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High Temperature Stress in Chickpea: Effects on Physiological Processes, Nitrogen Fixation, Pollination and Reproductive Growth

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Authors' contributions

This work was carried out in collaboration between all authors. All authors read and approved the final manuscript.

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ABSTRACT

Plants face various abiotic stresses such as drought, salinity, chilling, freezing, and high temperatures etc. during their lifespan. Chickpea (*Cicer arietinum* L.) is an important food legume crop and heat stress affects chickpea ontogeny over a range of environments. The crop often experiences abnormally high temperature (>35℃) during the reproductive stage. Heat stress at the reproductive stage is thus increasingly becoming a serious constraint to chickpea production in northern India due to climate change. Heat stress (≥ 35℃) during flowering and pod development results in severe yield losses due to the impact of high temperatures on different physiological processes. The most significant 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. This review describes the recent status of chickpea production, the effects of high temperature on chickpea, and the scopes for genetic improvement of chickpea to high-temperature tolerance. Recent field screening at ICRISAT has identified several heat tolerant germplasm, which can be used in successful breeding programs for improved heat tolerance in chickpea. It is observed that the detrimental effects of high temperature on membrane

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integrity, chlorophyll content, nitrogen-fixing ability, pollen and stigma function etc. are comparatively less in the tolerant genotypes than the sensitive ones. Therefore, identification and development of heat tolerant genotypes is an important aspect of chickpea breeding, especially in the aspect of the continuously changing global climate scenario.

Keywords: Chickpea; high-temperature stress; reproductive phase; genetic variation; tolerance.

1. INTRODUCTION

Chickpea (*Cicer arietinum* L.), commonly known as 'Bengal gram or garbanzo', is one of the world's most important grain legumes. This crop is a significant contributor to agricultural sustainability through nitrogen fixation and as a rotation crop allowing the diversification of agricultural production systems. India contributes a major share (64%) to the global chickpea production. India shares 90.75 lakh tones of chickpea production from an area of 95.39 lakh ha with the productivity of 951.36 kg/ha [1].

The production potential of chickpea is greatly constrained by high temperatures. Increases in air temperature, even by one degree above a threshold level, is considered heat stress in the plant. Temperature more than 32℃-35℃ for tropical and sub-tropical crops is considered high-temperature stress (Bita and Gerats, 2013); however, a daily maximum temperature above 25℃ is considered the upper threshold for heat stress in cool-season crops. The impact of heat stress varies with the intensity, duration of exposure, and the degree of the elevated temperature.

Plants have to interact with several abiotic stresses during its growth period. Among the abiotic stress, the high temperature is a major factor, associated with yield reduction. A minimum reduction of 53 kg/ha in the yield chickpea was noticed per 1˚C increase in mean seasonal temperature in India [2]. In case of late sown chickpea, this crop faces low temperature during sowing time and high temperature at the end of its cropping season. The low temperature at the initial stage of crop growth results in poor and slow vegetative growth whereas high temperature at the end of cropping season leads to forced maturity and problem of poor biomass (Chaturvedi and Dua, 2003). Heat stress at the reproductive stage is thus increasingly becoming a serious constraint to chickpea production in northern India due to climate change.

2. EFFECTS OF HIGH TEMPERATURE

High-temperature stress (HTS) alters several physiological and metabolic processes in cells. The vulnerability of plants to HTS differs according to developmental stage, but it affects both vegetative and reproductive phases to some extent. The level and extent of those effects are dependent on species and genotype [3] of plants.

2.1 Physiological Processes

High-temperature stress decreases leaf chlorophyll content. The loss of chlorophyll during high-temperature stress resulted in change in the chlorophyll a:b ratio due to premature leaf senescence. The degradation of chlorophyll molecules may be associated with the production of reactive oxygen species under high-temperature stress [4].

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

During sowing, high-temperature stress has direct impacts on crop germination and establishment. Reduced seed germination at high temperatures has been reported in many legumes including soybean [5], pea [6] Ren et al. [5], lentil [7], mungbean [8,9,10], and chickpea [11,12]. Chickpea seed germination decreases at supra-optimum temperatures. Covell et al. [13] observed that germination was faster in rate at higher temperatures between 31.8ºC and 33ºC. However, at high temperature, the mobilisation of cotyledon reserves and embryo growth are adversely affected. The germination percentage of chickpea was nil within the temperature range between 45ºC to 48ºC [14].

2.1.2 Photosynthesis

Photosynthetic rate and chlorophyll content of plants are two major physiological parameters. The direct effect of heat stress on photosynthesis includes photosystem II (PS II) in chickpea. High temperature stress hastens to damage of thylakoid membrane [15]. Peak photosynthetic rate was observed at sub-optimal temperatures (22ºC) under controlled environments [16]. At Hissar in north India, the net photosynthetic rate at 25˚C was in linear relation with photon flux density and reduced at ≥ 28˚C [17].

2.2 Effect of Heat Stress on Nitrogen Fixation

High temperatures affect nitrogen fixation and its symbiosis in chickpea [18]. High temperature induces reduction in nodule formation and impaired nodule function and affects nodule structure [19]. The detrimental effect on nodule formation and nitrogen fixation efficiency of chickpea was observed in simultaneous warm days of 30/18°C of day/night temperatures [20]. Slightly increased day temperature (32.5°C) delayed nodulation, decreased total plant nitrogen fixation and longevity of the symbiotically active nodule population [21].

However, the effect of heat stress on nitrogen fixation in chickpea has genotypic dependence [22]. Thus, further investigation of heat stress and *Rhizobium* culture in chickpea is utmost need. Most nitrogen fixation in chickpea occurs during the vegetative phase (biomass accumulation) and declines after pod filling [23]. In the spring season, chickpea sown is exposed to a warm temperature in most cases during flowering. But in South Asia (north, central and south India), the vegetative phase is subjected to a high temperature of 31˚C to 33˚C [24]. From the available data, it is clear that temperature above 30˚C is detrimental to 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 a hot environment. There is a need for greater knowledge of plant physiological response to nitrogen fixation by different rhizobial strains under heat stress [9].

2.3 Effect of High-temperature Stress on Developing Seeds

Seed filling, the ultimate stage of growth for any grain crop, It involves transport of constituents and biochemical related to the synthesis of carbohydrates, proteins and lipids in seeds [25,26]. Legumes are reported to be highly sensitive to abiotic stresses during pod and seed set phase [27,28]. The declined rate of leaf photosynthesis during seed filling stage in chickpea plants exposed to high-temperature stress are a major reason for reduced seed size with water shortage.

2.4 Effect of High-temperature Stress on Pollen and Anther Development/ Effect of Heat Stress on Reproductive Development and Yield

Heat stress above 30℃ from early meiosis to pollen maturity reduces the pollen viability in chickpea resulting in failure of fertilization that directly reduces seed set [29]. In chickpea, heat stress during the later growth period was found to produce more structural abnormalities in anthers and pollen grains such as changes in anther locule number, anther epidermis wall thickening and pollen sterility in high-temperature sensitive genotypes [10].

In flowering plants, the process of sexual reproduction which, in general, requires flowers producing male and female gametophytes, can be restricted because the formation of the male gametophyte is more sensitive to the growing environment [30,31]. Pollen tends to be more sensitive than the female gametophyte to HTS across plant species, including chickpea (*Cicer arietinum*) [32,33], rice [34], tomato (*Lycopersicon esculentum*) [35], and *Vigna unguiculata* [36].

High temperature stress affects reproductive development in legumes such as chickpea [33,37], mungbean [38,39], and lentil [40,41]. Reproductive growth's sensitivity to HTS includes effects such as depletion of buds, flowers, fruits, pods, and seeds, resulting in marked reductions in yield potential [42,29].

High temperature after flower opening decreases chickpea seed yield by reducing the number of seeds per plant and weight per seed [43]. In chickpea, Summerfield et al. [44] suggested that the longer exposure to reproductive development to a high day temperature of 35°C lowers the yield. Pod set in most chickpea genotypes fails when temperatures reach >35ºC [45]. High-temperature effects on pre-anthesis are related to the development of anther, pollen sterility and pollen production. Temperature stress at post-anthesis is associated with significant pod abortion and decreased grain filling.

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 to 34°C	≥ 35ºC	Singh and Dhaliwal [14]
Air temperature	31.8 to 33ºC	≥ 35ºC	Covell et al. [13]
Growth and development			
Seedling growth	20 to 24ºC	≥ 28ºC	Sivaprasad and Sundrasarma [46]
Leaf growth	10 to 25ºC	≥ 27ºC	Khanna-Chopra and Sinha [47]
Early growth	20 to 26ºC	≥ 27ºC	Van der Maesen [48]
Flowering			
In vitro Pollen germination	25 ºC	35 ºC	Jaiwal and Mehta [49]
In vitro Pollen tube growth	25 ºC	45 ºC	Jaiwal and Mehta [49]

Table 2. Effect of heat stress on both reproductive function, male and female reproductive tissue in some legume crops

Crop species	Temperature stress	Effects	Reference
Soybean	Above 35ºC	Flower abscission, reduced yield	Koti et al*.,* [50]; Salem et al*.,* [51]
	38/28ºC	Decreased *in-vitro* pollen germination	Djanaguiraman et al*.,* [52]
Cowpea	33/30ºC	Anther indehiscence due to degeneration of tapetal cells	Ahmed et al*.,* [36]
Common bean	33/29ºC	Degeneration of tapetal cells	Suzuki et al.,*[53]*
Chickpea	33/27ºC	Anther indehiscence and pollen sterility	Gross and Kigel, [54]
	35/20ºC	Lack of pollen germination and tube growth in style	Devasirvatham et al*.,* [55]
	32/26ºC	Abnormal embryo sac development	Polowick and Sawhney, [56,57]
	45/35ºC	Reduced stigma receptivity	Kumar et al*.,* [37]
	≥40/30ºC	Reproductive failure, reduced yield	Gaur et al*.,* [58]

3. BREEDING PROGRAMME FOR HIGH-TEMPERATURE STRESS TOLERANCE AND RECENT SUCCESSES IN INDIA AND ABROAD

Chickpea improvement is aimed to increase yield potential and regional adaptation through resistance and tolerance to abiotic and biotic stresses, plant type and grain characteristics. A simple but effective field screening technique for heat tolerance at the reproductive stage in chickpea has been developed at ICRISAT [58]. It involves advancing sowing date to synchronize the reproductive phase of the crop with the occurrence of higher temperatures (≥35°C). Eighteen heat tolerant chickpea genotypes were screened by Krishnamurthy et al. (2011) from southern and central Indian field trials. Short-duration, high-yielding, heat-tolerant genotypes were identified by Upadhyaya et al. (2011). Outside India, Kaloki (2010) identified ICCV 92318 as a source of heat tolerance in the semi-arid environments of Kenya through the African

Climate Change Breeding Program. Assessment of genetic diversity by using an eco-geographic approach broadens the opportunity to select chickpea germplasm for crossing [59].

4. CONCLUSION

High temperature above ≥35°C is detrimental to pollen fertility, *in vitro* pollen germination, and pollen tube growth, thus reducing subsequent pod set. High temperatures during pre-anthesis result in poor pollen fertility. Pollination is the most critical condition of flower development during chickpea under high temperature condition. Therefore, pre-anthesis and anthesis are the most sensitive stages to high temperature in chickpea. High temperature stresses result in grain yield loss of chickpea due to the failure of pod set. So, for screening of heat tolerance at reproductive stage in chickpea, pollen germination, pollen tube growth and per cent pod set can be employed. Although screening for tolerance to high-temperature stresses has identified many promising sources of tolerance in chickpea, but still, there has been little attempt to extrapolate these findings across the world's core chickpea production areas. Overall, the heat stress can be studied using an integrated approach that integrates genetic and physiological characterization of plant response to achieve plant breeding targets.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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