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Review

High temperature tolerance in chickpea and its implications for plant improvement

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Abstract. Chickpea (*Cicer arietinum* L.) is an important food legume and heat stress affects chickpea ontogeny over a range of environments. Generally, chickpea adapts to high temperatures through an escape mechanism. However, heat stress during reproductive development can cause significant yield loss. The most important effects on the reproductive phase that affect pod set, seed set and yield are: (1) flowering time, (2) asynchrony of male and female floral organ development, and (3) impairment of male and female floral organs. While this review emphasises the importance of high temperatures >30°C, the temperature range of 32–35°C during flowering also produces distinct effects on grain yield. Recent field screening at ICRISAT have identified several heat-tolerant germplasm, which can be used in breeding programs for improving heat tolerance in chickpea. Research on the impact of heat stress in chickpea is not extensive. This review describes the status of chickpea production, the effects of high temperature on chickpea, and the opportunities for genetic improvement of chickpea tolerance to high temperatures.

Additional keywords: genetic variation, legumes, pollen, semi-arid tropics, tolerance.

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Introduction

Chickpea is a major grain legume used for food from ancient days. It is one of the essential semi-arid tropical legume crops. Chickpea is either grown during the post-rainy season on stored soil moisture (south Asia and spring-sown Mediterranean) or as a Mediterranean winter crop on in-season rainfall; in both instances the crop is exposed to terminal drought which is accompanied by rising temperatures. The south Asian crop may also experience high temperatures in the seedling phase if planted early (Berger and Turner 2007). Chickpea productivity is constrained by several abiotic stresses (Singh *et al*. 1994; Gaur *et al*. 2007) and temperature is one of the most important determinants of crop growth over a range of environments (Summerfield *et al*. 1990) and may limit chickpea yield (Basu *et al*. 2009).

The effects of heat stress during the vegetative and reproductive growth stages using agronomic, phenological, morphological and physiological assessment has been studied in various crops such as wheat (Sharma *et al*. 2005), rice (Weerakoon *et al*. 2008) and cotton (Cottee *et al*. 2010) while only limited research has been conducted in chickpea (Wang *et al*. 2006). The detrimental effects of high temperature on various growth and reproductive stages are difficult to assess when growing conditions are favourable in the short-term (few days) as the plant continues vegetative growth but sets fewer pods because of indeterminate plant type and plasticity (Liu *et al*. 2003). The relatively narrow genetic base of chickpea is another reason why high temperature has such a detrimental effect on growth and reproductive physiology (Abbo *et al*. 2003*a*). For these reasons chickpea tends to be sensitive to high temperature during the growth and reproductive stages. In general, the cool season food legumes (peas, lentil, chickpea and faba bean) are more sensitive to heat than warm season legumes (cowpea, soybean, groundnut, pigeonpea, and mung bean). Among cool season legumes, chickpea is less sensitive to high temperature (Wery *et al*. 1993; McDonald and Paulsen 1997). Although chickpea is exposed to warm temperatures (>30°C) in certain regions, limited yield loss was found at 30°C, which is higher than other cool season legumes such as field peas, faba bean and lentil (Summerfield *et al*. 1984; Erskine *et al*. 1994; McDonald and Paulsen 1997; Patrick and Stoddard 2010). Therefore, a base level of heat tolerance is found in chickpea. However, there is no clear evidence to show the mechanism of heat tolerance. This review outlines the occurrence of high temperature stress, the state of chickpea production, the effects of high temperature on growth and physiology of chickpea, and explores strategies to improve chickpea breeding for heat tolerance.

State of chickpea production

Climates favourable for chickpea production fall into two general groupings; Mediterranean and summer-dominant rainfall semi-arid subtropical climates (Berger and Turner 2007). Chickpea production is also grouped into three regions globally: West Asia and North Africa (WANA), the Indian subcontinent region and recently emerged regions. The details of these regions, their climate and relative intensity of the principal stresses are discussed by Berger and Turner (2007). Chickpea is extensively cultivated in the Mediterranean climate regions of northern Pakistan, Iran, Iraq, Turkey, southern and south-western Australia and the Mediterranean basin. In these areas, chickpea is widely sown in winter at a maximum air temperature of 10°C (Berger 2007) and high temperatures occasionally occur during reproductive development in the spring (Iliadis 1990).

In the Indian subcontinent region and recently emerged regions (e.g. eastern, northern and southern Australia), the crop experiences cool (5–10°C) and frosty nights (0 to −1°C) in the early vegetative stage and warm (20–27°C) to hot (>30°C) air temperature during the day over the reproductive phase (Summerfield *et al*. 1984, 1990; Berger and Turner 2007). During the last two decades, south Indian and eastern Australian late-sown chickpea has been exposed to heat stress in the growing season, mainly in reproductive phase. In south India, if the rainy season (*kharif*) is extended, then the chickpea sowing in the *rabi* season will be delayed (Ali 2004). This delay exposes the crop to high temperatures during the reproductive stage. Ninety percent of Australian chickpea is produced in Tamworth. In Australia, particularly in northern NSW and depending on the climatic conditions, sowing can be delayed until the last week of June to reduce the incidence of *Ascochyta* blight (Moore and Knights 2009). However, late-sown crops may experience high temperatures during the reproductive phase. Berger and Turner (2007) and Berger *et al*. (2011) described the global chickpea distribution based on climate analysis and current production trends. The climate analysis showed that the current chickpea-growing area is under threat from increasing temperature and production may extend to cooler regions.

The nature of heat stress and plant response

High temperature often occurs in combination with high solar irradiance, drought, and strong wind, all of which can aggravate plant injury even in well-watered plants (Hall 1992). Heat stress is a function of plant genotype, high temperature, water status and soil type. The occurrence and severity of heat stress varies in different regions from year to year. Depending on timing, duration and interaction, observed heat stress can be grouped into chronic and acute, each of which involve different coping mechanisms, adaptation strategies and ultimately, breeding techniques (Blum 1988; Wery *et al*. 1993). Chronic heat stress occurs at any stage of crop growth and generally results in substantial yield loss and even crop failure. Acute heat stress of relatively short duration can occur at any stage of crop growth, often leading to lower yield. Acute heat stress is more prevalent than chronic heat stress in the spring-sown chickpea regions of WANA (e.g. Turkey) and the Indian subcontinent region. In the spring crop, the mean seed yield of 1627 kg ha^{-1} decreased compared with the autumn crop due to seasonal temperature fluctuation (26–38°C) during the reproductive stage (Ozdemir and Karadavut 2003). In north India, chickpea grain yield decreased by 53 kg ha^{-1} in Uttar Pradesh and 301 kg ha^{-1} in Haryana per 1°C increase in seasonal temperature (Kalra *et al*. 2008). Pod development is clearly impaired at above optimum (>30°C) temperatures (Summerfield *et al*. 1984). Nevertheless, different genotypes have a range of tolerance or resistance mechanisms that help them cope.

Genotypic variability for heat tolerance

During the Greek and Roman period, chickpea was grown as a summer crop (sown in March–April and harvested in June–July) (Kumar and Abbo 2001). In the Mediterranean and near-eastern gene pools, the wild *Cicer reticulatum* germinates after autumn rain and the crop matures in spring. During the spring the crop is exposed to rising temperature which influences the flowering period, accelerates maturity and may limit yield. However, the shift of chickpea sowing from autumn to spring occurred early in the crop's history (Abbo *et al*. 2003*b*) and was driven by high fungal disease (*Ascochyta* blight) incidence in the autumn-sown crop (Kumar and Abbo 2001). This shift of season has likely caused a genetic bottleneck which narrowed the genetic diversity (Abbo *et al*. 2003*a*) and most probably genetic variation for heat tolerance. Therefore, the origin and diversity of genetic resources must be considered when screening germplasm for heat tolerance if the plant breeder is to improve the temperature tolerance of modern chickpea in the target environments.

A decade ago, the heat-tolerant genotypes ICCV 88512 and ICCV 88513 were identified from among 25 genotypes (Dua 2001). Recently, a reference collection of 280 diverse chickpea germplasm was screened in the field for heat tolerance in two locations (Patancheru and Kanpur) in India during the post-rainy season (optimum) and summer season (late heat). Based on a Heat Tolerance Index (HTI) (≥1.00), ICC 3362, ICC 6874 and ICC 12155 were identified as heat-tolerant lines. ICC 16374, ICC 4567 and ICC 10685 were classified as heat-sensitive lines based on low HTI (negative values) (Krishnamurthy *et al*. 2011). Upadhyaya *et al*. (2011) identified ICC 14346 as a heat-tolerant genotype among 35 early maturing germplasm under ideal crop management (irrigation, nitrogen application) conditions in field screening at Patancheru based on yield (kg ha^{-1}). At present, genotypic diversity of chickpea global germplasm collections and chickpea production environments, particularly those affected by high temperature have not been amply studied. The heat tolerance of chickpea is likely to be multi-genic and the components of heat tolerance are probably controlled by different sets of genes (Upadhyaya *et al*. 2011).

Plant responses to heat

Effect of heat stress on crop establishment (germination and crop development)

Heat stress at sowing directly affects crop germination and crop establishment. Chickpea seed germination decreases at supra-optimum temperatures (Singh and Dhaliwal 1972; Ellis *et al*. 1986). Ellis *et al*. (1986) indicated that the optimal temperature for germination is 10–15°C and noted that high germination temperatures are considered to be 22–35°C. Covell *et al*. (1986) showed that germination was faster at higher temperatures between 31.8 and 33°C. However, at high temperatures the mobilisation of cotyledon reserves and embryo growth are adversely affected. While chickpea showed genotypic variation in the rate of germination under various temperatures (Ellis *et al*. 1986), the germination percentage of chickpea was zero when temperature ranged between 45 and 48°C (Singh and Dhaliwal 1972). High mean maximum temperature and low relative humidity can have a marked influence on seedlings (Saxena 1987). Low photosynthetic rates and high transpiration rates occur during high temperature stress and tend to reduce plant establishment in chickpea (Singh and Dhaliwal 1972). Recent climate data from field experiments in south India (Patancheru – 18°N, 78°E) during sowing time after the rainy season (last week of October) showed a temperature range of 28–31°C (Upadhyaya *et al*. 2011). Sowing temperature is an important determinant of yield, and will become a significant constraint should predicted climate change lead to higher future sowing temperatures.

Though early phenology was mentioned in the heat escape mechanism section, the importance of early phenology in chickpea breeding for heat tolerance will be discussed in greater detail in this section. Higher temperature and photoperiod can modify plant phenology (e.g. opening of first flower), particularly if crops are exposed to warming temperatures and long days in summer (van der Maesen 1972; Summerfield *et al*. 1984). An understanding of these effects and their interactions with genotype are needed in field screening under stress. Breeders generally use days to first flowering as an indicator of crop duration (Anbessa *et al.* 2006). The photoperiod-sensitive genotype (Chafa) produced flowers in 25 days under optimum temperature (26°C) and 15-h photoperiod compared with 52 days in the late flowering genotypes (K 850, G 130) (ICRISAT 1979). The flowering model studies of Summerfield *et al*. (1985) indicated that the rate of progress towards flowering was a linear function of mean temperature and there was no interaction between photoperiod and mean temperature. However, the linear development of the plant through to flowering only occurs within a defined range above which the rate of development declines. These critical temperatures vary among genotypes with tolerant lines having higher optimum temperatures compared with sensitive genotypes.

Effect of heat stress on reproductive development and yield

Chickpea has small flowers and the stamens are diadelphous (9 + 1 anthers). Self pollination takes place before the flower opens and pods form within 5–6 days (Singh 1997). Heat stress during the reproductive phase in legumes is generally allied with lack of pollination, abscission of flower buds, flowers and pods with substantial yield loss (Nakano *et al*. 1997, 1998). Hot (>30°C) and dry atmospheric conditions lead to profligate loss of flower buds and open flowers in chickpea (Sinha 1977).

High temperature after flower opening decreases chickpea seed yield by reducing the number of seeds per plant and weight per seed (Wang *et al*. 2006). In chickpea, Summerfield *et al*. (1984) suggested that the longer the exposure during reproductive development to a high day temperature of 35°C, the lower the yield. Most chickpea genotypes do not set pods when temperatures reach >35°C (Basu *et al*. 2009). However, there is considerable variation among genotypes for response to high temperature. The period of anthesis and seed set are clearly critical stages for exposure to heat stress (Gross and Kigel 1994). Nayyar *et al*. (2005) suggested that the development of male (pollen, anthers) and female (stigma-style, ovary) parts are the most sensitive organs to abiotic stress in reproductive biology. Therefore, pollen viability, stigma receptivity and ovule viability are useful indicators of sensitivity to abiotic stress (Nayyar *et al.* 2005). However, the effect of stress on either male or female organs depends upon the stage of sporogenesis (micro or mega). Due to heat stress, meiosis and pollen development are the most affected part in micro-sporogenesis. Megaspore formation in the ovule and fertilisation are the most important events in mega-sporogenesis under high temperature stress (Gross and Kigel 1994).

High temperature effects on pre-anthesis are related to anther development, pollen sterility and pollen production. The study of pollen may help to predict genetic variation among genotypes for reproductive phase heat tolerance. Pollen sterility is one of the key factors limiting legume yield under high temperature (Porch and Jahn 2001). Eight stages of chickpea pollen development, from pollen mother cell development to mature pollen can be distinguished (Fig. 1). Two of the stages, microspore mother cell meiosis and mature microspores at anthesis, appear to be detrimentally affected by

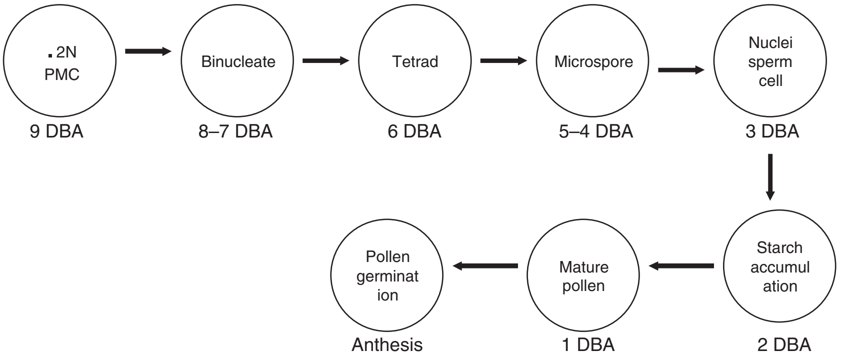

Fig. 1. Sequences of chickpea pollen development.

high temperature (Iwahori 1965; Ahmed *et al*. 1992). The microspore mother cell meiosis, particularly early meiosis I, II is also sensitive to high temperature (Iwahori 1965). Ahmed *et al*. (1992) reported that tapetal cells (meiosis II) did not become binucleate and the locular cavity was less developed in anthers under high temperatures (33°C day/30°C night) resulting in premature pollen development. Such information is lacking in chickpea at meiosis stage. Most of the pollen studies in chickpea have focussed on cold tolerance (Srinivasan *et al*. 1999; Clarke *et al*. 2004) and the meiosis stage [9 days to 5–6 days before anthesis (DBA)] of chickpea was found to be sensitive to cold (<3°C) (Clarke and Siddique 2004).

Reduced pollen viability is common in legumes during pre-anthesis. In chickpea, 80–90% pollen germination occurs in the range 7–25°C (assessed after 4 h incubation *in vitro*). During germination pollen hydration is inhibited by low temperature (Clarke and Siddique 2004). *In vitro* pollen germination after 60 min incubation was higher (61%) at 25°C in chickpea compared with 45°C (33%) (Jaiwal and Mehta 1983). Therefore, both high and low temperatures reduce pollen germination. Pollen abnormalities were observed in cowpea at 33/30°C when plants were exposed to heat 3 DBA (Ahmed *et al*. 1992). Anther indehiscence in bean occurred at 32/27°C when subjected to heat stress during the period 9–13 DBA (Gross and Kigel 1994; Porch and Jahn 2001). Pollen production was reduced ~30–50% at 38/30°C compared with 30/22°C in soybean (Koti *et al*. 2005). Therefore, pre-anthesis flower abortion is caused by male sterility resulting from abnormal pollen development and anther indehiscence (Warrag and Hall 1984). In chickpea there is genotypic variability for high temperature sensitivity. At 35/20°C day/night exposure for 24 h before anthesis, the chickpea genotype ICC 5912 became sterile, while pollen from the genotype ICCV 92944 was fertile (Devasirvatham *et al*. 2010) (Fig. 2).

High temperature effects post-anthesis are associated with loss of stigma receptivity (Kakani *et al*. 2002), poor pollen germination, pollen tube growth on the stigma (Talwar and Yanagihara 1999) and failure of pollen fertilisation and ovule formation (Ormrod *et al*. 1967). Heat stress sometimes has a combined effect on male and female parts, thus creating asynchrony between male and female organs (Zinn *et al*. 2010). There is a lack of information about asynchrony in chickpea under heat stress. Nevertheless, progress has been made in chickpea reproductive biology under cold stress. The stigma receptivity is reported to be low at low temperatures (12/7°C) in chickpea (Nayyar *et al*. 2005). At 12/7°C, decline in pollen germination and pollen tube growth on the stigma may be associated with stigma receptivity (Clarke and Siddique 2004). This might occur due to low amounts of exudates on the stigma (Nayyar *et al*. 2005). Lack of pollen germination and tube growth in the style was found in the heat-sensitive genotype ICC 5912 at 35/20°C due to sterile pollen (Devasirvatham *et al*. 2010). In this study, stigma receptivity was not affected by high temperature stress. However, the observed reduction in pollen germination at high temperature on the stigma is not clear. Therefore, it is essential that the effect of heat stress on pollen function (pollen germination and tube growth) and stigma receptivity of genotypes in the field be studied.

Pre-anthesis heat stress resulted in flower abortion indicating that this stress limits pod formation. In addition, the number of days of exposure to high post-anthesis temperatures is important in legumes. The timing of pre- and post-anthesis heat stress was studied in cowpea (Hall 1992) and groundnut (Vara Prasad *et al*. 2001). A combination of pre- and post-flowering stress reduced pod set in bean at 34/29°C (Agtunong *et al*. 1992). The maximum sensitivity to hot day temperatures (38°C) in groundnut occurred anywhere between 6 days before and 15 days after flowering which can reduce the fruit set, i.e. the proportion of flowers producing pegs or pods (Vara Prasad *et al*. 1999, 2001). These examples indicate that the period of anthesis (pre-anthesis; anthesis and post-anthesis) and number of days of exposure to heat during flowering play an essential role in the development of reproductive organs, i.e. pods.

Generally, the responses of plants to high temperature are assessed under high day temperature. However, high night temperature might also play a significant role in legumes and can influence seed set. Anthers failed to dehisce and pod

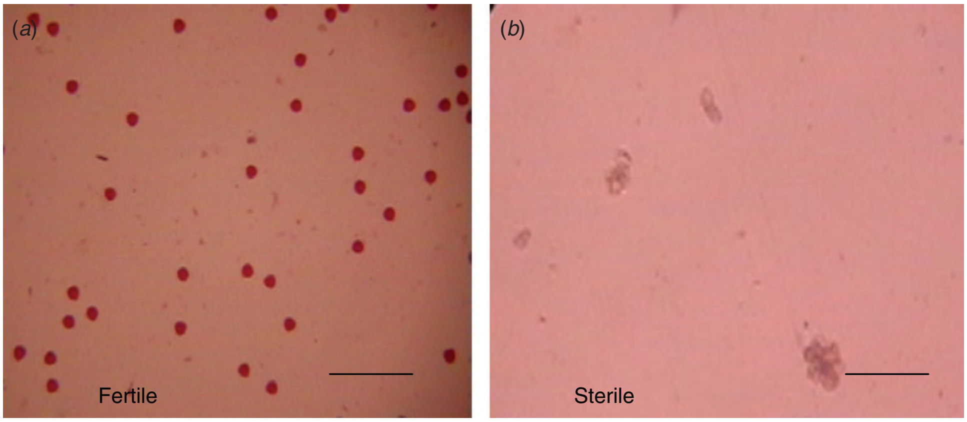

Fig. 2. Fertile and sterile pollen of chickpea at 35/20°C (pollen grains stained with 2% acetocarmine). (*a*) Fertile pollen of ICCV 92944 (picked up stain); (*b*) sterile pollen of ICC 5912 (no stain) (Devasirvatham *et al*. 2010) (bars = 10 µm).

development was affected by a high night temperature of 27°C in bean (Konsens *et al*. 1991). In cowpea, high night temperature (33/30°C) increased the occurrence of small and shrunken pollen leading to zero pod set compared with low night temperature (33/20°C) (Ahmed *et al*. 1992). Therefore diurnal temperatures play an important role in legume male reproductive organs (Ahmed *et al*. 1992). However, little is known about these effects in chickpea.

Seed development in legumes is a function of the rate and duration of embryo growth, which is in turn influenced by abiotic stress that may lead to embryo abortion (Warrag and Hall 1983), or small endosperms (Davies *et al*. 1999). Finally endosperm filling in the seed is affected by high temperature resulting in small or wrinkled seeds (Egli *et al*. 2005). The probable reason for small endosperm or smaller seed size after post-anthesis heat stress is that the remobilisation of photosynthates to the grain is reduced. A large proportion of carbohydrate is generally utilised to fill the grain in legumes (Davies *et al*. 1999), thus influencing seed weight and number. Under heat stress seeds are not fully developed in sensitive genotypes at agronomic maturity (Sivakumar and Singh 1987). More research is needed to address the remobilisation of the photosynthates to chickpea seeds under heat stress.

Seed quality (uniformity of seed size, shape, colour and texture of the seed coat) is important for grain marketing and is subjected to genotypic × environmental effects that seem to be related to abiotic stress, particularly in kabuli chickpea (Sivakumar and Singh 1987; Leport *et al*. 1999). While heat stress is expected to play a role here, its effects have not been well studied.

In summary, available evidence indicates that chickpea crop establishment (seedling growth) has a lower supra-optimal temperature (20–24°C) than pollen germination or pollen tube growth (25°C) (Table 1). However, high temperature frequently occurs during the reproductive stage in chickpea production areas. Heat stress has important effects on the reproductive period that influence time to pod set, seed set and yield including: (1) flowering time, (2) asynchrony of male and female organ development, and (3) impairment of male and female organs (Craufurd and Wheeler 2009; Zinn *et al*. 2010). Therefore, improved understanding of chickpea response to heat stress (both day and night temperatures) combined with the timing and duration (short or acute/long or chronic) of heat stress is important for chickpea breeding.

Effect of heat stress on physiology

Photosynthetic rate and chlorophyll content are important physiological parameters in plants. Heat stress directly affects photosynthesis including photosystem II in chickpea (Srinivasan *et al*. 1996). The rate of photosynthesis has a negative linear relationship with temperature (Grace 1988). Peak photosynthetic rate was observed at suboptimal temperatures (22°C) in chickpea under controlled environments (Singh *et al*. 1982). At Hissar in north India, the net photosynthetic rate at 25°C was linearly related to photon flux density and reduced at ≥28°C (Singh *et al*. 1987). Singh *et al*. (1987) also reported that transpiration efficiency (photosynthesis/transpiration) of chickpea decreases with increasing temperature. Photosynthetic rates are higher during 50% flowering to pod formation than the vegetative stage in chickpea. Photosynthetic duration is controlled by the requirement of assimilates in the growing organs (e.g. leaves) and the reproductive organs (e.g. pods) (Singh *et al*. 1987) and also by the environment.

Membrane stability of leaf tissue can be used as another physiological indicator of heat stress, and is determined by electrolyte leakage measured as electrical conductivity (Stoddard *et al*. 2006). Genotypic variation for heat tolerance in chickpea was evaluated during vegetative, flowering and pod-filling stages by testing cell membrane thermostability (using electrolyte leakage). The chickpea lines Annigeri, ILC 482 and ICCV 10 were more thermostable at 45°C than K 850 and injury decreased with crop development (Srinivasan *et al*. 1996). However, there is no evidence of a relationship between cellular integrity under heat stress and grain yield. Tongden *et al*. (2006) used cell membrane stability as a screening technique at the seedling stage of chickpea to identify heat-tolerant and sensitive cultivars.

The plant is unlikely to show any significant yield difference due to short duration (acute) heat stress and distinguishing genotypes may be difficult. Under such situations, testing

Table 1. Summary of findings on the effect of high temperature on germination, growth and development and flowering of chickpea

Crop stage	Optimum temperature	Detrimental high temperature	References
		Germination	
Soil temperature	15–34°C	≥35°C	Singh and Dhaliwal (1972)
Air temperature	31.8–33°C	≥35°C	Covell *et al.* (1986)
		Growth and development	
Seedling growth	20–24°C	≥28°C	Sivaprasad and Sundrasarma (1987)
Leaf growth	10–25°C	≥27°C	Khanna-Chopra and Sinha (1987)
Early growth	20–26°C	≥27°C	van der Maesen (1972)
		Flowering	
In vitro pollen germination	25°C	35°C	Jaiwal and Mehta (1983)
In vitro pollen tube growth	25°C	45°C	Jaiwal and Mehta (1983)
Flowering and pod development	20–26°C	≥30°C	Summerfield *et al.* (1980)

membrane stability and photosynthesis may be more suitable screening techniques if they can be linked with injury to tissue or physiological process.

The rate of assimilate partitioning and leaf senescence are important physiological responses that influence pod set and yield. Carbohydrates (accumulated at the time of photosynthesis) supplied to the reproductive organs (e.g. flowers and pods) directly influence grain filling (Hendrix 2001). The rapid growth and development of reproductive organs arises through partitioning of a large proportion of the net-accumulated biomass from leaves under heat stress (Evans 1993). However, there are limited physiological studies on chickpea heat tolerance and the interaction between germplasm and environments.

In general, the success of heat screening physiological techniques depends on the frequency of heat stress in the field and the relevance of managed screening techniques to the target environment (Wery *et al*. 1994). Limited screening techniques have been developed for heat tolerance in chickpea (Singh *et al*. 1994) because significant genotypic × environmental interaction and differences in phenology make screening difficult (Wery *et al*. 1994). Hence, the improvement of heat tolerance in chickpea is dependent upon access to reliable and accurate phenotyping procedures.

Effect of heat stress on nitrogen fixation

High temperatures affect nitrogen fixation and symbiosis in chickpea (Rodrigues *et al*. 2006). Generally, high temperature reduces nodule formation, impairs nodule function and affects nodule structure (Roughley 1970; Kurdali 1996). Detrimental effect on nodule formation and nitrogen fixation efficiency of chickpea was observed in continuous warm days of 30/18°C day/night temperatures (Minchin *et al*. 1980). Slightly increased day temperature (32.5°C) delayed nodulation, decreased total plant nitrogen fixation and longevity of the symbiotically active nodule population (Rawsthorne *et al*. 1985). Nodules were not formed at >32°C soil temperature and recovery of nitrogenase activity failed after plant roots were exposed to 35°C. The optimum soil temperatures for chickpea growth lie between 18 and 22°C for nodulation and nitrogen fixation (Dart *et al*. 1975). When the chickpea cultivar ILC 482 was inoculated with *Rhizobium leguminosarum* L., strain CP 37A, the initial growth rate was encouraged at 40/25°C under controlled conditions (Laurie and Stewart 1993). However, the effect of heat stress during nitrogen fixation could vary in different genotypes (Summerfield *et al*. 1981). Thus, further investigation of heat stress and rhizobium culture in chickpea is needed.

Most nitrogen fixation in chickpea occurs during the vegetative phase (biomass accumulation) and declines after pod filling. Most of the spring-sown chickpea is exposed to warm temperature during flowering. But in south Asia (north, central and south India), the vegetative phase is subjected to high maximum temperature of 31–33°C (Berger *et al*. 2011). From the available data, it is clear that temperature >30°C has detrimental effect on nitrogen fixation. Therefore, particular consideration is needed in these regions.

The heritability of nitrogen fixation traits, under heat stress may be important to obtaining higher, more sustainable yields in hot environments. However, most research of this nature has focussed on water stress and very little has been published on heat stress. There is a need for greater knowledge of plant physiological response to nitrogen fixation by different rhizobial strains under heat stress.

Adaptation mechanism

Chickpea performance over different environments under high temperature has been covered in the previous sections. The adaptive strategies to high temperature stress are classified into the following three groups (Wery *et al*. 1993).

Adaptation mechanisms of crop plants to high temperatures

1. Heat escape: plants can escape heat stress with early phenology. Though flower initiation is sensitive to rising temperature in chickpea (Toker and Canci 2006), early flowering and maturity is a heat escape mechanism (Toker *et al*. 2007) particularly in the Mediterranean spring-sown environments and south Indian germplasm (Berger *et al*. 2011).
2. Heat avoidance: leaf reflectance, reduction of non-photosynthetic energy intercepted by the canopy and transpiration are important physiological components of heat avoidance. Leaves play a vital role in heat avoidance by changing their orientation, transpiration rate and reflectance (Wery *et al*. 1993). The mechanism of heat avoidance has not been studied in chickpea and screening germplasm for heat avoidance may lead to improve productivity in heat-stressed environments.
3. Heat tolerance: heat tolerance is linked to membrane stability, alteration of membrane lipid composition, accumulation of heat shock proteins and specific solutes (proline and glycine) particularly in pollen (Blum 1988). The role of protein functional properties (e.g. heat shock proteins) has not been studied in chickpea and their assessment may assist plant breeders in the development of heat-tolerant cultivars.

Strategies to improve breeding for heat tolerance in chickpea

Visual selection, selection for physiological traits linked to plant response to high temperature, empirical selection for yield and marker-assisted selection (MAS) are four important selection methods used to improve heat tolerance through breeding (Howarth 2005). However, the first step in the breeding process is identification of genetic diversity for economically important traits. Genetic diversity can be measured by quantifying variation in morphological characters that are targeted for selection for adaptation to heat stress. This approach has been used in south India (Krishnamurthy *et al*. 2011; Upadhyaya *et al*. 2011). Genetic diversity is also assessed using an eco-geographic approach to select chickpea germplasm for crossing (Berger 2007). In addition, new DNA-based fingerprinting technologies can be used to quantify the extent of diversity among potential parental lines (Lin *et al*. 2008).

The next step in the breeding process is selection of superior heat tolerant germplasm from the progeny of each cross. A suitable screening environment is essential. Some breeders use late planting to induce high levels of heat stress from anthesis through the grain-filling period (Krishnamurthy *et al*. 2011). Others use more sophisticated techniques such as field-based heat chambers or controlled environment chambers (Cottee *et al*. 2010). The primary consideration when choosing a screening method is relevance to the target environment. If quantitative trait loci (QTL) linked to superior heat tolerance has been identified then molecular markers associated with these QTL can be used at any time during the selection process to conserve these chromosomal regions in the progeny. While molecular markers for heat tolerance have been identified in rice (Xiao *et al*. 2011) and wheat (Al-Doss *et al*. 2010), there are currently no effective markers available in chickpea. Nevertheless, contrasting parents of chickpea for heat tolerance were crossed and used to develop recombinant inbred lines (Krishnamurthy *et al*. 2011), which will later be assessed for heat tolerance and QTL mapping.

Conclusions and presumption for the future

Although classification of heat responses of chickpea has been documented (Krishnamurthy *et al*. 2011; Upadhyaya *et al*. 2011), there has been little attempt to extrapolate these findings across the world's chickpea production areas. The determination of a heat response phenotype through screening is vital if the genetic control of heat tolerance in chickpea is to be understood and significant progress made through plant breeding. Clearly, the research under high temperature stress shows that early phenology is the most important mechanism and pod set the primary yield component to be considered in heat tolerance breeding. Overall, the heat stress can be studied using a holistic approach that integrates genetic and physiological characterisation of plant response to help define plant breeding targets. These combined approaches which include molecular tools and agronomic practices, will be pivotal to developing improved heat-tolerant chickpea cultivars. However, research gaps include:

- Development of simple screening methods to identify heat tolerance in chickpea genotypes relevant to the target environment,
- Determination of the physiological response of chickpea to heat stress across a range of concurrent factors such as moisture availability and evaporative demand and the underlying genetic control of these traits,
- Classification of genetic material to determine diversity groupings and establishment of genetic correlations between the traits linked to heat stress response,
- Identification of molecular markers linked to major QTL that explain a significant portion of the variation in heat tolerance.

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