to embolism, with the water potential inducing 50% embolism accumulation (P_{50}) being −4.2 MPa for leaves, −5.4 MPa for stems, and −5.5 MPa for roots (Li et al., 2020). These resistances are considered high relative to other annual herbaceous crops (Cardoso et al., 2025) but similar to those observed in woody angiosperms (Cardoso et al., 2022). The importance of high embolism resistance to the function and survival of woody plants in response to drought has been widely documented in the literature (Choat et al., 2018; Mantova et al., 2022), but its role in sustaining crop function and production remains uncertain (Cardoso et al., 2025). Given the positive association between leaf embolism and leaf mortality (Brodribb et al., 2021; Cardoso et al., 2020; Tonet et al., 2023), we hypothesized that cotton varieties with greater leaf embolism resistance would exhibit lower leaf mortality than varieties with lower resistance when they are exposed to similar dehydration levels. Naturally, this response would only be observed under drought events in which dehydration levels are severe enough to cause leaf embolism.

This study was designed with the overarching goal of broadening our understanding of leaf- and canopy-level traits associated with drought avoidance, tolerance, and recovery capacity in cultivated cotton. Our experiments were designed to test the following three hypotheses: (1) higher leaf turgor loss and early decline in canopy transpiration underpin drought avoidance; (2) greater leaf resistance to embolism is an important tolerance trait, reducing canopy mortality during drought; and (3) plants experiencing lower canopy mortality during drought would exhibit more efficient recovery from drought. Experiments were performed using six high-yielding cotton varieties that are commercially available in the USA so that our research findings would be informative for both plant scientists and cotton growers. We also evaluated field-based yield data to potentially associate drought resistance with the yield potential. The yield data were obtained from North Carolina State Official Variety Trials and the North Carolina On-Farm Cotton Variety Evaluation Programs.

2. Materials and methods

2.1. Plant material and growing conditions

The six cotton varieties selected for this study included three Deltapine® varieties (DP2038, DP2115, and DP2127) (Bayer AG, Leverkusen, Germany), two PhytoGen® varieties (PHY443 and PHY360) (Corteva Agriscience Inc., Indianapolis, IN, USA), and one Stoneville® variety (ST4990) (BASF SE, Ludwigshafen, Germany). On average, these varieties produce approximately 1,400 kg lint ha^{-1} (Supplementary Dataset), which is 40% more than the average productivity in the USA when all varieties are combined (USDA, 2026). Plants of each variety were grown from seeds in 10-L plastic pots containing a mixture of 50% river bottom sand and 50% Sun Gro Propagation Growing Mix (Canadian sphagnum peat moss, vermiculite, dolomitic lime, silicon dioxide). Two sets of plants of each variety were cultivated: one set (n = 8 plants per variety) was used to determine several leaf hydraulic traits, and the other (n = 6 plants per variety) was used for the drought experiment.

Each plant was considered a biological replicate. Plants were approximately 50 d old when experiments were initiated.

The experiment was conducted between September and November, 2024 in a greenhouse at North Carolina State University (Raleigh, NC, USA; 35°46′30″ N, 78°38′24″ W). Temperatures in the greenhouse were 36±3°C (mean ± SD) during the day and 21±1°C during the night. Plants received natural sunlight supplemented with photosynthetic photon flux density of 450 μmol m^{-2} s^{-1} on a 12-h photoperiod. During cultivation, plants were irrigated daily to field capacity. Every two weeks, each plant received 5 g of slow-release fertilizer (Vigoro All Purpose Plant Food, Wilmington, DE, USA) containing nitrogen (12%), phosphorus (5%), potassium (7%), iron (0.2%), copper (0.05%), manganese (0.05%), zinc (0.05%), boron (0.02%), and molybdenum (0.0005%).

2.2. Functional hydraulic traits at the leaf level

Several leaf hydraulic traits associated with drought avoidance and tolerance were evaluated for each variety using fully expanded leaves from the middle canopy. Traits associated with drought avoidance were the leaf turgor loss point, leaf capacitance before and after the turgor loss, and leaf residual conductance. The trait associated with drought tolerance was the leaf resistance to xylem embolism.

Pressure-volume curves were performed using leaves from five plants of each variety (n = 5). Leaves were collected, placed into small sealable plastic bags with damp paper towels, and transported to the laboratory. They were scanned (Perfection V850 Pro Photo, Epson, Tokyo, Japan), and their area was obtained using ImageJ (https://imagej.nih.gov). Petioles were then recut under water, and leaves remained immersed for approximately 12 h to allow complete rehydration (LWP < −0.1 MPa). Leaf mass and LWP were synchronously measured while leaves slowly dehydrated on a bench at approximately 23°C and 43% relative humidity until the linear portion of the pressure-volume curve was established. Leaf mass was determined using an analytical balance (ML503T; Mettler Toledo, LLC, Columbus, OH, USA), and LWP was measured using a pressure chamber (Model 1000, PMS Instruments, Albany, OR, USA). Leaves were then dried at 70°C for 3 d to obtain dry weight. Leaf dry weight was used to calculate relative water content, and curves were constructed by plotting the inverse of LWP against relative water content (Tyree and Hammel, 1972). From each curve, the following parameters were estimated: turgor loss point, capacitance pre-turgor loss, and capacitance post-turgor loss.

Leaf residual conductance was determined using leaves from eight plants of each variety (n = 8). This trait was measured through the weight loss method for detached leaves (Duursma et al., 2019). Leaves were collected early in the morning from well-watered plants, placed in sealed plastic bags, and transported to the laboratory. Leaf petioles were sealed with parafilm, and each leaf was positioned so that both the adaxial and abaxial surfaces remained exposed to the atmosphere throughout the measurement period, allowing water loss from both sides. Leaves were then weighed on an analytical balance at 15 min intervals for 3 h. Initial and final leaf areas were determined using a scanner, and images were processed with ImageJ. Leaf residual conductance was calculated from the slope of the linear relationship between leaf mass and time ($R^2 > 0.99$) and normalized by leaf area (average between initial and final leaf areas and the sum of both adaxial and abaxial areas), atmospheric pressure, and vapor pressure deficit.

Leaf embolism resistance was determined using leaves from five plants of each variety (n = 5). Leaf embolism curves were constructed using the optical vulnerability method (Brodribb et al., 2016). Plants were brought to the laboratory the day before the analysis and kept overnight in a well-saturated atmosphere, with the pot substrate irrigated to field capacity. The following morning, plants were removed from their pots, roots were gently washed with tap water, and leaves were used to construct the optical vulnerability curves. Leaves were imaged with a stereomicroscope using transmitted light (LCD Digital Microscope, New York Microscope Company, NY, USA). The images were taken every 180 s as plants were dehydrated under dark conditions. To ensure that all embolism events were captured, images were taken for at least 24 h after the last embolism event was detected. To ensure that this was the case, images were analyzed daily to check for new embolisms during the last 24 h, starting when leaves looked crispy dry. This approach required SD cards to be removed from the stereomicroscopes, and new images could not be captured in the meantime. The process of transferring photos from the SD cards to a desktop computer took less than 5 min. Embolism quantification was performed by subtracting subsequent images to reveal light transmission changes associated with xylem embolism (http://www.opensourceov.org). Embolized pixels were expressed as a percentage of the total embolized pixel area. To construct the optical curves, each embolism event was associated with the LWP measured at that time. The LWP was measured every 4 h using a pressure chamber. The P_{50} was obtained for each curve and averaged for each variety.

2.3. Drought stress and post-drought recovery

A dry-down experiment was initiated approximately 50 d after emergence using the second set of plants. We initiated the experiments using six plants of each variety. However, we had to remove one repetition from the variety DP2127 and one from the variety PHY360 because these plants dehydrated too fast, and we could not properly monitor their water status. Therefore, the final replicate number for this experiment was n = 5 for DP2127 and PHY360 and n = 6 for all other varieties.

On the first day of the experiment, at 6:00 p.m., all pots were saturated with water and allowed to drain freely. The soil surface of each pot was then covered with a plastic bag to prevent soil evaporation. Evapotranspiration was quantified by placing each pot on individual balances (SP6001, Ohaus Scout, Parsippany, NJ, USA) (Fig. S1) and recording the weight loss over the 12-h light period, with measurements taken between 7:00 a.m. and 7:00 p.m. each day. The daytime transpiration under well-watered conditions was assessed as the average transpiration rate of 3 d before irrigation was stopped. During these days, irrigation was applied at 7:00 p.m., replacing the water lost on the previous day (24-h period). After these 3 d, irrigation was suspended (day zero), and plants were allowed to slowly and gradually experience declines in soil water levels. Plants remained under drought until the mean LWP for each genotype reached −4.11 MPa, which corresponds to the mean leaf P_{50} of all varieties. Once this threshold LWP was reached, irrigation was resumed at 7:00 p.m. and repeated daily to maintain soil moisture near field capacity for seven consecutive days. After this recovery period, plants were harvested for destructive analyses.

To avoid the removal of an excessive number of leaves from each plant, LWP was only assessed after plant wilting. The LWP was measured using fully expanded leaves from the middle canopy 8 d after irrigation was stopped, followed by measurements on every other day after that. Leaves were collected at midday, bagged with damp paper towels for 10 min, and measured using a pressure chamber. The time for plants to reach the P_{50} was assessed by comparing the observed LWP on each day with the P_{50} value of each variety.

After the rehydration period, we assessed the total leaf area of living and dead leaves. Green leaves with soft texture and that were firmly attached to the branches were considered alive. Brown, crispy leaves that could be easily detached from the branches were considered dead. Leaves that abscised during the drought and rehydration phases were also included as dead leaves. While for some species it may be difficult to differentiate between dead and living leaves without more sophisticated analysis, such as chlorophyll fluorescence or electrolyte leakage, this is not the case for cotton. Cotton plants appear to shed their dead leaves through the active formation of an abscission zone, so that leaves fall easily by lightly shaking the plants. The area of living leaves (final canopy leaf area composed of remaining and new leaves) was measured

using a leaf area meter. After measurement, living and dead leaves were oven-dried separately at 70°C for 72 h. The area and dry mass of the living leaves were used to calculate the mean leaf mass per area of each variety, which was used to convert the dry mass of the dead leaves into the estimated leaf area of dead leaves. Canopy mortality was estimated as the percentage of dead leaves of the total leaf area. Finally, the transpiration recovery was assessed as the percent recovery of canopy transpiration of each plant compared with the daytime transpiration prior to the drought.

2.4. Statistical analysis

Single-point measurements were compared using discrete analyses. Differences among varieties were assessed using ANOVA ($P < 0.05$) (when ANOVA's assumptions were met) and Scott-Knott's test ($P < 0.05$). For the time to reach P_{50}, differences among varieties were assessed using Kruskal-Wallis and Dunn's test with a Bonferroni correction, as the data did not meet the ANOVA's requirements. These analyses were performed using *agricolae* and *multcomp* packages in R Studio v. 4.5.0 (R Core Team, 2025). Leaf dehydration over time was analyzed using a fixed model linear regression analysis. Models were fit using the *nlme* package in R Studio. A higher-order polynomial analysis, including the fixed effect of variety, was conducted. Residuals were inspected for heteroscedasticity, which was not observed. The final parameters were selected based on the significant highest-order polynomial and model parsimony.

3. Results

3.1. Functional hydraulic traits at the leaf level

We assessed several functional hydraulic traits at the leaf level for the six cotton varieties. All varieties exhibited similar turgor loss point (−1.42 MPa), leaf capacitance before the turgor loss point (1.20 mol m^{-2} MPa^{-1}), and leaf residual conductance (2.60 mmol m^{-2} s^{-1}) (Table 1). The leaf capacitance after turgor loss of DP2038, PHY360, and ST4990 was, on average, 24% greater than that of the remaining varieties. The leaf resistance to embolism (as indicated by the P_{50}) of ST4990 was approximately 0.9 MPa less negative than that of the remaining varieties.

3.2. Drought avoidance

The overall drought avoidance of the cotton varieties was assessed by monitoring leaf dehydration as plants experienced gradual declines in soil water levels. The LWP was assessed every other day, starting when wilting was first detected (i.e. 8 d after irrigation stopped) (Fig. 1A). After 8 d without irrigation, the LWP of all the varieties decreased with increasing drought duration, with differences among the varieties in terms of the intensity of LWP declines over time ($P = 0.0003$). The varieties DP2115 and DP2127 exhibited much more negative slopes (indicating greater declines in LWP over time) than the remaining varieties. Slopes for DP2115 and DP2127 were −0.17 and −0.28, respectively, which contrasted with the slope of DP2038 (−0.02) and also with the slopes of PHY443, PHY360, and ST4990 (−0.08 on average).

Differences in the ability to prevent dehydration during drought between the two varieties (DP2115 and DP2127) and the other varieties were also confirmed by the LWP after 16 d without irrigation (Fig. 1B). The two varieties exhibited more negative LWP than all other varieties on this day. This day was selected for a discrete analysis because it corresponded to the last day when all varieties were under drought simultaneously. A strong correlation was found between the LWP on day 16 and the slope of curves describing declines in LWP over time ($R^2 = 0.92$, $P = 0.0015$), indicating that the selection of this particular day is a good proxy for the ability of plants to prevent dehydration during drought. Based on the greater ability of DP2038, PHY443, PHY360, and ST4990 to minimize dehydration over time during a drought event, these varieties were considered to have higher drought avoidance than DP2115 and DP2127 (Table 2).

The threshold LWP selected to define the end of the drought was −4.11 MPa, which corresponds to the mean leaf P_{50} of all varieties. After reaching the LWP threshold, plants of each variety were rehydrated and received daily irrigation thereafter. After 16 d without irrigation, three varieties reached the selected threshold LWP: DP2115 with a mean±SD LWP of −4.73±1.29 MPa, DP2127 with a LWP of −5.56±1.07 MPa, and ST4990 with a LWP of −4.12±1.04 MPa. Two varieties reached the threshold LWP after 18 d without irrigation: PHY443 with a LWP of −4.54±0.90 MPa and PHY360 with a LWP of −5.16±0.90 MPa. Finally, DP2038 reached the threshold LWP after 20 d without irrigation, with a LWP of −5.07±1.89 MPa. These LWP values corresponded to the minimum LWP experienced by these varieties during the drought period, and they were similar across all varieties ($P = 0.49$) (Fig. 1C). Nevertheless, a large variation in LWP among plants of the same variety was noticeable for all varieties.

3.3. Water loss and transpiration decline during drought

Throughout the experiment, whole-plant water loss (i.e. canopy transpiration) was assessed using balances (Fig. 2A). Prior to the initiation of the drought, plants of all varieties increased the daytime canopy transpiration, likely due to increases in evaporative demand (increases in air temperature, decreases in relative humidity, or both) in the greenhouse. Plants continued to exhibit high rates of canopy transpiration within the first day after irrigation stopped, until gradual declines in transpiration were observed. Transpiration was nearly zero on the last day of the drought. Daytime transpiration rates were assessed as the mean rate of the 3 d before irrigation stopped. Transpiration differed among varieties, with DP2127, PHY360, and ST4990 exhibiting greater mean daytime transpiration than DP2038, DP2115, and PHY443 (Fig. 2B). The time taken for plants to decline the daytime transpiration by 50% and 80% also varied among varieties, with DP2127, PHY360, and ST4990 declining transpiration earlier than DP2038, DP2115, and PHY443 (Fig. 2C, D). By analyzing the response of individual plants, we could establish that plants with greater mean daytime transpiration and earlier declines in transpiration by 50% and 80% experienced more negative LWP on day 16 (Fig. 2E–G).

In addition to evaluating the time for plants to decline transpiration during drought, we constructed curves describing the decline in

Table 1
Functional leaf hydraulic traits for six commercial varieties of cotton. Data are means±SD (n = 8 for leaf residual conductance and n = 5 for all other traits).

Variety	Turgor loss point (MPa)	Capacitance pre-turgor loss (mol m^{-2} MPa^{-1})	Capacitance post-turgor loss (mol m^{-2} MPa^{-1})	Leaf residual conductance (mmol m^{-2} s^{-1})	Water potential at 50% leaf embolism (MPa)
DP2038	−1.32±0.1	1.37±0.2	4.74±0.7 a	3.06±0.4	−4.11±0.4 a
DP2115	−1.36±0.1	1.05±0.1	4.14±0.7 b	2.21±0.4	−4.05±0.5 a
DP2127	−1.46±0.1	1.15±0.3	4.26±0.6 b	2.11±0.3	−4.14±0.4 a
PHY443	−1.50±0.1	1.13±0.1	3.67±0.5 b	2.28±0.6	−4.56±1.0 a
PHY360	−1.47±0.1	1.29±0.2	4.67±1.0 a	3.20±1.1	−4.48±0.6 a
ST4990	−1.43±0.1	1.22±0.2	5.51±1.2 a	2.77±0.5	−3.39±0.5 b

Different letters indicate differences among varieties using Scott-Knott's test ($P < 0.05$).

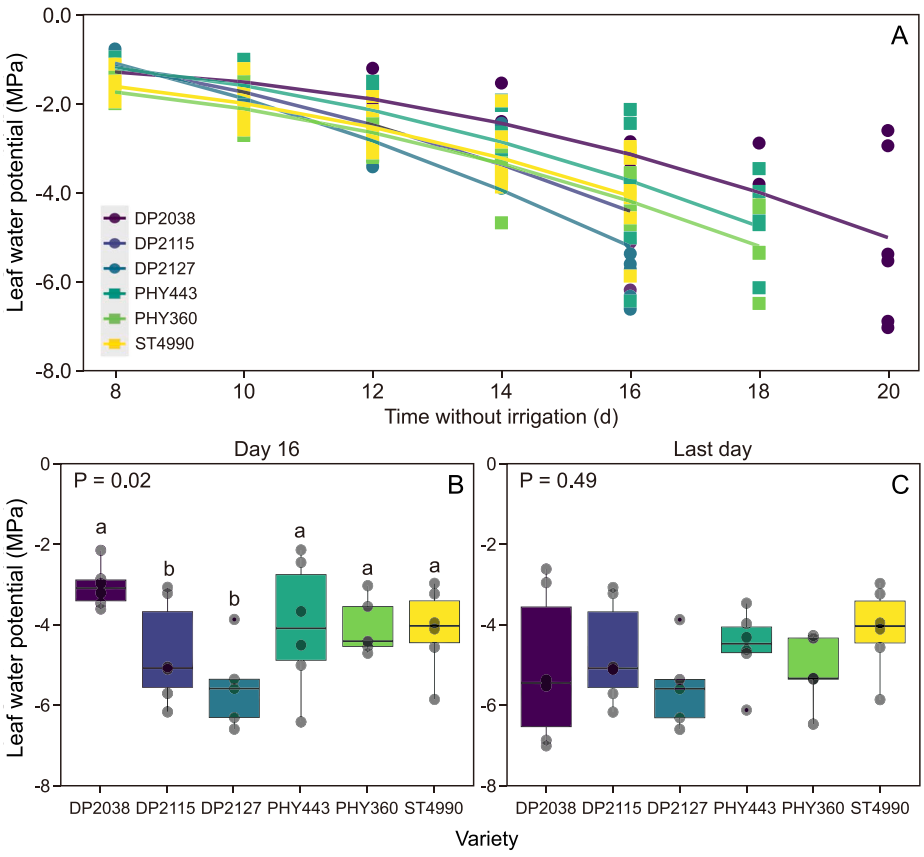

Fig. 1. (A) Declines in leaf water potential (LWP) after withholding irrigation. Data are for six commercial varieties of cotton (n = 5 plants for DP2127 and PHY360 and n = 6 plants for all other varieties). Data collection began after 8 d without irrigation, when plants started to show wilting. Lines represent model fits to the original data points. The test of fixed effects revealed statistical differences among varieties (P = 0.0003) for the rates of LWP decline over time. (B) The LWP of plants after 16 d without irrigation, which corresponded to the last day when all varieties were under drought simultaneously. (C) The LWP of plants on their respective last day of drought. ANOVA P-values are shown in (B) and (C). Different letters in (B) indicate differences among varieties using Scott-Knott's test (P < 0.05).

transpiration with decreasing LWP (Fig. 3A). The LWP at which plants declined daytime transpiration by 50% and 80% was essentially similar across all varieties, with differences of approximately 0.3 MPa between the two most constraining varieties for each of those traits. The LWP associated with 50% and 80% declines in transpiration could not explain the varietal differences in drought avoidance (P > 0.5), described as the LWP on day 16 (Fig. 3B, C), or the slope of the LWP decline curves over time without irrigation (Fig. 3D, E).

3.4. Drought tolerance and recovery capacity

All varieties experienced similar mean minimum LWP on the last day of the drought (Fig. 1C), such that drought tolerance and recovery capacity could be evaluated independently of the capacity to delay dehydration. All varieties experienced similar mean percent canopy mortality at the end of the drought (P = 0.15) (Fig. 4A), despite differences in leaf embolism resistance among them (Table 1). Across all plants, greater mortality correlated with lower minimal LWP experienced during drought (Fig. 4D). Canopy mortality was mostly observed as leaf shedding or leaves that were loosely attached to the stem.

While the percent canopy mortality was similar among varieties, varieties differed in their ability to sustain leaf area (mostly remaining, but also newly formed leaves) after the drought (Fig. 4B). Plants of DP2115 and ST4990 exhibited greater canopy leaf area after the drought than the remaining varieties. The relative drought tolerance of these varieties was defined based on the percent canopy mortality and the remaining canopy leaf area, and DP2115 and ST4990 were considered to have higher drought tolerance than the remaining varieties (Table 2).

The recovery capacity of plants was assessed as their ability to resume whole-plant gas exchange (i.e. canopy transpiration) after 7 d of recovery. Similar canopy transpiration recovery was observed among varieties (Fig. 4C), which were considered to have similar recovery capacity (Table 2). By analyzing the response of individual plants, we established that plants that experienced greater canopy mortality exhibited lower canopy leaf area (Fig. 4E) and lower recovery of daytime transpiration (Fig. 4F) at the end of the recovery phase. Differences in the final canopy leaf area for plants of all varieties, except for PHY360, can be observed in Fig. S2.

Table 2
Categorization of six commercial varieties of cotton based on their relative drought avoidance, tolerance, and recovery capacity. Drought avoidance was defined based on the slope of the curves describing the declines in leaf water potential (LWP) over time without irrigation and on the LWP after 16 d without irrigation, which corresponded to the last day that all varieties were under drought simultaneously. Drought tolerance was defined based on the percent canopy mortality and the remaining canopy leaf area. Recovery capacity was defined based on the transpiration recovery.

Variety	Drought avoidance	Drought tolerance	Recovery capacity
DP2038	High	Low	Intermediate
DP2115	Low	High	Intermediate
DP2127	Low	Low	Intermediate
PHY443	High	Low	Intermediate
PHY360	High	Low	Intermediate
ST4990	High	High	Intermediate

4. Discussion

4.1. Differences in drought avoidance among varieties were not explained by stomatal closure during drought

Contrary to our first hypothesis, neither of the functional hydraulic traits evaluated at the leaf level (turgor loss point, capacitance, and residual conductance) (Table 1) explained the differences in avoidance among the varieties at the plant level (Table 2). Even though the two varieties with lower drought avoidance (DP2115 and DP2127) were

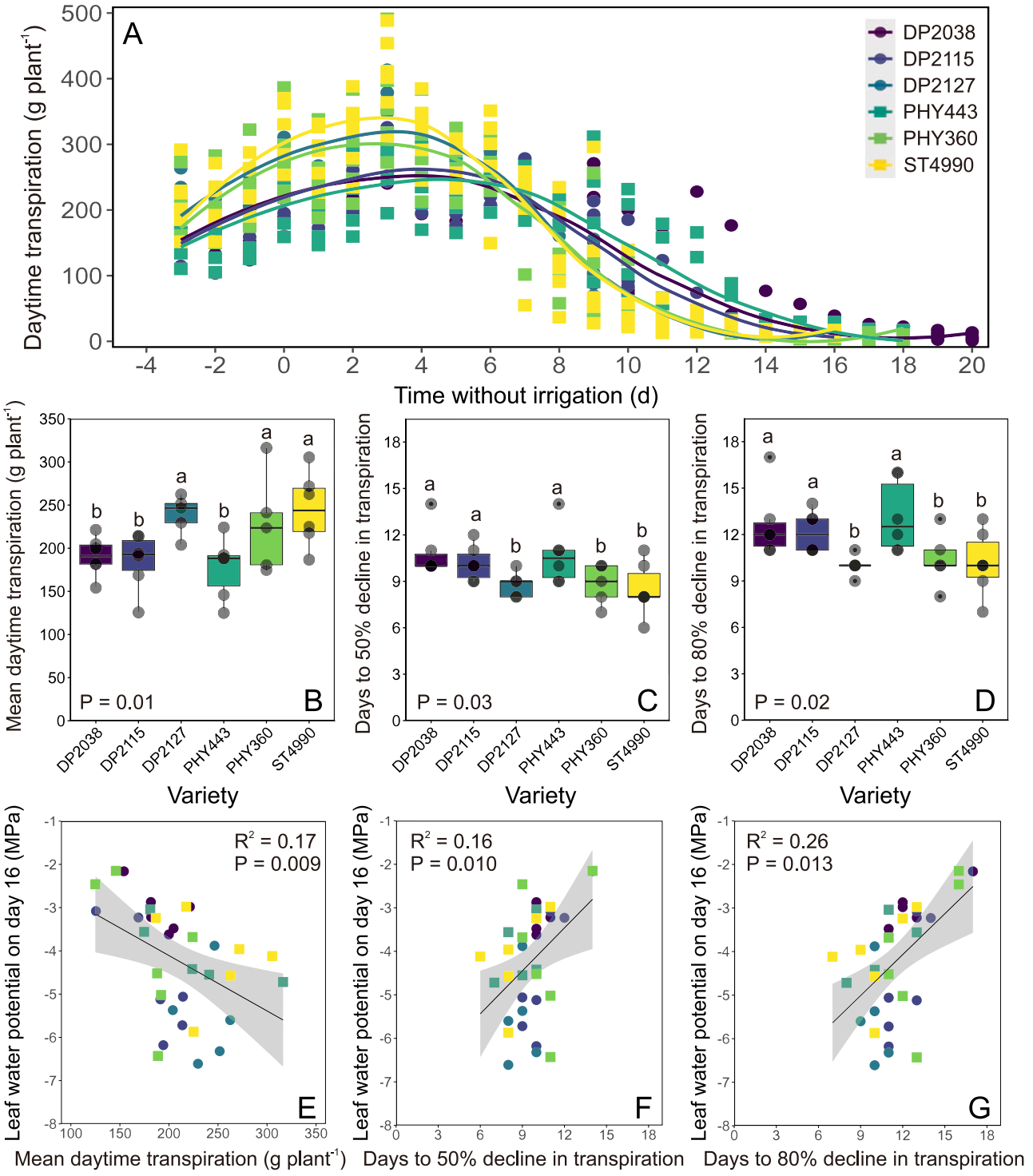

Fig. 2. (A) Declines in daytime transpiration at the canopy level after withholding irrigation (day zero). Data are for six commercial varieties of cotton (n = 5 plants for DP2127 and PHY360 and n = 6 plants for all other varieties). (B) Mean daytime transpiration during well-watered conditions (average of 3 d pre-drought). The number of days necessary for daytime canopy transpiration to decline by 50% (C) and 80% (D) from mean pre-drought levels. ANOVA P-values are shown in (B–D). Different letters in (B–D) indicate differences among varieties using Scott-Knott's test ($P < 0.05$). Relationships between the leaf water potential of plants after 16 d without irrigation and (E) mean transpiration during well-watered conditions, (F) days taken for transpiration to decline by 50%, and (G) days taken for transpiration to decline by 80%. The leaf water potential after 16 d without irrigation corresponded to the last day when all varieties were under drought simultaneously and was selected to reflect the drought avoidance capacity of each plant.

among those with lower leaf capacitance post-turgor, a significant relationship could not be established between capacitance and the LWP on day 16 ($P = 0.6$) or between capacitance and the slope of curves describing declines in LWP over time ($P = 0.5$). Early declines in whole-plant transpiration (in terms of days or LWP) also did not explain differences in avoidance among the varieties (Figs. 2, 3). For instance, one of the varieties with the lowest avoidance (DP2127) was among those declining transpiration on earlier days during the drought (Fig. 2C, D).

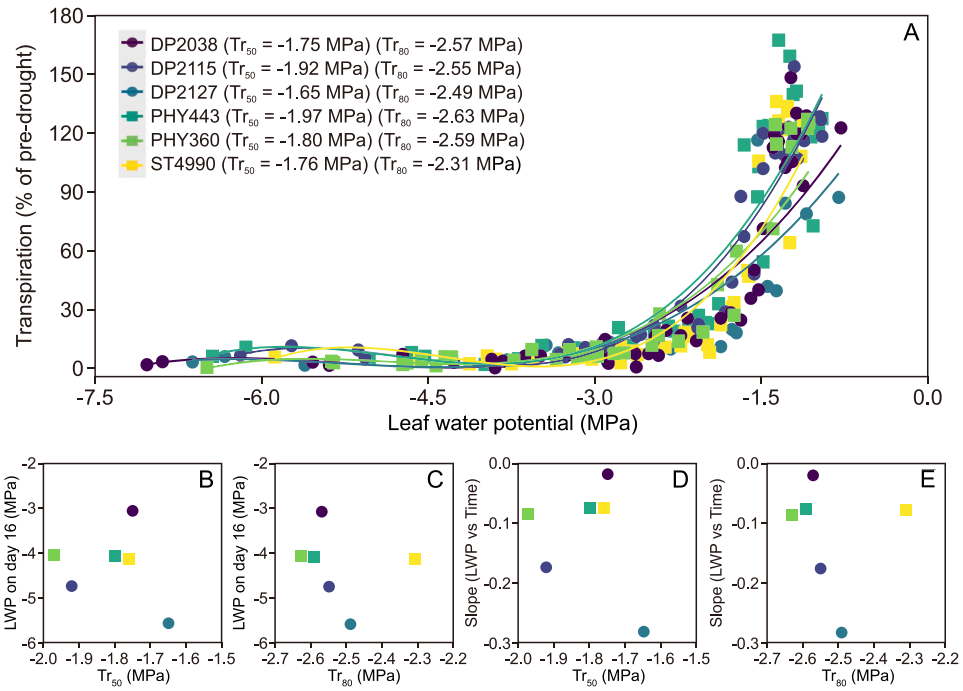

Fig. 3. (A) Relationship between daytime canopy transpiration (as a percentage of pre-drought) and leaf water potential (LWP). Data are for six commercial varieties of cotton (n = 5 plants for DP2127 and PHY360 and n = 6 plants for all other varieties). Lines represent model fits to the original data points. The Tr_{50} and Tr_{80} are the LWPs at which daytime transpiration declined by 50% and 80% from pre-drought levels, respectively, according to the model fits. The LWP after 16 d without irrigation against Tr_{50} (B) and Tr_{80} (C) using the means of each variety ($P > 0.5$). The slope of the curves describing the LWP declines over time without irrigation (Fig. 1A) against Tr_{50} (D) and Tr_{80} (E) using the means of each variety ($P > 0.5$).

This variety also exhibited the highest and second-highest LWP among all varieties at 50% and 80% transpiration declines, respectively (Fig. 3A). Finally, the evaluation of individual plant responses suggested that plants that experienced lower dehydration levels during drought (greater drought avoidance) required more days to decrease transpiration (Fig. 2F, G).

Stomatal closure and reductions in plant transpiration during drought are widely recognized as critical mechanisms contributing to drought avoidance in several plants and crops (Cardoso et al., 2025; Haverroth et al., 2023; Koehler et al., 2023; Vadez et al., 2024), including cotton (Li et al., 2020). Several studies have assessed differences in drought avoidance potential among genotypes by determining the threshold water levels of soils and plants for stomatal closure (Gholipoor et al., 2013; Sinclair et al., 2018). Genotypes exhibiting stomatal closure earlier during drought (i.e. at higher soil or plant water levels) are interpreted as those that exhibit greater drought avoidance potential. While stomatal closure certainly contributes to avoidance, other factors are important to prevent dehydration during drought, including the development of roots to efficiently scavenge and absorb soil water. Plants that absorb water from the soil more efficiently can sustain leaf hydration and gas exchange for longer as the soil dries. In this case, the delay of stomatal closure simply represents that leaf dehydration is not yet sufficient to induce such a response. These results demonstrate the importance of monitoring plant dehydration during drought in addition to assessing stomatal closure or hydraulic traits (such as those from pressure-volume curves or leaf residual conductance) when studying drought avoidance.

4.2. *Lower daytime transpiration delayed plant dehydration and physiological dysfunction*

When evaluating the responses of individual plants, we observed that plants with lower daytime transpiration experienced lower leaf dehydration during drought (Fig. 2E). Plants with lower transpiration also experienced declines in transpiration and leaf embolism later during drought (Fig. S3). These associations are in line with a scenario in which plants that lose more water through transpiration consume soil water faster, thus resulting in faster plant dehydration and impairment of physiological processes (Juenger and Verslues, 2023). Whole-plant transpiration relies on the rate of transpiration (or stomatal conductance) per unit of leaf area and on the total leaf area per plant. Excessive stomatal conductance beyond the point at which stomatal conductance contributes to photosynthesis (Daloso et al., 2026; Gilbert et al., 2011), as well as excessive leaf area per plant beyond the point at which leaf area contributes to solar radiation interception and whole-plant photosynthesis (Brodrick et al., 2013; Li et al., 2022), will inevitably result in wasteful water loss and reductions in water use efficiency (Leakey et al., 2019). In addition, if a high canopy leaf area is not matched with a well-developed and deep root system, this might result in plants consuming the soil water in the rhizosphere faster, ultimately experiencing greater dehydration and physiological dysfunction in water-limited soils. Altogether, these results highlight the importance of minimizing excessive water loss at the leaf and canopy levels to improve water use efficiency and drought avoidance (Cardoso et al., 2025).

4.3. *Leaf mortality and shedding as drought-induced damage in the context of cotton production*

Drought tolerance and rehydration capacity were assessed by dehydrating all varieties to a common mean LWP and evaluating the plant responses. In this case, we selected the mean leaf P_{50} of all varieties, which represents a moderate to severe stress level. In contrast to our second hypothesis, leaf embolism resistance did not govern drought-induced canopy mortality across cotton varieties. Specifically, the variety with the lowest resistance to leaf embolism (ST4990) experienced similar canopy mortality to all other varieties when exposed to similar dehydration levels. This demonstrated that leaf P_{50} was not a good predictor for canopy mortality during drought in cotton. This result also suggests that the positive association between canopy mortality and leaf embolism experienced during drought (Fig. S4) might not constitute a causal relationship.

In a similar way that leaf embolism has been associated with the mortality of individual leaves (Brodribb et al., 2021; Cardoso et al., 2020; Tonet et al., 2023), stem embolism might contribute to leaf mortality at the canopy level, in which plants with greater stem embolism would experience greater canopy mortality. Another hypothesis is that leaf shedding might be actively triggered by cotton plants during drought (Li et al., 2020), similar to the abscission of flowers and

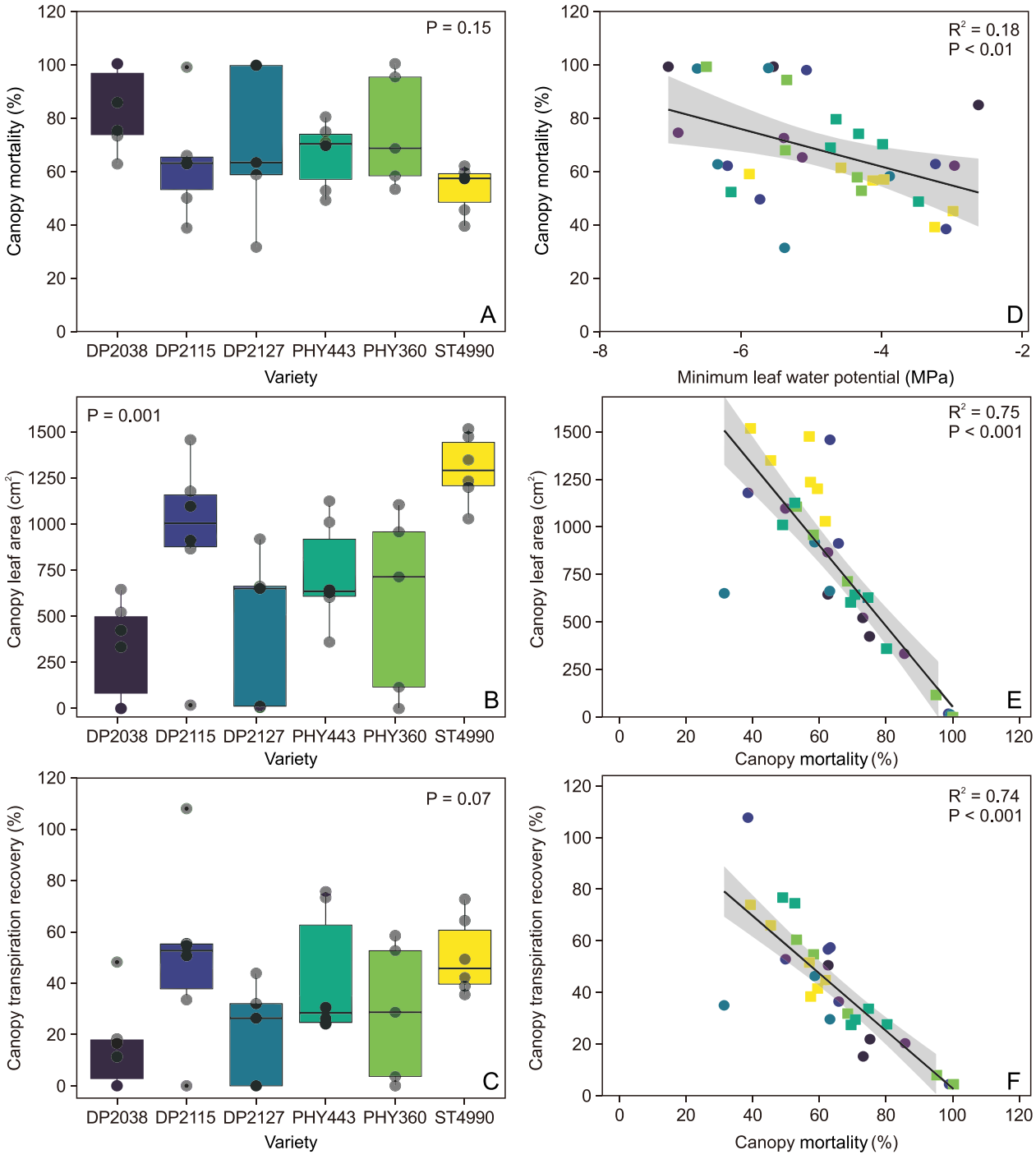

Fig. 4. (A) Canopy mortality, (B) canopy leaf area, and (C) canopy transpiration recovery (percentage of the pre-drought levels) after 7 d of drought recovery. Data are for six commercial varieties of cotton (n = 5 plants for DP2127 and PHY360 and n = 6 plants for all other varieties). ANOVA P-values are shown in (A–C). Different letters in (B) indicate differences among varieties using Scott-Knott's test ($P < 0.05$). (D) Relationship between canopy mortality and the minimum leaf water potential during drought. (E) Relationship between canopy leaf area and canopy mortality. (F) Relationship between canopy transpiration recovery and canopy mortality.

developing bolls, and that this response is independent of leaf or stem embolism. This last hypothesis might be supported by the fact that canopy mortality in cotton plants was mostly observed as leaf shedding or leaves that were loosely attached to the stem, which contrasts with leaf mortality in other woody crops in which dead leaves remain attached to plants (Cardoso et al., 2020; Oliveira et al., 2022).

From an ecophysiological perspective, leaf shedding can be interpreted as a strategy in which a plant sacrifices some leaves to reduce total plant transpiration, prevent extensive stem embolism, and ensure the survival of the individual (Volaire et al., 2026). In cotton, leaf shedding has been recently demonstrated to prevent stem embolism (Li et al., 2020). Even though we did not monitor the dehydration or

embolism accumulation in stems, we showed that plants that experienced lower canopy mortality were able to sustain greater canopy leaf area and more efficient transpiration recovery after drought (Fig. 4). This suggests that the stems of plants with lower canopy mortality and shedding remained at least partially functional after the drought.

The production of lint and seeds by cotton plants has long been associated with the capacity of plants to photosynthesize (Chastain et al., 2014; Pettigrew, 2004; Pettigrew and Gerik, 2007). Reductions in leaf area due to shedding can certainly reduce whole-plant photosynthesis and thus, the production of lint, which is the ultimate goal of cotton production (Pettigrew and Gerik, 2007). In addition, the ability of plants to efficiently and quickly recover from drought is critical to resume photosynthesis and minimize the production losses after the drought, which has been demonstrated to be impaired in plants with greater canopy mortality. This finding is in line with several studies showing that drought-induced damage to leaves in woody species results in slower recovery of gas exchange (Cardoso et al., 2020; Skelton et al., 2017; Tonet et al., 2024). Therefore, preventing leaf mortality and shedding appears to be of ultimate importance for cotton to sustain plant function during the post-drought, which supports our third hypothesis. These findings also suggest that leaf shedding manifests as a physiological dysfunction in the context of high-yielding cotton production, where the goal is maximizing productivity rather than survival.

4.4. Drought resistance and yield capacity: selecting the right variety for each field condition

None of the varieties evaluated in this study combined high avoidance, tolerance, and recovery capacity (Table 2). However, ST4990 exhibited high avoidance and high tolerance, while DP2127 exhibited low avoidance and low tolerance. Interestingly, DP2127 exhibits the greatest yield potential among the varieties selected for this study, producing on average over 1,450 kg lint ha^{-1} (Supplementary Dataset). In addition, a recent report evaluating cotton production across multiple years and locations in North Carolina revealed that DP2127 consistently achieves the greatest lint yield (approximately 1,635 kg ha^{-1}) among all cotton varieties evaluated in the North Carolina State University Official Variety Testing (Phillips et al., 2025). This potential trade-off between yield potential and stress resilience in DP2127 might be rooted in the high canopy transpiration rates, which likely support high canopy photosynthetic rates under well-watered conditions while resulting in faster plant dehydration under water limitation. A recent field study also suggested a trade-off between yield potential and stress resilience in cotton varieties by establishing positive associations between lower leaf osmotic potential (as a proxy for leaf drought tolerance) and lower lint yield and fiber quality (Dong et al., 2023). It is important to emphasize that we can not rule out the possibility that DP2127 exhibits high drought avoidance at the field level through the development of a deep root system. In this case, DP2127 could potentially sustain high yields not only under well-watered conditions but also under water-limited conditions. In any case, based on our greenhouse experiments, we would caution against selecting DP2127 for production areas prone to soil drought before a thorough assessment of its yield potential in water-limited environments.

For dryland production in water-limited environments, the variety ST4990 might be a more consistent performer. In addition to other varieties, ST4990 was shown to effectively minimize plant dehydration during drought, a trait associated with greater seed and lint production during drought (Dong et al., 2023; Quisenberry et al., 1985). Greater drought avoidance has also been demonstrated to result in greater productivity for several other crops, particularly in environments exposed to terminal droughts, because of the increases in soil water availability during the reproductive stages resulting from the lower water use early in the growing season (Vadez et al., 2024). In addition to its superior drought avoidance, the plants of ST4990 were also shown to better tolerate dehydration, sustaining greater canopy leaf area after the drought. Interestingly, this variety was recently shown to yield at satisfactory levels (1,019 kg lint ha^{-1}) under dryland production in Texas, USA, exhibiting a lint yield greater than the average rate across the 17 varieties tested (Dong et al., 2023), which supports our findings.

4.5. Limitations and future directions

Given that root structure and function are limited by the pot size (Dambreville et al., 2016; Poorter et al., 2012), we recognize the importance of replicating this experiment under field conditions to confirm the potential drought avoidance of these varieties under more realistic conditions. We also recognize that the lack of statistical differences in canopy mortality among varieties might have resulted from the large variation in mortality among plants within each variety. Variation in canopy mortality among plants of the same variety might have been partially caused by differences in dehydration among them (Fig. 1C). Using data of all plants and varieties, we revealed that greater canopy mortality was associated with lower minimum LWP experienced during drought ($R^2 = 0.18$) (Fig. 4D) and higher levels of leaf embolism ($R^2 = 0.11$) (Fig. S4). Even greater significance was observed for these associations ($R^2 = 0.33$ for minimum LWP and $R^2 = 0.30$ for leaf embolism) when a new experiment was performed to increase the number of observations. An experimental design in which each plant is allowed to dehydrate to a selected threshold LWP likely represents a more accurate method to test differences in the tolerance of these varieties (Juenger and Verslues, 2023).

5. Conclusions

The selected cotton varieties differed in their drought avoidance and tolerance. The variety DP2127, which achieves the greatest lint production in the field, exhibited both low avoidance and low tolerance. The variety ST4990, which efficiently sustains lint production in the absence of irrigation in the semi-arid state of Texas, exhibited both high avoidance and high tolerance. Based on our findings, selecting cotton varieties that limit transpiration per leaf area instead of varieties that trigger leaf shedding during drought can result in greater avoidance and recovery in combination. Field-based studies integrating both aboveground and belowground traits are needed to confirm the patterns of avoidance, tolerance, and recovery capacity for these six cotton varieties and to determine how these strategies contribute to yield stability in cotton under water limitation.

Abbreviations

LWP leaf water potential
P50 Water potential inducing 50% embolism accumulation

Availability of data and materials

Data will be shared upon request by the readers.

Authors' contributions

MM: Methodology, Data Curation, Visualization, Writing – review & editing. LAO: Methodology, Writing – review & editing. MTA: Methodology, Writing – review & editing. GC: Writing – review & editing. DS: Visualization, Validation, Writing – review & editing. KG: Conceptualization, Funding acquisition, Writing – review & editing. AAC: Conceptualization, Data Curation, Visualization, Validation, Funding acquisition, Writing – review & editing. All authors read and approved the final version of this manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.crope.2026.100142.

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