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Characterizing plant trait(s) for improved heat tolerance in field pea (*Pisum sativum* L.) under subtropical climate

Ashok K. Parihar[1] · Kali K. Hazra[1] · Amrit Lamichaney[1] · Girish P. Dixit[1] · Deepak Singh[2] · Anil K. Singh[1] · Narendra P. Singh[1]

Abstract

Field pea is highly sensitive to climatic vagaries, particularly high-temperature stress. The crop often experiences terminal heat stress in tropical climates indicating the need for the development of heat-tolerant cultivars. Characterization and identification of stress-adaptive plant traits are pre-requisites for breeding stress-tolerant/adaptive cultivar(s). In the study, a panel of 150 diverse field pea genotypes was tested under three different temperature environments (i.e., normal sowing time or non-heat stress environment (NSTE), 15 days after normal sowing time or heat stress environment-I (LSHTE-I), and 30 days after normal sowing time or heat stress environment-II (LSHTE-II)) to verify the effect of high-temperature environment, genotype, and genotype×environment interaction on different plant traits and to elucidate their significance in heat stress adaptation/tolerance. The delayed sowing had exposed field pea crops to high temperatures during flowering stage by +3.5 °C and +8.1 °C in the LSHTE-I and LSHTE-II, respectively. Likewise, the maximum ambient temperature during the grain-filling period was +3.3 °C and +6.1 °C higher in the LSHTE-I and LSHTE-II over the NSTE. The grain yield loss with heat stress was $25.8 \pm 2.2\%$ in LSHTE-I, and $59.3 \pm 1.5\%$ in LSHTE-II compared to the NSTE. Exposure of crops to a high-temperature environment during the flowering stage had a higher impact on grain yield than the heat stress at the grain filling period. Results suggested that the reduced sink capacity (pod set (pod plant^{-1}), seed set (seed pod^{-1})) was the primary cause of yield loss under the heat stress environments, while, under the NSTE, yield potential was mostly attributed to the source capacity (plant biomass). The high-temperature stress resulted in forced maturity as revealed by shrinkage in crop period (5–11%) and reproductive period (15–36%), prominently in long-duration genotypes. The failure of pod set in the upper nodes and higher ovule abortion (7–16%) was noticed under the high-temperature environments, particularly in the LSHTE-II. Multivariate analysis results revealed seed set, pods plant^{-1}, last pod bearing node, and plant biomass as a critical yield determinant under the heat stress. The GGE biplot suggested that the genotypes G-112, G-114, and G-33 had higher potential to sustain yield coupled with higher stability across the environments and, thus, could serve as a source for breeding heat-tolerant high yielding cultivars.

Keywords Terminal heat stress · Phenology · Traits association · Subtropical climate · Field pea · GGE biplot

Introduction

The global ambient temperature is expected to increase by 2–4 °C by the end of twenty-first century (IPCC 2007). Such elevation in ambient temperatures could constrain food crop productivity in near future, especially in tropical climates (Zinn et al. 2010; Vadez et al. 2012). The ambient temperature beyond the threshold limit, particularly at the reproductive stages, causes significant yield loss and affects produce quality (Bita and Gerats 2013; Farooq et al. 2017; Liu et al. 2019; Al Mahmud et al. 2021). Therefore, crop-breeding approach to improve heat tolerance in field crops is essential to ensure food and nutritional security. Field

✉ Kali K. Hazra
  kalikrishna123@gmail.com

✉ Amrit Lamichaney
  amritiarisst@gmail.com

[1] ICAR-Indian Institute of Pulses Research, Kanpur, Uttar Pradesh 208024, India

[2] ICAR-Indian Agricultural Statistics Research Institute, New Delhi 110012, India

pea (*Pisum sativum* L.) is one of the important cool-season legumes, grown across the world for food, feed, and fodder (Holdsworth et al. 2017; Rubiales et al. 2019). Field pea, being a cool-season legume, has higher sensitivity to high-temperature environments than most warm season legumes (Hall 2001). According to Guilioni et al. (2003) and Sadras et al. (2012), the productivity of field pea declines when maximum ambient temperature during the flowering exceeds 25 °C. Also, flowering to seed filling period has been reported to be the most sensitive stage to heat stress in field pea (Jeuffroy et al. 2010; Jiang et al. 2019a). Previous studies have reasoned that a higher ambient temperature above threshold limit can reduce crop biomass, flowering nodes, number of pods plant^{-1}, flower and young pod abortion, and forced maturity, which ultimately affects the crop yields (Guilioni et al. 2003; Sadras et al. 2012; Bueckert et al. 2015). To date, the sensitivity of field pea to high-temperature environments and its inherent genotypic potential with reference to high-temperature adaptation/tolerance at field scale are still uncertain in tropical climates.

Over the years, a notable shift in the growing environment of cool-season legumes has been observed from the cooler, long-season environments of northern India to the warmer, short-season environments of central and southern India (Gaur et al. 2019; Gowda et al. 2009). Particular to field pea growing areas in sub-tropical climates, the crop is often exposed to high temperature environments (> 25 °C) during flowering and grain filling period (Dixit et al. 2006). Concerning this, strategic deployment of potential heat tolerant lines in crop improvement program is increasingly being realized for this heat-sensitive crop (Sita et al. 2017; Gogoi et al. 2018). Identification and characterization of heat stress inductive plant traits are prerequisites for strategic crop improvement under stressful environments. Heat tolerance is often viewed as a complex trait (Paul et al. 2018). An effective and simple screening method with well-defined traits for selecting heat-tolerant genotypes under field conditions is necessary for breeding heat tolerant cultivars (Devasirvatham et al. 2013). To date, much progress has been made to characterize/utilize the heat-tolerant/sensitive traits in cool-season legumes like chickpea and lentil (Pareek et al. 2019; Kumar et al. 2020); however, the research progress on high-temperature tolerance in field pea is still lagging. Also, very limited efforts have been made to explore the genetic capacity of heat tolerance attributed to plant traits like phenological stability, floral position with reference to nodes, pod and seed set, grain filling (or grain weight), source and sink capacity within a diverse group of field pea genotypes. Therefore, in the present investigation diverse group of field pea genotypes (150) were used to understand the sensitivity of different plant traits to high temperature stress which may provide an insight on crop adaptive strategy with reference to heat tolerance.

A systematic investigation of high-temperature environment, genotype, genotype × environment interaction (G × E) effects, and associations of plant traits among themselves provide a baseline information to identify and characterize stress-adaptive trait(s) of interest (Parihar et al. 2014a, 2014b). Several multivariate analysis approaches such as GGE biplots, linear mixed regression model, and size effect plot are widely used for trait association studies and representativeness of plant traits across crop growing environments. A prior knowledge on the relative magnitudes of genetic, G × E interaction, and environmental variance can be helpful for designing a heat tolerance breeding program. Therefore, the present study was undertaken with the objective of testing diverse field pea genotypes under three different temperature regimes and to verify the effect of environment, genotype, and genotype × environment interaction on different plant traits and to elucidate their significance in heat stress adaptation/tolerance. The major hypothesis were (i) differential contribution of heat responsive traits in heat robust and susceptible genotypes, (ii) genotypic sensitivity to high temperature stress hinged on the temperature intensity during reproductive period, (iii) staggered sowing exposes the reproductive period of field pea genotypes to high temperature stress.

Materials and methods

Site characteristics

The field experiment was conducted at the main research farm of ICAR-Indian Institute of Pulses Research, Kanpur, India, during the *rabi* season of 2017–2018. The site experiences a sub-tropical humid climate with average annual rainfall and temperature of about 720 mm and 26 °C, respectively. The weather parameters prevailing during the crop-growing season are presented in Fig. 1. The soil of the experimental site is sandy-loam in texture with an electrical conductivity of 0.342 dS m^{-1}, pH value of 7.98, 4.3 g kg^{-1} soil organic carbon, 102 mg kg^{-1} available nitrogen (KMnO$_4$-N), 7.1 mg kg^{-1} available phosphorus (Olsen-P), and 113 mg kg^{-1} available-potassium (NH$_4$OAC-K).

Planting material and experimental details

In the present study, a total of 150 field pea genotypes including a diverse panel of germplasm, breeding lines, and high-yielding released cultivars were used as an experimental material (Supplementary Table 1). To expose the crop, especially the reproductive period to heat stress, the genotypes were staggered planted on three different dates of sowing, i.e., 15th November, 30th November, and 15th December. The first date of sowing (15 November) is considered an optimum time for

Fig. 1 Diurnal variation in ambient temperature (DVT) and relative humidity (RH) during the study period. The vertical green, orange, and red lines indicate the sowing time in the NSTE, LSHTE-I, and LSHTE-II, respectively
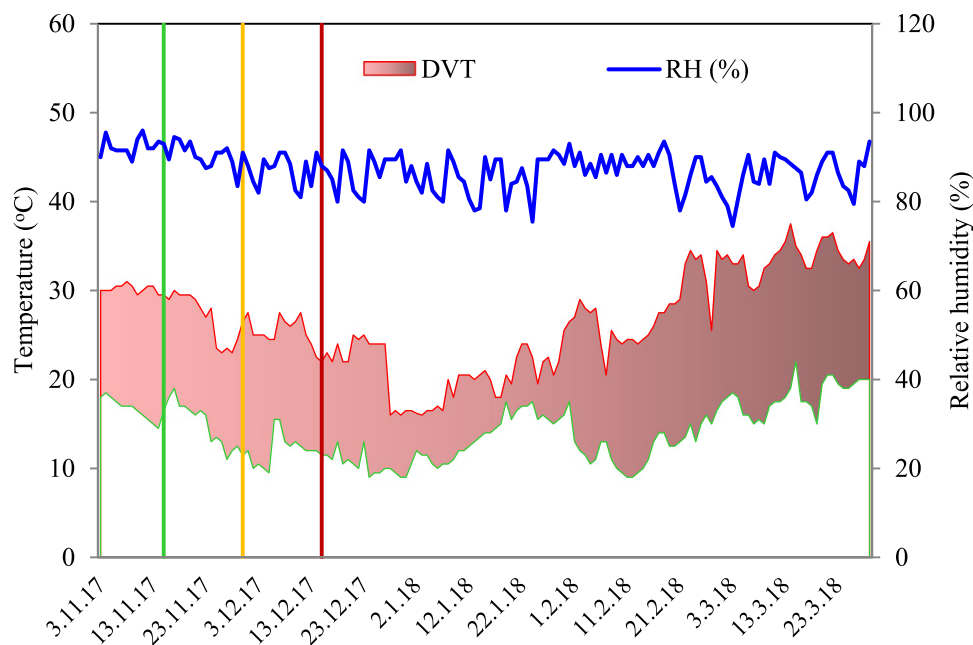
planting field pea in Kanpur. From this point onwards, the staggered sowing-induced heat stress treatments are designated as late-sown high-temperature environment-I (LSHTE-I) (30 November) and late-sown high-temperature environment-II (LSHTE-II) (15 December), whereas non-heat stress environment (15 November) as NSTE. The genotypes in each environment were randomly allocated in the plot following the augmented block design, comprising of six blocks and two checks (IPF 99–25 and IPF 5–19) in each block.

Crop management

The field was properly ploughed before sowing followed by a harrowing and planking to produce a fine tilth. Each genotype was sown in 3 lines of 4 m length following standard plant geometry of 30 cm × 5 cm, between rows and plant, respectively. At the time of sowing, nitrogen (20 kg N ha^{-1}), phosphorus (50 kg P$_2$O$_5$ ha^{-1}), and potassium (50 kg K$_2$O ha^{-1}) were applied as a basal dose. Field pea crops under different environments were irrigated based on irrigation water/cumulative pan evaporation (IW/CPE) ratio of 0.75, such that irrigation was given at 40 and 78 days after sowing (DAS) in NSTE, while the irrigation was given at 30 and 67 DAS in LSHTE-I and 51 and 73 DAS in LSHTE-II. One hand-weeding was done after 25 days of sowing to control the weeds. Necessary plant protection measures were taken to control the insect pests and diseases.

Observations on phenology

The flowering behavior of each genotype was daily observed visually and the day in which about 50% of the total pant

recorded flowering was taken as days to 50% flowering (DTF). Likewise, the day when almost all the pods appeared fully dried and yellowish was considered the maturity date for each genotype, and the number of days taken for a genotype from sowing to achieve maturity was calculated and denoted as days to maturity (DTM). The period (days) taken by a genotype from DTF to DTM was considered the reproductive period (RP) for that particular genotype.

Crop growth and yield attributing parameters

Plant biometric observations like plant height (PH), first pod bearing node (FPBN), last pod bearing node (LPBN), number of pods plant^{-1}, pod length, number of grains pod^{-1}, and ovules pod^{-1} were recorded in five randomly selected plants at maturity. The plants were oven dried at 65 ± 2 °C for 48 h and dry weights were recorded to determine the aboveground biomass plant^{-1}. For the calculation of seed set percentage, the number of fully developed seeds and ovules per pod was counted and computed in ten pods selected from the top four pod bearing nodes. For determining grain yield, among the three rows, the inner row was separately harvested and weighed at 12% moisture content and expressed as kg ha^{-1}. One hundred grains of each genotype in three replications were counted and weighed for determination of 100-grain weight. The dry weight of grains plant^{-1} was recorded to represent grain weight plant^{-1}. The harvest index was calculated using the following formula:

$$Harvest\ index\ (\%) = \frac{Grain\ weight\ per\ plant\ (g)}{Above\ ground\ plant\ weight\ (g)} \times 100$$

Temperature intensity and growing degree-day (GDD) calculation

The intensity of temperature during flowering ($TMAX_F$) and reproductive period ($TMAX_{RP}$), GDD for vegetative (GDD_{VEG}), reproductive (GDD_{RP}), and full crop season (GDD_{FS}) of each genotype were calculated following the protocol as detailed by Lamichaney et al. (2021).

Statistical analyses

The analysis of variance (ANOVA) of augmented block design was performed to determine the significance of genotype and environment factors and to obtain the adjusted mean value of each parameter for each genotype, which was used for the correlation studies. The principal component analysis was carried out using the software PAST 3.14. The biplots of genotype + genotype-by-environment (GGE) were developed using "GGEBiplotGUI" package in R studio (Yan and Tinker 2006). The procedure followed by Parihar et al. (2018) was used for constructing the GGE biplots. To determine the relative contribution of different yield attributing traits toward grain yield under normal and heat stress environments, size effect plot analysis was done using the R software. The regression line for a multivariable regression is as follows:

$$Y = a + b_1 X_1 + b_2 X_2 + ...b_n X_n$$

where Y is the dependent variable, X_{1-n} is the independent variables, a is the constant (y-intersect), and b_{1-n} is the regression coefficient of the variable. We assessed model predictions by plotting and calculating the linear regression equations of each paired (observed values) and (predicted values) vectors, for OP values, and then plotted the distribution of slope and intercept parameters predicted in the linear model.

Results

Heat events and growing degree days

Results showed that late-sown induced high-temperature effect was prominent and significant on field pea crop. Maximum ambient temperature during flowering ($TMAX_F$) was highest (30.5 °C) in the LSHTE-II, followed by LSHTE-I (25.9 °C) and NSTE (22.4 °C) (Fig. 2). Likewise, mean maximum temperature during reproductive period ($TMAX_{RP}$) was in the order LSHTE-II (33.3 °C) > LSHTE-I (30.5 °C) > NSTE (27.2 °C) ($p < 0.001$). On an average, the crop in the NSTE, LSHTE-I, and LSHTE-II, 61%, 84%, and 100% of the reproductive period, was exposed to maximum temperature > 25 °C,

respectively. Growing degree days of reproductive period (GDD_{RP}) was 762 °C-days in the NSTE, which was reduced to 686 °C-days (− 10%) and 281 °C-days (− 63%) in the LSHTE-I and LSHTE-II, respectively. Non-significant differences were observed in GDD of vegetative period (GDD_{VEG}) across the three studied environments (Fig. 2).

Crop phenology

Results revealed that the crop growing environments did not alter the days to 50% flowering ($p > 0.05$). However, the mean days to maturity in the NSTE were 109 days, which reduced to 104 and 98 days in the LHSTE-I and LHSTE-II, respectively. Subsequently, a significant reduction in reproductive period was noted in the LHSTE-I and LHSTE-II (reproductive period 27–31 days) as compared to NSTE (reproductive period 37 days) (Fig. 3).

Crop growth, yield, and yield parameters

Late-sown induced high-temperature environments (LHSTE-I and LHSTE-II) resulted in a reduction in seed set (7–17%), grain pod^{-1} (9–36%), pod plant^{-1} (12–86%), pod length (5–17%), last pod bearing node (5–16%), 100-seed weight (7–19%), grain weight plant^{-1} (20–144%), and aboveground plant biomass (17–79%) (Fig. 4). However, the plant height and first pod bearing node remain unchanged within the different growing environments (Table 1, Fig. 4). The average grain yield in the NSTE, LHSTE-I, and LHSTE-II was 1260, 928, and 484 kg ha^{-1} accounting for 26–62% yield loss in the heat stress environments as compared to the non-heat stress environment (Fig. 5a).

Weather variables and plant trait associations with yield

The relationship between weather variables and grain yield is presented in Fig. 2. Under the NSTE, the correlations of $TMAX_F$ and $TMAX_{RP}$ with grain yield were non-significant ($p > 0.05$). $TMAX_F$ and $TMAX_{RP}$ had significant negative associations with grain yield in LSHTE-II, while in LSHTE-I, the association was significantly negative only for $TMAX_F$. The association of GDD_{VEG} with grain yield was significant in only LHSTE-II. However, GDD_{RP} and the ratio of GDD_{RP} with GDD_{VEG} had significant and positive associations with grain yield in all the three environments. The association of GDD_{FCS} with grain yield was significant only in NSTE. Crop phenological parameters like days to 50% flowering, days to maturity, and reproductive period exhibited strong positive association with grain yield (Fig. 2). Among the crop growth and yield parameters, plant height, last pod bearing nodes, pod plant^{-1}, and aboveground biomass had positive associations with grain yield across the environments, and the
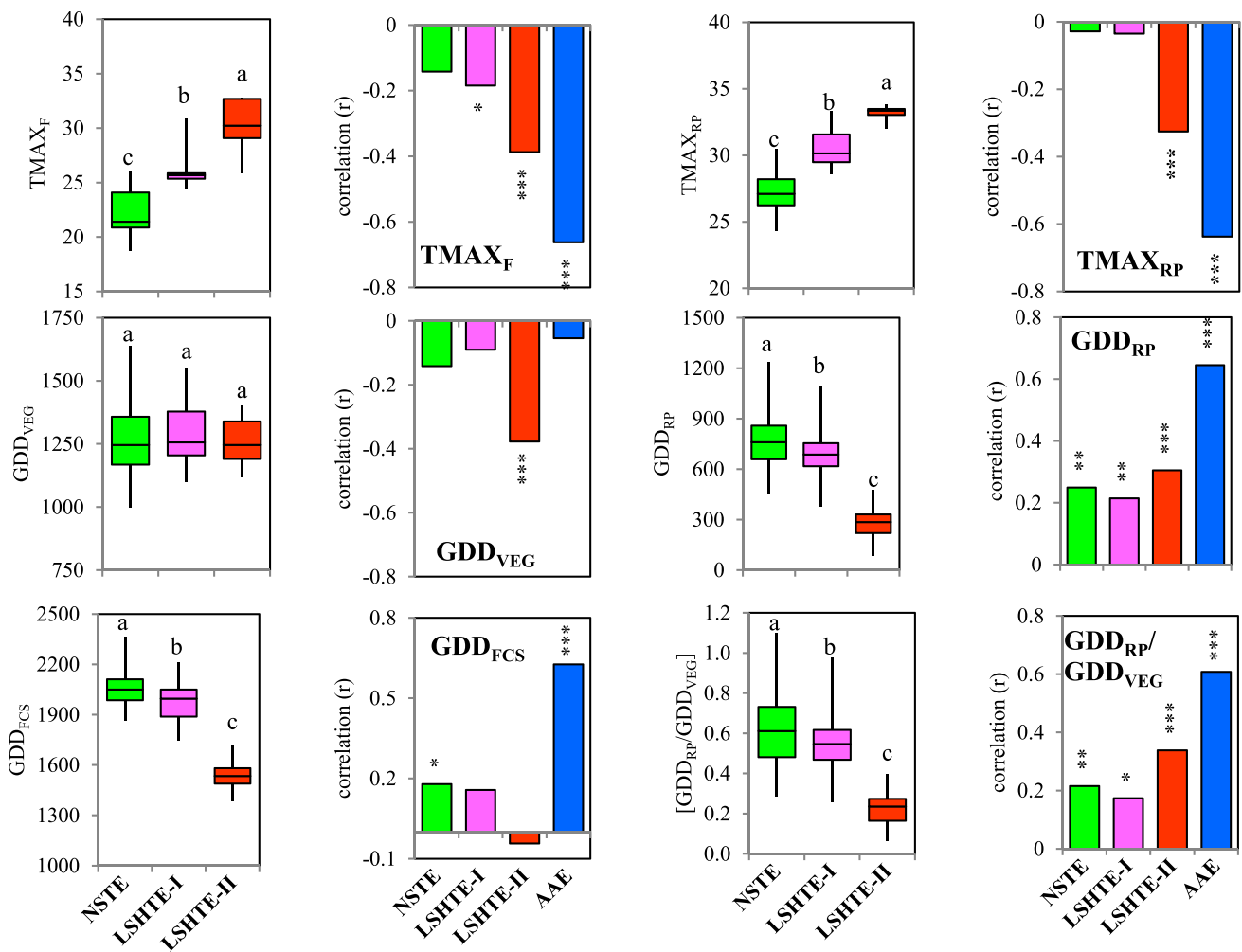
Fig. 2 Maximum temperatures during flowering (TMAX_F), reproductive period (TMAX_RP), and cumulative growing degree days of vegetative (GDD_VEG), reproductive (GDD_RP), and full crop season (GDD_FCS) of field pea genotypes as altered by different crop growing environments. The bar graphs represent the correlations of temperature and GDD parameters with grain yield (Pearson correlation coefficient). *a–c* Different lowercase letters represent significant difference at $p = 0.05$ according to Duncan's multiple range test. AAE, across all the environments. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$

correlation was highest in the LSHSE-II (Fig. 3). Correlation results further revealed that the genotype yield potential (grain yield under normal sown condition, NSTE) had significant and positive association ($p < 0.001$) with grain yield loss under the late-sown induced high temperature environments (LHSTE-I and LHSTE-II) (Fig. 5). Likewise, the crop maturity duration shows significant positive association with yield loss in LHSTE-II ($p < 0.05$), but not in the case of LHSTE-I ($p > 0.05$). Seed weight was negatively correlated with grain yield loss in LHSTE-I; in contrast, the correlation was found positive in LHSTE-II (Fig. 5).

Multivariate analysis and trait associations

Linear mixed model results indicated that high temperature at the flowering stage had more detrimental impact on crop

yield than the reproductive period (Table 2). The cumulative GDD of reproductive period exhibited a positive impact on crop yield. The relationship between observed and predicted grain yield was highly significant in all the three environments ($p < 0.001$) (Fig. 6). The size effect analysis revealed that under the NSTE, the aboveground biomass had prominent influence on grain yield (Table 3). While, under the LHSTE-I, pod plant^{-1} and last pod bearing node had the highest size effect with their corresponding log value of 3.247 and 1.435, respectively. Likewise, under the LHSTE-II, the traits with higher size effect were seed set (4.49), pod plant^{-1} (1.948), last pod bearing node (1.918), and ovule pod^{-1} (1.711). The PCA results indicated that the traits like crop biomass, pod plant^{-1}, last pod bearing node, and seed set percentage had prominent contribution toward the variation in grain yield (Fig. 7). The PCA graph
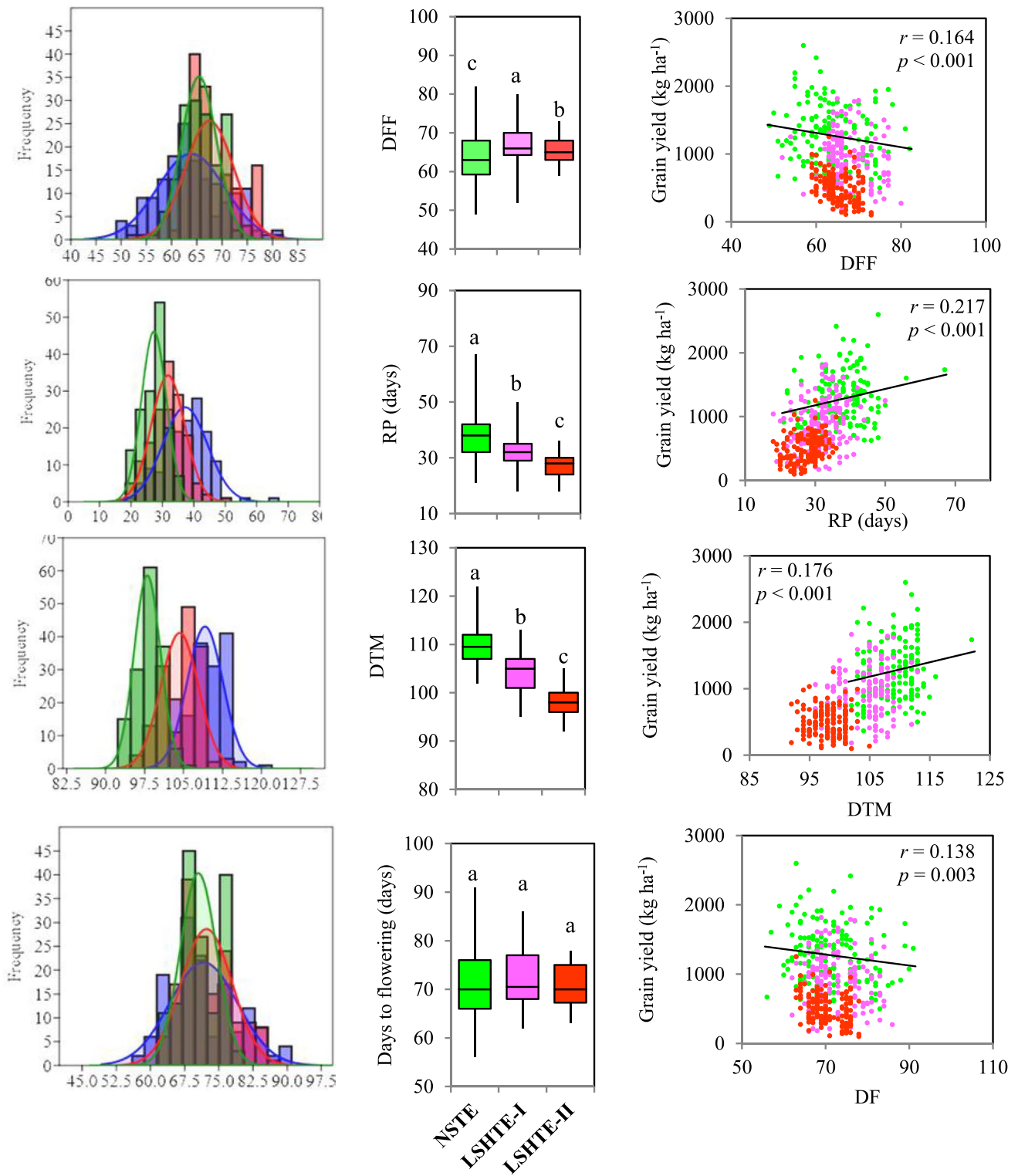
Fig. 3 Histogram and box plot presentation of crop phenology of field pea as influenced by late-sown induced high temperature environments and their association with grain yield. DFF, days to first flowering; RP, reproductive period (days); DTM, days to maturity; DF, days to 50% flowering. *a–c* Different lowercase letters represent significant difference at $p = 0.05$ according to Duncan multiple range test. Scatter green, pink, and red color points in correlation graphs represent genotypic variation in the NSTE, LSHTE-I, and LSHTE-II, respectively
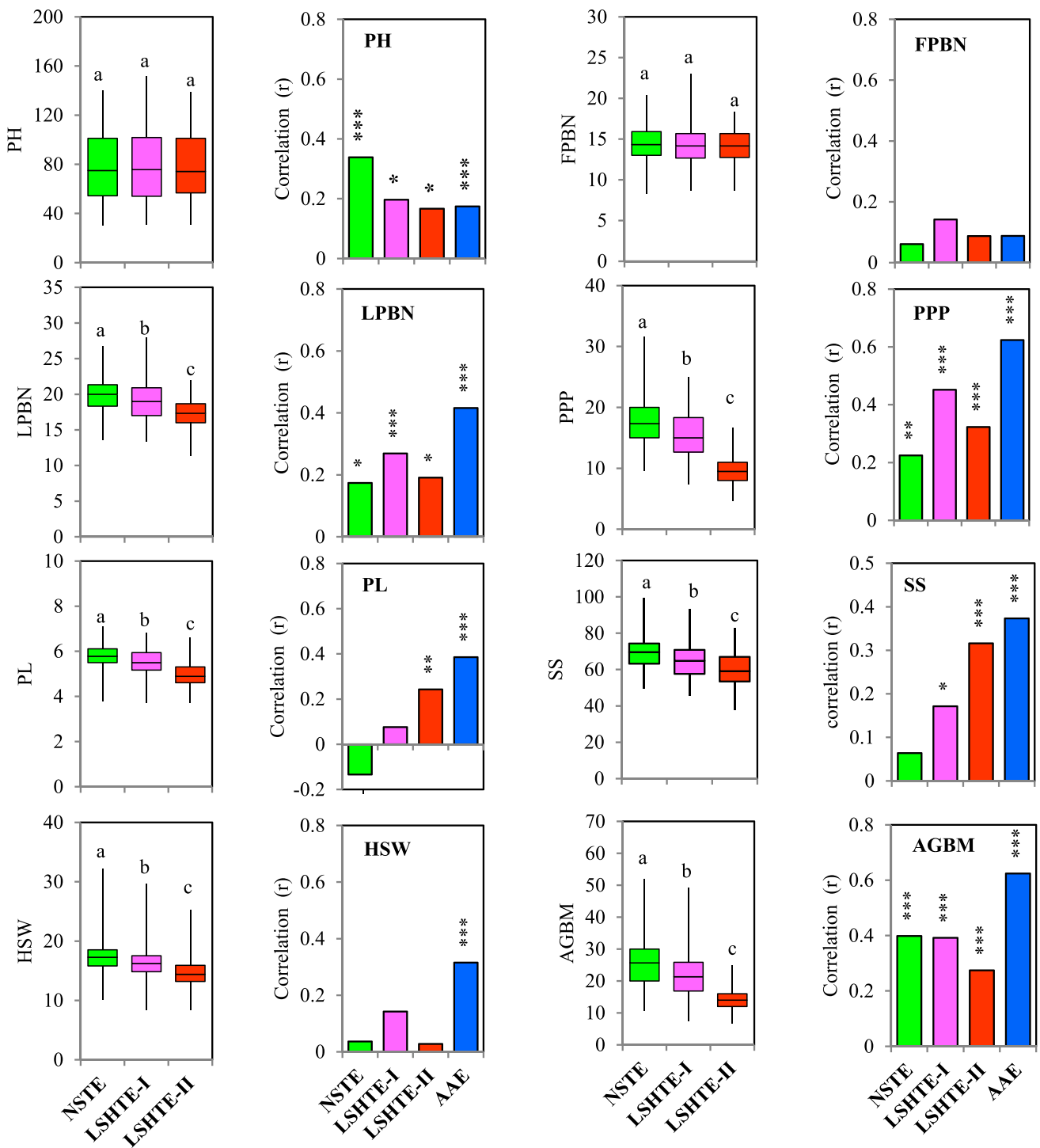
Fig. 4 Effect of high temperature environments on crop growth and yield parameters of field pea genotypes and their relation with grain yield (Pearson correlation coefficient). *a–c* Different lowercase letters represent significant difference at *p* = 0.05 according to Duncan multiple range test. AAE, across all the environments; PH, plant height (cm); FPBN, first pod bearing node; LPBN, last pod bearing node; PPP, pods per plant (nos.); PL, pod length (cm); SS, seed set (%); HSW, 100-seed weight (g); AGBM, aboveground dry biomass (g). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

illustrates reduced genotypic variability under the high temperature environments as compared to NSTE. Particularly, the genotypes with very late-sown condition are distinctly positioned on the PCA coordinates. Results revealed that temperature intensity and grain yield were negatively associated. The late-sown induced variation in days to flowering

Table 1 Analysis of variance for grain yield and yield attributes in field pea under different temperature regimes during winter season 2017–2018

Parameter	Source of variation		Mean squares	
	Environment	Genotype	Error	Total
Degrees of freedom (*df*)	2	150	300	452
Days to first flowering (DFF)	506.10**	61.43**	9.29	576.81
Days to 50% flowering (DF)	128.12**	80.09**	9.71	217.93
FTFF (DF-DFF)	462.52**	7.72**	3.68	473.92
Reproductive period	4162.82**	67.31**	21.97	4252.09
Days to maturity	5254.18**	17.47**	12.62	5284.28
Plant height	9.51	1837.68**	276.84	2124.03
First pod bearing node	1.47	7.99**	3.77	13.22
Last pod bearing node	299.62**	11.51**	4.19	315.32
Pods plant^{-1}	2897.89**	29.97*	22.01	2949.87
Pod length	26.75**	0.42**	0.28	27.44
Ovules pod^{-1}	39.33**	0.94	0.77	41.03
Grains pod^{-1}	59.12**	0.61**	0.33	60.05
Seed set percentage	3656.47**	112.41**	80.35	3849.23
100-seed weight	290.83**	13.52**	4.4	308.75
Grain weight plant^{-1}	1311.88**	10.84*	7.19	1329.91
Aboveground biomass plant^{-1}	4942.72**	53.41*	40.67	5036.8
Grain yield	328,531.19**	3458.40**	2197.38	334,187
Harvest index	5080.57**	94.58*	71.99	5247.13

and reproductive period was also noticeable, where it was marginal for the 100-seed weight. The yield-attributing traits like ovule pod^{-1}, seed set, pod plant^{-1}, last pod bearing node and 100-seed weight exhibited positive associations with grain yield, being higher for above-ground biomass. Grain yield had a negative association with and pod length. However, the days to flowering and first pod bearing node did not show any direct associations. GGE biplot graphs illustrate that environment and G × E effects were distinct on grain yield (Fig. 8). Based on the yield potential, the genotypes G-112, G-144, and G-33 were identified as superior as these genotypes possessed both higher yield and stability across the environments.

Discussions

The results verify that the late sown conditions expose field pea crops to high-temperature stress as the maximum ambient temperatures during the flowering and reproductive period were 22.4 °C and 27.2 °C in the normal sown condition (NSTE), and 30.5 °C and 33.3 °C in very late-sown condition (LHSTE-II), respectively. Meanwhile, the average maximum temperatures during the flowering and reproductive stages were higher than the threshold limit of 25 °C (Guilioni et al. 2003; Lamichaney et al. 2021) in both the late-sown conditions (LSHTE-I and LSHTE-II) indicating heat stress particularly at the terminal growth stages. Across the environments, uniform crop management practices were

followed and IW/CPE ratio based irrigation schedule was employed to avoid temperature-induced soil moisture stress. So, the observed variations in the crop parameters were certainly attributed to the differences in temperature intensity as differed within the normal and late-sown conditions. Stress-induced forced maturity is viewed as a plant adaptation strategy; however, this is often coupled with reduced yields. Our result verifies that the late-sown induced high temperature stress causes forced maturity in field pea mainly because of the shrinkage in the reproductive period. Such reduction in seed filling period (or reproductive period) due to high temperature can limit the transfer of assimilates and their accumulation in seed, resulting in reduced seed weight (Basu et al. 2009; Prasad et al. 2017). Although, stress-induced forced maturity is considered as a plant adaptation strategy, it is often accompanied by reduced yield (Fahad et al. 2017; Kumari et al. 2021) and poor quality (Lamichaney et al. 2021). Moreover, our results indicated no alteration in the vegetative period of field pea across the crop growing environments, hence the flowering stage of late-sown crops were exposed to higher temperatures as compared to the normal sown crop.

At moderately late-sown condition (LSHTE-I), the highest adverse impact was observed on crop biomass (17%) followed by pod plant^{-1} (12%), grain pod^{-1} (9%), seed set (7%), and seed weight (7%), while the most affected traits in very late-sown condition (LSHTE-II) were pod plant^{-1} (86%) > crop biomass (79%) > grain pod^{-1} (36%) > 100-seed weight (19%) > seed set (17%). Hence, there are

Fig. 5 Grain yield of field pea under different growing environments (**a**, **b**). Linear correlation of grain yield loss under high temperature environments (LSHTE-I, LSHTE-II) with genotype yield potential (NSTE), 100-seed weight (NSTE), and maturity duration (NSTE) (**c**–**h**). *a*–*c* Different lowercase letters represent significant difference at $p = 0.05$ according to Duncan multiple range test
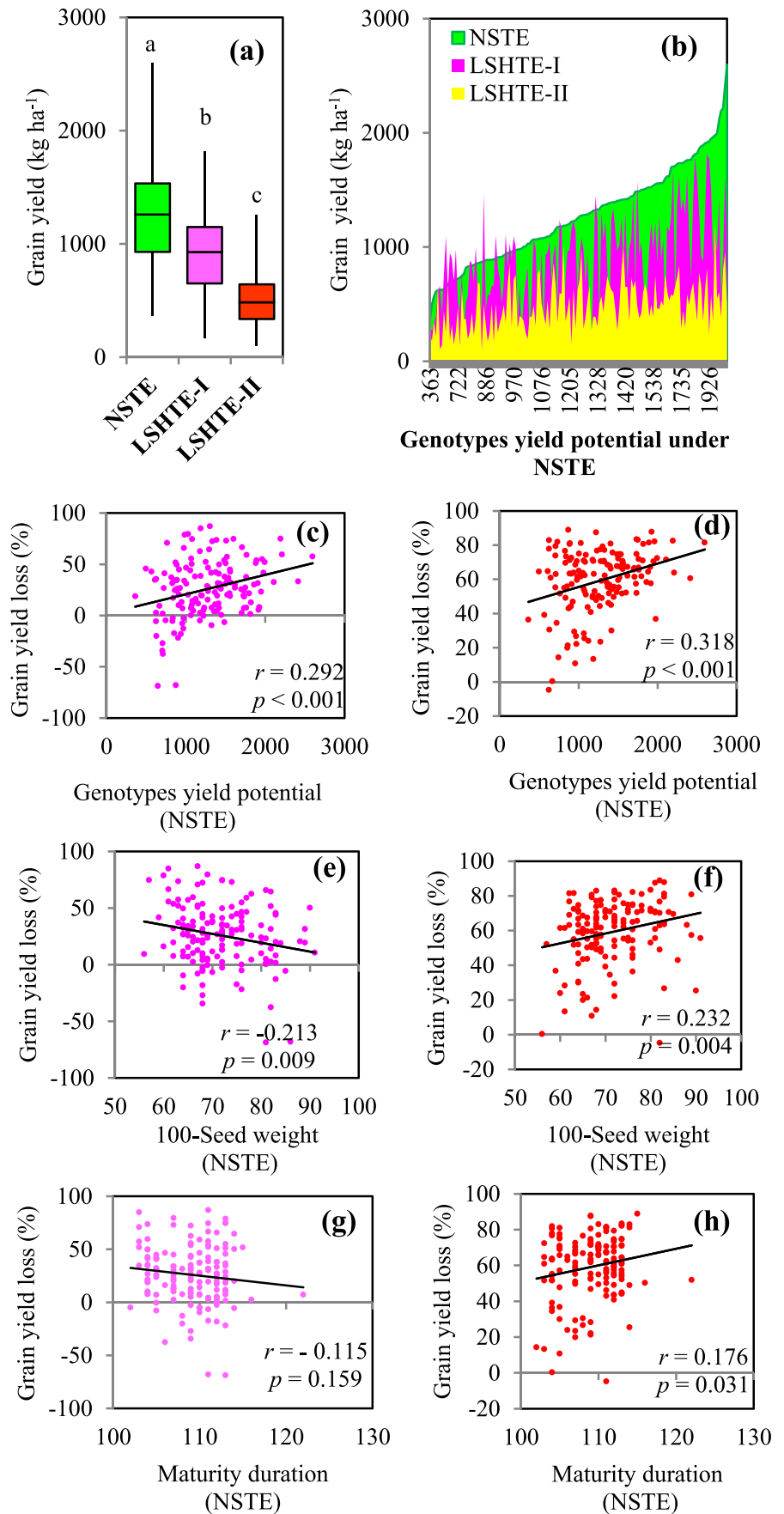
Table 2 Regression equations and association between grain yield (GY) with ambient maximum temperatures and growing degree days (GDD) in field pea

Genotype group	n	Regression equation	R^2	Adj. R^2	p value					
					Regression	Intercept	$TMAX_F$	$TMAX_{RP}$	GDD_V	GDD_{RP}
NSTE	150	$GY = -2184 + 1.61TMAX_F + 215.4TMAX_{RP} - 1.98\ GDD_V + 0.126GDD_{RP}$	0.087	0.062	0.010	0.173	0.976	0.161	0.359	0.885
LSHTE-I	150	$GY = 3109 - 1722.9TMAX_F - 155.6TMAX_{RP} + 3.29GDD_V + 3.07GDD_{RP}$	0.089	0.063	0.009	0.060	0.070	0.129	0.075	0.019
LSHTE-II	150	$GY = 2806 - 66.3TMAX_F - 22.7TMAX_{RP} + 0.114\ GDD_V + 0.336GDD_{RP}$	0.154	0.130	<0.001	0.422	0.058	0.711	0.899	0.476
AAE	450	$GY = 3.6 - 45.6TMAX_F + 13.4TMAX_{RP} - 0.92\ GDD_V + 0.887GDD_{RP}$	0.883	0.880	<0.001	0.852	0.002	0.331	<0.001	<0.001

$TMAX_F$, T_{MAX} during flowering; $TMAX_{RP}$, average T_{MAX} during reproductive period; GDD_V, cumulative growing degree-day of vegetative period; GDD_{RP}, cumulative growing degree-day of reproductive period

inefficiencies both at the level of source and sink under the high-temperature environments, which contributes to yield losses. To sustain yield under stressful conditions, it is crucial to maintain a higher sink capacity coupled with an optimal source. Reduction in crop biomass due to high temperature stress in field pea may be attributed to reduced leaf area, leaf chlorophyll content, which affected the photosynthetic efficiency of the crop (McDonald and Paulsen 1997; Vijaylaxmi 2013). Moreover, excessive production of reactive oxygen species (ROS) under stress condition reduces plants ability to fix carbon dioxide and thereby the photosynthetic efficiency (Hussain et al. 2021). The severity of oxidative damage under stress depend on the production and accumulation of ROS as well as the antioxidants activities (enzymatic and non-enzymatic components) in plant system (Hossain et al. 2021). Since plant growth, development and productivity are largely dependent on photosynthesis, its reduction under high temperature stress certainly has yield-limiting impacts (Ahammed et al. 2018; Brestic et al. 2018). Grain filling depends upon two major sources, i.e. transfer of current assimilates directly to developing grains and redistribution from pre- or post-anthesis vegetative reserve pools (Yang and Zhang 2006). However, high-temperature stress equally affects the current photosynthesis assimilation during the grain filling period (Subramanyam et al. 2006; Sehgal et al. 2018).

Jeuffroy et al. (1990) reported a reduction in seed yield when flowering and seed filling period of pea was exposed to a temperature above 25 °C, attributed mainly to seed abortion, reduced number of fruitful node, number of pods plant^{-1} and seed weight (Duthion et al. 1987; Laconde et al. 1987; Guilioni et al. 2003; Lamichaney et al. 2021). McDonald and Paulsen (1997) reported that high temperature exposure during the flowering stage plays detrimental role in field pea and reduced seed yield, seed weight, seed number and harvest index. For instance, a reduction at the source level (crop biomass) develops less flowers and set fewer seeds to maintain the source-sink balance. The seed size and weight are often limited at the level of source capacity and reduced intra-plant reserve mobilization efficiencies at the post-flowering stages.

The finding of the present investigation suggests that the mean vegetative period is found to be least influenced by high temperature stress, therefore, the average plant height also remained unaffected. Nevertheless, a reduction in crop biomass without changes in plant height may result into development of weaker stems and subsequently prone to lodging, which is also an important cause of yield loss in field pea (Smitchger and Weeden, 2019; Gali et al. 2018). Interestingly, the pea genotypes prone to lodging were found to be very sensitive to high temperatures stress as compared to the genotypes with better lodging tolerance (Tafesse et al. 2019). Being the component of direct yield
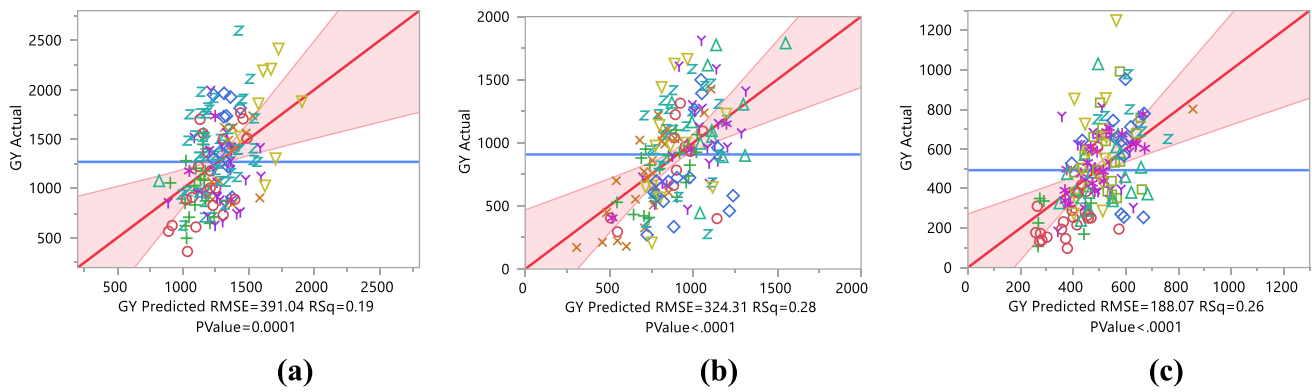
Fig. 6 Regression model of actual and predicted grain yield of field pea in NSTE (a), LSHTE-I (b), and LSHTE-II (c), respectively

Table 3 Size effects (LogWorth) and estimates of the variables used in the multivariate regression model (coefficients of the variables used in the linear model) for non-heat stress environments

Environment	Variable	Estimate[1]	Std error[2]	t-ratio[3]	LogWorth	p-value[4]
NSTE	AGDM	23.820	4.739	5.03	5.83	<.0001
	LPBN	22.463	11.825	1.9	1.225	0.0595
	PPP	−5.076	5.640	−0.9	0.432	0.3697
	HSW	−5.299	12.436	−0.43	0.173	0.6707
	OPP	−8.447	42.819	−0.2	0.074	0.8439
	PL	6.220	54.168	0.11	0.042	0.9087
	SS	0.167	3.818	0.04	0.015	0.9653
	Intercept	423.817	652.672	0.65		0.5172
LSHTE-I	PPP	31.233	8.856	3.53	3.247	0.0006
	LPBN	28.157	13.351	2.11	1.435	0.0367
	SS	5.872	3.195	1.84	1.167	0.0681
	PL	81.651	49.902	1.64	0.983	0.104
	HSW	15.715	9.643	1.63	0.977	0.1054
	OPP	43.327	34.992	1.24	0.662	0.2177
	AGDM	3.037	5.650	0.54	0.228	0.5917
	Intercept	−1459.69	527.15	−2.77		0.0064
LSHTE-II	SS	7.94	1.85	4.29	4.49	<.0001
	PPP	19.73	7.68	2.57	1.948	0.0113
	LPBN	6.08	2.39	2.54	1.918	0.0121
	OPP	41.70	17.64	2.36	1.711	0.0194
	AGDM	4.32	5.53	0.78	0.361	0.4356
	HSW	2.54	6.99	0.36	0.145	0.7169
	PL	5.61	17.94	0.31	0.122	0.7549
	Intercept	−658.45	234.42	−2.81		0.0057

[1]The estimated coefficient value of the variable in the model. [2]The standard error on estimated coefficient value. [3]The t-ratio of the estimated variable in the model. [4]The significance of the variable in the model. *AGDM*, aboveground dry matter; *LPBN*, last pod bearing node; *PPP*, pods plant^{-1}; *HSW*, 100-seed weight; *OPP*, ovules pod^{-1}; *PL*, pod length; *SS*, seed set percentage

functions, the parameters plant biomass, pods plant^{-1}, and grains pod^{-1} exhibited strong positive correlations with crop yield. The positive association between the last pod bearing node and grain yield suggest the significance of last pod bearing node in maximizing yield under heat stress condition. In field pea, the flowering and pod formation occurs acropetally, occurring first in lower nodes and the later in the upper nodes. Since, the flowering at upper nodes occurs later, thus exposes itself to higher temperature as compared to the flower at lower nodes. The mean number of pod bearing nodes in our experiment varied between 20, 19 and 17 in NSTE, LHSTE-I, and LHSTE-II, respectively, suggesting that high temperature environments affects pod setting in upper nodes. Therefore, the genotypes with productive
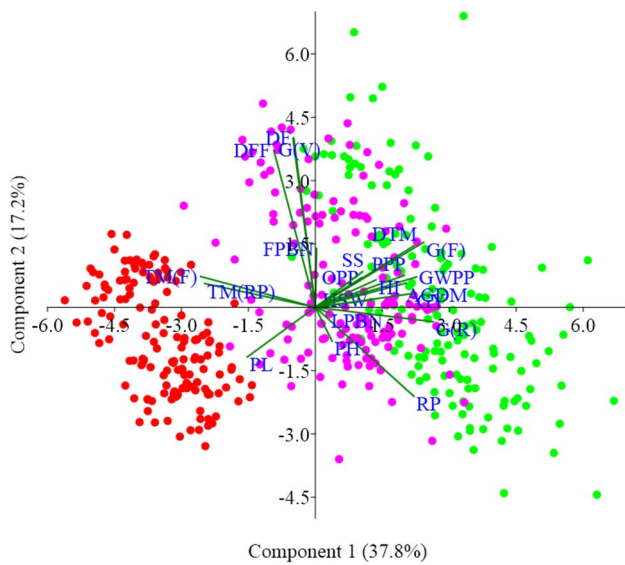
Fig. 7 Scatter plot of field pea genotypes on PCA coordinates based on the phenology, growth, yield attributes, growing degree days, and weather parameters under three growing environments (NSTE (green dots), LSHTE-I (pink dots), and LSHTE-II (red dots)). PH, plant height (cm); FPBN, first pod bearing node; LPBN, last pod bearing node; PPP, pods per plant (nos.); PL, pod length (cm); GWPP, grain weight per plant (g); HSW, 100-seed weight (g); AGBM, above-ground dry biomass (g); OPP, ovules per pod; SS, seed set percentage; DFF, days to first flowering, DF, days to 50% flowering; DTM, days to maturity; RP, reproductive period; G(V), cumulative GDD of vegetative period; G(R) cumulative GDD of reproductive period; G(F), cumulative GDD of full crop season; TM(F), maximum temperature during flowering; TM(RP), maximum temperature during reproductive period

upper nodes are the preferred genotypes under heat stress conditions. The high yielding genotypes underwent a greater yield penalty than the low yielding genotypes under heat stress environments, indicating that the expression of yield

attributing traits are highly environment-specific. Likewise, long duration and large seeded genotypes appear to be more susceptible to high temperature stress than the early maturing and small seeded genotypes suggesting development of short duration and small seeded varieties for improved heat tolerance.

The linear regression model explains higher temperature stress at flowering to have more detrimental effect on yield than during the grain filling period. In legumes, loss/reduction in viability of pollen, formation of empty pollen grains or shrunken pollen, abnormal pollen germination and pollen tube growth, failure in fertilization, and embryo abortion are some of the abnormalities linked with high-temperature stress (Liu et al. 2019; Jiang et al. 2019b). The estimates of LogWorth value demonstrated a higher impact of source limitation on grain yield in non heat stress environment. Whereas, the higher LogWorth weightage of sink attributes (seed set, pods plant^{-1}, last pod bearing node and ovules pod^{-1}) in the heat stress environments suggests breeding for improving sink efficiency for mitigating heat stress. According to Jiang et al. (2020), the high temperature tolerant genotypes retain higher number of pod and ovule as compared to the susceptible genotypes. Sadras et al. (2013) found that low pod wall ratio was associated with better adaptation to heat stress and therefore could serve as selection trait for heat tolerance in field pea. Hossain et al. (2021) suggested that under abiotic stress, selecting genotypes based solely on yield potential could be misleading and inefficient due to low heritability. Plant makes several important biochemical and physiological adjustments to develop mechanisms for tolerating stress. Tafesse et al. (2019) reported semi-leafless and erect plant type to have better tolerance to heat stress by maintaining lower canopy temperature. Thus, the selection criteria for improved heat tolerant genotype(s) should essentially include secondary traits that have a high association

Fig. 8 GGE biplot mean vs. stability (**a**) and genotype ranking (**b**) across the three growing environments (NSTE, LSHTE-I, and LSHTE-II) for field pea genotypes. Please see supplementary Table 1 for genotype detail
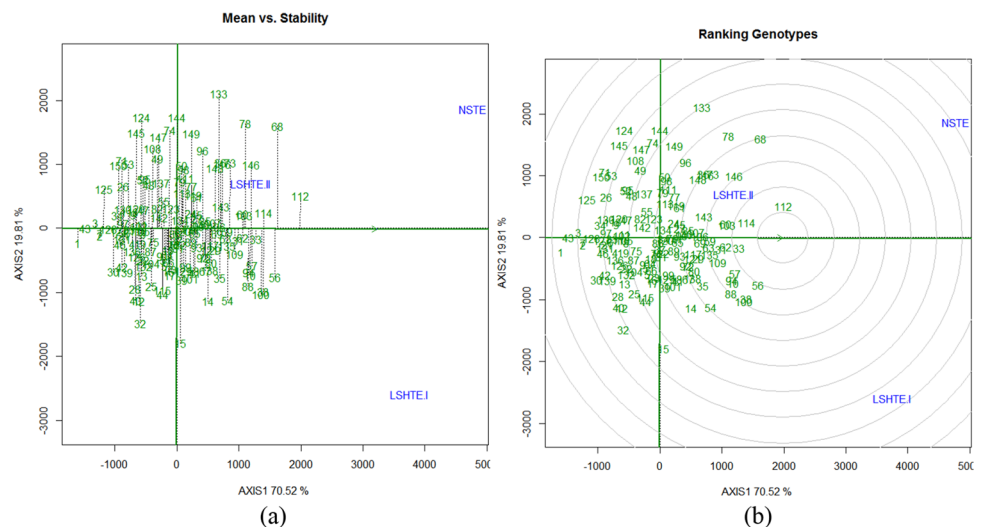
with yield. Also, several indices may be useful to identify and select heat tolerant genotypes (Rosielle and Hamblin 1981; Al Mahmud et al. 2021). Hence, for screening field pea genotypes under heat stress, strategic phenotypic selection will lead to successful results.

The PCA analysis provides information about the cluster of traits explaining maximum variability in the population under a given environment. The biplot graphs explains the associations among different traits, where the cosine of angle between the trait vectors approximates the correlation between the variables they represent. The acute and obtuse angles amidst traits represent the positive and negative correlation between each other, respectively. The PCA results confirm the results of linear correlations within the plant traits and non-significant associations of parameters days to flowering and first pod bearing node with grain yield, whereas, a negative association between pod length and grain yield was observed. The PCA results further explain that the genotypic variability for plant traits is reduced with the intensity of heat stress; hence, late planting is to be avoided for judicious characterization of germplasm.

The polygon or convex hull of GGE biplot was constructed considering multi-environment standardized data and environment-cum-genotype-focused singular-value partition (symmetric scaling). The biplot demonstrated that the first two principal components, i.e., PC1 (mean performance) and PC2 (stability), collectively explained 90.3% of the total variation and individually accounted for 70.5% and 19.81 of the total variation, respectively (Fig. 7a). Those genotypes, which are positioned at the vertices of polygon, contributed the greatest to the interaction, i.e., either highest or the lowest yelded genotypes. The GGE biplot depicted that the genotypes at the left side of the convex hull had low grain yield potential, while those on the right side had high grain yield potential across the environments. Consequently, genotype G-112 had the highest yield and G-1 had lowest yield across the environments. The means vs. stability GGE biplot ranked the genotypes along the average tester axis (or ATC abscissa), considering their mean performance across the environments (Fig. 7b). The single arrowed line is the ATC abscissa and the arrow point indicating toward the higher mean performance. The stability of the genotypes is approximated by their projection onto the central parallel line. The greater the length of the projection of a genotype, the less stable it is and vice versa. Overall, in terms of high mean grain yield, the best performing genotype was G-112 with fair stability. However, based on high grain yield and high stability, the best performing genotypes are G-114 and G-33. Conversely, genotypes such as G-133, G-124, G-100, and G-15 were positioned farthest away to the ATC abscissa and, accordingly, these were highly sensible to the environmental fluctuations.

Conclusions

The present study conducted using a diverse panel of genotypes concluded existence of large genotypic variability with respect to the high temperature stress, enabling possibility of enhancing tolerance to heat stress in field pea through breeding. The identified potential heat-tolerant and stable genotypes could be utilized for improving heat tolerance in field pea. Our study suggests seed set, last pod bearing node, pods plant^{-1} and plant biomass to be considered as a selection parameter for identification of heat tolerant field pea genotypes.

Declarations

Conflict of interest The authors declare there are no conflicts of interest.

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