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Trait association and identification of heat-tolerant genotypes in cotton (*Gossypium hirsutum* L.) under contrasting temperature regimes

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ABSTRACT

Temperature is one of the vital climatic factors influencing the growth and development of upland cotton (*Gossypium hirsutum* L.), with wild cotton species predominantly found in tropical and subtropical regions. Recent climate changes and global warming have exposed cotton crops to unprecedented temperature extremes, highlighting their susceptibility to heat stress. In this direction current study was aimed to evaluate 204 cotton germplasm for heat tolerance by screening them for morpho-physiological and phenological traits under two different temperature field regimes during Kharif 2016. The association study results revealed that canopy temperature was negatively associated with seed-cotton yield. Using Stress Susceptibility Index (SSI) and Yield Index (YI), 33 genotypes were identified as highly heat tolerant and 64 as moderately heat tolerant. The top-performing genotypes including CPD-437 (0.31, 1.85) and PRS-74 (-1.75, 1.77) exhibited promising Stress Susceptibility Index (heat tolerance) and high yield potential respectively. Overall, the study provides robust evidence that substantial exploitable genetic variability exists for key yield and physiological traits, offering an effective basis for breeding cotton varieties resilient to rising temperatures. The study identified 33 highly heat tolerant genotypes which can be used for introgression of heat tolerant traits to develop novel cultivar.

Keywords: Heat tolerance, Upland cotton, Stress susceptibility index and yield index

Introduction

Cotton (*Gossypium spp.*) is a major commercial crop in India and a key contributor to the agricultural and industrial economy. India is one of the largest cotton producers globally, with cultivation spread across diverse agro-climatic regions. Despite having the largest area under cotton, productivity remains moderate. The adoption of Bt cotton has improved yields and reduced bollworm damage; however, challenges such as pink bollworm incidence, climate variability, and nutrient imbalances persist. Cotton, often termed “white gold,” is the backbone of the textile industry and supports millions of livelihoods across farming and allied sectors. It also contributes significantly to export earnings. This establishes cotton as one of the most important commercial crops in India (Palanis Singh *et al.*, 2017) [1]. In India, cotton is predominantly cultivated under rainfed conditions, which contribute more to overall cotton production compared to irrigated systems. Although cotton plants can regulate their temperature under irrigated conditions, they remain vulnerable to the adverse impacts of high-temperature stress. Temperature stress is one of the most significant abiotic stresses affecting rainfed cotton, as it disrupts normal growth and development by altering a wide range of biochemical and physiological processes within plant cells. From a phenological perspective, the reproductive growth phase of cotton is particularly sensitive to heat stress (Rahman, 2006) [2]. When peak flowering coincides with high temperatures, reproductive performance is impaired, leading to reduced lint quality and yield (Snider and Oosterhuis, 2012). Moreover, the detrimental effects of heat stress have also been reported during germination and seedling stages, where plant survival is compromised (Ashraf *et al.*, 1994) [3]. Collectively, these findings highlight that heat stress is a major constraint to cotton production in regions with elevated temperature regimes.

Although *Gossypium* species are ecologically adapted to a wide range of habitats, many occur in arid regions. Temperature plays a critical role in the growth and development of cotton, and wild species are predominantly distributed across tropical and subtropical regions (Fryxell, 1986) [4]. Among cultivated species, upland cotton is the most widely grown fibre crop and is generally regarded as a warm-adapted species. However, recent exposure to unprecedented temperature extremes, driven by global warming and climate change, has revealed the vulnerability of upland cotton to heat stress. This indicates that existing cultivars and traditional management practices have limited historical adaptation to elevated temperatures. Consequently, there is an urgent need to enhance heat tolerance in upland cotton through breeding and improved agronomic strategies to ensure sustainable fibre production and meet the growing demand for clothing in a changing climate (Dendage *et al.*, 2018) [5]. Estimation of heat tolerance indices is essential in cotton

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ton (*Gossypium spp.*) for identifying genotypes that maintain yield stability under high-temperature stress. Heat stress significantly affects cotton growth, especially during flowering and boll development, leading to reduced productivity (Susan *et al.*, 2021).

Screening of advanced breeding lines, cultivars, and germplasm under high-temperature conditions is essential to identify variation and utilize it for improving heat tolerance in cotton. Several screening approaches have been developed, ranging from controlled growth chamber studies to field-based evaluations. Among these, field experiments are considered more reliable, as results obtained under natural conditions better reflect the crop's performance and adaptability. Moreover, the spectrum of gene expression can vary considerably between controlled environments and field conditions. Although limited reports are available on the variability of morpho-physiological and biochemical traits associated with high-temperature tolerance, recent studies (Majeed *et al.*, 2019; Jamil *et al.*, 2020) [7, 6] have highlighted the potential for improving heat tolerance in cotton. This underscores the scope for genetic enhancement of upland cotton to withstand the challenges of a warming climate. Developing heat-tolerant cultivars remains the most economical and sustainable strategy to mitigate the negative impacts of heat stress on cotton production. In this context, the present study undertakes the screening of available germplasm for various morpho-physiological, yield, and phenological traits under two temperature regimes, with the objective of assessing genotype responses, identifying trait associations, and estimating genetic variability among genotypes.

Materials and methods

Plant materials and experimental site

A total of 204 *Gossypium hirsutum* lines were evaluated, comprising 153 germplasm accessions that included indigenous types, exotic collections, and released varieties from the Agricultural Research Station, Dharwad along with 47 advanced breeding lines obtained from the All India Coordinated Research Project on Cotton. These lines were identified under rainfed and irrigated trials across the south, central, and northern zones. Four checks *viz.*, Sahana, Surabhi, MCU 5 and ARBH 813 were also selected for present study for the evaluation of seed cotton yield, its attributes and physiological traits. The experiment was evaluated at two temperature regimes *viz.*, Agricultural Research Station, Dharwad Farm (15°29'21" N latitude and 74°58'58" E longitude) and Main Agricultural Research Station, UAS, Raichur (16°12' N latitude and 77°21' E longitude) during kharif 2016.

Experiment design and sowing conditions

At both the temperature regimes during kharif 2016, the augmented design was used for screening 200 cotton genotypes with 4 checks, 10 blocks and each treatment was hand dibbled in single rows of 4.2 m length with inter-row spacing of 90 cm and 30 cm between plants within the row. The crop raised in rainfed condition at ARS, Dharwad farm during Kharif 2016 received a total rainfall of 352.50 mm in 36 rainy days. While, the crop raised in irrigated conditions at MARS, Raichur received a total rainfall of 547.30 mm in 32 rainy days (Fig 1 and 2).

Data collection and statistical analysis

The observations on morphological and seed cotton yield attributing traits were recorded on five randomly selected plants for number of dried squares (DS), number of monopodia (NM), number of sympodia (NS), number of nodes on main stem (NN), number of fruiting points (NFP) and plant height (PH), boll retention percentage (BR), boll number (BN), boll weight (BW) and seed cotton yield per hectare (SCY). Similarly, physiological traits *viz.*, SPAD chlorophyll meter reading (SPAD), canopy temperature (CT), relative water content (RWC) specific leaf weight (SLW) and leaf area (LA) were recorded at peak flowering (90 days after sowing) and boll development stages (120 DAS) which are critical as well as sensitive stage for heat stress. Apart from above traits, the phenological traits *viz.*, days to square

initiation (DSI), days fifty percent squaring (DFS), days to flower initiation (DFI) and days to 50 per cent flowering (DFF) were also recorded in present study. The recorded data was subjected for analysis of variance, estimation genetic variability parameters using Windostat software version 9.1.. Stress susceptibility index (SSI) was calculated using the formula $SSI = (1 - (Y_s/Y_p)/H)$, given by Fischer *et al.*, (1978) [8], while yield index was worked out using formula $YI = Y_s/X_s$ given by Gavuzzi *et al.* (1997) [9]. Based on these parameters promising genotypes suitable for heat stress environments was identified.

where,

Heat stress intensity, $H = (1 - (X_s/X_p))$ Eq.1

X_s – average yield of all the genotypes under stress environment

X_p – average yield of all the genotypes under normal environment

Y_p - genotype's yield under normal condition (MARS, Raichur)

Y_s - genotype's yield under high-temperature stress (ARS, Dharwad)

In the present experiment, the H value was estimated as 0.54, indicating that the yield under normal conditions was approximately twice that under stress conditions. This H value was further utilized to calculate the Stress Susceptibility Index (SSI) for individual genotypes.

Which statistical methods, which ANOVA method, which statistical software (of which version), which mean comparison method, were used in your statistical analysis?

Results and discussion

The analysis of variance (ANOVA) for the genotypes screened under Dharwad (rainfed) revealed significant differences among the genotypes for all the morpho-physiological, yield, and yield-attributing traits. Similarly, genotypes evaluated under Raichur (irrigated) also indicated significant differences for most of the traits related to yield, yield attributes, physiological, and phenological characteristics. However, exceptions were observed for the number of monopodia, number of nodes on the main stem, and specific leaf weight at 90 DAS, which did not show significant variation among the genotypes.

Threshold ambient temperature and severity of heat stress across two temperature regimes

The prevalence of high temperatures, *i.e.*, above 32 °C, during cotton cultivation has been reported to cause adverse effects on crop growth and development, ultimately leading to significant yield losses (Liu *et al.*, 2006; Pettigrew, 2008) [10, 11]. A threshold ambient temperature of 32 °C is widely considered detrimental for cotton cultivation and has been used as a critical benchmark to ascertain the presence of heat stress, as temperatures above this threshold sharply reduce seed cotton yield (Schlenker *et al.*, 2009) [12]. Accordingly, in the present investigation, the number of days with maximum temperature exceeding 32 °C was recorded for the entire crop growth period, as well as specifically from flower initiation to maturity, for each experimental location. This criterion was used to analyse the two environments in which the experiments were conducted. Since the heat tolerance screening was undertaken under open field conditions, the phenological phases of the experimental crop across environments were naturally exposed to high temperatures above the 32 °C threshold. Under rainfed (Dharwad), the cotton crop experienced a total of 32 warm days above 32 °C between flower initiation and maturity. These stress-inducing warm days occurred predominantly during the 18th, 19th, 20th, and 23rd weeks after sowing in 2016, thereby subjecting the crop to relatively severe heat stress. In contrast, temperatures above 32 °C were recorded during the 4th, 5th, and 6th weeks after sowing, amounting to only 6 warm days between flower initiation and maturity under irrigated (Raichur) regime. Thus, among the two experimental environments, the rainfed experiment at Dharwad experienced comparatively more severe heat stress than the irrigated experiment at Raichur. Weather data further confirmed that the two environments differed considerably in terms of ambient temperature patterns

throughout the crop growth period, validating their use as contrasting temperature regimes for heat tolerance screening.

Phenotypic and genotypic coefficients of variability

To assess the extent to which the observed variation among genotypes was attributable to genetic factors, the phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) were computed for all 34 traits across the two screening experiments. The differences between PCV and GCV were relatively small, suggesting that environmental influence was minor and hence phenotypic variability could serve as a reliable indicator of underlying genotypic variability.

Seed cotton yield and yield attributing traits

In the present study, remarkably high estimates of PCV and GCV were observed under the rainfed temperature regime (Dharwad) for traits such as the number of dried squares, number of fruiting points, boll number, seed cotton yield per hectare, and boll retention (Table 1a). A similar trend was also observed under the irrigated temperature regime (Raichur), indicating that these traits contributed substantially to the total variability at both temperature regimes (Table 2a). These results suggest that the genetic material used in this study possesses considerable variation, which can be effectively exploited for breeding higher-yielding cultivars under high-temperature conditions. In contrast, traits such as boll weight, number of sympodia, number of monopodia, number of nodes on the main stem, plant height, seed index, and lint index, which also contribute to seed cotton yield, exhibited moderate PCV and GCV estimates under both rainfed (Dharwad) and irrigated (Raichur) regimes. These findings are in agreement with [Abro et al., \(2015\) \[13\]](#), who also reported substantial genetic variation among genotypes for yield and yield attributing traits. On the other hand, ginning outturn recorded low PCV and GCV estimates under both environments, indicating limited variation for this trait in the evaluated genetic material. Overall, the results highlight that certain yield-contributing traits exhibit high genetic variability and can be prioritized in breeding programs aimed at improving heat tolerance and productivity in cotton.

Under both rainfed (Dharwad) and irrigated (Raichur) temperature regimes, high estimates of broad-sense heritability (H^2) coupled with high genetic advance as a percentage of mean (GAM) were recorded for key yield-attributing traits, including number of sympodia, number of fruiting points, boll number, boll retention, boll weight, and seed cotton yield per hectare. These findings indicate that phenotypic selection for these traits is likely to be effective across the evaluated temperature regimes. Similarly, [Dabbert et al., \(2017\) \[14\]](#) reported higher broad-sense heritability for lint yield under well-watered conditions compared to water-limited environments, where drought-induced heat stress prevailed. Moreover, lint percentage exhibited the highest estimates of broad-sense heritability, further highlighting the importance of heritable traits for effective selection under stress conditions.

Further, traits such as number of nodes on the main stem, seed index, and ginning outturn, which exhibited high broad-sense heritability, were accompanied by moderate genetic advance as a percentage of mean (GAM). This indicates that these characters are relatively stable and minimally influenced by the environment, making selection based on them effective. Since seed cotton yield is primarily determined by boll number and boll weight for a given genotype and environment, the present study observed nearly 50% reduction in seed cotton yield under the rainfed regime (Dharwad) compared to the irrigated regime (Raichur). This reduction was largely due to significant decreases in key yield-attributing traits: boll number (52.64%), boll retention (38.87%), and boll weight (7.34%). These findings are consistent with previous studies by [Dabbert et al. \(2017\) \[14\]](#) and [Chattha et al., \(2020\) \[15\]](#). Earlier heat tolerance studies in cotton have also identified boll number, boll retention, boll weight, and seed cotton yield as crucial traits for screening heat-tolerant genotypes ([Abro et al., 2015\) \[13\]](#). According to [Hall \(2004\) \[16\]](#), a heat-tolerant genotype is defined

as one that is more productive than other genotypes under heat stress conditions. Therefore, biological yield (seed cotton yield) serves as the ultimate indicator of heat tolerance, reflecting the potential and viability of a genotype for commercial cultivation under high-temperature and changing climatic conditions ([Singh et al., 2007\) \[17\]](#).

Physiological traits

High seed cotton-producing genotypes are often characterized by low canopy temperature and high chlorophyll content, making these two traits essential physiological parameters for screening heat tolerance in cotton germplasm ([Saranga et al., 2004\) \[18\]](#). Genotypes with higher chlorophyll content generally perform better under heat stress, and the stay-green trait has been closely associated with heat tolerance ([Reynolds et al., 2000\) \[19\]](#). Canopy temperature is influenced by ambient temperature, water availability in the root zone, and various physiological factors, making it a powerful integrative trait. It serves as an indirect selection criterion for improving crop yields, as it reflects the overall fitness of genotypes in a given environment ([Reynolds et al., 2001](#)). High-yielding advanced lines of Pima cotton have been associated with reduced leaf area, lower leaf temperatures, and higher stomatal conductance ([Lu et al., 1994\) \[20\]](#). Leaf area functions as the primary site of photosynthesis and determines both biomass accumulation and transpiration efficiency ([Akram-Ghaderi et al., 2007\) \[21\]](#). Cotton leaf development is highly temperature-sensitive, with 26 °C reported as the optimum temperature for leaf growth, indicating that elevated temperatures can adversely affect leaf area expansion and, consequently, overall plant productivity ([Reddy et al., 1992 a, b\) \[22\]](#).

Among the physiological traits evaluated in the present study, leaf area at 90 and 120 DAS exhibited high estimates of PCV and GCV under both rainfed (Dharwad) and irrigated (Raichur) temperature regimes (Tables 1b and 2b), indicating substantial genetic variation for leaf area in the tested material. Specific leaf weight (SLW) at 90 DAS showed high PCV and GCV estimates only under the rainfed condition (Dharwad), whereas SLW at 120 DAS and relative water content (RWC) at 120 DAS recorded moderate PCV and GCV under the same regime. Additionally, SPAD value at 120 DAS exhibited moderate PCV and GCV under the irrigated condition (Raichur). These results suggest that these physiological traits contributed significantly to total variability and can be considered useful indicators for selection in both rainfed and irrigated cotton environments.

Specific leaf weight (SLW) at 90 DAS, which exhibited moderate PCV and GCV under the irrigated condition (Raichur), recorded high PCV and GCV under the rainfed condition (Dharwad). Similarly, canopy temperature at 120 DAS showed low PCV and GCV under the irrigated regime but nearly moderate estimates under the rainfed regime. Relative water content (RWC) at 120 DAS also displayed low PCV and GCV under irrigated conditions but moderate estimates under rainfed conditions. These contrasting estimates indicate that traits such as SLW at 90 DAS, canopy temperature at 120 DAS, and RWC at 120 DAS vary in their expression across temperature regimes. In contrast, low PCV and GCV estimates for SPAD value, canopy temperature, and RWC at 90 DAS under both irrigated (Raichur) and rainfed (Dharwad) conditions suggest minimal variability at this stage. However, the same traits exhibited contrasting variability at 120 DAS under the two environments. Thus, the differential expression of these physiological traits across temperature regimes highlights their importance in contributing to genetic variability for heat tolerance among the cotton genotypes evaluated in this study.

In this study, leaf area at 90 and 120 DAS exhibited high heritability coupled with high genetic advance as a percentage of mean (GAM) under both rainfed (Dharwad) and irrigated (Raichur) temperature regimes. Relative water content (RWC) and specific leaf weight (SLW) at 120 DAS recorded high heritability accompanied by moderate GAM under both environments. Canopy temperature and SPAD value at 120 DAS under the regime (Dharwad), which exhibited high broad-sense heritability, were associated with moderate GAM, indicating additive gene action and suggesting that selection for these

traits would be effective across both temperature regimes. Similarly, under the irrigated regime (Raichur), SPAD value at 90 DAS and RWC at 120 DAS exhibited high broad-sense heritability with moderate GAM, indicating minimal environmental influence on their expression and that variation in these traits is largely due to additive genetic effects. Such patterns of heritability and genetic variability are known to increase under stressful temperature conditions, and previous cotton heat tolerance studies have also reported high heritability coupled with high GAM for chlorophyll content and relative cell injury percentage (Jamil *et al.*, 2020) [6]. In contrast, SPAD value at 90 DAS under rainfed (Dharwad) recorded moderate heritability with low GAM, while under irrigated conditions (Raichur), RWC at 90 DAS and SPAD value at 90 DAS exhibited moderate heritability coupled with low GAM. These results indicate that the expression of these traits is more strongly influenced by the environment under both temperature regimes.

Phenological traits

The rate of plant growth and development is strongly influenced by weather parameters, with temperature being a key factor that governs the phenological stages of cultivated cotton species across different regions, ultimately affecting biological yield (Menzel *et al.*, 2006) [23]. The responsiveness to temperature fluctuations varies among cotton cultivars, and the interrelationship between vegetative and reproductive phases, as well as the time required to reach reproductive stages, is unique to each cultivar. In the present study, low estimates of PCV and GCV were recorded for all the phenological phases evaluated, including days to square initiation, days to fifty per cent squaring, days to flower initiation, days to fifty per cent flowering, and days to maturity, under both rainfed (Dharwad) and irrigated (Raichur) temperature regimes (Tables 1a and 2a). Although these phenological phases exhibited moderate to high heritability, all stages recorded low genetic advance as a percentage of mean (GAM) under both temperature regimes. This suggests that, while these traits are genetically controlled to some extent, their expression is strongly influenced by environmental factors, limiting the effectiveness of direct selection for phenological traits under varying temperature conditions (Venkatesh *et al.*, 2024).

Correlation studies among yield and yield attributing traits and physiological traits

Under both irrigated (Raichur) and rainfed (Dharwad) temperature regimes, seed cotton yield per hectare exhibited significant positive correlations with number of nodes on the main stem, number of fruiting points, plant height, boll retention, boll number, boll weight, and lint index (Table 3 and 4). Additionally, under the rainfed (Dharwad) regime, seed cotton yield per hectare showed significant positive correlations with days to square initiation, number of dried squares, number of sympodia, and ginning outturn, whereas under the irrigated (Raichur) regime, a positive significant association was observed with seed index. These positive character associations indicate that the listed traits contribute substantially to seed cotton yield and can be exploited for indirect selection of superior-yielding genotypes. Specifically, the significant positive correlation between number of dried squares and seed cotton yield under the rainfed regime suggests that genotypes experiencing square drying during episodes of high temperature were able to produce new squares during subsequent favourable cooler conditions, thereby contributing to overall seed cotton yield (Lu *et al.*, 1994) [20]. Yet, yield of cotton is primarily determined by the number of bolls produced per plant and the weight of individual bolls, as these two traits are strongly and positively correlated with seed cotton yield (Bechere *et al.*, 2014; Depar *et al.*, 2019) [24, 25]. Consequently, both traits play a crucial role in determining the quantum of seed cotton yield produced per plant under a given growing environment. Another important yield-determining parameter is the boll retention percentage, which reflects the proportion of fruiting squares that successfully develop into mature open bolls. This trait in-

dicates the plant's ability to retain fruit and is directly linked to final yield potential (Liu *et al.*, 2006) [10].

Character association among canopy temperature and yield attributing traits

Canopy temperature exhibited a significant negative association with seed cotton yield per hectare under both irrigated (Raichur) and rainfed (Dharwad) temperature regimes. Under the rainfed condition (Dharwad), when the crop was in the boll development stage canopy temperature at 120 DAS showed a significant negative correlation with both yield per hectare and boll retention. In contrast, under the irrigated regime (Raichur), canopy temperature at 90 DAS, corresponding to the peak flowering stage, was negatively associated with seed cotton yield per hectare and boll retention. It has been observed that shedding or burning of young bolls occurs when the average daily temperature exceeds 28 °C, and prolonged exposure to such supra-optimal temperatures increases the frequency of boll abscission (Reddy *et al.*, 1992a, 1999) [22]. Exposure of cotton genotypes to high temperatures during critical reproductive stages adversely affects productivity. Consistent with previous studies, genotypic differences in seed cotton yield were closely correlated with fruit retention, indicating that high temperatures during the reproductive phase induce square drying, flower, and boll abscission, thereby limiting seed cotton yield (Kariyannanavar *et al.*, 2023 and Abro *et al.*, 2015) [26]. These findings highlight that high temperatures negatively impact cotton during both flowering and boll development stages, underscoring the importance of selecting heat-tolerant genotypes.

Under the rainfed (Dharwad) temperature regime, canopy temperature at 90 DAS showed significant positive associations with number of nodes on the main stem, number of sympodia, and seed index. The average canopy temperature at 90 DAS was 23.35 °C, which appears to be favourable for the development of these traits. Reddy *et al.*, (1992) [22] similarly reported an increase in nodes on the main stem as temperatures rose from 20 to 40 °C. However, canopy temperature at 120 DAS under the same regime exhibited a significant negative association with node number, indicating that higher temperatures during later growth stages may adversely affect vegetative development. Under the irrigated (Raichur) temperature regime, canopy temperature at 90 DAS was significantly negatively associated with plant height and boll number, while canopy temperature at 120 DAS showed significant negative correlations with plant height, seed index, and lint index. These character associations indicate that episodes of high temperature during crop growth reduce seed cotton yield by affecting key yield-attributing traits such as plant height, boll retention, boll number, seed index, and lint index. These observations are consistent with findings by Sawan (2017) [27], who reported that maximum air temperature was negatively correlated with flower and boll production, as well as boll retention, across two consecutive cotton-growing seasons.

Character association among canopy temperature and physiological traits

Canopy temperature at 120 DAS under both irrigated (Raichur) and rainfed (Dharwad) temperature regimes showed a significant negative association with seed cotton yield, indicating that high temperatures during the boll development stage markedly reduce yield under both irrigated and rainfed conditions (Fig. 3). Additionally, canopy temperature at 120 DAS was significantly negatively correlated with SPAD value at 120 DAS, suggesting that elevated temperatures at this stage can lead to chlorophyll depletion, thereby adversely affecting photosynthesis. The use of canopy temperature as a selection criterion has been applied to assess tolerance to high-temperature stress in cotton breeding programs (Saranga *et al.*, 2004; Khan *et al.*, 2014) [18, 28]. In contrast, relative water content (RWC) at 120 DAS exhibited a significant positive association with seed cotton yield per hectare under both temperature regimes, indicating that higher leaf turgidity during the boll development stage enhances the yielding capacity of genotypes. These results highlight the critical role of canopy temperature

and leaf water status in determining cotton productivity under heat stress conditions.

Under the rainfed (Dharwad) temperature regime, seed cotton yield per hectare showed significant positive associations with SPAD value, specific leaf weight (SLW), and relative water content (RWC) at 90 DAS. This indicates that genotypes with higher chlorophyll content, thicker leaves, and greater leaf turgidity during the reproductive stage significantly enhance seed cotton yield under rainfed conditions. In contrast, seed cotton yield per hectare was negatively correlated with leaf area at 90 DAS and SPAD value at 120 DAS, suggesting that excessive allocation of photosynthates to vegetative growth—such as production of broad leaves during the reproductive phase—may delay or limit reproductive development. Reduced leaf area may also reflect an adaptive mechanism under heat stress, as high-yielding advanced breeding lines were previously reported to have smaller leaf area under elevated temperatures (Lu *et al.*, 1994) [20]. Additionally, canopy temperature at 120 DAS was negatively associated with RWC at 120 DAS, indicating that high temperatures deplete leaf water content through transpiration as a mechanism to maintain optimal canopy temperature. Akram-Ghaderi *et al.* (2007) [21] and Khan *et al.*, (2014) [28] reported that cultivars with cooler canopies exhibit higher heat tolerance. Under the irrigated (Raichur) temperature regime, seed cotton yield per hectare showed significant positive associations with SLW at 90 DAS and leaf area at 120 DAS, highlighting the importance of these traits in supporting yield under irrigated conditions.

Character association among canopy temperature and phenological stages

Under the rainfed (Dharwad) temperature regime, among the phenological stages, seed cotton yield per hectare exhibited a significant positive correlation only with days to square initiation, whereas other stages, including days to fifty per cent squaring, days to flower initiation, days to fifty per cent flowering, and days to maturity, showed significant negative associations (Table 3). This suggests that a longer square initiation period enhances yield potential, while delays in subsequent growth stages lead to significant yield reductions. Interestingly, canopy temperature at 120 DAS displayed significant positive correlations with days to flower initiation, days to fifty per cent flowering, and days to maturity, indicating that high temperatures during the flowering stage can delay boll formation due to square abscission, ultimately resulting in poor boll retention, as observed in the present study under rainfed conditions. Under the irrigated (Raichur) regime, days to fifty per cent flowering exhibited a significant negative association with seed cotton yield per hectare, suggesting that even under irrigated conditions, high temperatures during peak flowering can reduce yield (Table 4).

Identification of heat tolerant genotypes based on stress susceptible index and yield index

All the 204 genotypes were subjected to calculate stress susceptibility index (*SSI*) and Yield index (*YI*) represented in the Fig 4 and 5 respectively. The genotypes exhibiting stress tolerance index less than 0.5 value is considered as highly heat tolerant and in the present study as many as 33 genotypes were classified as highly heat tolerant based on *SSI* values. Similarly, about 64 genotypes which exhibited *SSI* values within 0.5 to 1.00 were categorised as moderately heat tolerant. Based on the yield index (*YI*) given by Gavuzzi *et al.*, (1997) [9], CPD-437, PRS-74, GJHV-407 and Sharada were showing highest yield index among 204 genotypes (Fig 5). Episodes of high temperature during the reproductive stage have been shown to cause significant square and boll abscission (Revanasiddhaya *et al.*, 2023 and Reddy *et al.*, 1999), thereby reducing boll retention and ultimately decreasing seed cotton yield (Tariq *et al.*, 2017) [29]. Thus, boll retention percentage, along with the number of bolls per plant and boll weight, represents

an important criterion for selecting heat-tolerant genotypes (Abro *et al.*, 2015) [13]. Boll weight itself is largely determined by the number of seeds per boll and the amount of fibre produced per seed. Heat stress adversely affects both components: a reduction in pollen load under elevated temperatures decreases fertilization events, leading to fewer seeds per boll, while high-temperature-induced carbohydrate starvation compromises fibre development. As a result, boll weight is significantly reduced under heat stress conditions. Interestingly, CPD-437 showed moderate peak in the *SSI* (Fig 4) and highest peak in the yield index (Fig 5). This trend was observed for most of the genotypes revealing susceptibility of the genotypes towards stress is negatively affecting its seed cotton yield and yield attributing traits. This association is limited to certain range of value between *SSI* and *YI*, beyond that correlation became deceptive. Thus, current study proposes that, use of alone *SSI* to identify drought tolerant genotypes (Zahid *et al.*, 2021) [30] may be ineffective breeding strategy as compared to combination of both *SSI* and *YI* (Devi *et al.*, 2021) [31] to identify heat-tolerant and high-yielding cotton genotypes.

Conclusion

The present investigation clearly demonstrated higher estimates of PCV, GCV and broad-sense heritability coupled with high genetic advance as per cent of mean for yield traits and key physiological parameters indicate that these characters are under additive gene control and amenable to direct selection for improving heat tolerance. In contrast, phenological stages exhibited low GAM, suggesting stronger environmental influence on their expression. Similarly, correlation studies further showed that canopy temperature was negatively associated with seed-cotton yield and major yield components, whereas higher chlorophyll content, higher leaf turgidity and moderated leaf area during reproductive stages were positively associated with yield under heat stress. These results confirm that boll number, boll retention, boll weight, canopy temperature, relative water content and chlorophyll content are reliable indirect selection criteria for identifying heat-tolerant, high-yielding cotton genotypes. Overall, the study provides robust evidence that substantial exploitable genetic variability exists for key yield and physiological traits, offering an effective basis for breeding cotton varieties resilient to rising temperatures. The study identified 33 highly heat tolerant genotypes which can be used for introgression of heat tolerant traits to develop novel cultivar.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

The datasets used and analysed in the current study are available from the corresponding author upon reasonable request.

Competing interests

The authors have no conflict of interest

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Author contributions

V and STK designed the experiment. V grew plants and performed the phenotypic evaluation. PK and V analyzed the data. PK and R wrote the draft manuscript. STK and JMN revised the draft manuscript. All authors made contributions and approved the final manuscript.

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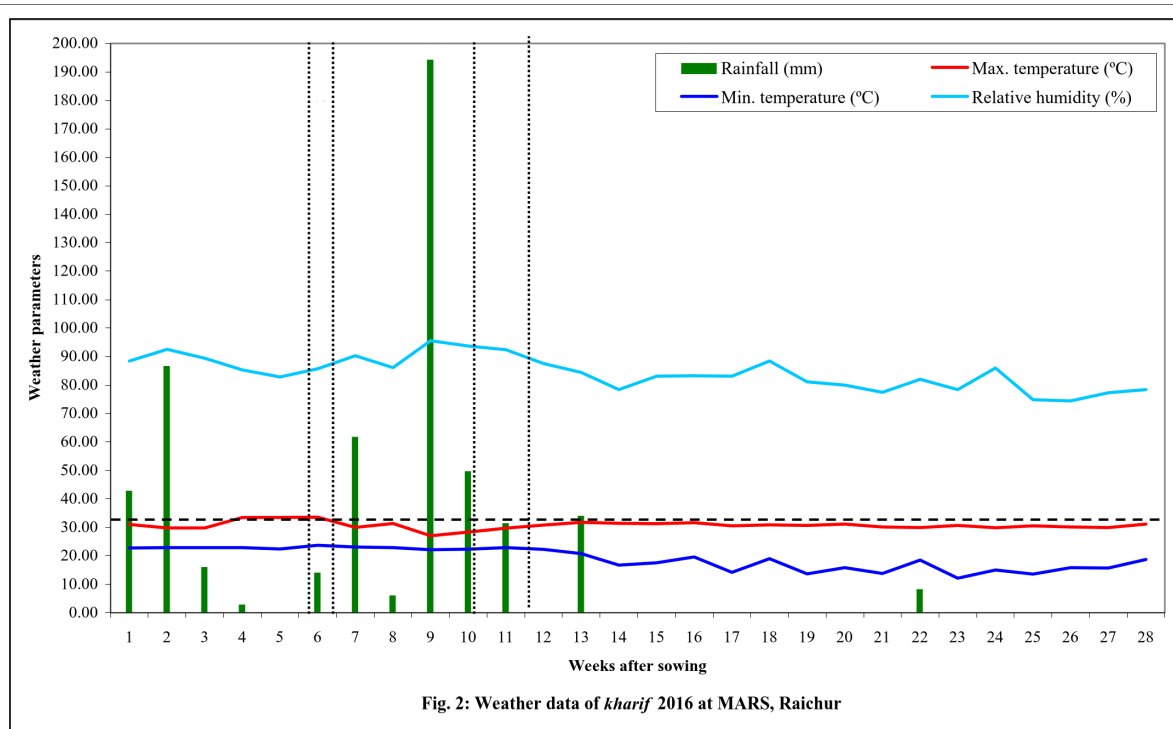
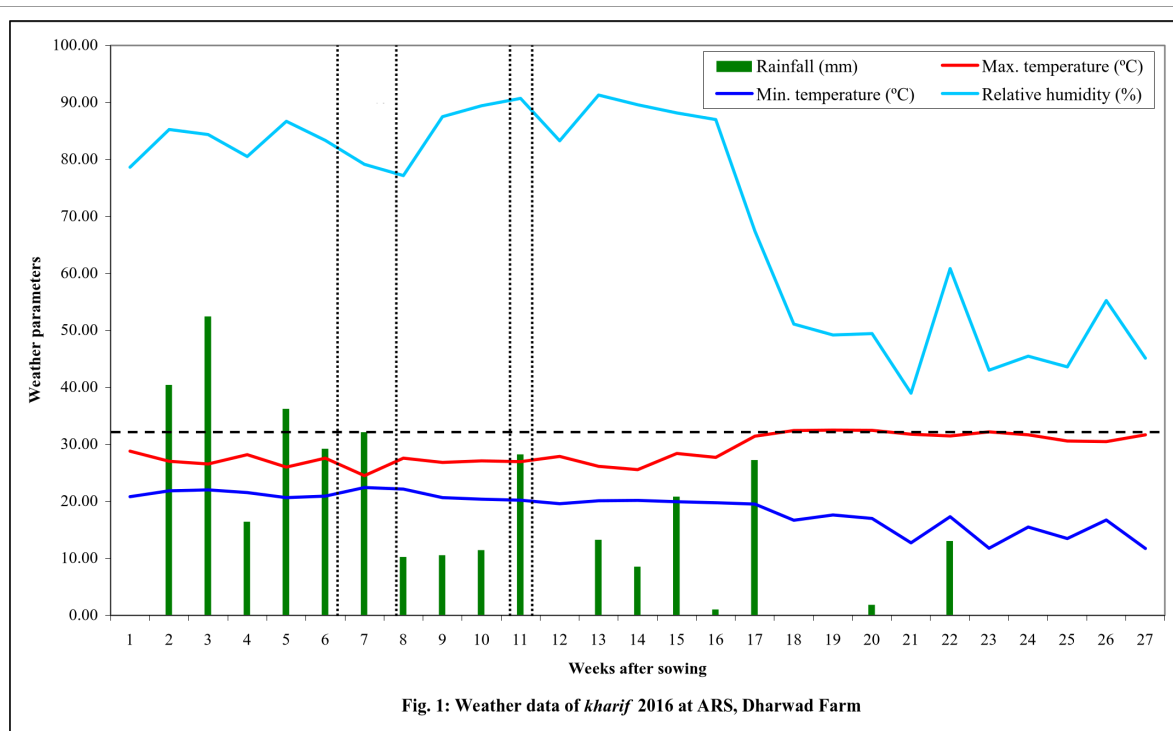


Table 1a. Estimates of genetic parameters for seed cotton yield and its attributes among the 204 *Gossypium hirsutum* lines at ARS, Dharwad

Yield attribut- ing traits	Range		Mean	GCV (%)	PCV (%)	h ² (broad sense) (%)	GA	GAM (%)
	Minimum	Maximum						
DSI	41.00	50.00	43.60	3.73	4.26	77.00	2.94	6.74
DFS	50.00	59.00	55.67	1.69	1.86	82.40	1.76	3.15
NDS	0.00	6.40	2.20	24.90	26.35	89.25	0.74	48.45
NM	0.20	4.00	1.89	10.31	12.33	69.91	0.27	17.75
NS	5.67	16.40	12.79	12.85	13.79	86.80	3.09	24.66
NN	8.00	20.80	16.22	10.57	12.37	73.02	2.97	18.60
NFP	13.40	58.67	34.71	23.02	23.59	95.26	15.50	46.29
DFI	64.00	83.00	75.09	3.80	5.17	54.04	4.33	5.76
DFE	71.00	95.00	82.61	4.12	4.84	72.45	6.00	7.23
DM	147.00	185.00	157.38	2.33	2.67	76.06	6.60	4.18
PH	33.00	113.80	88.39	11.96	13.21	82.05	19.54	22.32
BR	9.62	51.85	33.18	20.84	23.47	78.84	12.30	38.12
BN	1.67	20.67	11.38	27.60	29.05	90.29	5.80	54.03
BW	2.02	6.05	4.04	13.39	14.45	85.97	1.03	25.58
SCY	67.46	2305.56	1324.47	33.81	35.48	90.83	822.24	66.38
SI	6.67	12.56	9.32	9.95	10.54	89.09	1.82	19.35
GOT	28.00	46.29	36.58	7.73	7.88	96.20	5.69	15.61
LI	3.66	8.95	5.39	14.12	15.40	84.06	1.45	26.67

DSI: Days to square initiation	DFS: Days to 50 per cent squaring	NDS: Number of dried squares	NM: Number of monopodia	
NS: Number of sympodia	NN: Number of nodes on main stem	NFP: Number of fruiting points	DFI: Days to flower initiation	
DFF: Days to 50 per cent flowering	DM: Days to maturity		PH: Plant height (cm)	BR: Boll retention (%)
BN: Boll number	SCY: Seed cotton yield kg ha ⁻¹	SI: Seed index (g)	GOT: Ginning out-turn (%)	
	BW: Boll weight (g)			
LI: Lint index (g)				

Table 1b. Estimates of genetic parameters for physiological traits among the 204 *Gossypium hirsutum* lines at ARS, Dharwad

Physiological traits	Range		Mean	GCV (%)	PCV (%)	h ² (broad sense) (%)	GA	GAM (%)
	Minimum	Maximum						
<i>SPAD</i> ₉₀	32.00	44.77	39.54	4.93	6.72	53.78	2.93	7.45
<i>CT</i> ₉₀	21.27	27.00	23.35	3.94	4.42	79.40	1.69	7.23
<i>RWC</i> ₉₀	62.52	92.31	78.98	5.75	7.04	66.78	7.62	9.68
<i>SLW</i> ₉₀	3.10	7.99	5.52	20.29	21.00	93.38	2.25	40.39
<i>LA</i> ₉₀	36.80	188.31	103.80	22.86	23.62	93.66	47.96	45.58
<i>SPAD</i> ₁₂₀	29.63	46.83	38.85	8.94	11.10	64.92	5.78	14.84
<i>CT</i> ₁₂₀	30.27	46.17	33.67	9.78	9.90	97.59	6.74	19.89
<i>RWC</i> ₁₂₀	50.10	89.91	66.15	10.21	11.60	77.60	12.23	18.54
<i>SLW</i> ₁₂₀	4.57	8.90	7.46	10.66	12.65	71.06	1.39	18.51
<i>LA</i> ₁₂₀	27.75	162.44	85.31	20.97	21.53	94.84	36.31	42.07
<i>SPAD</i> ₉₀ : SPAD value at 90 DAS				<i>CT</i> ₉₀ : Canopy temperature at 90 DAS (°C)			<i>RWC</i> ₉₀ : Relative water content at 90 DAS (%)	
<i>SLW</i> ₉₀ : Specific leaf weight at 90 DAS (mg cm ⁻²)	<i>LA</i> ₉₀ : Leaf area at 90 DAS (cm ²)		<i>SPAD</i> ₁₂₀ : SPAD value at 120 DAS					
<i>CT</i> ₁₂₀ : Canopy temperature at 120 DAS (°C)	<i>RWC</i> ₁₂₀ : Relative water content at 90 DAS (%)		<i>SLW</i> ₁₂₀ : Specific leaf weight (mg cm ⁻²)					
<i>LA</i> ₁₂₀ : Leaf area at 120 DAS (cm ²)								

Table 2a. Estimates of genetic parameters for seed cotton yield and its attributing traits among the 204 *Gossypium hirsutum* lines at MARS, Raichur

Yield attributing traits	Range		Mean	GCV (%)	PCV (%)	h ² (broad sense) (%)	GA	GAM (%)
	Minimum	Maximum						
DSI	34.00	51.00	40.69	3.72	5.49	46.01	2.12	5.20
DFS	39.00	57.00	44.72	4.67	5.91	62.47	3.40	7.60
NDS	0.00	11.00	1.23	40.34	41.75	93.36	1.00	80.29
NM	0.00	3.00	1.14	8.47	19.00	19.88	0.10	7.78
NS	11.67	26.33	16.57	10.16	13.68	55.16	2.55	15.54
NN	3.50	27.00	17.54	9.12	15.14	36.27	1.97	11.31
NFP	22.33	100.00	44.72	22.91	23.38	96.03	20.53	46.26
DFI	61.00	83.00	70.22	3.30	4.66	50.33	3.39	4.83
DFF	75.00	92.00	80.93	2.28	3.51	42.15	2.47	3.05
DM	152.00	196.00	171.32	1.82	2.17	70.40	5.39	3.14
PH	65.00	178.67	110.94	13.36	15.07	78.51	27.17	24.38
BR	10.00	82.80	54.28	21.33	22.05	91.88	22.96	42.48
BN	7.00	51.67	24.03	27.51	28.70	93.52	12.78	54.32
BW	2.33	6.13	4.36	13.54	15.58	75.51	1.06	24.23
SCY	121.69	4970.90	2747.94	32.32	33.94	90.72	1724.66	63.42
SI	4.81	12.42	8.76	11.84	12.33	92.20	2.06	23.43
GOT	25.43	42.69	35.26	5.06	6.37	62.96	2.91	8.27
LI	2.72	6.99	4.76	10.46	13.99	55.91	0.77	16.11

DSI: Days to square initiation	DFS: Days to 50 per cent squaring	NDS: Number of dried squares	NM: Number of monopodia	
NS: Number of sympodia		NN: Number of nodes on main stem	NFP: Number of fruiting points	DFI: Days to flower initiation
DFF: Days to 50 per cent flowering	DM: Days to maturity		PH: Plant height (cm)	BR: Boll retention (%)
BN: Boll number			BW: Boll weight (g)	SCY: Seed cotton yield (kg ha ⁻¹)
SI: Seed index (g)		GOT: Ginning out-turn (%)		LJ: Lint index (g)

Table 2b. Estimates of genetic parameters for physiological traits among the 204 *Gossypium hirsutum* lines at MARS, Raichur

Physiology traits	Range		Mean	GCV (%)	PCV (%)	h ² (broad sense) (%)	GA	GAM (%)
	Minimum	Maximum						
<i>SPAD</i> ₉₀	22.85	45.25	37.07	7.00	8.28	71.48	4.57	12.19
<i>CT</i> ₉₀	24.60	29.67	27.16	3.06	3.57	74.00	1.47	5.41
<i>RWC</i> ₉₀	63.00	91.38	77.70	5.90	7.98	54.68	6.96	8.99
<i>SLW</i> ₉₀	4.10	8.95	6.83	8.75	17.45	25.14	0.62	9.04
<i>LA</i> ₉₀	29.20	134.53	68.88	22.67	24.00	89.23	30.70	44.11
<i>SPAD</i> ₁₂₀	30.33	58.10	44.40	12.21	12.49	95.52	10.97	24.58
<i>CT</i> ₁₂₀	26.13	35.50	30.63	5.28	6.45	67.09	2.73	8.91
<i>RWC</i> ₁₂₀	58.54	92.17	78.59	6.26	7.12	77.27	8.90	11.34
<i>SLW</i> ₁₂₀	4.48	8.95	7.81	7.32	10.17	51.79	0.84	10.85
<i>LA</i> ₁₂₀	26.29	189.13	93.87	20.71	22.31	86.15	36.71	39.60

*SPAD*₉₀: SPAD value at 90 DAS

*CT*₉₀: Canopy temperature at 90 DAS (°C)

*RWC*₉₀: Relative water content at 90 DAS (%)

*SLW*₉₀: Specific leaf weight at 90 DAS (mg cm⁻²)

*LA*₉₀: Leaf area at 90 DAS (cm²)

*SPAD*₁₂₀: SPAD value at 120 DAS

*CT*₁₂₀: Canopy temperature at 120 DAS (°C)

*RWC*₁₂₀: Relative water content at 90 DAS (%)

*SLW*₁₂₀: Specific leaf weight (mg cm⁻²)

*LA*₁₂₀: Leaf area at 120 DAS (cm²)

Table 3. Phenotypic correlation coefficients for seed cotton yield and its attributes among the 204 *Gossypium hirsutum* lines at ARS, Dharwad

	DSI	DFS	NDS	NM	NS	NN	NFP	DFI	DFF	DM	PH	BR	BN	BW	SI	GOT	LJ	CT90	CT120	SCY
DSI	1.00	0.18*	0.05	0.11	0.06	0.05	0.03	0.05	0.06	0.06	0.06	0.23**	0.23**	0.25**	-0.03	0.18**	0.13	0.04	-0.03	0.45**
DFS		1.00	-0.34**	0.09	-0.23**	-0.32**	-0.29**	0.13	0.23**	0.19**	-0.26**	-0.10	-0.26**	-0.19*	-0.11	-0.03	-0.09	-0.01	0.10	-0.39**
NDS			1.00	-0.07	0.24**	0.32**	0.30**	-0.23**	-0.22**	-0.29**	0.10	0.18**	0.32**	0.09	-0.03	0.10	0.05	0.03	-0.19**	0.40**
NM				1.00	-0.07	0.03	0.12	0.19**	0.25***	0.19**	0.02	0.06	0.13	0.02	0.21**	0.08	0.23**	0.13	-0.01	0.06
NS					1.00	0.75**	0.43**	-0.04	-0.11	-0.16*	0.72**	0.25**	0.45**	0.22**	0.13**	-0.04	0.05	0.19**	0.05	0.39**
NN						1.00	0.38***	-0.12	-0.20**	-0.24**	0.58**	0.18*	0.38**	0.24**	0.12	0.09	0.16	0.19**	-0.18*	0.37**
NFP							1.00	-0.13	-0.09	-0.14*	0.33**	-0.10	0.64**	0.19**	0.11	0.03	0.10	0.11	0.08	0.42**
DFI								1.00	0.66**	0.64**	0.03	0.04	-0.05	-0.09	-0.11	0.00	-0.06	-0.04	0.24**	-0.21**
DFF									1.00	0.81**	-0.04	0.03	-0.03	-0.02	0.01	-0.04	-0.02	0.07	0.22**	-0.17*
DM										1.00	-0.07	-0.01	-0.08	-0.07	-0.02	-0.01	-0.01	0.01	0.19**	-0.21**
PH											1.00	0.22**	0.36**	0.18**	0.13	-0.04	0.06	-0.02	-0.05	0.31**
BR												1.00	0.67**	0.21**	-0.15*	0.11	-0.02	-0.04	-0.17*	0.53**
BN													1.00	0.30**	-0.04	0.13	0.07	0.05	-0.06	0.71**
BW														1.00	0.37**	0.16*	0.37**	0.12	-0.10	0.52**
SI															1.00	-0.17**	0.56**	0.24**	-0.01	0.12
GOT																1.00	0.72**	-0.05	0.00	0.21**
LJ																	1.00	0.12	0.00	0.25**
CT90																		1.00	0.10	0.09
CT120																			1.00	-0.24**
SCY																				1.00

*** : Significance at 5% and 1% probability respectively.

DSI: Days to square initiation	NS: Number of sympodia	DFS: Days to 50 per cent squaring	NDS: Number of dried squares	NM: Number of monopodia	NN: Number of nodes on main stem	NS: Days to maturity	NFP: Number of fruiting points	DFI: Days to flower initiation	DFF: Days to flower initiation	DM: Days to maturity	PH: Plant height (cm)	BR: Boll retention (%)	BN: Boll number	BW: Boll weight (g)	SI: Seed index (g)	GOT: Ginning outturn (%)	LJ	CT90	CT120	SCY
DSI	1.000	0.930**	-0.022	-0.155*	-0.085	-0.149*	-0.125	0.762**	0.929**	0.709**	0.042	0.018	-0.065	0.125	0.061	0.046	0.087	0.011	-0.007	-0.092
DFS		1.000	-0.018	-0.141*	-0.060	-0.121	-0.093	0.732**	0.887**	0.674**	0.079	0.002	-0.072	0.090	0.061	0.048	0.090	0.005	0.020	-0.073

Table 4. Phenotypic correlation coefficients for seed cotton yield and its attributing traits among the 204 *Gossypium hirsutum* lines at MARS, Raichur

	DSI	DFS	NDS	NM	NS	NN	NFP	DFI	DFF	DM	PH	BR	BN	BW	SI	GOT	LJ	CT90	CT120	SCY
DSI	1.000	0.930**	-0.022	-0.155*	-0.085	-0.149*	-0.125	0.762**	0.929**	0.709**	0.042	0.018	-0.065	0.125	0.061	0.046	0.087	0.011	-0.007	-0.092
DFS		1.000	-0.018	-0.141*	-0.060	-0.121	-0.093	0.732**	0.887**	0.674**	0.079	0.002	-0.072	0.090	0.061	0.048	0.090	0.005	0.020	-0.073

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NDS	1.000	-0.048	0.061	0.055	0.158*	0.022	0.048	0.059	0.063	-0.291**	-0.173*	-0.273**	-0.189**	-0.110	-0.253**	0.039	0.071	-0.249**
NM	1.000	1.000	0.129	0.331**	0.139*	-0.124	-0.162*	-0.080	0.069	0.175*	0.211**	0.014	-0.023	0.033	-0.012	0.109	0.120	0.050
NS	1.000	1.000	1.000	0.903**	0.409**	-0.031	-0.069	-0.043	0.650**	-0.230**	0.038	0.095	0.274**	-0.182**	0.108	-0.026	-0.037	0.080
NN				1.000	0.412**	-0.069	-0.135	-0.086	0.587**	-0.155*	0.108	0.108	0.241**	-0.186**	0.077	-0.013	0.007	0.146*
NFP				1.000	1.000	-0.127	-0.127	-0.004	0.533**	-0.306**	0.426**	-0.057	0.140*	-0.123	0.030	-0.068	-0.163*	0.226**
DFI						1.000	0.819**	0.653**	0.072	0.022	-0.066	0.162*	0.062	0.054	0.095	0.062	0.081	-0.121
DFF							1.000	0.728**	0.021	-0.017	-0.092	0.110	0.037	0.039	0.058	0.050	0.063	-0.146*
DM								1.000	0.104	0.026	0.025	0.166*	0.124	-0.009	0.099	-0.026	0.027	0.019
PH									1.000	-0.054	0.291**	0.098	0.287**	-0.236**	0.085	-0.165*	-0.173*	0.324**
BR										1.000	0.673**	0.294**	-0.119	0.104	-0.034	-0.178*	-0.010	0.529**
BN											1.000	0.257**	-0.037	0.058	0.003	-0.228**	-0.128	0.721**
BW												1.000	0.302**	0.124	0.360**	-0.090	-0.113	0.354**
SI													1.000	-0.249**	0.723**	0.028	-0.218**	0.160*
GOT														1.000	0.484**	-0.021	-0.016	0.036
LI															1.000	0.012	-0.197**	0.164*
CT ₉₀																1.000	0.089	-0.236**
CT ₁₂₀																	1.000	-0.250**
SCY																		1.000

*, **: Significance at 5% and 1% probability respectively.

DSI: Days to square initiation	DFS: Days to 50 per cent squaring	NDS: Number of dried squares	NM: Number of monopodia	DFI: Days to flower initiation	BR: Boll retention (%)
NS: Number of sympodia	NN: Number of nodes on main stem	NFP: Number of fruiting points	PH: Plant height (cm)	YPP: Seed cotton yield per plant (g)	SCY: Seed cotton yield (kg ha ⁻¹)
DFF: Days to 50 per cent flowering	DM: Days to maturity	BW: Boll weight (g)	LI: Lint index (g)		
BN: Boll number					
SI: Seed index (g)	GOT: Ginning out-turn (%)				

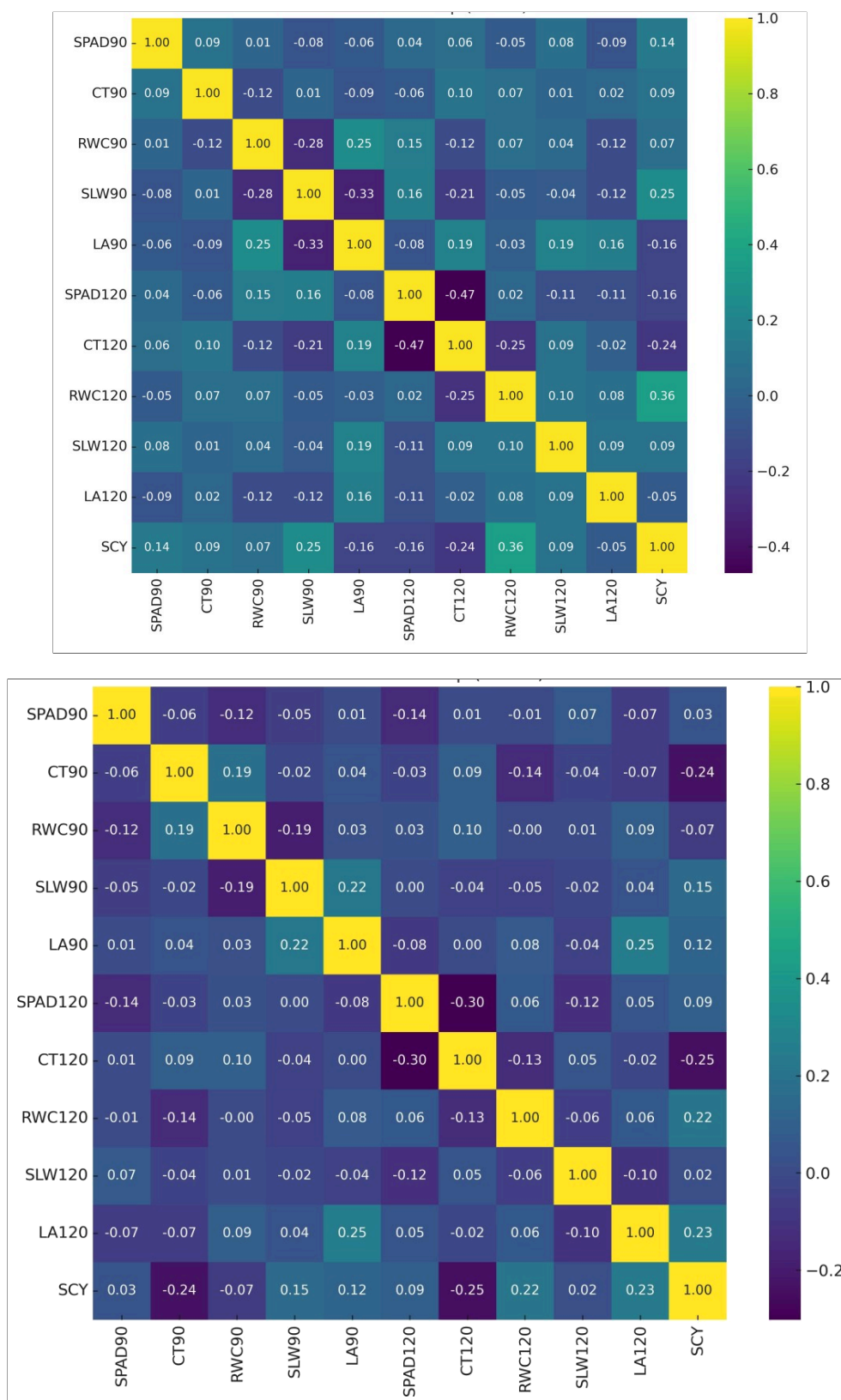


Figure 3. Phenotypic correlation coefficients for physiological traits among the 204 *Gossypium hirsutum* lines. at ARS Dharwad and MARS, Raichur

Rainfed (Dharwad) Irrigated (Raichur)

*SPAD*₉₀: SPAD value
at 90 DAS

*SLW*₉₀: Specific leaf
weight at 90 DAS
(mg cm⁻²)

*LA*₉₀: Leaf area at 90
DAS (cm²)

*CT*₉₀: Canopy tem-
perature at 90 DAS
(°C)

*SPAD*₁₂₀: SPAD value
at 120 DAS

*RWC*₉₀: Relative wa-
ter content at 90 DAS
(%)

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CT₁₂₀: Canopy temperature at 120 DAS (°C) RWC₁₂₀: Relative water content at 90 DAS (%) SLW₁₂₀: Specific leaf weight (mg cm⁻²)

LA₁₂₀: Leaf area at 120 DAS (cm²) SCY: Seed cotton yield



Figure 4. Stress Susceptible Indices of 204 genotypes estimated under two temperature regimes

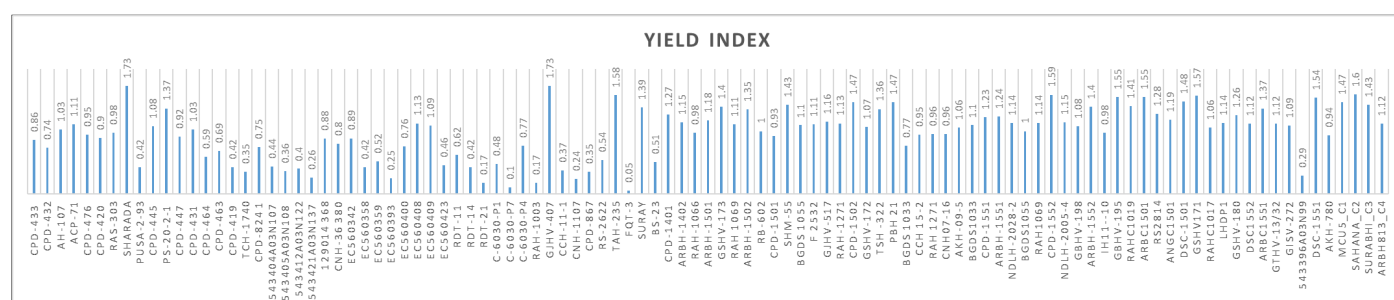


Figure 5. Yield Indices of 204 genotypes estimated under two temperature regimes

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