Field Crops Research 172 (2015) 59–71

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Field response of chickpea (*Cicer arietinum* L.) to high temperature

V. Devasirvatham[a,b,*], P.M. Gaur[b], T.N. Raju[a], R.M. Trethowan[a], D.K.Y. Tan[a]

[a] Plant Breeding Institute, Faculty of Agriculture and Environment, University of Sydney, Cobbitty, NSW 2570, Australia
[b] International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502324, Telangana, India

ARTICLE INFO

Article history:
Received 24 November 2014
Accepted 27 November 2014
Available online 4 January 2015

Keywords:
Canopy temperature depression
Genetic variability
High temperature
Heat tolerance index
Phenology

ABSTRACT

High temperature is an important factor affecting chickpea growth, development and grain yield. Understanding the plant response to high temperature is a key strategy in breeding for heat tolerance in chickpea (*Cicer arietinum* L.). This study assessed genetic variability for heat tolerance in chickpea and identified sources of heat tolerance that could be used for crop improvement. One hundred and sixty-seven genotypes were grown in two environments (heat stressed/late sown and non-stressed/optimal sowing time) in 2 years (2009–2010 and 2010–2011) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India. Large genetic variation was observed for phenology, growth, yield components and grain yield. While phenology (assessed as days to first flower, days to 50% flowering and days to first pod) was negatively correlated with grain yield at high temperature; plant biomass, pod number, filled pod number and seed number per plant were positively correlated. Genotypes were classified into short and long duration groups based on their maturity. Days to first flowering (DFF) of long duration genotypes were negatively associated with grain yield under stressed conditions in both years compared with medium to short duration genotypes. However, genotypes varied in their heat sensitivity and temperatures ≥35 °C produced yield losses up to 39%. A heat tolerance index (HTI) classified the genotypes into five groups: (i) stable heat tolerant (>0.5), (ii) moderately heat tolerant (0.1–0.49), (iii) stable heat sensitive (−ve values), (iv) heat tolerant to moderately sensitive (−0.10 to 1) and (v) heat sensitive to moderately tolerant (−0.5 to 0.4). Pod characteristics, including days to first pod and pod number per plant, were correlated with grain yield whereas canopy temperature depression (CTD) was generally not correlated. Heat tolerant genotypes in a range of maturities were identified that could be used to improve the heat tolerance of chickpea.

1. Introduction

Chickpea (*Cicer arietinum* L.) is a cool season legume and high temperature during the reproductive period can limit grain yield. High temperature (>30 °C) regulates floral initiation and grain yield in chickpea (Summerfield et al., 1984). At present, chickpea is generally produced in warm environments (Devasirvatham et al., 2012a) in rotation with cereals. However, there is potential to increase the area of chickpea rotation in future, especially in the warmer areas of India, Australia and Myanmar (Subbarao et al., 2001; Gentry, 2011; Than et al., 2007). Furthermore, heat stress is expected to increase due to predicted climate change further impacting chickpea production and productivity in current production areas.

A threshold day/night temperature for chickpea growth and reproductive development is between 29/21 °C and 21/15 °C (Imtiaz et al., 2011). However, most of the chickpea growing regions experience >30 °C during the reproductive period (Devasirvatham et al., 2012a). Grain yield is reduced by high temperature (≥35 °C) during flowering and pod development (Wang et al., 2006) and this is linked to reduced pollen viability (Devasirvatham et al., 2012b). Stigma receptivity can also be affected at high temperature (≥40/30 °C) which causes failure of fertilisation (Kumar et al., 2012a). The mechanism of heat stress tolerance is therefore, related to growth, seed set and grain yield. The response to heat stress in chickpea is also governed by abscisic acid (ABA) (Kumar et al., 2012b) and high temperature can affect root nodulation and nitrogen fixation (Saxena et al., 1988).

Generally, the assessment of whole plant response to heat stress in the field is an effective screening method. The chickpea plant response was studied by comparing two growing environments

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[*] Corresponding author at: Plant Breeding Institute, Faculty of Agriculture and Environment, University of Sydney, Cobbitty, NSW 2570, Australia.
Tel.: +61 438572589.
E-mail address: violawre@yahoo.com (V. Devasirvatham).

http://dx.doi.org/10.1016/j.fcr.2014.11.017
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(cool and warm regions) using available cultivars in Kenya and the cultivar ICCV 92318 which was classified as heat tolerant (Kaloki, 2010). A farmers' field survey concluded that chickpea yielded better in warmer environments than bean, cowpea, green gram and maize in Kenya (Kaloki, 2010). The whole plant response of chickpea was observed in the field using different sowing dates and temperatures (normal and late seasons) at ICRISAT (Krishnamurthy et al., 2011; Upadhaya et al., 2011). Krishnamurthy et al. (2011) identified new sources of heat tolerance from a chickpea reference collection of chickpea germplasm and Upadhaya et al. (2011) characterised early maturing heat tolerant chickpea genotypes suitable for semi-arid environments. They concluded that grain yield loss varied from 10 to 15% among these early maturing genotypes for every 1 °C rise above optimum temperature. Krishnamurthy et al. (2011) identified heat tolerant genotypes from a reference set of chickpea ($n = 280$). However, the current study attempts to extrapolate their findings using different genotypes ($n = 167$) classified for maturity groups that represents a range of global chickpea production environments. In addition to whole plant response to heat stress, canopy temperature depression (CTD) should be further investigated as potential indirect selection criteria for yield under heat stress. Several studies report genetic variation for canopy temperature under abiotic stress in wheat and food legumes (Rosyara et al., 2010; Ibrahim, 2011; Zaman-Allah et al., 2011). Generally leaf temperature is associated with leaf water content which is influenced by soil moisture and ambient temperature (Gardner et al., 1981). Tanner (1963) suggested that the temperature difference between stressed and unstressed leaves gave a quantitative indication of differences in transpiration potential. In such situations, transpiration is a tolerance mechanism that may help dissipate the heat load. Therefore, canopy temperature variation under stress during the reproductive period should be further investigated.

Chickpea production mostly occurs on residual soil moisture under rainfed conditions and terminal drought and heat stresses are the major limitations to chickpea grain yield (Summerfield et al., 1990). These rainfed regions are accompanied by variable rainfall patterns. Therefore, screening for heat stress tolerance is frequently confounded by interaction with drought stress. Experiments were conducted to investigate the field response of chickpea to heat stress in semi-arid environments in south India. The objective of this research was to assess genetic variability for heat tolerance in a diverse group of chickpea materials by screening in heat stressed (late sown) and non-stressed (optimally sown) environments. Furthermore, traits that were likely to be associated with grain yield under heat stress were investigated.

2. Materials and methods

2.1. Experimental design and management

One hundred and sixty-seven chickpea genotypes were obtained from the gene bank at the International Crops Research Institute for the Semi-arid Tropics (ICRISAT) for field evaluation under high temperature. The genetic background of the 167 genotypes studied are summarised in Supplementary Table 1. A randomised complete block design with two replications was used for field experiments during year 1 (2009–2010) and year 2 (2010–2011) at ICRISAT on a Vertisol soil at Patancheru approximately 30 km west of Hyderabad, south India (17.53° N; 78.27° E; 545 m). The field used for the experiments was solarised using polythene mulch during the preceding summer to sanitise the field, mainly to eradicate the wilt causing fungus *Fusarium oxysporum* f. sp. *ciceri*. After soil solarisation, the field was kept fallow. The optimally sown experiment was conducted on 31st October in year 1 and 13th November in year 2. The late season equivalent was sown on 3rd February in both years. Both optimal and late season experiments were sown on row ridges with inter- and intra-row spacing of 60 cm × 10 cm. A 4 m long row was considered as a replication plot. Seeds were treated with 0.5% Benlate® (E.I. DuPont India Ltd., Gurgaon, India) + Thiram® (Sudhama Chemicals Pvt. Ltd., Gujarat, India) mixture in both experiments. The optimally sown crop was supported with post-sowing irrigation, while the late sown crop received irrigation 0, 20, 28, 35, 45, 55, 65 and 75 days after sowing. Two seeds per hill were sown and later thinned to one seedling. The experiments were maintained weed free by manual weeding. Insecticide was sprayed to control pod borer (*Helicoverpa armigera*) based on need.

Supplementary Table 1 related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2014.11.017.

2.2. Weather data

Daily maximum and minimum temperatures were recorded in both seasons (Fig. 1).

2.3. Measurements

2.3.1. Crop phenology

Days to first flower (DFF), days to 50% flowering (D50%F), days to first pod formation (DFP) and days to physiological maturity (DPM – defined as the date when 80% of the pods in a plot were mature) were recorded for each genotype.

2.3.2. Plant height and canopy width

Five plants were randomly selected at physiological maturity and plant height (cm) and width (cm) was measured for each genotype. An average of five plants were calculated and recorded per genotype.

2.3.3. Harvest and yield components

At physiological maturity, the aerial parts of the plants were harvested from 2 m row length of each genotype, air dried at 38 °C for 48 h and total shoot dry weight recorded. At harvest, five plants were randomly collected and yield components per plant (pod number, filled pod number, unfilled pod number, seed number per plant and grain yield per plant) were recorded. Harvest Index (%) was calculated as (grain yield/total shoot dry weight) × 100.

2.3.4. Canopy temperature depression

Canopy temperature depression (CTD) is an indicator of the difference between the plant canopy and ambient air temperature. The plants continue to transpire through open stomata and the canopy temperature is maintained at a metabolically comfortable range. However, plants close stomata for considerable periods due to stress, and this is known to increase canopy temperature (Kashiwagi et al., 2008). The canopy temperature in a plot was captured using thermal images during the reproductive stage. The thermal images were captured from 50% flowering (approximately 42 days after sowing) to two weeks before physiological maturity. These observations were recorded on six different days with 4 day intervals in heat stressed environments in both years. An infrared camera IR FLEXCAM (Infrared Solutions, Inc., USA) was used to capture the images between 1300 and 1500 h. As the maximum plant height of chickpea was approximately 40 cm, the top view of the thermal images was captured. The target area of the image captured was about 30 cm × 20 cm at the centre of each plot, and the images were captured from the north to avoid shading of the target area. The thermal images were analysed using the colour analysis function of the image analysis software Smart View 2.1 (Fluke Thermography, USA) to estimate the canopy temperature occupied by each colour. The background thermal image of the soil was removed using a colour threshold. This method followed that previously

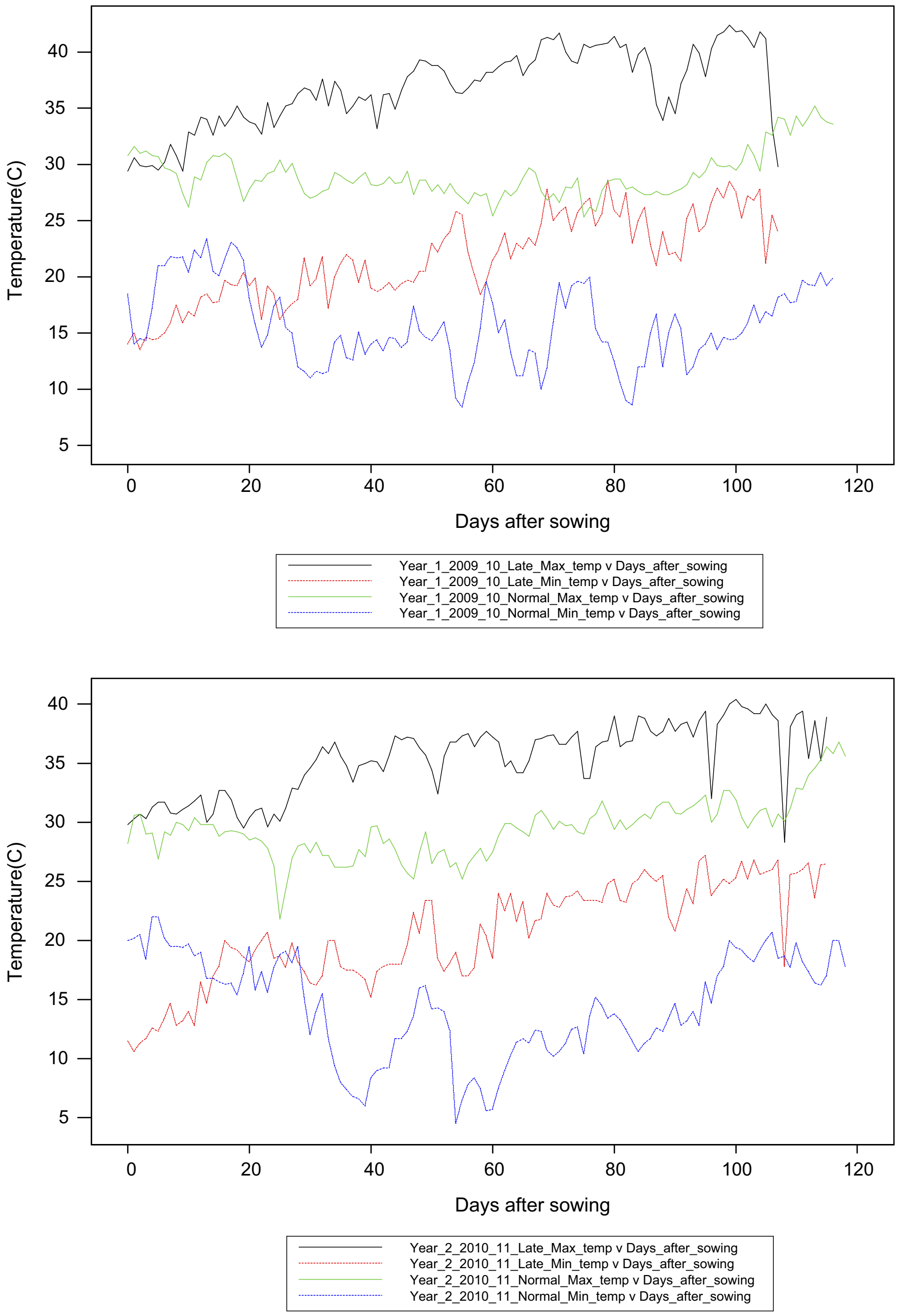

Fig. 1. Maximum and minimum temperatures of non-stressed (optimally sown) and stressed environments (late sown) during 2009–2010 (year 1) and 2010–2011 (year 2) at ICRISAT.

reported in chickpea by Zaman-Allah et al. (2011). In each plot, five temperature values were randomly selected from each thermal image and average canopy temperature was calculated. Finally, the average of five spots was considered as an average temperature for each genotype. Canopy temperature depression (CTD) was calculated as the difference between ambient and canopy temperature for each genotype.

2.4. Genotypes

Genotype variability in phenology can confound efficient phenotyping for stress tolerance. A previous study by Krishnamurthy et al. (2011) reported a confounding effect because peak heat stress periods occurred at different the phenological stages for different genotypes. To remove this confounding effect, the 167 genotypes were classified into two groups: long duration (≥111 days) and medium to short duration (≤110 days) based on crop maturity in the normal cropping season. Only seven short duration genotypes were observed and no significant statistical differences among traits were observed.

2.5. Estimation of heat tolerance

2.5.1. Heat tolerance index (HTI)

The grain yield under stressed and non-stressed conditions was used to predict the stress tolerance of genotypes. However, there were higher yields in short duration genotypes compared with long duration materials under heat stress. To eliminate the differences in

Table 1
Mean square values and season mean for 12 traits of 167 chickpea genotypes under normal (non-heat stressed) and late (heat stressed) seasons in the field during 2009–2010 (year 1) and 2010–2011 (year 2) at ICRISAT.

Traits	Season		Genotypes		Season × genotypes		Season mean of each trait		Year 1		Year 2	
	df	Mean squares	df	Mean squares	df	Mean squares	Normal	Late	Normal	Late	Normal	Late
DFF (days)	1	2508.08***	166	703.39***	166	87.12***	49	47	50	46	49	46
D50%F (days)	1	12,103.83***	166	534.94***	166	209.08***	54	48	54	47	55	49
DFP (days)	1	19,988.29***	166	500.96***	166	231.03***	57	49	57	48	57	52
DPM (days)	1	51,225.0***	166	220.98***	166	32.63***	110	97	111	92	108	102
Plant biomass (g/plant)	1	46,538.68***	166	92.30***	166	72.38*	30.0	18.1	23.3	9.7	27.9	26.3
Plant height (cm)	1	20.57NS	166	141.93***	166	36.66NS	35.9	36.2	44.3	30.1	50.7	41.9
Plant width (cm)	1	54,165.32***	166	129.05***	166	62.0**	45.2	32.4	39.5	23.1	36.5	41.2
TNP	1	163,419.0***	166	2730.0***	166	557.5***	61	37	54	15	68	61
NFP	1	140,060.8***	166	2436.9***	166	533.0***	57	36	50	14	64	58
NS	1	172,735.5***	166	4840.7***	166	961.4***	70	47	61	18	78	75
GY (g/plant)	1	6965.21***	166	60.46***	166	16.42NS	11.9	7.3	10.6	2.4	13.2	12
HI	1	7.38***	166	0.16***	166	0.02***	0.46	0.31	0.46	0.17	0.46	0.45

DFF, days to first flower; D50%F, days to 50% flowering; DFP, days to first pod formation; DPM, days to physiological maturity; TNP, total number of pods per plant; NFP, number of filled pods per plant; GY, grain yield; HI, harvest index; df, degrees of freedom.
Significant difference at:
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
NS, non significant.

crop phenology and heat escape, the multiple regression approach of Bidinger et al. (1987) under abiotic stress was used. Briefly this approach considers grain yield under heat stress conditions (Y_s) to be a function of yield potential (Y_p), time to 50% flowering (F), and a heat tolerance index (HTI) such that the yield of a genotype can be expressed as follows:

$$Y_{si} = a + bYp + cFi + HTIi + E,$$

where E is random error. The difference between the estimated late season grain yield and estimated optimal season grain yield plus standardised residuals from regression analysis indicated the heat tolerance of genotypes. HTI was calculated for each genotype. One way analysis of variance (ANOVA) was then conducted to identify the genotypic differences. This approach was used previously to identify heat tolerant and sensitive chickpea genotypes by Krishnamurthy et al. (2011).

2.6. Temperature at different developmental stages of chickpea

The plant growing days at different developmental stages (vegetative, flowering and grain filling period) were calculated for each genotype. Vegetative period (V) was defined as the number of days from sowing to one day before flowering date. The days from first flower to first pod was considered the flowering period (F). The grain filling period (GF) was defined as the number of days from first pod to maturity. The average maximum and minimum temperatures were then calculated at different developmental stages (V_{Max}; V_{Min}; F_{Max}; F_{Min}; $\mathrm{GF}_{\mathrm{Max}}$ and $\mathrm{GF}_{\mathrm{Min}}$).

2.7. Statistical analysis

One way analysis of variance (ANOVA) was conducted for 12 traits assessed on 167 genotypes with two replications over two years. Two way analysis (genotype × season) was conducted for all traits for heat stressed and non-stressed environments. The correlation of 12 traits for both environments and years was also studied. One way analysis of CTD was calculated for six days in stressed environments. The relationship between chickpea grain yield and average CTD during the reproductive period in heat stressed environments in both years was determined using regression analysis. GenStat 12th version from VSN International Ltd was used for all statistical analyses.

3. Results

3.1. High temperature effects on phenology, growth and yield of chickpea

Significant differences in crop phenology were observed among the 167 chickpea genotypes in both environments (stressed and non-stressed) and years. ANOVA revealed a large treatment difference between stressed and non-stressed conditions for DFF, D50%F, DFP and DPM (Table 1). There were 4–5 day differences in crop phenological duration. The overall crop cycle was reduced by 13 days in the heat stressed treatment (Table 1). This was associated with high temperature in the stressed environments. In heat stressed environments, DFF, D50%F and DFP had significant ($R^2 \geq 0.50$) negative associations with maximum temperature during the first year (data not shown). In year 2, DFF and D50%F were negatively associated with high temperature and DFP was positively associated with high temperature (data not shown). The experiments were exposed to temperatures up to 42 °C in year 1 and 38 °C in year 2 (Fig. 1).

Significant variation in plant height, plant width and plant biomass at harvest were also observed in both environments and these were considered as growth parameters. At high temperature plant height was not significantly affected (Table 1). But, the plant biomass at high temperature was approximately half (18 g plant^{-1}) that of non-stressed (30 g plant^{-1}) materials. The interaction of season and genotypes was significant for plant width and biomass and non-significant for plant height.

There was significant variation in grain yield and pod number, filled pod number and seed number per plant in both seasons. High temperature reduced pods from 61 (optimal season) to 37 per plant ($P < 0.001$). Similarly, grain yield was also reduced from 11.9 to 7.3 g plant^{-1} ($P < 0.001$). Thus pod number per plant and grain yield were reduced by 39% in the stressed conditions (late sown) compared to non-stressed (optimally sown) materials (Table 1).

3.2. Contribution of yield and its components to heat tolerance

Days to first flower (DFF) were negatively associated with grain yield (Fig. 2). The genotypes were subsequently classified in two

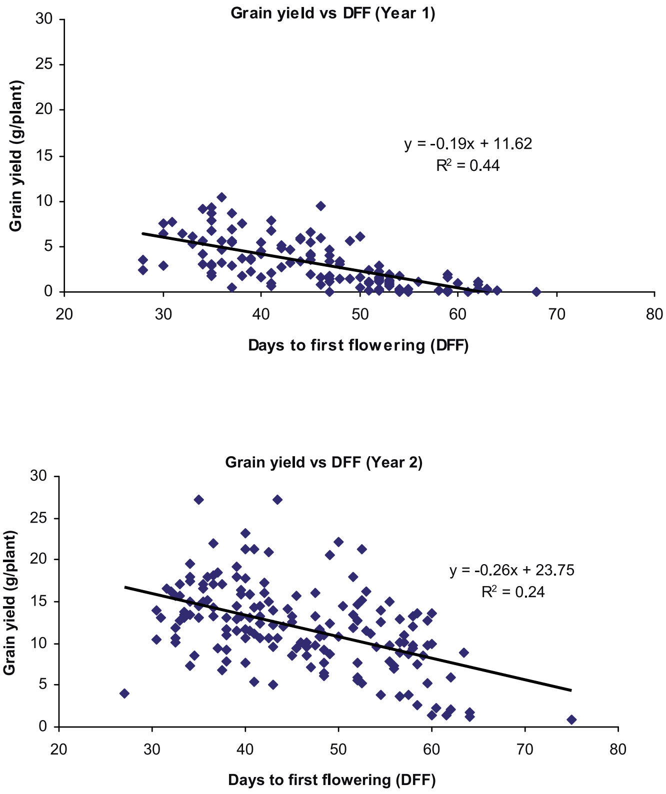

Fig. 2. Relationship of days to first flower (DFF) with grain yield in heat stressed environments (late sown) during 2010 (year 1) and 2011 (year 2).

groups (long duration and medium to short duration) based on their maturity date. The phenology of genotype groups were regressed against grain yield (Figs. 3–5) and DFF, D50%F and DFP were observed to be negatively associated with grain yield in both years under late season heat stress. This negative association was strong in medium to short duration genotypes in year 1 and in long duration genotypes in year 2 (Figs. 3–5).

Harvest index was regressed against grain yield under high temperature and showed a positive association (Fig. 6). Therefore, yield components such as pod number per plant, filled pod number per plant, seed number per plant and harvest index were regressed against grain yield in both environments and years. Among yield components, pod number per plant and harvest index were most strongly related to grain yield under heat stress ($R^2 > 0.5$) (Fig. 7).

3.3. Correlation among 12 traits measured in the field

The phenological traits DFF and DPM showed significant and negative correlation under heat stress in year 1 (Table 2). However, plant biomass, pod number, filled pod number and seed number per plant were positively correlated with grain yield ($P < 0.001$) while crop phenology (DFF, D50%F, DFP) was significantly negatively correlated with grain yield in year 2 (Table 3). Plant width, plant biomass, pod number, filled pod number and seed number per plant were all positively correlated with grain yield ($P < 0.001$). Similar trends were observed in the non-stressed experiments in both years (Tables 2 and 3).

3.4. Classification of heat response

There was a significant difference between genotypes and years for heat response (data not shown). Hierarchical cluster analysis classified the genotypes into five groups based on means. The score value of the similarity index was 0.80. However, the classification of genotypes did not reflect similarities in maturity. The groups were classified as (i) stable heat tolerant (>0.5), (ii) moderately heat tolerant (0.1–0.49), (iii) stable heat sensitive (−ve values), (iv) heat tolerant to moderately sensitive (−0.10 to 1) and v) heat sensitive to moderately tolerant (−0.5 to 0.4) (Table 4). The

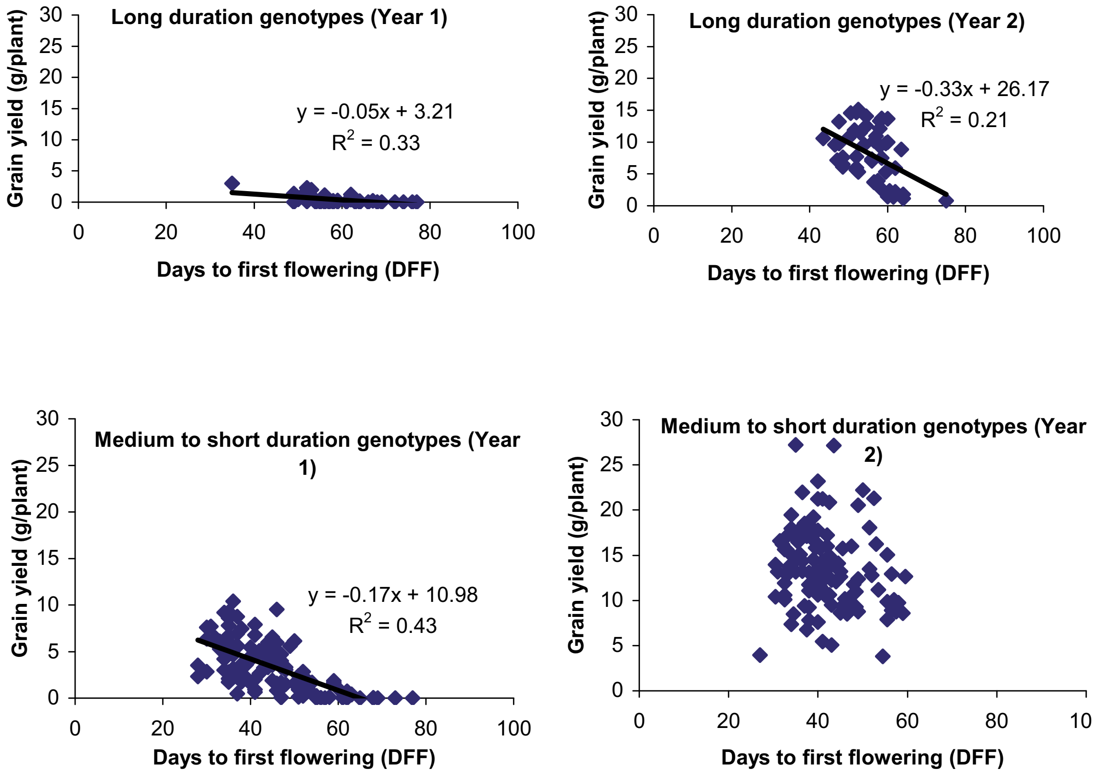

Fig. 3. Relationship of days to first flower (DFF) with grain yield based on maturity group in heat stressed environments (late sown) during 2010 (year 1) and 2011 (year 2).

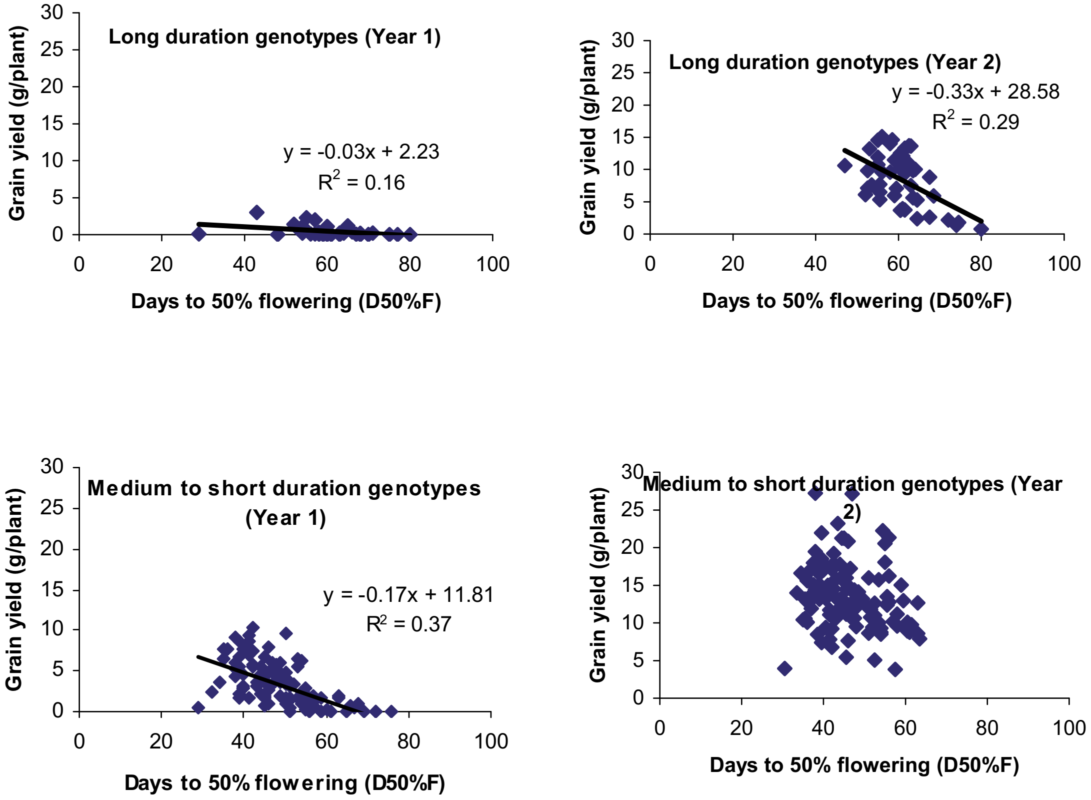

Fig. 4. Relationship of days to 50% flowering (D50%F) with grain yield based on maturity group in heat stressed environments (late sown) during 2010 (year 1) and 2011 (year 2).

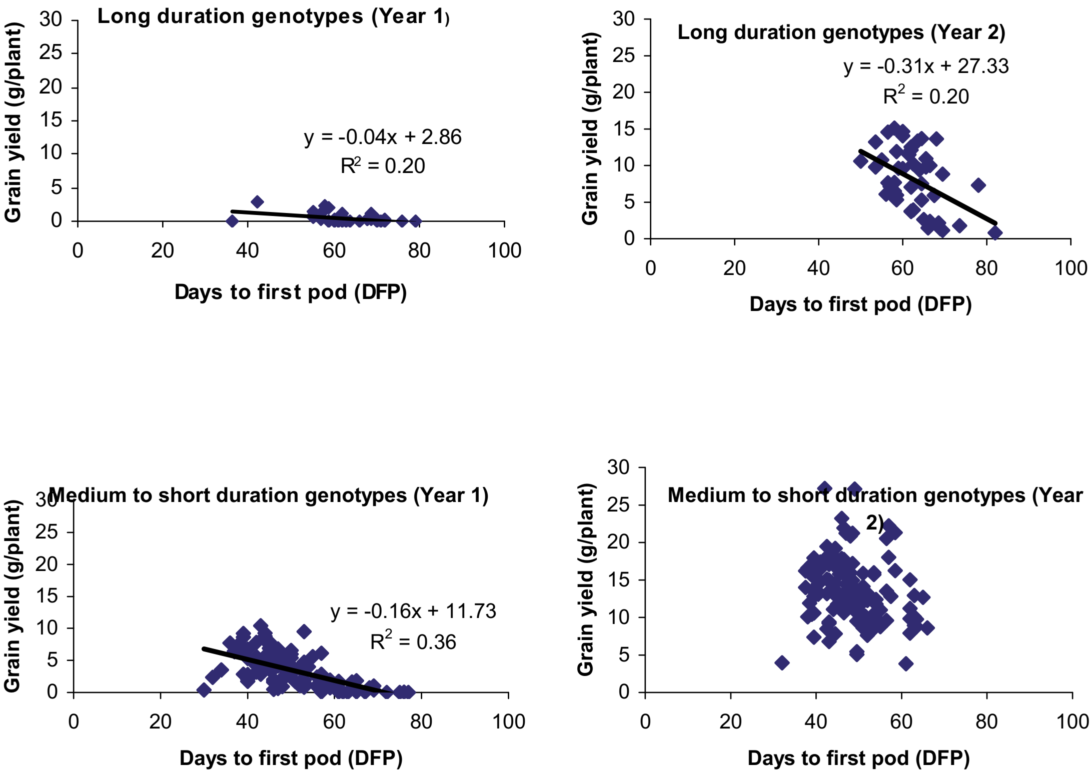

Fig. 5. Relationship of days to first pod (DFP) with grain yield based on maturity group in heat stressed environments (late sown) during 2010 (year 1) and 2011 (year 2).

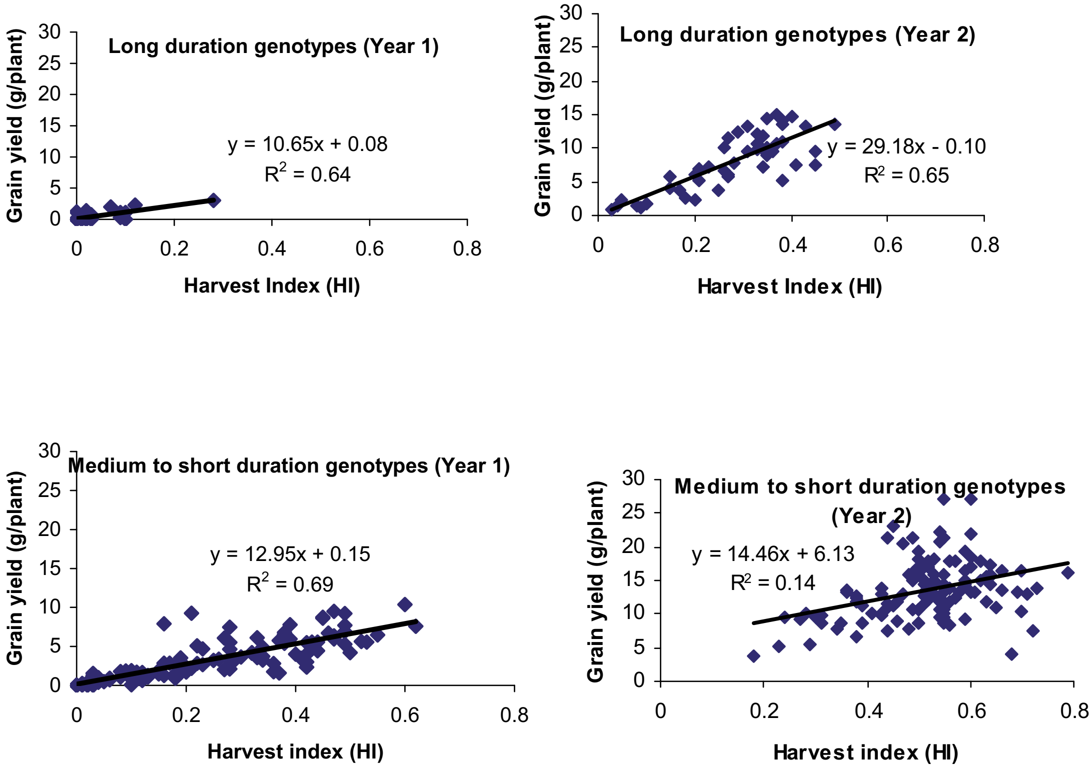

Fig. 6. Relationship of harvest index (HI) with grain yield based on maturity group in heat stressed environments (late sown) during 2010 (year 1) and 2011 (year 2).

most stable heat tolerant genotypes were ICCV 95311, ICCV 98902, ICCV 07109, ICCV 92944 and ICC 12312. The most heat sensitive genotypes included ICCV 07117, ICC 5566, ICC 7570 and ICC 5912. The genotypes were subsequently arranged into maturity groups to negate the confounding effect of phenology ($n = 167$ data not shown). Traits such as days to first flower, days to 50% flowering, days to first pod, harvest index and canopy temperature depression were then associated with maturity groups (data shown in Figs. 3–8 and Tables 5 and 6).

3.5. Canopy temperature depression

CTD at 50% flowering showed significant differences among genotypes in both years (Tables 5 and 6). The CTD of selected genotypes were listed with their response to high temperature (Tables 5 and 6). In both years, sensitive genotypes had lower CTD than tolerant genotypes. The medium to short duration heat tolerant genotypes ICCVs 95311, 98902, 07109 and 92944 recorded greater CTD compared with sensitive genotypes (Tables 5 and 6). Some of the sensitive genotypes, such as ICCV 07116, ICCV 07117 and ICC 14592 produced negative CTD values (i.e., no temperature depression) further highlighting their sensitivity to heat stress (data not shown). The average CTD of both genotype groups regressed against grain yield under heat stress showed a positive relationship in year 1 (Fig. 8), however, this was not significant among medium to short duration genotypes in year 2 (Fig. 8).

3.6. Effect of temperature at different developmental stages

Genotypes showed differences in average maximum and minimum temperatures during vegetative, flowering and grain filling periods in both heat stressed and non-stressed environments. These data help define the critical temperature for each genotype under heat stress. Chickpea genotypes were arranged based on maturity groups in Table 7. In year 1, stable heat tolerant and moderately tolerant genotypes experienced maximum temperature of 33 ± 1 °C during the vegetative period. In comparison, the stable heat sensitive genotypes were exposed to maximum temperatures ranging from 34 to 35 °C. In year 1, the maximum flowering and grain filling period temperature varied from 35 to 39 °C. However, a maximum temperature of 37.8 °C was observed in year 2. The most heat tolerant medium duration genotype ICCV 98902 encountered 38.5/21.6 °C during flowering and 39.4/24.1 °C during the grain filling period and produced grain yield of 9.5 g plant^{-1} (Table 7). Conversely, the same genotype produced grain yield of 27.2 g plant^{-1} at 36.7/22.3 °C during the grain filling period in year 2 (Table 7).

4. Discussion

Field screening demonstrated that delayed sowing is a successful strategy to detect heat tolerance in chickpea. These data confirmed the earlier studies of Krishnamurthy et al. (2011) and Upadhaya et al. (2011) in semi-arid environments. Using delayed sowing, Canci and Tokar (2009) studied the combined effect of drought and heat in the Mediterranean environment. They used visual scoring on a 1–9 scale to screen 377 lines in the field. Krishnamurthy et al. (2011) used HTI as a tool to identify the most heat tolerant and sensitive genotypes among 280 genotypes. Later, Upadhaya et al. (2011) found a correlation between climatic factors and plant traits. The current research used plant growth and yield traits, plant physiological traits (CTD), a stress index (HTI) and temperature exposure at different developmental stages (V_{Max}; V_{Min}; F_{Max}; F_{Min}; GF_{Max} and GF_{Min}) as tools for screening heat tolerance in chickpea.

Crop phenological duration (DFF, D50%F and DFP) was negatively correlated to high temperature (Fig. 2) and the shortened growth cycle reduced grain yield reduction at high temperature (Table 1). This was highlighting the advantages of early flowering and shorter crop cycles in heat stressed environments. However, in sensitive genotypes, reproductive failures (flower abortion, poor

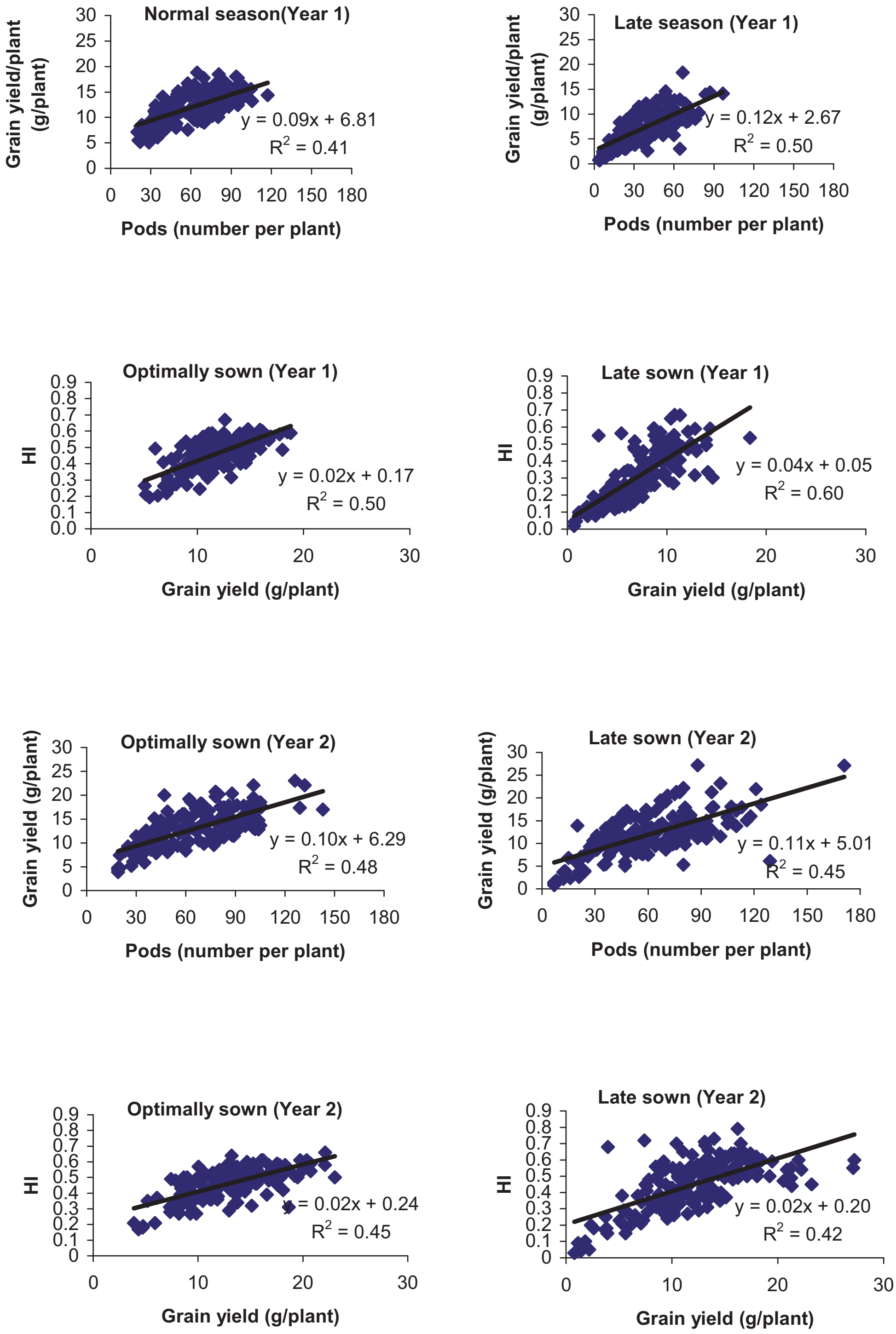

Fig. 7. Relationship of pod number per plant with grain yield (g/plant) and harvest index (HI) in heat stressed (late sown) and non-stressed (optimally sown) conditions.

pollen viability) can cause poor grain yield (Devasirvatham et al., 2013). Krishnamurthy et al. (2011) suggested that D50%F was delayed and DPM was hastened at high temperature, although Upadhaya et al. (2011) observed early flowering and forced maturity under the same conditions. In the current study heat stress shortened the grain filling period by accelerating the rate of plant development, an observation supported by Gan et al. (2004). Plant biomass under stress was low which indicates poor water use efficiency under heat stress. Lower biomass also suggests a disturbance in photosynthesis under heat stress (Prasad et al., 2008). Plant width was reduced by heat stress resulting in poor ground cover.

Controlled environment studies suggest that high temperature (35 °C) during the grain filling period reduces grain yield more significantly than stress during early flowering (Wang et al., 2006; Summerfield et al., 1984). Under these conditions, high temperature accelerates the rate of senescence and shortens the duration of the reproductive period (Wang et al., 2006; Summerfield et al., 1984). Grain yield under heat stress is therefore reduced due to lack of assimilate partitioning from leaves to seed (Wardlaw, 1974). However, in the current field based study, the yield related traits most affected by temperature stress were pod number per plant and harvest index. These observations support the findings of

Table 2

Correlation of 12 traits under normal (non-heat stressed) and late (heat stressed) seasons in the field during 2009–2010 (year 1) at ICRISAT.

Non-heat stressed condition												
DFF												
D50F	0.989***											
DFP	0.981***	0.977***										
DPM	0.639***	0.640***	0.641***									
PH	0.175*	0.176*	0.174*	0.272***								
PW	−0.052	−0.057	−0.049	0.023	0.598***							
Biomass	0.187***	0.194***	0.179	0.291***	0.491***	0.437						
NP	0.065	0.060	0.073	0.059	−0.079	0.140	0.475***					
NFP	0.076	0.073	0.087	0.045	−0.095	0.108	0.435***	0.967***				
SN	0.097	0.090	0.108	0.041	−0.073	0.138	0.391***	0.889***	0.880***			
GY	0.207***	−0.198***	−0.206***	−0.088	0.135	0.358***	0.641***	0.686***	0.676***	0.665***		
HI	0.571***	−0.578***	−0.566***	−0.555***	−0.384***	−0.023	−0.186*	0.327***	0.347***	0.339***	0.477***	
	DFF	D50F	DFP	DPM	PH	PW	Biomass	NP	NFP	SN	GY	HI
Heat stressed condition												
DFF												
D50F	0.989***											
DFP	0.981***	0.977***										
DPM	0.639***	0.640*	0.641									
PH	0.187	0.193	0.178	0.290								
PW	0.174	0.176	0.174	0.271	0.491***							
Biomass	−0.052	−0.056	−0.049	0.023***	0.436***	0.597***						
NP	0.065***	0.060	0.072	0.059***	0.474	−0.078	0.139***					
NFP	0.075***	0.072	0.087	0.045***	0.434	−0.095	0.107***	0.966***				
SN	0.096***	0.090	0.108	0.041***	0.391	−0.072	0.138***	0.888***	0.880***			
GY	−0.206***	−0.197	−0.205	−0.087***	0.641	0.134	0.358***	0.685***	0.675***	0.664***		
HI	−0.570***	−0.577	−0.566	−0.555***	−0.185	−0.384	0.022***	0.327***	0.347***	0.338***	0.477***	
	DFF	D50F	DFP	DPM	PH	PW	Biomass	NP	NFP	SN	GY	HI

DFF, days to first flower; D50F, days to 50% flowering; DFP, days to first pod formation; DPM, days to physiological maturity; PH, plant height; PW, plant width; NP, total number of pods per plant; NFP, number of filled pods per plant; SN, seed number; GY, grain yield; HI, harvest index.

Significant difference at:

[*] $P < 0.05$.

[***] $P < 0.001$.

Krishnamurthy et al. (2011). The advantage of earliness and the link between pod and seed number and eventual yield under heat stress, suggests that manipulation of these traits will improve yield in warmer environments. Generally, high temperature reduces grain yield and its occurrence during the grain filling period can reduce seed size at maturity which may lower grain yield per plant (Ong, 1983). Grain yield was observed to reduce by 53–330 kg ha^{-1} for every 1 °C seasonal temperature rise in India (Kalra et al., 2008).

Table 3

Correlation of 12 traits under normal (non-heat stressed) and late (heat stressed) seasons in the field during 2010–2011 (year 2) at ICRISAT.

Non-heat stressed condition												
DFF	0.962***											
D50F	0.971***	0.967***										
DFP	0.613***	0.636***	0.637***									
DPM	0.337***	0.354***	0.336***	0.435***								
PH	−0.125	−0.079	−0.110	0.052	0.172*							
PW	−0.021	0.014	0.006	0.079	0.155	0.011						
Biomass	−0.120	−0.095	−0.097	−0.255***	−0.259***	−0.095	0.466***					
NP	−0.099	−0.071	−0.079	−0.241***	−0.254***	−0.078	0.465***	0.992***				
NFP	−0.056	−0.039	−0.051	−0.253***	−0.276***	−0.092	0.411***	0.917***	0.929***			
SN	−0.305***	−0.289***	−0.283***	−0.299***	−0.198***	−0.052	0.722***	0.721***	0.711***	0.673***		
GY	−0.482***	−0.499***	−0.483***	−0.604***	−0.519***	−0.102	−0.014	0.519***	0.516***	0.512***	0.578***	
	DFF	D50F	DFP	DPM	PH	PW	Biomass	NP	NFP	SN	GY	HI
Heat stressed condition												
DFF												
D50F	0.690***											
DFP	0.980***	0.692***										
DPM	0.525***	0.368***	0.543***									
PH	0.590***	0.494***	0.590***	0.538***								
PW	0.0421	0.170	0.037	0.240***	0.312***							
Biomass	0.548***	0.426***	0.553***	0.549***	0.586***	0.152*						
NP	−0.274***	−0.131	−0.274***	−0.127	−0.050	0.527***	−0.354***					
NFP	−0.292***	−0.148	−0.292***	−0.150***	−0.073***	0.519***	−0.374***	0.984***				
SN	−0.251***	−0.117	−0.249***	−0.149*	−0.062	0.486***	−0.375***	0.933***	0.949***			
GY	−0.401***	−0.226***	−0.408***	−0.168	−0.127	0.726***	−0.305***	0.738***	0.761***	0.708***		
HI	−0.726***	−0.471***	−0.736***	−0.670***	−0.637***	−0.057	−0.739***	0.440***	0.477***	0.446***	0.546***	
	DFF	D50F	DFP	DPM	PH	PW	Biomass	NP	NFP	SN	GY	HI

DFF, days to first flower; D50F, days to 50% flowering; DFP, days to first pod formation; DPM, days to physiological maturity; PH, plant height; PW, plant width; NP, total number of pods per plant; NFP, number of filled pods per plant; SN, seed number; GY, grain yield; HI, harvest index.

Significant difference at:

[*] $P < 0.05$.

[***] $P < 0.001$.

Table 4
Heat response classification of chickpea genotypes from cluster groups.

No	Genotypes	HTI year 1	HTI year 2
Stable heat tolerant			
1	ICCV 95311	0.89	1.19
2	ICCV 98902	0.97	1.15
3	ICCV 07109	0.96	0.78
4	ICCV 92944	1.49	0.43
5	ICC 6969	0.45	1.25
6	ICCV 07108	0.48	0.74
7	ICCV 98903	0.56	0.60
8	ICCV 96836	0.23	0.82
9	ICC 14406	1.06	0.28
10	ICC 16173	0.92	0.33
Stable moderate tolerant			
1	ICCX 820065(GG2)	0.54	0.34
2	ICCL 87207	0.6	0.28
3	ICC 4902	0.62	0.18
4	ICC 14315	0.62	0.12
5	ICCV 89314	0.61	0.12
6	ICC 13941	0.4	0.26
7	ICC 14497	0.42	0.21
8	ICC 16181	0.4	0.22
Stable sensitive			
1	ICC 988	−0.24	−0.47
2	ICC 8261	−0.25	−0.45
3	ICC 10090	−0.27	−0.47
4	ICC 7294	−0.21	−0.40
5	ICC 6231	−0.22	−0.56
6	ICC 7292	−0.21	−0.53
7	ICC 16453	−0.18	−0.49
8	ICC 5912	−0.3	−0.51
9	ICC 7308	−0.26	−0.54
10	ICC 5566	−0.22	−0.92
11	ICC 7570	−0.30	−0.87
Tolerant to moderate sensitive			
1	ICC 1017	−0.19	0.94
2	ICCV 94916-8	−0.24	0.92
3	ICC 9125	−0.15	0.88
4	ICC 12169	−0.12	1.05
Sensitive to moderate tolerant			
1	ICC 982	−0.32	0.05
2	ICC 16298	−0.31	0.01
3	ICC 14183	−0.26	0.10
4	ICCV 07116	0.03	0.10
5	ICC 14592	−0.24	0.19
6	ICC 1025	−0.27	0.47

Similarly, in spring sown crops the mean grain yield is reduced compared with autumn sowing due to greater seasonal temperature fluctuations (26–38 °C) during the reproductive stage (Ozdemir and Karadavut, 2003). In Bangladesh, a six week delay in sowing from the optimum period reduced the grain yield by 40% and flowering and maturity was also accelerated (Ahmed et al., 2011).

In the current study, heat tolerant genotypes produced more grain yield than sensitive genotypes (Tables 5 and 6). Some of the released cultivars listed in Tables 5 and 6 (ICCVs 98902, 98903, 95311, 92944, 07109, 07108 and 96836) represent good sources of heat tolerance for crop improvement. The genotype ICCV 92944 (JG 14) was previously reported as heat tolerant by Gaur et al. (2010). This line can be either deployed directly in farmer fields or used as a parent in a plant breeding programme. In addition, ICC 6969, ICC 14406 and ICC 16173 were identified as potential new sources of heat tolerance from among the 167 genotypes tested. These selected heat tolerant genotypes were strongly correlated with grain yield under heat stress. Heat tolerant genotypes believed to produce enzymatic and non-enzymatic antioxidants which are useful to defend against oxidative stress thus improving tolerance to heat (Kumar et al., 2012a).

Canopy temperature depression was used as a method of screening for heat tolerance in cereals (Rosyara et al., 2010). It was

Table 5
Canopy temperature depression (CTD – °C) of selected chickpea genotypes (from cluster groups) grown in the field under heat stressed conditions during 2010 (year 1).[a]

Genotypes	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
Medium to short duration heat tolerant						
ICCV 92944	4.7	6.2	8.2	9.6	11.0	12.3
ICCV 95332	2.6	3.9	2.6	5.7	7.7	8.9
ICCV 07109	4.2	4.5	2.3	8.6	7.3	7.2
ICCV 98902	3.6	2.6	4.8	5.0	10.3	6.3
ICCV 95311	1.9	6.1	3.3	8.5	8.1	6.5
ICC 12289	4.4	7.1	1.8	7.1	5.7	6.3
Medium to short duration heat sensitive						
ICC 3485	4.4	5.2	4.3	8.5	6.2	5.2
ICCV 94954	1.5	4.4	2.2	5.7	4.3	1.7
ICC 16181	3.0	4.6	4.3	4.7	6.2	5.8
ICCV 89509	2.1	1.8	2.0	5.2	6.6	6.5
ICCV 90201	2.4	5.9	1.9	3.8	9.5	6.7
ICC 3935	1.2	7.2	5.4	7.9	6.7	6.5
Long duration heat tolerant						
ICC 7292	0.9	3.0	4.0	7.1	4.9	6.4
ICC 16774	1.6	4.0	3.3	2.9	5.7	3.6
ICC 15795	0.1	3.0	3.1	2.9	7.1	2.8
Long duration heat sensitive						
ICC 15367	2.0	2.0	0.9	1.5	2.9	2.2
ICC 15807	2.2	3.0	3.7	2.2	5.7	1.5
ICC 988	2.3	3.8	0.8	3.6	5.9	5.0

ANOVA for 167 genotypes

	df	Mean squares	Mean of 167 genotypes	LSD
CTD	166	2.87	4.04[*]	2.8

Note: selected genotypes based on maturity from chickpea germplasm ($n = 167$) were presented in this table).

[*] $P < 0.05$.

Table 6
Canopy temperature depression (CTD – °C) of selected chickpea genotypes grown in the field under heat stressed conditions during 2011 (year 2).[*]

Genotypes	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
Medium to short duration heat tolerant						
ICCV 92944	3.0	6.4	7.3	4.7	5.4	6.7
ICCV 95332	4.2	4.8	7.8	4.7	5.3	7.0
ICCV 07109	3.7	5.3	7.0	5.4	6.5	8.6
ICCV 98902	3.4	5.3	5.8	5.5	5.2	5.9
ICCV 95311	3.0	5.7	9.2	4.8	5.8	6.8
ICC 12289	5.3	7.4	10.9	7.9	9.0	9.7
Medium to short duration heat sensitive						
ICC 3485	3.4	4.5	6.0	5.2	4.8	6.2
ICCV 94954	2.4	4.4	8.5	6.7	6.3	9.1
ICC 16181	3.5	4.9	7.3	5.1	5.7	7.0
ICCV 89509	2.1	4.7	7.5	6.0	6.8	8.1
ICCV 90201	2.4	5.2	6.1	5.7	5.7	5.6
ICC 3935	5.0	6.8	8.8	7.3	9.0	9.6
Long duration heat tolerant						
ICC 7292	4.2	5.6	7.4	6.5	5.6	7.6
ICC 16774	4.6	4.8	5.7	4.4	2.8	5.0
ICC 15795	3.3	5.1	6.8	4.8	4.8	5.9
Long duration heat sensitive						
ICC 15367	4.5	4.9	6.8	8.5	6.3	7.4
ICC 15807	1.5	4.3	7.2	5.2	6.5	6.5
ICC 988	3.0	4.5	6.7	5.1	5.1	4.2

ANOVA for 167 genotypes

	df	Mean squares	Mean of 167 genotypes	LSD
CTD	166	1.75	5.9[a]	2.2

Note: selected genotypes based on maturity from chickpea germplasm ($n = 167$) were presented in this table.

[*] $P < 0.05$.

Table 7
Maximum and minimum temperatures at different developmental stages of selected chickpea genotypes and their response to grain yield in heat stressed conditions during 2009–10 (year 1) and 2010–11 (year 2).

Genotypes	V_{Max} (°C)	V_{Min} (°C)	F_{Max} (°C)	F_{Min} (°C)	GF_{Max} (°C)	GF_{Min} (°C)	Grain yield (g/plant)
Year 1							
Medium to short duration heat tolerant							
ICCV 92944	33.1	17.4	36.1	20.6	38.6	23.0	6.5
ICCV 95332	33.3	17.5	35.7	20.3	38.8	23.2	5.6
ICCV 07109	33.5	17.8	35.5	19.7	39.1	23.6	5.7
ICCV 98902	33.9	18.2	38.5	21.6	39.4	24.1	9.5
ICCV 95311	33.7	18.0	35.9	19.2	39.1	23.8	4.5
ICC 12289	34.3	18.3	37.5	22.7	39.1	24.1	1.6
Medium to short duration heat sensitive							
ICC 3485	33.5	17.9	35.9	19.5	38.8	23.7	1.8
ICCV 94954	33.7	18.1	37.1	19.5	39.0	24.0	5.1
ICC 16181	33.3	17.5	35.7	20.3	38.9	23.4	4.2
ICCV 89509	34.5	18.5	37.1	22.8	39.2	24.4	1.5
ICCV 90201	34.8	19.0	38.9	22.0	39.7	25.2	1.7
ICC 3935	34.0	18.2	38.3	22.4	39.4	24.1	4.0
Long duration heat tolerant							
ICC 7292	34.5	18.6	37.1	22.2	39.3	24.4	2.0
ICC 15795	34.5	18.5	37.8	23.7	39.4	24.3	1.0
ICC 16774	35.0	19.1	39.6	23.7	39.5	25.2	1.2
Long duration heat sensitive							
ICC 15367[a]	–	–	–	–	–	–	0
ICC 15807	34.7	19.0	38.6	21.5	39.6	25.1	0
ICC 988	35.1	19.2	39.8	23.9	39.2	25.0	0
Year 2							
Medium to short duration heat tolerant							
ICCV 92944	33	17.1	37.1	18.7	37.3	23.9	16.2
ICCV 95332	33.0	17.1	36.7	17.7	37.0	23.4	15.6
ICCV 07109	31.7	16.2	35.1	17.4	36.7	22.3	22.2
ICCV 98902	32.1	16.5	35.7	17.3	36.7	22.3	27.2
ICCV 95311	31.6	16.1	35.2	18.1	36.8	22.2	20.9
ICC 12289	32.3	16.4	36.2	18.7	37.1	23.1	13.2
Medium to short duration heat sensitive							
ICC 3485	32.0	16.4	34.8	17.2	37.1	22.7	15.1
ICCV 94954	32.4	16.5	36.8	19.4	37.0	23.0	8.5
ICC 16181	32.1	16.4	35.3	17.2	36.8	22.5	13.2
ICCV 89509	33.3	17.2	36.8	20.2	37.1	23.9	14.1
ICCV 90201	32.9	16.8	35.4	20.1	37.1	23.1	15.0
ICC 3935	32.4	16.5	36.3	20.4	36.9	22.7	9.5
Long duration heat tolerant							
ICC 7292	33.0	17.1	36.8	18.2	37.3	24.0	6.5
ICC 15795	33.0	17.1	36.9	18.5	37.2	24.1	13.3
ICC 16774	33.1	17.2	37.2	18.7	37.3	24.0	3.7
Long duration heat sensitive							
ICC 15367	32.2	16.5	36.0	17.7	37.0	22.9	11.5
ICC 15807	32.0	16.4	34.8	17.1	36.9	22.6	14.6
ICC 988	33.6	17.4	35.4	22.2	37.6	24.4	5.9

V = one day before first flower – sowing day; F = days to first pod – days to first flower; GF = harvest date – one day after pod formation. Average temperature at each period was calculated.

[a] ICC15367 did not flower under heat stressed conditions in year 1.

also used to identify a relationship between canopy conductance and transpiration rate under drought in chickpea (Zaman-Allah et al., 2011). In the current study, the heat tolerant genotypes showed some degree of temperature depression. However, all medium to short duration genotypes did not show higher CTD than long duration genotypes in all observations in both years (Tables 3 and 4). This revealed that canopy temperature could be regulated by changing the level of soil moisture. Since ambient temperatures in the field experiments were high, it can be concluded that an increase in soil moisture during stress may result in heat stress relief. A similar response was found in wheat screened for heat tolerance in the field (Rosyara et al., 2010). Earlier work by Ibrahim (2011) reported a lack of significant differences among chickpea genotypes for CTD under high temperature at vegetative stage. However, in the current study, CTD was measured during the reproductive period in some instances showed a significant relationship with grain yield. CTD during the grain filling period was correlated with yield under heat stress (Reynolds et al., 1998). Heat stress during grain development can affect the availability and translocation of assimilates to the grain thus reducing starch synthesis and deposition resulting in lower grain weight (Wiegand and Cuellar, 1981). Those genotypes with lower CTD (1–3 °C) tended to have lower grain yield than those with higher CTD (>4 °C) (Fig. 8). Therefore, few genotypes showed cooler canopies during grain development indicating another mechanism for high temperature tolerance during this stage of lifecycle.

Maximum temperatures estimated at different developmental stages influenced genotype performance under heat stress. Clearly, temperatures >37 °C are the primary reason for grain yield reduction in the current study. The average maximum temperature also determines the critical temperature for each individual genotype. The critical temperature of two heat tolerant medium duration

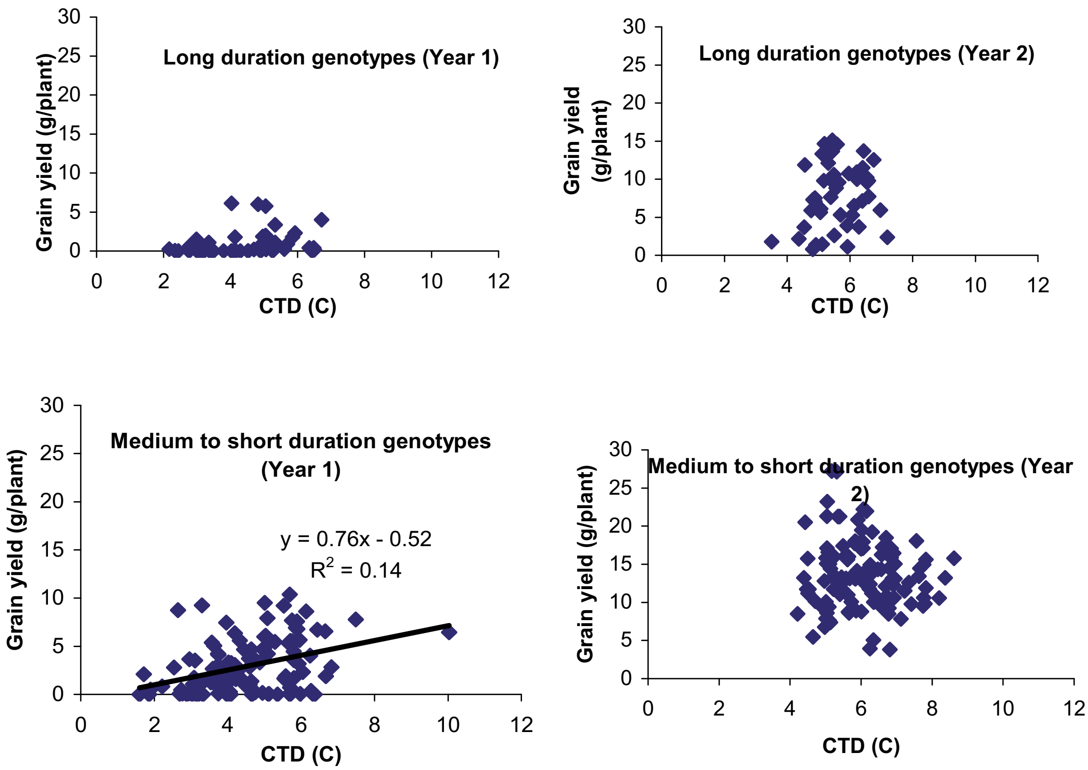

Fig. 8. The relationship of chickpea grain yield and average canopy temperature depression (CTD) in reproductive period under heat stressed conditions (late sown) during 2010 (year 1) and 2011 (year 2).

genotypes (ICCVs 98902 and 95311) was ≥38 °C (Tables 5 and 6). At and above this temperature, both genotypes suffered an average yield reduction of up to 50%. Generally, chickpea is a cool season legume and has a higher base level of heat tolerance compared with other cool season legumes (Malhotra and Saxena, 1993). This experiment confirmed the findings of Malhotra and Saxena (1993) and validates the need to breed for heat tolerance to provide food security in warmer environments.

5. Conclusions

This study found genetic variation in chickpea for phenology, plant growth and yield traits under heat stress. There was also significant genetic variation for canopy temperature depression and a heat stress index. Medium to short duration genotypes tended to have a yield advantage under heat stress compared with long duration genotypes. Generally, heat stress reduced plant biomass and grain yield and the most heat sensitive traits were pod number per plant and harvest index. This research identified a group of heat tolerant genotypes based on their maturity that can be used in a breeding programme targeting the selection of plant growth and physiological traits, grain yield and a heat tolerance index.

Acknowledgements

We thank the Grains Research and Development Corporation of Australia (GRS 180) and National Food Security Mission (NFSM), Ministry of Agriculture, Government of India for financial support.

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