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FULL-LENGTH RESEARCH ARTICLE

# Evaluation of Groundnut (*Arachis hypogaea*) Genetic Variability for High-Temperature Tolerance in Controlled and Field Conditions

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## Abstract

High-temperature stress poses a serious threat to groundnut production in semi-arid tropical regions due to climate change and global warming. It is important to develop tolerant cultivars that can adapt and produce higher yields. Thirty-six groundnut genotypes were evaluated for tolerance to high temperatures at the seedling stage using the Temperature Induction Response technique, followed by comparing seedling responses to yield performance under field conditions. This aids in understanding genotype responses to high-temperature stress at various growth stages and the possibility of early selection to accelerate breeding for high-temperature tolerance. In the TIR experiment, variability in seedling survival and growth reduction was observed, and the induced genotypes exhibited higher seedling survival and lower growth reduction compared to the non-induced genotypes. Field screening revealed significant genotype, environment, and genotype×environment differences for pod yield and associated traits under high-temperature stress. Heat-tolerant genotypes recorded higher pod yield and associated traits than sensitive genotypes. However, genotypes with seedling tolerance did not exhibit superior pod yields under high-temperature stress, which implies distinct mechanisms governing high-temperature tolerance at different growth stages. This recommends comprehensive screening of genotypes under high-temperature stress for future research and genetic improvement of groundnut high-temperature tolerance.

**Keywords** Groundnut · G × E interaction · High-temperature stress · Partitioning of assimilates · Relative injury · TIR · Yield

## Introduction

In semi-arid tropical areas, temperature is a significant environmental factor that determines crop growth and development. Prolonged exposure of plants to high temperatures causes high-temperature (HT) stress, resulting in negative effects on crop growth and productivity. HT stress causes the wilting of plants, reduces photosynthesis, and alters plant metabolism and physiological processes [7, 10]. This can ultimately lead to reduced yield, quality, and economic losses for farmers [13]. With climate change and global warming, the severity and incidence of HT stress are projected to increase, posing a significant risk to crop production worldwide [15].

Groundnut, also referred as peanut (*Arachis hypogaea* L.), is a significant economic crop cultivated in 113 countries in a 30.53-million-hectare area, with global groundnut production estimated at 54.23 million tons and an average productivity of 1.70 tons per hectare [16]. The optimum temperature for the growth of groundnut is between 25°C and 30°C, but the pod yield can be significantly reduced if the air temperature exceeds 35°C [42]. High temperatures during the flowering period cause flower buds to drop, resulting in fewer pods and affects the pod quality by reducing their size, weight, and oil content, further reducing the yield and productivity of the crop [29]. In addition, high temperatures impact the partitioning of

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assimilates from source to sink, resulting in a reduction in pod yield [1, 30].

Typically, plants exhibit basal tolerance to survive under HT stress. They can also acquire tolerance when exposed to lethal and sub-lethal temperatures, known as acquired HT tolerance [36]. However, HT tolerance is a complex trait controlled by many genes in plants [39]. The yield reduction due to HT stress is influenced by various factors, including the severity and extent of the high temperatures and the particular growth stage of the crop exposed to high temperatures. Since HT stress is a significant factor affecting groundnut production in semi-arid tropical regions, it is crucial to develop tolerant cultivars capable of adapting and producing higher yields even under stress.

Several techniques were employed to screen genotypes under HT stress, such as Temperature Induction Response (TIR), glasshouse screening, and field screening [43]. TIR is a highly effective and reliable technique commonly used to screen genotypes at the seedling stage [33, 48]. Seedling tolerance is a critical factor for crop establishment, especially in semi-arid tropical areas where soil temperatures are high [10]. Plants naturally develop adaptation mechanisms to survive under HT stress. Thus, it is necessary to evaluate the performance of identified tolerant genotypes at the seedling level under field conditions [43]. Field screening of genotypes for HT tolerance involves evaluating them in heat-stress environments, considering yield and associated traits [25]. The pod yield under HT stress is important in identifying tolerant genotypes in crop breeding and selection programs. Several physiological traits, namely pod growth rate (PGR), crop growth rate (CGR) [1], partitioning factor (PF) [42], SPAD chlorophyll content [38], and relative injury [12, 38], have been employed in the assessment of the HT tolerance of genotypes.

Screening for HT tolerance under both controlled and field conditions is useful to identify heat-tolerant genotypes across the growth stages, evaluate the effectiveness of screening methods, and explore the possibility of early selection at the seedling stage to accelerate the breeding for HT tolerance. To answer these questions, the present study included screening of groundnut genotypes under controlled conditions for seedling tolerance, evaluating agronomic performance in field conditions, and examining genotype responses under HT stress at various growth stages.

## Materials and Methods

### Plant Materials

The study was conducted with thirty-six (36) advanced breeding lines of groundnut, including two tolerant checks (ICGV 13249 and ICGV 16553) and two sensitive checks (ICGV 16516 and ICGV 16690) (Supplementary Table 1), which were selected based on a previous study on HT tolerance in groundnut (Rachana et al. unpublished data). These genotypes were assessed both in TIR and field screening experiments.

### Screening for High-Temperature Tolerance Under Controlled Conditions

The TIR experiment works on the principle of subjecting plantlets to sub-lethal temperatures, followed by exposure to lethal temperatures, and subsequently assessing their growth and recovery. Lethal temperatures were defined as the ones at which 100% mortality of seedlings was determined. The temperatures at which high recovery and less reduction in growth of seedlings were identified as induced temperatures [23].

The TIR experiment was carried out in a WGC-450 programmable plant growth chamber. Surface sterilization of seeds was done with a 0.1% mercuric chloride ($HgCl_2$) solution for 30 s and washed three times with distilled water and allowed to germinate in petri plates for 48 h at 30°C. Later, the seedlings that were uniformly germinated were selected and sown in aluminum trays filled with sterilized sand, soil, and vermicompost in 3:2:1 ratio. The seedlings were then subjected to high temperatures in two different treatments. The induced treatment involved exposing the seedlings to sub-lethal temperatures of 38–54°C at a 0.5°C rise in temperature every 10 min for 5 h, followed by exposure to lethal temperatures of 58°C for 3 h and then recovering at 30°C with 60% relative humidity (RH) for 72 h. In contrast, in the non-induced treatment, the seedlings were directly exposed to lethal temperatures of 58°C for 3 h, followed by the same recovery process similar to the induced treatment. A control treatment was also maintained, where the seedlings were kept at 30°C with 60% RH for 72 h (Fig. 1). The trial was designed in a completely randomized design (CRD), with each treatment having three replications and each replication consists of ten seedlings. After the recovery

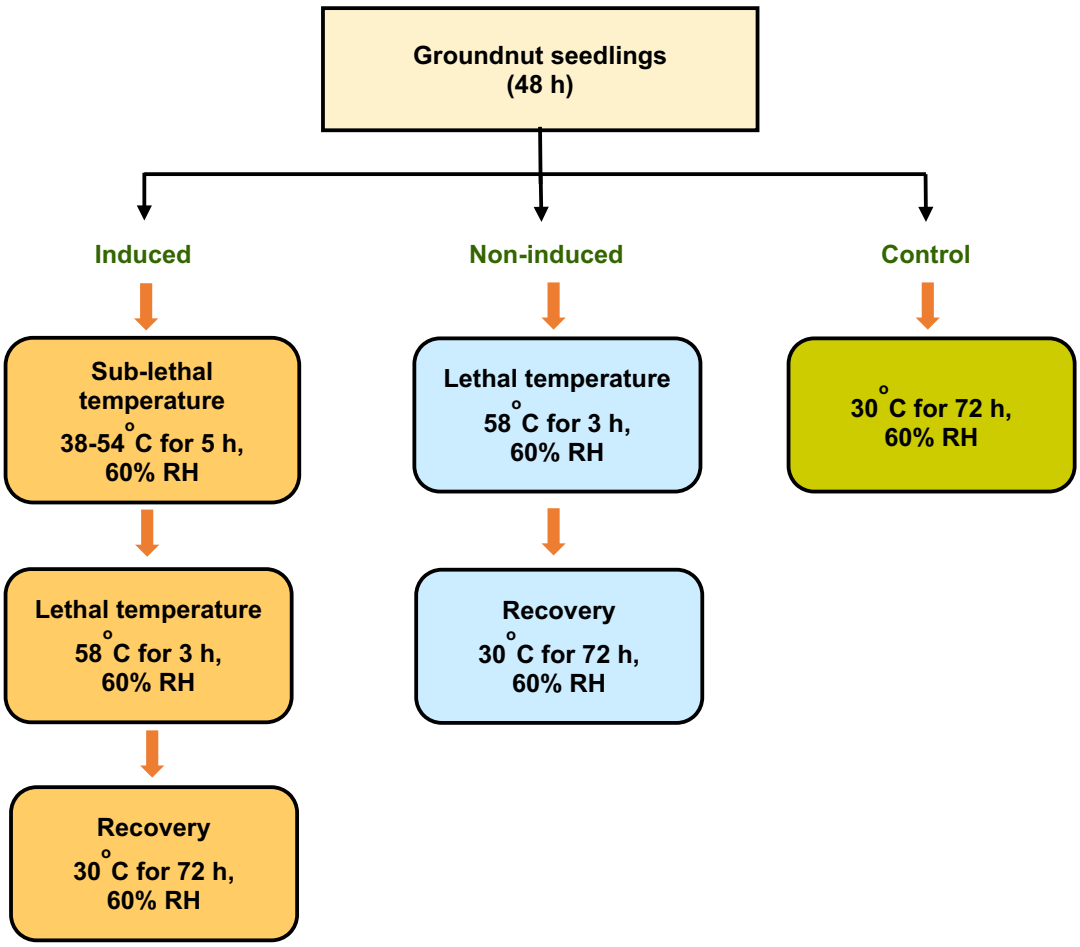


**Fig. 1** Temperature Induction Response (TIR) protocol to screen thirty-six genotypes for high-temperature (HT) tolerance. *Note*: h = hours; RH = relative humidity

period, observations such as the percent survival of seedlings and the percent reduction in shoot and root growth over control were estimated [23].

(a) Percent survival of seedlings =

$$\frac{\text{No. of seedlings survived at the end of recovery period}}{\text{Total no. of seedlings sown}} \times 100$$

(b) Percent reduction in root growth =

$$\frac{\text{Root growth of control seedlings} - \text{Root growth of treated seedlings}}{\text{Root growth of control seedlings}} \times 100$$

(c) Percent reduction in shoot growth =

$$\frac{\text{Shoot growth of control seedlings} - \text{Shoot growth of treated seedlings}}{\text{Shoot growth of control seedlings}} \times 100$$

Physiological traits, including Relative Injury (RI) and SPAD Chlorophyll Meter Reading (SCMR) were measured. Recordings of observations were made from three

randomly selected plants of each genotype in each replication. The RI is a measure of cell membrane damage in biological systems when exposed to stress. A fresh leaf sample weighing 100 mg was collected from the fully expanded quadrifoliate leaf of the groundnut genotypes after the recovery period. The leaf sample was incubated in a beaker filled with ten ml of distilled water and shaken gently for 3 h. The light absorbance values were recorded at 273 nm (initial absorbance, Ia) using a UV 1800 visible spectrophotometer (Shimadzu). The beakers were then placed in a hot water bath (100°C) for 30 min. The final absorbance values were recorded at 273 nm (final absorbance, Fa) using the spectrophotometer, and the percent leakage of ions was computed utilizing the formula [24].

$$\text{Relative injury } (\%) = \frac{\text{Ia}}{\text{Fa}} \times 100$$

After the recovery period, the quadrifoliate leaves were collected and placed in a Minolta handheld portable Soil Plant Analytical Development (SPAD) chlorophyll meter (SPAD-502 plus Minolta, Tokyo, Japan) to measure the plant's chlorophyll content (SCMR). For each genotype, an average of eight readings was recorded to calculate the chlorophyll content [20].

## Screening for High-Temperature Tolerance Under Field Conditions

The trial was conducted at the International Crops Research Institute for the Semi-arid Tropics (ICRISAT), Hyderabad, India, during the summer season 2021. To examine genotype×temperature interactions, the trial was sown on two different dates, *i.e.*, Environment 1 (E1) on February 1st, 2021, and Environment 2 (E2) on February 25th, 2021. The experiment was designed in an alpha-lattice design with two replications, and each replication consisted of three blocks, with block size 12. The plot area was 4.8 $m^2$ and spaced 30 × 10 cm apart between rows and plants. Standard agronomic practices, including irrigation, herbicide application, and intercropping operations, were implemented to ensure crop establishment.

Recordings of observations were made from three randomly selected plants of each genotype from each of the replications. For each genotype, plant height (PH), days to 50% flowering (DFF), pod yield per plant (PY), kernel yield per plant (KY), shelling outturn (SP), hundred kernel weight (HKW), haulm yield per plant (HY), sound mature kernel (SMK), and harvest index (HI) were recorded [1]. To monitor the development of genotypes during vegetative and reproductive stages, two physiological traits—CGR and PGR were recorded. CGR (g $m^{-2}$ $day^{-1}$) refers to the rate at which a crop accumulates biomass or grows over a specific period of time, while PGR (g $m^{-2}$ $day^{-1}$) refers to the degree at which the pods increase in size or weight over a given period of time [1]. To adjust the varying differences in energy requirements to produce dry matter in pods by the reproductive parts relative to the vegetative parts, a correction factor of 1.65 is applied to the pod yield during the evaluation of PGR [14]. Further, a PF was estimated to determine the rate of assimilation of photosynthates by different plant parts and their partitioning to sink from source. The PF is computed as the proportion of the PGR to the CGR [1].

$$\text{Crop Growth Rate(CGR)}\left(\text{g m}^{-2}\text{day}^{-1}\right) = \frac{\text{HY} + (\text{PY} \times 1.65)}{T2}$$

$$\text{Pod Growth Rate(PGR)}\left(\text{g m}^{-2}\text{day}^{-1}\right) = \frac{\text{PY} \times 1.65}{T2 - T1 - 15}$$

where, HY = Haulm yield (g $m^{-2}$); PY = Pod yield (g $m^{-2}$); $T1$ = No. of days from sowing to days to 50% flowering; $T2$ = No. of days from sowing to harvest; 15 = No. of days from days to 50% flowering to the start of pod expansion; pod yield was multiplied by a correction factor of 1.65 to adjust for the variation in the energy required to produce dry matter in pods compared to the vegetative parts [1]. In addition, RI and SCMR were measured from the collected fresh leaf samples of groundnut genotypes.

## Statistical Analysis

Data collected from the two experiments, *i.e.*, TIR and field screening, were analyzed separately. In the TIR experiment, normal Z-distribution analysis was conducted for the distribution of genotypes determined by their growth and recovery. A combined analysis of variance (ANOVA) was performed to assess the main and interaction effects of treatments and genotypes, considering genotypes as fixed effects and treatments as random effects. The individual differences among treatments were estimated and modeled using the residual maximum likelihood (REML) procedure in SAS Mixed procedure [34]. Best linear unbiased estimates (BLUEs) were calculated for genotypes from the combined ANOVA (Supplementary Table 2). Within the field experiment, a combined ANOVA was performed to assess the main and interaction effects of genotypes and environment, considering genotype, environment, and replication nested within the environment as fixed effects and block as a random effect. The individual variances of environments were estimated and modeled to the error distribution using the residual maximum likelihood (REML) procedure in SAS Mixed procedure [34]. Best linear unbiased estimates (BLUEs) were calculated for both environment and genotypes from the combined

ANOVA (Supplementary Table 3). Centered scatter plots [46] have been generated to compare the performance of genotypes across the two environments.

## Results

### Controlled Experiment

After the recovery period, in the induced treatment, significantly higher percent survival of seedlings was observed, with percent varying from 40% to 94%. In contrast, the non-induced treatment exhibited a lower percent survival of seedlings, ranging from 12% to 70%. These findings indicate the recovery potential of induced genotypes to withstand HT stress. The control treatment exhibited a survival rate of 100% in seedlings (Supplementary Fig. 2a). Genotype variation for percent reduction in shoot and root growth was computed for induced and non-induced treatments by comparing them with the control treatment. In the induced treatment, the percent reduction in shoot growth ranged from 24% to 47%, while in the non-induced treatment, it was between 41% and 70% (Supplementary Fig. 2b). About the percent reduction in root growth, the induced treatment exhibited 16% to 48% reduction, whereas in the non-induced treatment, it was 50–77% (Supplementary Fig. 2c). Notably, the genotypes exposed to the induced treatment displayed a lower percent reduction in shoot and root growth in contrast to the genotypes exposed to the non-induced treatment.

Among the physiological characteristics, RI was 3.16–11.78% in the induced treatment and 3.95–16.04% in the non-induced treatment. Conversely, in the control treatment, RI was 1.61–7.74% (Supplementary Fig. 2d). The range of chlorophyll content (SCMR) was 29.04–41.34 in the induced treatment and 21.31–35.24 in the non-induced treatment, whereas in the control treatment, SCMR ranged from 34.70 to 48.76 (Supplementary Fig. 2e). Individual ANOVA revealed significant differences ($p < 0.05$) between genotype means for the traits, percent survival of seedlings, percent reduction in shoot and root growth, RI, and SCMR. Additionally, the random effect of treatment and the treatment×genotype interaction effect were significant ($p < 0.05$) for all the recorded traits (Table 1).

### Field Experiment

The weather data recorded during the field experiment revealed that two environments, E1 and E2, were subjected to high temperatures exceeding 35°C. In E1, the flowering stage experienced high temperatures above 35°C for a total of 11 days, while the pod-filling stage had high temperatures for 63 days. Interestingly, E1 managed to escape HT stress during flowering but was exposed during the pod-filling stage. On the contrary, the E2 experienced high temperatures exceeding 35°C for 15 days during the flowering stage and for 44 days during the pod-filling stage. Therefore, E2 was subjected to HT stress during both flowering and pod-filling stages (Supplementary Fig. 1).

In E1, the range of PH was 21.40–40.01 cm, while in E2, it was 17.41–46.77 cm. DFF were 35–39 days across two environments. The PY range was 7.93–23.81 g in E1 and 8.44–27.95 g in E2. KY ranged from 3.00–11.53 g in E1 and 4.50–19.00 g in E2, with significantly higher yields in E2. The range of SP was 30.85–56.45% in E1 and 47.75–74.23% in E2. HKW ranged from 28.50–43.50 g in E1 and 26.00–56.50 g in E2. The range of SMK was 74.00–92.50% in E1 and 54.87–82.00% in E2. The range for HY was 9.20–9.26 g in the two environments.

In E2, CGR was higher (15.50 g $m^{-2}$ $day^{-1}$) compared to E1 (12.50 g $m^{-2}$ $day^{-1}$). Additionally, PGR was higher

**Table 1** Analysis of variance for the recorded traits among thirty-six genotypes screened in TIR experiment

| | Percent survival of seedlings | Percent reduction in shoot growth | Percent reduction in root growth | Relative injury | SPAD chlorophyll meter reading |
|---|---|---|---|---|---|
| *Fixed effect* | | | | | |
| Genotype | 7.72*** | 7.72*** | 2.39*** | 5.77*** | 4.87*** |
| *Random effect* | | | | | |
| Treatment | 0.05*** | 4.75*** | 2.29*** | 0.99*** | 1.00*** |
| Treatment×Genotype | 0.01*** | 0.15*** | 0.13*** | 5.12*** | 2.56* |
| Residual (control) | 0.01 | 2.21 | 0.62 | 4.28 | 3.36 |
| Residual (induced) | 0.01 | 0.57 | 0.42 | 4.47 | 5.07 |
| Residual (non-induced) | 0.00 | 0.22 | 0.15 | 3.98 | 4.20 |

Significant differences are indicated: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

** typically signifies a statistically significant interaction or main effect at a specific alpha level, commonly $p < 0.01$

**Table 2** Mean, range, and estimated genetic parameters for yield and associated traits among thirty-six genotypes screened under field conditions

| Trait | Mean | Minimum | Maximum | Heritability (%) | Genetic advance (% of mean) |
|---|---|---|---|---|---|
| *E1* | | | | | |
| PH | 28.86 | 21.40 | 40.01 | 45.64 | 15.71 |
| DFF | 37 | 36 | 39 | 73.02 | 3.84 |
| PY | 15.57 | 7.93 | 23.87 | 62.15 | 32.66 |
| KY | 6.44 | 3.00 | 11.53 | 66.34 | 42.11 |
| HKW | 33.11 | 28.50 | 43.50 | 26.03 | 6.03 |
| SMK | 85.01 | 74.00 | 92.50 | 36.00 | 10.00 |
| HY | 9.23 | 9.20 | 9.25 | 20.63 | 0.05 |
| SP | 41.51 | 30.85 | 56.45 | 48.29 | 15.77 |
| PGR | 12.53 | 6.92 | 18.80 | 58.62 | 30.71 |
| CGR | 9.46 | 6.00 | 12.50 | 41.32 | 15.48 |
| PF | 1.29 | 1.06 | 1.48 | 52.01 | 8.53 |
| HI | 71.81 | 58.50 | 79.50 | 51.95 | 8.00 |
| RI | 3.74 | 1.63 | 6.94 | 52.45 | 36.59 |
| SCMR | 45.26 | 36.00 | 52.50 | 40.00 | 9.00 |
| *E2* | | | | | |
| PH | 32.46 | 17.41 | 46.77 | 68.77 | 25.17 |
| DFF | 37 | 35 | 39 | 89.22 | 5.36 |
| PY | 18.17 | 8.44 | 27.95 | 88.50 | 54.20 |
| KY | 11.47 | 4.50 | 19.00 | 87.97 | 58.69 |
| HKW | 35.07 | 26.00 | 56.50 | 84.60 | 31.75 |
| SMK | 70.15 | 54.87 | 82.00 | 40.00 | 11.08 |
| HY | 9.23 | 9.21 | 9.26 | 47.37 | 0.10 |
| SP | 63.54 | 47.75 | 74.23 | 63.43 | 12.36 |
| PGR | 14.77 | 6.95 | 22.49 | 87.59 | 53.06 |
| CGR | 10.69 | 6.00 | 15.50 | 83.56 | 39.36 |
| PF | 1.33 | 1.07 | 1.48 | 89.69 | 15.82 |
| HI | 74.78 | 60.50 | 83.50 | 88.80 | 15.38 |
| RI | 1.70 | 0.18 | 7.30 | 92.97 | 174.70 |
| SCMR | 44.24 | 35.50 | 57.50 | 52.38 | 11.22 |

E, Environment; PH, Plant height (cm); DFF, Days to 50% flowering; PY, Pod yield per plant (g); KY, Kernel yield per plant (g); HKW, 100-kernel weight (g); SMK, Sound mature kernel (%); HY, Haulm yield per plant (g); SP, Shelling outturn (%); PGR, Pod growth rate (g $m^{-2}$ $day^{-1}$); CGR, Crop growth rate (g $m^{-2}$ $day^{-1}$); PF, Partitioning factor; HI, Harvest index; RI, Relative injury (%); SCMR, SPAD chlorophyll meter reading

in E2 (22.49 g $m^{-2}$ $day^{-1}$) compared to E1 (18.80 g $m^{-2}$ $day^{-1}$). Significant differences ($p < 0.05$) were observed for PF between the two environments, with values ranging from 1.06 to 1.48. HI was 58.50–83.50 across the two environments. The range of RI was 1.63–6.94% in E1 and 0.18–7.30% in E2. SCMR ranged from 35.50 to 57.50 in the two environments. High heritability (> 60%) was recorded for the traits PY, KY, and DFF in E1 and for the traits PH, DFF, PY, KY, SP, HKW, PGR, CGR, PF, HI, and RI in E2. High genetic advance as a percent of mean (> 20%) was recorded for PY, KY, PGR, and RI in E1 and for the traits PY, KY, HKW, PGR, CGR, and RI in E2. The estimated range, mean, and genetic parameters for PY and associated traits are provided in Table 2.

Individual ANOVA of each environment revealed significant differences ($p < 0.05$) between genotype means for all the traits, except SMK, HY, CGR, and SCMR in E1 and SMK and HY in E2. A combined ANOVA across the environments showed significant differences ($p < 0.05$) among the genotype means for all the traits, except SMK and SCMR. Additionally, the environment effect showed significant differences ($p < 0.05$) for all the traits, except PH, DFF, and SCMR. The genotype×environment (G × E) interaction effect was significant ($p < 0.05$) for all the traits, except PH, SMK, and HY (Table 3).

**Table 3** Analysis of variance for yield and associated traits among thirty-six genotypes screened under field conditions

| Traits | PH | DFF | PY | KY | HKW | SMK | HY | SP | PGR | CGR | PF | HI | RI | SCMR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *E1* | | | | | | | | | | | | | | |
| Fixed effect | | | | | | | | | | | | | | |
| Genotype (G) | 1.90* | 4.07*** | 2.91** | 3.25*** | 1.31 | 0.78 | 1.30 | 1.98* | 2.70** | 1.76* | 2.14* | 2.21* | 2.24* | 0.91 |
| Replication | 0.24 | 0.09 | 0.00 | 7.51 | 0.65 | 0.14 | 57.43 | 2.90 | 0.00 | 0.00 | 0.51 | 0.00 | 1.79 | 0.22 |
| Random effect | | | | | | | | | | | | | | |
| Block (replication) | 14.76** | 0.17 | 2.00 | 0 | 0.81 | 0 | 0 | 0 | 1.31 | 0.09 | 0.00 | 1.87 | 0.08 | 2.75 |
| Residual | 20.69 | 0.44 | 10.06 | 2.27 | 17.76 | 51.17 | 0.00 | 41.42 | 7.07 | 3.09 | 0.00 | 24.73 | 1.10 | 27.74 |
| *E2* | | | | | | | | | | | | | | |
| Fixed effect | | | | | | | | | | | | | | |
| Genotype (G) | 3.41*** | 9.89*** | 8.77*** | 8.22*** | 6.48*** | 1.24 | 1.74* | 2.91** | 8.10*** | 6.07*** | 9.61*** | 8.93*** | 14.34*** | 2.11** |
| Replication | 0.09 | 1.25 | 0.22 | 0.30 | 0.40 | 0.75 | 9.33 | 1.30 | 0.25 | 0.45 | 1.38 | 2.03 | 0.01 | 4.73 |
| Random effect | | | | | | | | | | | | | | |
| Block (Replication) | 2.34 | 0.03 | 0 | 0 | 0 | 0 | 0 | 1.12 | 0 | 0 | 0 | 0 | 0 | 0 |
| Residual | 18.57 | 0.23 | 6.54 | 3.15 | 12.61 | 71.27 | 0.00 | 23.54 | 4.56 | 1.97 | 0.00 | 8.88 | 0.21 | 20.22 |
| *Combined (E1 & E2)* | | | | | | | | | | | | | | |
| Fixed effect | | | | | | | | | | | | | | |
| Environment (E) | 3.98 | 0.08 | 17.90* | 304.31*** | 8.78** | 127.81*** | 10.67** | 410.01*** | 17.17* | 21.44*** | 13.44*** | 18.22*** | 169.05*** | 1.53 |
| Genotype (G) | 3.85*** | 8.52*** | 6.07*** | 7.50*** | 5.06*** | 1.02 | 1.80* | 2.81*** | 5.68*** | 4.19*** | 4.98*** | 4.54*** | 5.96*** | 1.05 |
| G × E | 1.34 | 3.00*** | 3.41*** | 4.72*** | 1.95** | 1.09 | 1.16 | 1.67* | 3.21*** | 2.64*** | 2.87*** | 3.18*** | 3.66*** | 1.66* |
| Replication (environment) | 0.20 | 0.42 | 0.00 | 3.84 | 0.67 | 0.44 | 32.91 | 1.84 | 0.06 | 0.22 | 0.94 | 1.00 | 1.72 | 2.55 |
| Random effect | | | | | | | | | | | | | | |
| Block (Env × Rep) | 8.03* | 0.08* | 0.37 | 0 | 3.47E-18 | 0 | 0 | 0.68 | 0.35 | 0 | 0 | 0 | 0 | 0 |
| Residual (E1) | 21.25 | 0.46 | 10.88 | 2.27 | 18.32 | 51.16 | 0.00 | 41.08 | 7.50 | 3.15 | 0.00 | 26.02 | 1.17 | 29.63 |
| Residual (E2) | 18.24 | 0.22 | 6.49 | 3.15 | 12.61 | 71.27 | 0.00 | 23.77 | 4.48 | 1.97 | 0.00 | 8.88 | 0.21 | 20.21 |

Significant differences are indicated: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; E, Environment; PH, Plant height (cm); DFF, Days to 50% flowering; PY, Pod yield per plant (g); KY, Kernel yield per plant (g); HKW, 100-kernel weight (g); SMK, Sound mature kernel (%); HY, Haulm yield per plant (g); SP, Shelling outturn (%); PGR, Pod growth rate (g $m^{-2}$ $day^{-1}$); CGR, Crop growth rate (g $m^{-2}$ $day^{-1}$); PF, Partitioning factor; HI, Harvest index; RI, Relative injury (%); SCMR, SPAD chlorophyll meter reading

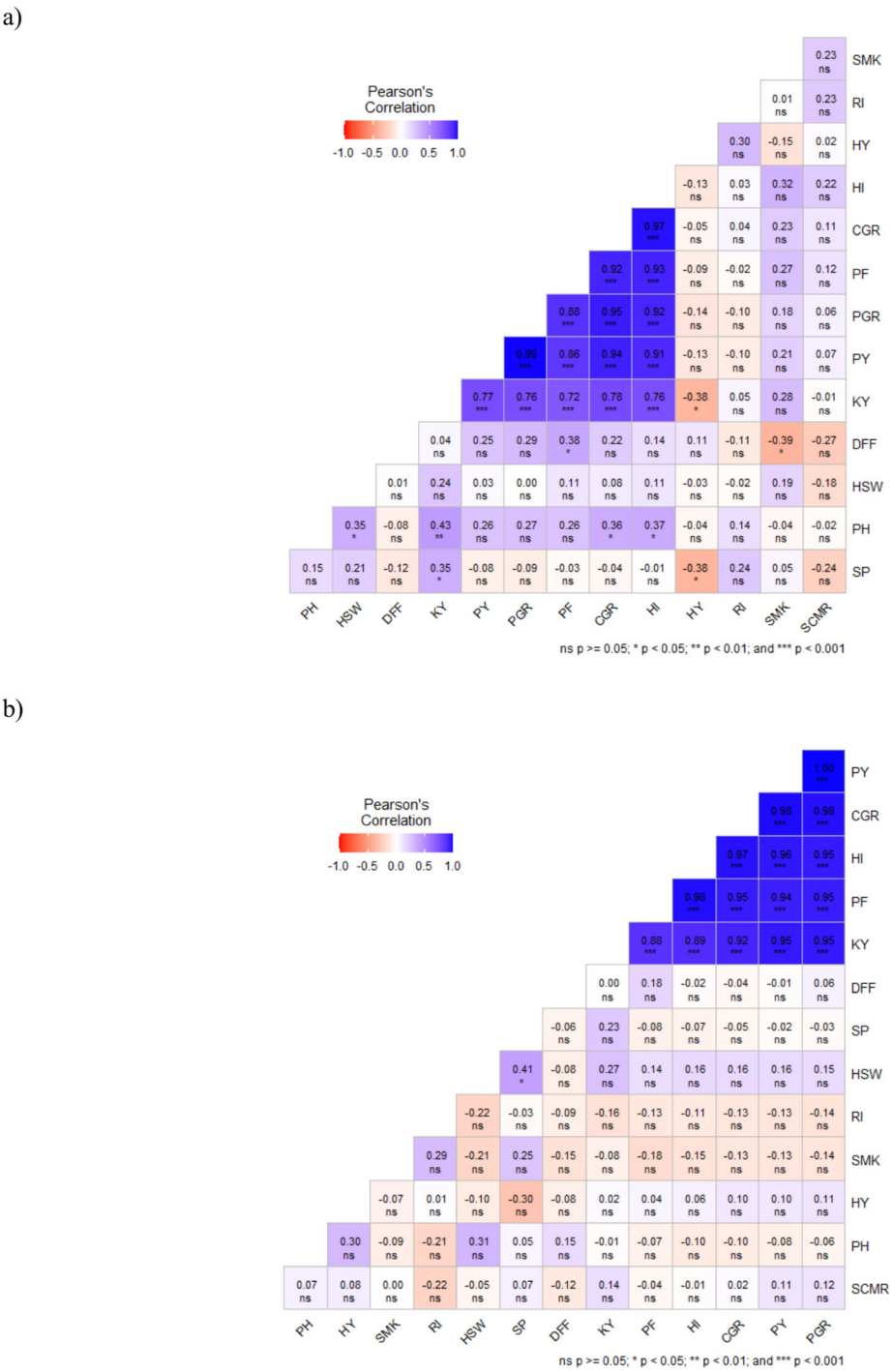


**Fig. 2** Correlation analysis of yield and associated traits among thirty-six genotypes screened under field conditions, i.e., **a** E1—Environment 1 and **b** E2—Environment 2. Significant differences are indicated: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, non-significant. PH, Plant height (cm); DFF, Days to 50% flowering; PY, Pod yield per plant (g); KY, Kernel yield per plant (g); HKW, Hundred kernel weight (g); SMK, Sound mature kernel (%); HY, Haulm yield per plant (g); SP, Shelling outturn (%); PGR, Pod growth rate (g $m^{-2}$ $day^{-1}$); CGR, Crop growth rate (g $m^{-2}$ $day^{-1}$); PF, Partitioning factor; HI, Harvest index; RI, Relative injury (%); SCMR, SPAD chlorophyll meter reading

Correlation analysis revealed positive and significant correlations of PY with KY ($r = 0.77$**), PGR ($r = 0.99$**), CGR ($r = 0.94$**), PF ($r = 0.86$**), and HI ($r = 0.91$**). Additionally, HY showed a negative and significant correlation with KY ($r = -0.38$*), and SP ($r = -0.38$*) and SMK with DFF ($r = -0.39$*) in E1 (Fig. 2a). In E2, PY had positive and significant correlations with KY ($r = 0.95$**), PGR ($r = 1.00$**), CGR ($r = 0.98$**), PF ($r = 0.94$**), and HI ($r = 0.96$**) (Fig. 2b). Overall, PY recorded positive correlations with KY, PGR, CGR, PF, and HI in both environments.

## Identification of Tolerant and Sensitive Genotypes

To further analyze the TIR results, normal Z-distribution analysis was conducted for the recorded traits. A normal Z-distribution graph was plotted, which categorized the

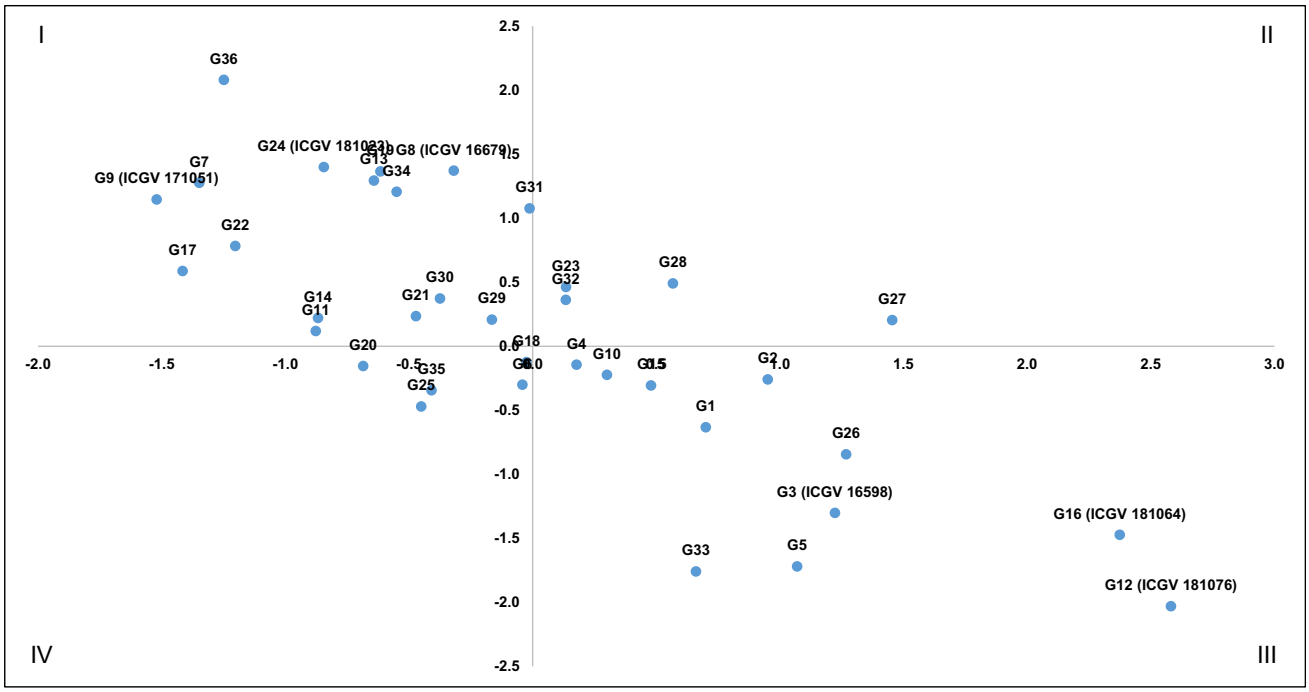


**Fig. 3** Normal Z-distribution of thirty-six genotypes based on percent reduction in growth (*Y*-axis) and actual growth during recovery (*X*-axis). *Note:* I quadrant—heat sensitive, III quadrant—heat tolerant, II and IV quadrants—moderately tolerant. G—Genotype

genotypes into three categories, i.e., heat-tolerant (III quadrant), moderately tolerant (II and IV quadrants), and heat sensitive (I quadrant). Out of 36 genotypes, eleven were classified as tolerant, nine as moderately tolerant, and sixteen as sensitive (Fig. 3). Among the genotypes, ICGV 16598, ICGV 181064, and ICGV 181076, located in quadrant III, and ICGV 181023, ICGV 16679, and ICGV 171051, located in quadrant I, were classified as heat-tolerant and sensitive genotypes in both induced and non-induced treatments, respectively. The heat-tolerant check, ICGV 13249, located in quadrant III, and the heat-sensitive check, ICGV 16690, located in quadrant I, displayed lower and higher percent reductions in shoot and root growth, respectively.

In the field experiment, centered scatter plots were used to assess the performance of genotypes across two environments. Genotypes falling under the II coordinate exhibit high performance in both environments (E1 and E2). Genotypes falling under I and III coordinates explain high performance in E2 and E1, respectively. Genotypes falling under the IV coordinate demonstrate low performance in both environments. Among the genotypes tested, ICGV 16606, ICGV 13312, and ICGV 07222, positioned in coordinate II, recorded higher PY in two environments. Conversely, ICGV 181023, ICGV 10365, and ICGV 16599, positioned in coordinate IV, exhibited lower PY across the two environments. The heat-tolerant check, ICGV 16553, and the sensitive check, ICGV 16690, recorded higher and lower PY in two environments, respectively (Fig. 4). Furthermore, the centered scatter plots for yield-associated traits, such as KY, HKW, SP, PF, PGR, CGR, and HI, revealed the performance of genotypes (Supplementary Fig. 3a–g). Specifically, ICGV 16606, ICGV 13312, and ICGV 07222 were identified as heat-tolerant, while ICGV 181023, ICGV 10365, and ICGV 16599 were considered heat-sensitive genotypes. Heat-tolerant checks, ICGV 16553 exhibited high performance for KY, PGR, and SCMR (Supplementary Fig. 3i), and ICGV 13249 reported low RI levels across the environments (Supplementary Fig. 3h).

## Discussion

HT stress is a significant abiotic constraint on groundnut cultivation as it impacts crop growth, development, and yield. Due to climate change and global warming, the severity and incidence of HT stress are projected to increase, posing a significant risk to crop production in most cropping systems [30]. Kadiyala et al. [21] predicted a − 34% to 43% change in pod yield in the groundnut growing areas of India due to elevated temperatures in 2021. When exposed to high temperatures, groundnut undergoes various physiological changes, resulting in reduced growth, increased water loss, and decreased nutrient uptake, all of which contribute to reduced yields.

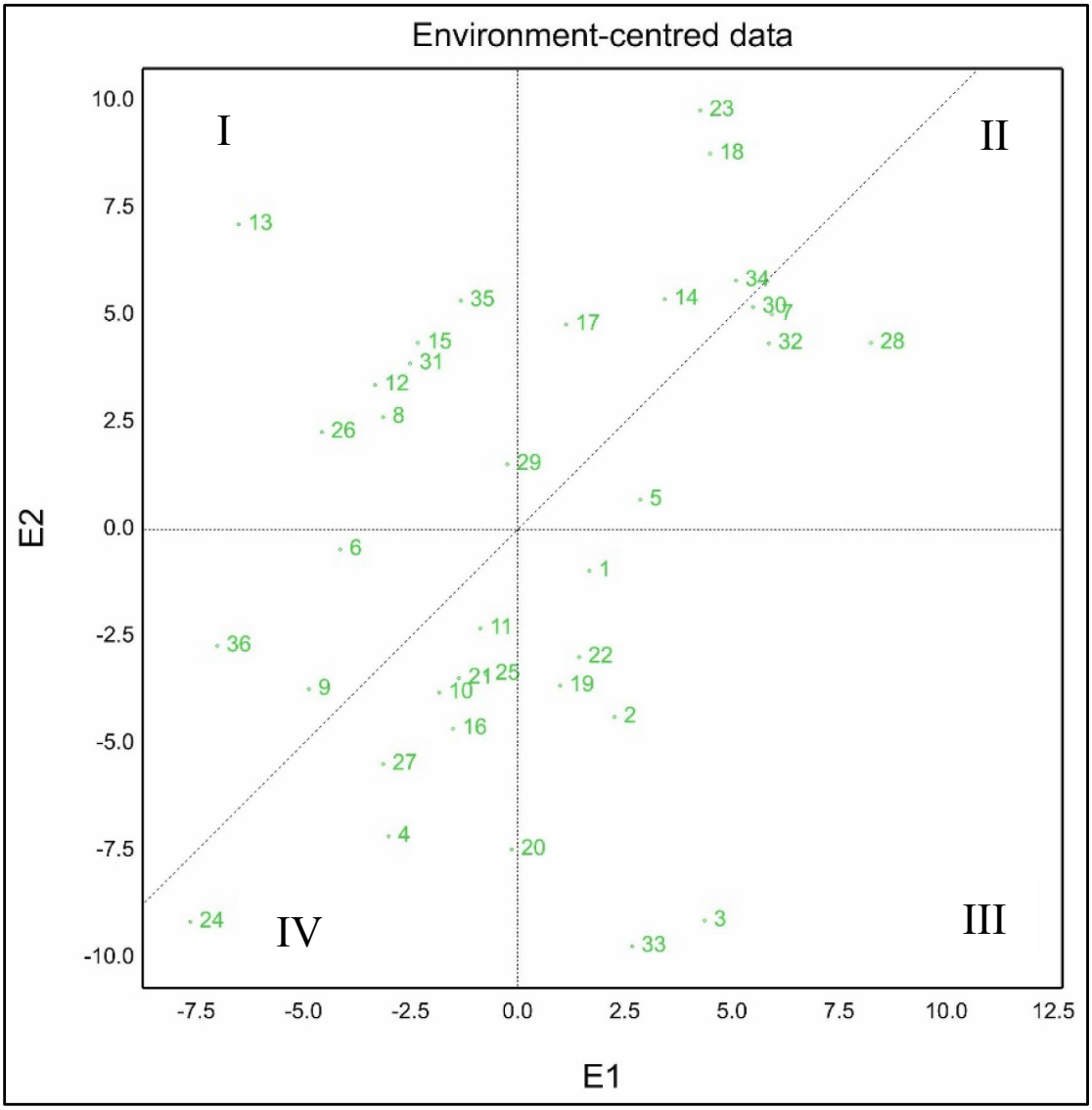


**Fig. 4** Centered scatter plot representing the performance of thirty-six genotypes screened under field conditions in E1 and E2 for Pod yield per plant (g). *Note*: I = first coordinate, II = second coordinate, III = third coordinate, IV = fourth coordinate

Therefore, it is critical to develop tolerant varieties to reduce the effects of HT stress on groundnut. Screening genotypes in various conditions help to improve genotype performance, adaptability to climate change, and advance our understanding of the HT tolerance mechanisms. Researchers have used both controlled environment assays [17, 23, 35] and field screening assays [1, 8, 18, 28] to assess groundnut response for tolerance to HT stress. In this study, a controlled environment TIR assay was employed to assess the genotypes response to HT stress during the seedling stage. Subsequently, seedling responses were compared to the pod yield performance of the genotypes under field conditions.

The TIR technique is an effective approach to evaluating genotypes for HT tolerance during the seedling stage. This method was applied to identify HT tolerant genotypes in various crop species, such as mung bean [32], chickpea [31], rice [5], groundnut [23], pea [44], and finger millet [33]. In the present study, the groundnut genotypes in the induced treatment exhibited a higher percent survival of seedlings (40–94%) compared to the non-induced treatment (12–70%) (Supplementary Fig. 2a). An increase in temperature has adverse effects on cellular functions, such as damaging cell membranes, disrupting photosynthesis, and increasing oxidative stress [30]. These impacts collectively contribute to reduced seedling viability and survival in the non-induced treatment [47]. Raghavendra et al. [31] indicated the significance of the percent survival of seedlings in identifying HT tolerant genotypes in chickpea. Additionally, a reduction in shoot and root growth was

observed in response to high temperatures. The induced treatment exhibited a lower percent reduction in shoot growth (24–47%) and root growth (16–48%) compared to the non-induced treatment (Supplementary Fig. 2b and c) because of the metabolic changes that occur by the induced treatment's acclimatization process [45]. Hence, percent survival of seedlings and percent reduction in growth can be used as essential indicators for evaluating genetic variability for HT tolerance at the seedling level in groundnut [22].

Field screening revealed significant genotypic differences ($p < 0.05$) for PY and associated traits in two heat environments, suggesting the possibility of exploiting varied genotype responses to improve heat tolerance in groundnut. Earlier studies have emphasized significant genotype responses ($p < 0.05$) in determining HT tolerance, specifically related to PY, KY, HKW, SP, HI, SMK [1, 2], PGR, CGR [1], and SCMR [2]. PY is a key selection criterion for identifying tolerant genotypes, as it directly impacts overall crop productivity [1, 28]. This study observed a higher PY in E2 (27.95 g), which experienced lower HT stress for 44 days, than in E1 with a lower PY (23.87 g), which experienced higher HT stress for 63 days (Supplementary Fig. 1). This suggests that an increased number of days of HT stress (> 35°C) during the pod-filling stage in E1 affected pod filling, resulting in reduced pod yield. Akbar et al. [1] reported similar reductions in PY (1.5–43.2%) with an increase in temperature. Additionally, higher KY (19.00 g), HKW (56.50 g), and SP (74.23%) were recorded in E2 compared to E1 (Table 2), as a consequence of fewer days of HT stress (> 35°C) in E2 than in E1. The extent of pod yield reduction in groundnut positively corresponds to the duration of HT stress during the pod-filling stage, with a lower reduction in pod yield when the crop experiences fewer days of HT stress during the pod-filling stage.

Elevated temperatures have an effect on the partitioning of assimilates into pods, resulting in reduced yield [1]. The identified tolerant genotypes exhibited a higher CGR (10.50–15.50 g $m^{-2}$ $day^{-1}$) and PGR (16.06–22.49 g $m^{-2}$ $day^{-1}$) under HT stress, indicating efficient photosynthate accumulation and partitioning to pods, contributing to a higher PY. Ntare et al. [28] recognized CGR and PGR as criteria for selecting HT tolerant genotypes in groundnut. The PF was identified as a crucial factor influencing groundnut yield under HT stress [1]. This study observed a difference in PF (1.06–1.48) between the genotypes of two environments, resulting in different yield performances. The pod-filling stage in E1 experienced more heat days (63 days), which likely disrupted the partitioning of assimilates and led to reduced yield. Conversely, E2, with fewer heat days (44 days) during the pod-filling stage, exhibited increased yield. These findings highlight PF as a significant determinant of genotype responses under HT stress and use as a selection criterion to identify HT tolerant genotypes.

HI, a measure of harvested components proportioned to the total biomass, was higher in E2 (83.50) compared to E1 (79.50). HT stress during key growth stages negatively affects crop development and growth, leading to reduced HI and ultimately lower crop yields [40]. This difference in HI was attributed to several factors, including higher values of CGR, PGR, and PF in E2. Positive and significant correlations were recorded between HI and PY ($r = 0.91^{***}$ to $r = 0.96^{***}$), PGR ($r = 0.92^{***}$ to $r = 0.95^{***}$), CGR ($r = 0.97^{***}$), and PF ($r = 0.93^{***}$ to $r = 0.98^{***}$) in two environments (Fig. 2), indicating that genotypes with efficient PY, PGR, CGR, PF, and HI can maintain productivity under HT stress. Ashutosh et al. [3] reported a positively significant correlation between PY and HI. High heritability (> 60%) for PY and KY in two environments indicated the additive gene action role in the inheritance of traits and suggested potential genetic gains by selection (Table 2). Tirkey et al. [41] and Chandrasekhara et al. [9] reported high heritability in groundnut for PY and KY. In summary, the study highlights the genetic variability of genotypes under HT stress in groundnut, with key indicators such as PY, CGR, PGR, PF, and HI influencing yield performance under challenging environmental conditions.

In assessing HT tolerance during the vegetative stage, physiological traits such as estimation of chlorophyll content and relative injury are important for the identification of tolerant genotypes [10]. Elevated temperatures induce lipid peroxidation and denaturation in the cellular components. This damage increases membrane fluidity, allowing ion leakage, measured as RI [4]. In the controlled experiment, genotypes subjected to the induced treatment exhibited a lower RI (3.16–11.78%) compared to the non-induced treatment (3.95–16.04%) and the lowest in the control treatment (1.01–7.74%) (Supplementary Fig. 2d). A lower RI indicates less damage to the cell membrane, indicating increased HT tolerance and suggesting no significant alteration in membrane stability. The adaptive reaction in the induced treatment genotypes resulted in less injury to the cell membrane, leading to lower reductions in root (16–48%) and shoot growth (24–47%). In the field experiment, the study revealed a higher RI value in E2 (7.30%) compared to E1 (6.94%). However, the identified tolerant genotypes showed lower RI in E2 (0.49–2.88%) compared to E1 (2.25–3.99%), indicating their ability to tolerate HT stress due to their tendency to acclimatize under HT stress [19]. Thus, RI is a reliable selection criterion for the identification of tolerant genotypes with lower relative injury under field conditions [6].

Chlorophyll content plays a pivotal role as an indicator of plant tolerance under HT stress and provides insights

into a plant's ability to maintain photosynthetic efficiency [6]. An increase in temperatures (> 38°C/32°C) leads to reduced chlorophyll content and ultimately less photosynthesis [30]. In the TIR experiment, higher chlorophyll content (29.04–41.34) was noted in the induced treatment genotypes, followed by the non-induced treatment (21.31–35.24), while the control treatment exhibited the highest chlorophyll content (34.70–48.76) (Supplementary Fig. 2e). This illustrates the acclimatization response and photosynthetic efficiency of the induced genotypes when exposed to HT stress, preventing the degradation of chlorophyll molecules in photosystem II (PSII) [26]. In the field experiment, higher chlorophyll content was recorded in E2 (57.50) compared to E1 (52.50), suggesting a limited effect of high temperatures (> 35°C). Correlation studies revealed a non-significant positive correlation of SCMR with PY ($r$ = 0.07 in E1 and $r$ = 0.11 in E2) under HT stress (Fig. 2). A similar association was reported in tomato [6], and hence, SCMR can be employed as a criterion of selection for identifying genotypes with higher chlorophyll content. However, the identified tolerant genotypes indicated lower levels of RI and less chlorophyll degradation, as evidenced by the elevated SCMR values, potentially resulting in increased yields. By focusing on traits like RI and SCMR, cultivars that withstand high temperatures and maintain yield can be selected.

A comprehensive screening for HT tolerance must include a controlled TIR assay as well as a field screening assay. This helps to identify potential genotypes that function well across various conditions, where genotypes are exposed to high temperatures at various stages of crop growth. Studies in other crops, such as cotton [11], Indian mustard [37], pepper [27], and wheat [25], have employed screening in both controlled and field conditions to assess HT tolerance. These studies demonstrated that the genotypes exhibited comparable performance in both conditions, highlighting the potential of a comprehensive screening approach for HT tolerance. In the present study, genotypes showing seedling tolerance under controlled conditions are different from the genotypes that recorded superior performance under field conditions. Differential genotype responses at various stages of crop growth when exposed to high temperatures have led to this variability [7, 10]. This proposes that various mechanisms are responsible for the seedling tolerance and yield performance of groundnut under HT stress.

In summary, the study's findings provided significant implications for enhancing groundnut resilience and adaptability under climate change, considering the variability in genotype responses to high temperatures across growth stages. Future research should focus on using these screening approaches and identifying additional factors which contribute to high-temperature tolerance in groundnut.

## Conclusions

Groundnut genotypes were assessed for HT tolerance using both the TIR technique and field screening. The results of the two experiments revealed significant variability in HT tolerance among the genotypes. The study revealed that induced seedling tolerance achieved through the controlled TIR assay is not associated with pod yield under field conditions. This indicates that genotype responses to high temperatures vary with growth stages under different genotype×temperature interactions. Although the association was not found, both controlled and field experiments were informative in assessing HT tolerance. Furthermore, the utilization of physiological traits such as PGR, CGR, and RI emphasized the importance of selecting adaptable genotypes. While the TIR technique can aid as an initial screening tool, field screening is crucial for validating the results and assessing agronomic performance under high-temperature conditions. Finally, our research provides important information for the development of HT tolerant groundnut cultivars for sustainable crop production in semi-arid tropical areas.

**Author Contributions** Conceptualization was performed by Padma Vemulapalli, Janila Pasupuleti, and Anurag Mathew; methodology was presented by Janila Pasupuleti; implementation was done by Anurag Mathew; coordination was followed by Rachana Bagudam, Sai Rekha Kadirimangalam, Lal Ahamed Mohammad, and Raghavendra M; article draft preparation was drafted by Anurag Mathew and Janila Pasupuleti; data curation and analysis were presented by Anilkumar Vemula. All the authors had approved the available version of the manuscript.

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**Data Availability** The data supporting the results of this study are available within the article and its supplementary material.

## Declarations

**Conflict of interest** The authors declare no conflicts of interest.

**Supplementary Information**

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