

We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,000

Open access books available

148,000

International authors and editors

185M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com



Chapter

Physiological Mechanisms of Tolerance to Drought and Heat in Major Pulses for Improving Yield under Stress Environments

Partha S. Basu, Sushil Kumar Chaturvedi, Pooran Mall Gaur, Biswajit Mondal, Surendra Kumar Meena, Krishnashis Das, Vaibhav Kumar, Kalpana Tewari and Kusum Sharma

Abstract

Reduction in biomass and pollen fertility are the two major constraints resulting in poor grain yield in major pulses grown under rainfed agrosystem. Generally, pulses are encountered into both heat and drought stresses during terminal reproductive stages. Though pulses have many adaptive features to counter the adverse effects of various abiotic stresses but yield is substantially reduced when the magnitude of these stresses is very high. The factors have been identified to enhance grain yield under stress environments which include promotion of biomass in the above ground part enabling crops to reserve a maximum amount of photosynthesis and water in the plant system itself before the onset of drought and heat stresses during reproductive stages. Various physiological mechanisms and fertility enhancement components including genetic diversity in key traits have been discussed here to improve yield of pulses under stressed conditions.

Keywords: pollen fertility, root, antioxidant, osmotic adjustment, photosynthesis, remobilization, chlorophyll fluorescence, pod

1. Introduction

The earth's climate system is experiencing a warmer phase. Increase in temperature and atmospheric CO₂ concentration are the major effects of climate, besides increase or decrease in the local rainfall. The climate modeling systems envisage that as the twenty-first century progresses, there will be rise in temperature from 2 to 6°C. Rainfed agriculture accounts for more than 40% of total food grain production, and nearly 90% of it is occupied by cultivation of pulses. Thus, country like India which is a major producer and consumer of pulses, there are about 100 million hectare cultivated areas dependent on rainfall. In general, crop productivity is adversely affected by high temperature and drought [1]. The rise in global mean temperature

and drought has affected agricultural productivity worldwide [2]. According to IPCC (2013), decreasing water availability and increasing temperature are posing a great threat to food security. Therefore, it is an urgent need to identify tolerant plant species for these stresses [3]. The pulses or food legumes are rainfed crops grown under diverse soil types and agro-ecosystems in low rainfall areas of semi-arid regions including India, Pakistan, Bangladesh, Myanmar, and Nepal. The pulses find an extremely important place in the agricultural system as they require less chemical fertilizers and limited moisture. The legumes or pulse crops include chick pea (*Cicer arietinum* L.), pigeon pea (*Cajanus cajan* L.), green gram (*Vigna radiata* L.), black gram (*Vigna mungo* L.), lentil (*Lens culinaris* L.), as major pulse crops (**Figure 1**) while field pea (*Pisum sativum* L.), kidney bean or rajmash (*Phaseolus vulgaris* L.), lathyrus, cowpea, horsegram, etc. are considered as minor pulses because of their lesser consumption by people. These pulses are broadly categorized into cool-season legumes constituting chick pea, lentil, field pea, rajmash, and lathyrus while warm-season legumes include pigeon pea, green gram, black gram, cowpea, horsegram, etc. The pulse seeds have high nutritive values with a low glycemic index comprising of approximately 18–30% protein which varies among legume species. The pulses also supplement essential amino acids, resistant starches, complex oligosaccharides, fibers, minerals, vitamins, phenolics, tannins, phytic acids, antioxidants, and folic acids which have enormous health benefits [4]. Additionally, pulses improve soil health by contributing soil nitrogen through fixing atmospheric nitrogen by a symbiotic association of N_2 fixing *Rhizobium* in their root nodules and host a number

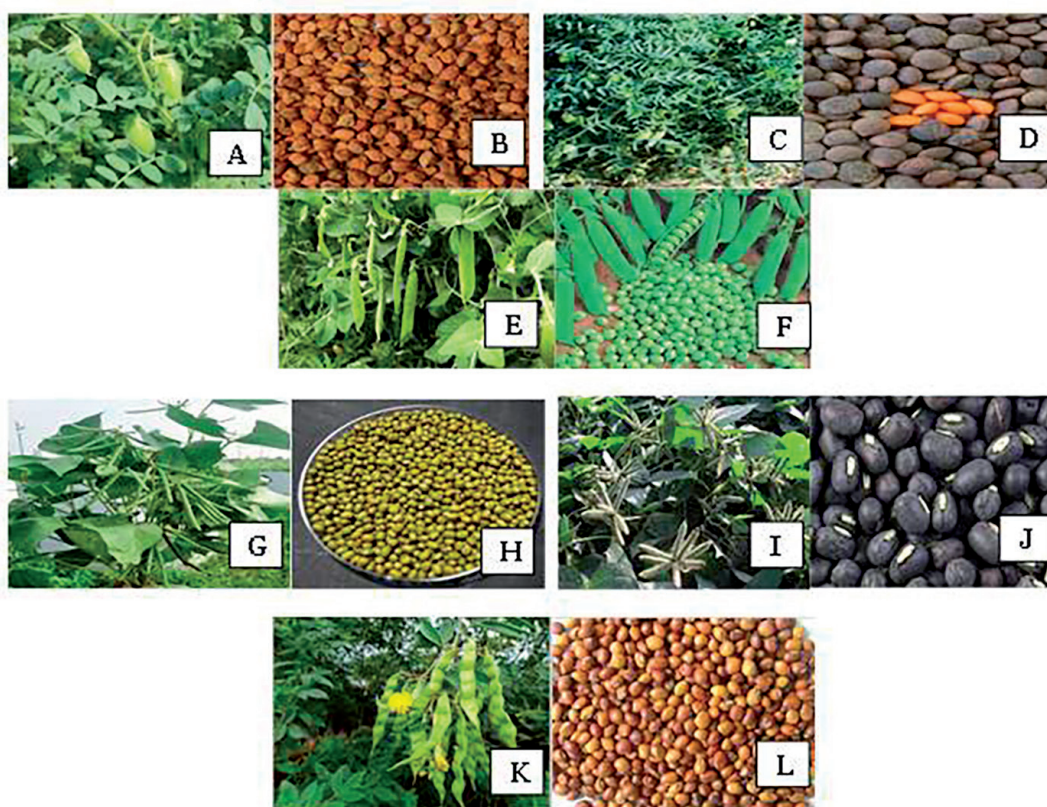


Figure 1.

Major pulses of cool season (A–F). Chick pea leaf with pods (A), chickpea seeds (B); lentil leaf with pods (C), lentil seeds (D); field pea leaf bearing pods (E), field pea seeds (F); major pulses of summer season (G–L). Green gram leaf with podding cluster (G), green gram seeds (H); black gram leaf with podding clusters (I), black gram seeds (J); pigeon pea leaf with pods (K), pigeon pea seeds (L).

of beneficial microbes in their rhizosphere such as phosphate solubilizing bacteria (PSB) that solubilize insoluble phosphates in the soil. They are hardy crops thriving well with their vigorous root system and have strong ability to proliferate root system into the deep soil layers. Keeping in view of the growing demand, additional lands are required for expanding the areas of cultivation of pulses. The productivity of pulses had been always low as they are threatened by great challenges of climatic aberrations such as drought, heat, salinity, frost, and cold. Among several abiotic stresses, drought and heat are considered to be the major yield limiting factor followed by unprecedented high temperature during the reproductive phase [5, 6]. High temperature stress affects various physiological processes and alters the plant-water relationship [7]. The rise in temperature beyond 35°C may cause irreversible damage to growth and development of plants [8]. It is therefore imperative to analyze critically the implications of climate change on pulses. There are several knowledge gaps in our understanding toward low productivity of pulses particularly when drought and heat are combinedly imposed on crops [9]. Efforts are needed to make pulses more climate-resilient and productive [10]. Our current understanding is not sufficient to counter the challenges imposed by climate adversities [11]. Therefore, systematic approaches are to be taken to hit the primary targets of achieving higher productivity with limited resources and sustain our ecosystem, soil health, protecting environment keeping in view of the fact that pulses play a central role in sustaining our agro-ecosystem under the climate change scenario.

2. Effects of major abiotic stresses on pulses

2.1 Drought

Yield reduction in pulses has been directly correlated with the intensity of drought [5]. Among rainfed pulses, *Vigna* species green gram and black gram being warm season crops require four irrigations till crop maturity. Sources of drought tolerance in *Vigna* crops are very rare, though green gram is relatively better adapted to warm climates. The highest yield reduction was observed during the reproductive stage of many pulses. However, yield reduction in pigeon pea under drought was relatively lower than that of lentils, groundnut, cowpea, and green gram. In extra-short-duration pigeon pea, the impact of drought stress is evident at the vegetative, flowering, and pod-filling stages [12]. The germination and seedling growth, seedling vigor, hypocotyl length is adversely affected by drought stress in pigeon pea. Tolerance to drought in short-duration pigeon pea has been ascribed to the crop's ability to maintain total dry matter, a small pod size, few seeds in the pod, high seed mass, and low flowering synchronization [13]. The important mechanisms of drought tolerance in pigeon pea were included with high root resistance to water flow; slow shoot development; limited initial root development at depth; partitioning of assimilates into vegetative parts; leaflet movement during water stress; dehydration tolerance; and osmotic adjustment [14]. The lethal leaf water potential, i.e. the lowest water potential experienced by the last viable leaf, was a key measure of dehydration tolerance. The pigeon pea has more dehydration tolerance than others. The ability of cells to continue metabolism at low leaf water status is termed dehydration tolerance [15]. Membrane disorder is often measured as a leakage of solutes from the cell [16]. Water status parameters like relative water content may be a good indicator of drought tolerance in pigeon pea under semi-arid conditions [17]. Accumulation of proline in

cell in response to water deficit is another mechanism protecting protein structures as cell dehydrate, and as an organic nitrogen source. The relative drought tolerance in a range of pulses is based upon the physiological traits such as osmotic adjustment, root system, and lethal leaf water potential. Thus, the order of drought tolerance in different pulses could be Pigeon pea > chick pea > lentil > black gram > green gram.

2.2 High temperature

High temperature results in an overall reduction in plant growth including roots, leaf area, and dry weight [18]. It has been predicted that an average 1°C increase will reduce yield by at least 3–4% in many crops [19]. The average surface temperatures are expected to rise by 3–5°C by the end of this century, posing a major threat to the production of many food crops including legumes worldwide, especially in the semi-arid tropics [20]. Moreover, increase in temperature will have more adverse effects on cool-season pulse crops (e.g. chick pea, lentil, and field pea) than the summer and rainy-season crops like green gram, black gram, and pigeon pea [21]. A temperature increase of 1–2°C above the threshold level is sufficient to reduce yield in many leguminous crops such as cowpea [22], groundnut [23], common bean [24], lentil [25], and chick pea [26, 27]. Heat stress causes considerable reduction in biomass production and grain yield in several crops [28]. A rise in temperature may limit the development of various yield components [29]. The majority of the food legumes including chick pea, lentil, pigeon pea, green gram, and black gram are grown by developing countries of south Asia under rainfed situation. They are often heavily influenced by climate variables. Crops grown at lower latitudes are often exposed to high temperatures above 40°C. Grain yield reduction in heat stress has been reported to be associated with a decrease in photosynthetic capacity because of altered membrane stability [30, 31] and enhanced maintenance respiration [32] along with a reduction in radiation-use efficiency. Photosynthesis is the most sensitive physiological process impaired by heat stress [33] which could be due to structural and functional disruptions of chloroplasts, reduction of chlorophyll, inactivation of chloroplast enzymes [34], or both stomatal and nonstomatal limitations [8]. High temperatures adversely affect starch and sucrose synthesis through a reduction in the activity of sucrose phosphate synthase and ADP-glucose pyrophosphorylase [35]. Crops exposed to high temperature are often subjected to oxidative stress-producing reactive oxygen species (ROS), which are highly toxic to cellular functions in plants because they damage nucleic acids and cause protein oxidation and lipid peroxidation; this oxidative damage eventually causes cell death [36, 37]. ROS toxicity during various stresses is considered to be one of the major causes of low crop productivity worldwide [38]. An increase in the activity of antioxidant enzymes, such as guaiacol peroxidase (GPX) and catalase (CAT), plays a significant role in minimizing the toxic effects of stress-induced ROS production [39]. High temperatures adversely affect nitrogen fixation in chick pea [40]. Increased day temperatures ranging from 32 to 35°C have shown reduction in nodule formation and nitrogen fixation in chick pea (**Figure 2**). It has been reported that high temperature delays nodulation, retards nitrogen fixation, and impairs nodule function and structure in chick pea [41–43].

2.2.1 Effect of high temperature on reproductive and seed development in pulses

The reproductive phase of major pulses is highly sensitive to temperature extremes [44]. High temperature inhibits flower set and flower retention, impair the

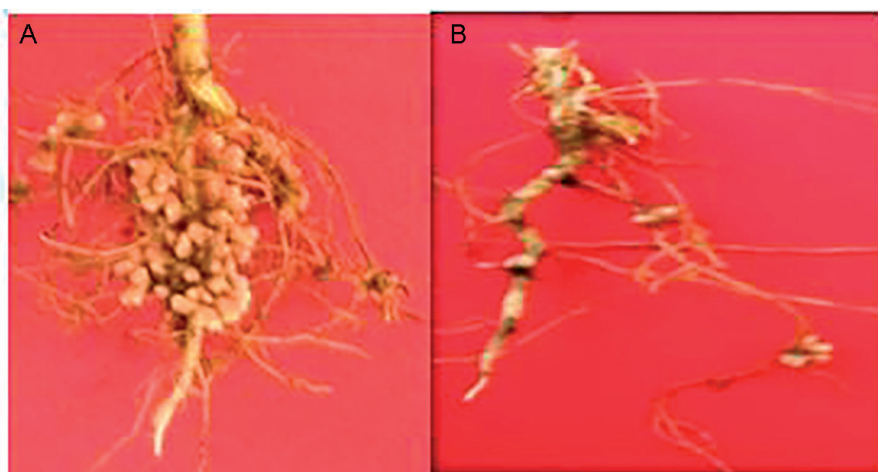


Figure 2.
Effect of high temperature on chick pea cv K 850 nodulation. (A) Normal sown chickpea nodule (25/15°C max/min), (B) late sown chick pea nodule (40/27°C max/min).

normal development of male and female gametophytes leading to ovule abortion, reduce pod settings, and impair grain filling which eventually results in significant yield loss. Several reports have indicated that heat stress caused reproductive failure due to impaired sucrose metabolism in the leaves, developing grains, and inhibition of sucrose transporters those results in decreased carbon-source to the anthers and developing pollen grains [45]. The heat stress results in drastic yield losses due to the decline of relative tissue water content (RWC) and leaf water potential (LWP) [46] pollen or ovule inactivity, flower abortion, and postfertilization impaired the growth and development of embryos or seeds in many pulses [47]. Ultrastructural studies revealed that pollen sterility could be due to degenerated tapetum owing to heat stress [48]. Temperature extremities have specifically detrimental effects on male gametophyte causing disrupted meiosis, tapetal hypertrophy, stunted development of pollen grains, anther protein degradation, pollen sterility, and pollen tube deformation [49] while heat stress adversely affects female gametophyte causing reduced size of style and ovary, disrupted meiosis, reduced stigma receptivity, callose deposits in style, damaged embryo sac components, and fertilization arrest. Flowering is either early or delayed, flowers abscised and become distorted and shedding occurs. Grain-filling process is impaired due to altered source-sink relations which lead to seed abortion and yield loss. However, the relative heat sensitivity varies for different crops [50]. High temperatures reduce yield and yield attributes such as dry matter accumulation and partitioning [51], pod set, pod weight, and harvest index in snap beans [52]. Temperatures above 40°C resulted in reduced pod set, seed production, and yield in soybean [53]. The water scarcity in floral parts and leaves due to high temperature driven increased transpiration causes heavy yield losses in snap bean (*P. vulgaris*) [54]. High temperature also adversely affects pollen germination and pollen tube growth. In cool-season legume lentils, pollen germination and pollen tube growth have been found to be retarded above 35°C [55]. Stressful temperatures often lead to impaired microsporogenesis and megasporogenesis at the pre-fertilization stage in various legumes such as chick pea (*C. arietinum*) [56]; and *P. vulgaris* [48, 57]. Loss of pollen viability and pollen germination have been reported at high temperatures in *C. arietinum* [58]; and *P. vulgaris* [57]; *Arachis hypogea* [59], loss of stigma receptivity, loss of ovule viability and flower abscission in *C. arietinum* [58]; *P. vulgaris*: [48]. Most of the pulse crops such as chick pea and lentil are sensitive to heat stress when

day temperature exceeds above 35°C resulting in reduced pollen germination, and decreased pod number and seed size. Arrest of fertilization and reduced embryogenesis have been reported at extreme temperatures in chick pea [60] and *Glycine max* [61]. The pigeon pea often experiences high temperature during the reproductive phase which results in pollen sterility, retards germination and pollen load on stigma, reducing the pollen receptivity on stigma and length of pollen tubes [58]. Consequently, heat stress has detrimental effects on both microsporogenesis and megasporogenesis causing incomplete cell division and eventually loss of viability of pollens and ovules [45]. Failure of anthesis would be a likely cause of flower abscission and also discontinuity of sustained photoassimilate mobilization to the developing grains results in pod abortion [62]. Identifying mechanisms of reproductive temperature tolerance in various legumes could be achieved through screening diversified germplasm available in gene banks. Warm-season legumes such as green gram, pigeon pea, black gram, and cowpea, though having higher temperature tolerance limits, are also affected negatively leading to a reduction in pod set in response to moderately-high night temperatures [63]. Thus, various legumes are sensitive to temperature extremities to different degrees from the vegetative to reproductive stage, resulting in metabolic and reproductive dysfunction and finally result in low yields.

2.3 Effect of combined stresses of drought and heat

There is a need to identify the tolerance mechanism of pulses in response to simultaneously occurring heat and drought stresses [64]. It is considered that the demand of water will proportionately increase with rise in temperature due to increase in soil-plant evapotranspiration water loss. To improve pulses for dual tolerance, traits that confer the tolerance to both heat and drought must be studied. The photosynthetic electron transport rate has been drastically declined when drought and heat superimposed simultaneously in chick pea. A high irradiance level had been found to be more deleterious for photosynthesis in chick pea under combined drought and heat stresses; however, genotypic variation was evident in light response of photosynthesis when different chick pea genotypes were subjected to combined stress (**Figure 3**). Similarly, it is urgently needed to inherit combined tolerance in pulses also. When both high temperature and drought stresses are superimposed, their combined effects are more detrimental and negative. The combined effects could be deleterious additive effects on phenology, growth, chlorophyll content, photosynthesis, grain number, fertility, grain-filling duration, and grain yield in several crops [65]. For example, the combined drought and heat stresses decrease leaf chlorophyll content by 49% while drought or heat alone reduce it by 9% or 27%, respectively [66]. Reproductive stages are more sensitive to combined heat and drought stresses than individual ones [1]. However, in some ways, drought and heat stresses are interlinked. Both the stresses significantly reduce photosynthetic efficiency, stomatal conductance, leaf area, and water-use efficiency in many crops, e.g. wheat, rice, chick pea [67]. Heat stress increases evapotranspiration from soil and plant canopy that leads to a disruption of water relations and plants often are succumbed to drought stress driven by high temperatures [68]. Crops may respond to drought and heat stresses individually or combinedly in a different manner [69] which eventually lead to yield reduction. Pigeon pea, chick pea, lentil, and field pea are often exposed to drought and high temperatures simultaneously particularly during reproductive stages [6]. The basic physiological mechanisms of tolerance to drought and heat may differ or be common with respect to some traits. For example, reduction of photosynthesis is a common

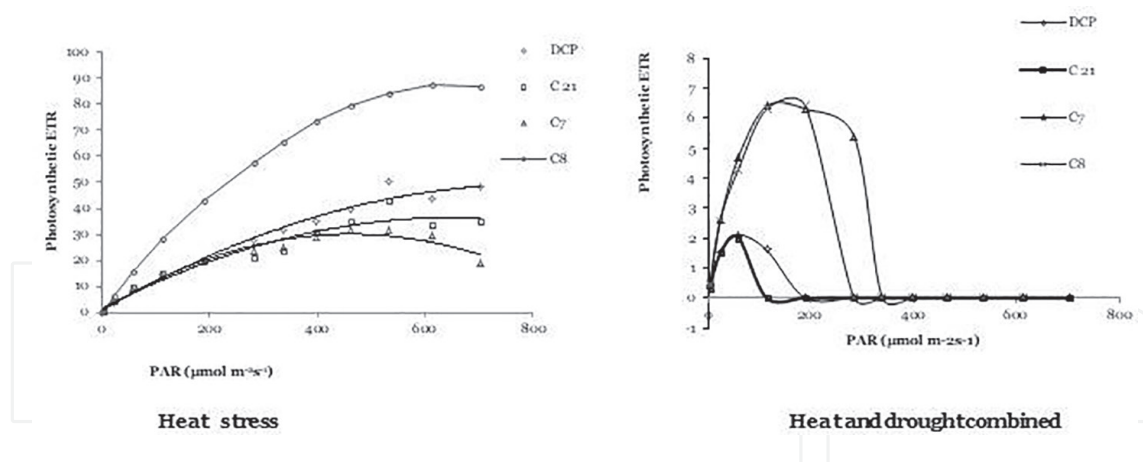


Figure 3.
 Genotypic variation in the light response of different chick pea genotypes under combined stress of drought and heat.

phenomenon under drought and heat; however, photosynthetic inhibition due to drought is largely attributed by stomatal closure, reduced biomass production, and decreased leaf size. Drought limits gaseous exchange by triggering stomatal closure and in this way modifies plant-water relations whereas heat stress inhibits photosynthetic electron transport and PSII activity, conformational changes in thylakoid proteins, and distortion of membranes, and alters Rubisco enzyme and change in the solubility of CO₂ and O₂ inside mesophyll cells. Heat stress has detrimental effects on reproductive parts such as microsporogenesis and megasporogenesis of male and female gametophytes, loss of pollen viability and retards pollen germination and pollen tube growth, decreased stigma receptivity and pollen load on stigma, cell division, and accelerated rates of respiration and inhibition of carbohydrate metabolism in developing grains. However, there are common tolerance or avoidance mechanisms against both heat and drought stresses such as generation of harmful reactive oxygen species (ROS) and to counteract the deleterious effects of ROS, both the stresses are induced to produce antioxidative enzyme complex that enables scavenging of superoxide radicals being generated when plants are exposed to high temperatures in combination with drought and heat. Several heat shock proteins (HSPs) are expressed in response to high temperatures that helps to protect the membrane and vital molecules from denaturation and allows cellular machinery to operate normally. Both heat and drought stresses adversely affect water relation characteristics of plant which include decline in leaf RWC, water potential, osmotic, and turgor potential.

3. Response of major food legumes to abiotic stresses

3.1 Cool-season legumes

3.1.1 Chick pea

Chick pea (*C. arietinum* L.) is the second largest grown food legume of the world after beans. India, Australia, Pakistan, Turkey, Myanmar, Ethiopia, Iran, Mexico, Canada, and USA are the major chick pea producing countries. Chick pea is a good source of protein (20–22%) and rich in carbohydrates (~60%) [70], dietary fiber, and minerals [71]. The demand of chick pea is increasing keeping in view of its enormous

health benefits which include prevention of cardiovascular diseases, type 2 diabetes, digestive diseases, and even cancer [72]. Chick pea fixes atmospheric nitrogen through symbiotic nitrogen fixer rhizobium resulting in lesser dependence on chemical fertilizers and residual nitrogen left in the soil after harvest benefits the subsequent crops. Drought and heat are the major abiotic stresses and constraints limiting chick pea production globally which together account for about 50% of the yield losses [73]. Chick pea is largely grown under rainfed on residual soil moisture after withdrawal of monsoon. The crop often experiences terminal drought if winter rain fails and the soil moisture starts receding and reaching below to a critical level at grain-filling stages causing heavy yield losses primarily due to water limitation. Exposure to heat stress ($\geq 35^{\circ}\text{C}$) at flowering and podding in chick pea results in drastic reductions in seed yields [74]. High temperature adversely affects seed germination, photosynthesis, respiration, membrane stability, fertilization, fruit maturation, quality of seeds, nutrient absorption, protoplasmic movement, transport of materials and also modulated levels of hormones, and primary and secondary metabolites [8, 75]. It has been observed that lower grain yields with greater exposure to hot days ($30\text{--}35^{\circ}\text{C}$), during the reproductive period [7]. Heat stress at reproductive stages is thus increasingly becoming a serious constraint to chick pea production due to climate change. The optimal temperatures for chick pea growth range between 15°C and 30°C [76].

3.1.2 Lentil

Lentil (*Lens culinaris* Medik) is another cool-season food legume grown widely and consumed for edible purposes and intensifying the cereal-based cropping systems. Lentil often experiences high temperatures ($>35^{\circ}\text{C}$) during flowering and pod filling stages, which leads to forced maturity and consequently affects seed yield and quality [77]. The delayed sowing of lentil coincides with terminal heat stress. Consequently, a large portion of cultivated areas (~ 11.7 million ha) in India remains fallow after the late harvest of rice [78]. In Australia, $\sim 70\%$ yield losses in lentil were observed due to a 6-day heat wave with a maximum temperature of 35°C or above [77]. In recent years, heat stress as a result of global warming has become a major challenge to crop production and productivity in general [79]. Development of heat-tolerant lentil cultivars is required to sustain production and productivity of lentil for semi-arid regions. These issues could be addressed by distinguishing the heat-tolerant and sensitive lentil genotypes at critical temperature [80]. Thus, identification of key physiological traits that impart heat tolerance can help to facilitate a breeding program for developing heat-tolerant lentil cultivars, leading to a reduction the yield losses under a changing climate scenario [81]. High and low temperatures cause photo damage to PSII [82] which could be due to damage of proteins that are involved in a photo damage-repair cycle [83]. However, cyclic electron transport around PSII constitutes an effective protective mechanism against photo-inhibitory damage [83], and some phenolic compounds have been identified in this protection [84]. In lentil, pollen and leaf traits could also be helpful in identifying heat-tolerant genotypes [47].

3.2 Warm-season legumes

3.2.1 Pigeon pea

Pigeon pea (*C. cajan* L.) Millsp. is a major grain legume of the arid and semi-arid regions of the world [85]. Drought and high temperature during the reproductive

stage are becoming a recurrent phenomenon in these regions resulting in significant yield loss in pigeon pea. Among pulses, pigeon pea is the hardiest crop which is cultivated in a wide range of climatic conditions from tropics to subtropics between 30°N and 30°S latitude. It is well adapted to semi-arid, arid, and marginalized regions receiving even less than 600 mm rainfall. This crop even tolerates as high as a temperature of 35°C if soil moisture is optimally available. Among pulses, the pigeon pea is an inherently drought and heat-tolerant crop to some extent [86]. High temperature leads to excessive water loss from crop canopy and soil through increased evapotranspiration. The decrease in soil moisture below a certain threshold level and the rise of temperature exceeding 35°C or more during the grain-filling stage often lead to poor yield in pigeon pea [87]. The high temperature causes oxidative damage, affects cell division, and may cause severe damage to the membranes and proteins and their synthesis, along with inactivation of major enzymes [88]. Even exposure to the high temperature for a shorter period during the seed filling can result in accelerated filling and eventually it results in incomplete grain development, poor quality, and reduction in the yield. High temperature beyond 35°C often leads to flower shedding, pod abortion, and incomplete grain development, inhibits photosynthesis [89] with increased respiration which cumulatively imbalance the source-sink relation [6]. Drought tolerance in pigeon pea is due to its deep-rooting tap root reaching up to 6 feet (2 m) in depth that helps to improve water infiltration into the deep soil [90]. Inherent drought tolerance in pigeon pea could be associated with the prolific root system with a higher number of thin lateral roots, higher hydraulic resistance to restrict flow of water or tends to conserve available water more efficiently, smaller but high stomatal density that regulates transpiration water loss to minimum level but maintain photosynthesis with lower order but not completely inhibited. Among all legumes, drought tolerance characters of pigeon pea also involve high osmotic adjustment and very low (more negative) lethal leaf water potential indicating a higher degree of dehydration postponement and dehydration tolerance. Genes expressing heat shock proteins (HSPs), dehydration responsive element-binding DREB, and cyclophilin have been found to be responsive to combined stresses of drought and heat in pigeon pea [91, 92]. Signaling effects of abscisic acid and reactive oxygen species (ROS), calcium, calcium-regulated proteins have been well characterized for their role in signal transmission under stress [93].

3.2.2 *Black gram or urdbean*

Black gram (*V. mungo* L. Hepper) is a popular food legume grown in many Asian countries including India, Pakistan, Myanmar, Bangladesh, Thailand, and China. India is the largest producer and consumer of black gram. It is a warm-season food legume, which requires 25–35°C temperature along with a high humidity for its normal growth and development. However, prevailing high temperature (>40°C) during flowering results in deformation of flower parts or flower drop leading to negative impact on yield. Nutritionally, urdbean is dense with protein (21–28%), dietary fiber (161–187 g/kg), iron (16–255 mg/kg), zinc (5–134 mg/kg), and other micronutrients like other pulses [94]. Urdbean is grown in different ecological conditions and seasons across the growing regions. In India, it is grown mainly in the rainy season (July-October) and in the southern part it is also cultivated as a winter season crop (November-February). However, its cultivation is not wide in the summer season due to excessive heat stress and a lack of humidity in the atmosphere. Thus, availability of heat-tolerant cultivars can bring more areas under urdbean cultivation. Urdbean is a close relative of mungbean, which is

extensively cultivated in identical ecological conditions. In this crop as well as in another *Vigna* pulse crop, e.g. cowpea, sources of heat tolerance have already been identified [49]. Knowledge of genetics underlying key traits imparting heat tolerance helps the breeder to make genetic improvements more precisely. In recent years, molecular markers helped to decipher the genetics of complex key morpho-physiological traits imparting heat tolerance in several crops [95].

3.2.3 *Green gram or mungbean*

Among all food legumes, green gram (*V. radiata* L. Wilczek), also known as mungbean, contains high amount of easily digestible seed proteins ranging between 24 and 28% which is higher than chick pea, lentil, and pigeon pea. The crop is grown during summer or rainy season and thrives most effectively at temperatures between 30°C and 40°C; however, significant flower shedding occurs at temperatures beyond 40°C [47]. It has been reported that the abscission of reproductive organs is the primary determinant of yield under heat stress in mungbean [24]. This is a short duration crop with a yield potential of about 1200–1500 kg/ha. During the reproductive stage, high temperatures cause flower drop, induce male sterility, impair anthesis, and shorten the grain-filling period. The productivity and adaptability of mungbean are seriously affected by a range of abiotic stresses including heat and drought. In mungbean, high temperature increases flower shedding [96] pollen sterility and dehiscence of anthers [22]. Being a summer crop, it is often exposed to temperature exceeding 40°C resulting in high turnover of sterile pollens, infertility, and flower abortion, and grain filling is adversely affected. High night temperature also affects grain filling and carbon partitioning. Further increase in the day maximum temperature to 44°C or above causes production of smaller and hard seeds. The pollen viability and germination were extremely sensitive to high temperature (>40°C) in mungbean, though a wide genotypic variation in the pollen germinability was observed. Seed size reduces; however, a majority of genotypes had reduced, shriveled, or deformed grains at high temperatures exceeding 40°C. The critical temperature range for damage of reproductive organs was found somewhere in between 40 and 45°C; however, sensitivity varied among genotypes. Earlier reports suggest that brief exposure of plants to high temperatures during seed filling accelerates senescence, diminishes seed set and seed weight, and reduces yield [97]. In mungbean, remobilization of pre-anthesis reserve carbohydrates and nitrogen in leaves, podwall, and stems contribute significantly towards grain filling. In the changing scenario of climate, sudden rise in the temperature beyond 35°C causes increase in the respiration rates and unusually high degradation of stored starch as major chloroplasts carbon source was observed. As a result, failure to set pods, reduced or incomplete grain development at high temperature could be partly due to inadequate supply of carbon and nitrogen from leaves or by decrease in the activity of sucrose synthase, the key enzyme playing a crucial role in grain development. Poor partitioning of carbon and nitrogen at high temperature leads to low harvest index and low productivity in mungbean. The productivity and adaptability of green gram are adversely affected by several abiotic stresses including heat, drought, salinity, and water-logging, which affect crop growth and development by altering physiological processes and the plant-water relationship [98]. Several studies have reported a reduction in the growth and development of legumes because of high-temperature stress [99].

4. Mechanism of drought and heat tolerance in pulses

Knowledge of key traits imparting heat and drought tolerance can help to improve the grain yield of food legumes [81]. Therefore, understanding of physio-biochemical mechanisms associated with these key traits imparting tolerance is essential for large-scale phenotyping of pulse germplasm under both field and controlled conditions [100]. In several crops, various physiological and biochemical traits such as accumulation of phenolic compounds, organic acids, photosynthetic activity, water-use efficiency, canopy temperature, rooting length, osmotic adjustment, membrane stability, and pollen viability [47, 101] have been used to identify heat and drought tolerant genotypes and a significant genetic variability has been reported for key physiological traits under stress conditions [102].

Under rainfed or water-limiting regions, pulses experience drought, heat stress, or both at the terminal end that is at the reproductive stage. There is enough scope to improve grain yield in pulses when drought or heat appears particularly during reproductive or grain-filling stages. This type of terminal stresses is better defined as there was no moisture limitation at initial growth stages or temperature remains conducive to support normal physiological activities. The crop productivity is largely determined by initial crop vigor, biomass, number of podding nodes, water retention capacity in the tissue through regulated ways of gaseous exchange making a balance between photosynthetic carbon gain and minimum water loss through transpiration. However, if drought or heat during germination or intermittent drought accompanied by unusual temperature prevails at initial growth stages, it could be more detrimental for the crop to cope up the situation even most tolerant species introduced under such conditions. Therefore, drought or heat tolerance in pulses is practically limited to the conditions when they appear at the later or terminal end of the crop. There are two types of mechanisms that are operating in pulses toward improving yield in pulses under terminal drought or heat. One of the important requirements of the plant is to avoid terminal stresses or to develop a mechanism to postpone dehydration with depletion of soil moisture. Another strategy is to develop cellular resistances to counter the stresses such as stable membrane system, higher water-use efficiency, efficient photosynthetic system, expression of heat shock proteins, etc. Different models have been proposed for drought resistance of pulses which includes traits associated with productivity such as dry matter, harvest index, and water-use efficiency and other drought resistance mechanisms comprising morpho-physiological traits conferring resistance to drought [103, 104].

4.1 Matching phenology

Matching the phenology to the water supply is the primary way in which chick pea crop yield can be improved in water-limited environments [105]. This involves the identification of plant with an early flower and pod initiation, rapid but short growth period.

4.2 Early biomass accumulation

Early extensive biomass accumulation and setting of reproductive organs before the onset of terminal drought are largely considered as drought escape mechanisms. In environments in which terminal drought is likely, selection for shorter time to

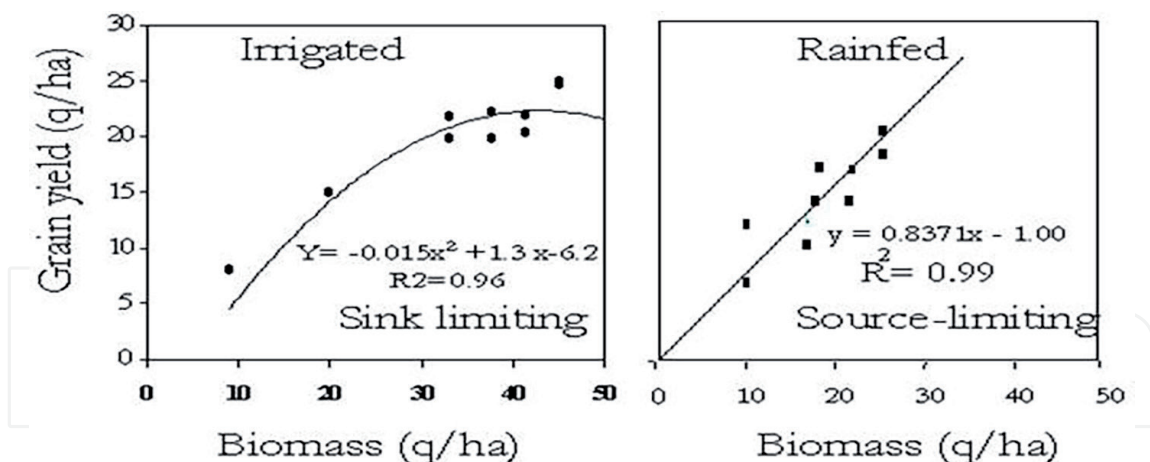


Figure 4. Biomass-yield relationship of chick pea under rainfed (stress) and irrigated (non-stress) conditions.

flowering has been highly successful [106]. Vegetative biomass in most of the pulses has been found to be the most sensitive to water stress. The leaf expansion is affected even under mild water stress with a leaf water potential declined to ≤ 1.2 MPa. The biomass showed a linear relationship with yield under rainfed indicating sources (leaves & stems) are the major limiting factor for low yield. Contrary to this, increasing biomass beyond a certain limit did not further increase in the grain yield in irrigated fields that suggests the sink limiting condition of irrigated crops (no stress) **Figure 4**.

4.3 Importance of plant types to improve yield under stress

Higher biomass does not always lead to contribute higher yield in pulses. Two distinct plant types in chickpea had shown significant yield difference in chick pea. The plant with multiple shoots having uniform height emerged at the seedling stage leads to profuse primary and secondary branches with a higher number of podding nodes (**Figure 5**). On the contrary a different plant type with a single erect branch,



Figure 5. Two distinct plant types in chick pea. High yielding plant type (left) with multiple primary branches and low yielding plant type with single stem (right).

with suppressed lateral branches at the base, has been observed to be a poor yielder due to lack of podding branches although these types of plant had shown vigorous root system and are better adapted to drought conditions (**Figure 5**). Therefore, it is essential to tag both attributes together that plant types with profuse branching and extensive root system.

4.4 High biomass with profuse branching leads to higher yield

Terminal drought markedly reduces leaf photosynthesis during grain filling in chick pea. Prestored assimilate reserve in the stems and leaves during the vegetative stage plays a major role in contributing carbon (C) and nitrogen (N) to the developing grains. The storing capacity of photosynthates (C and N reserve) is thus directly proportional to the biomass which includes stem and leaf reserves. The carbon and nitrogen fixed during vegetative growth is a potential source of assimilates for the developing seeds as photosynthetic gain during reproductive stages is substantially reduced due to stomatal closure or other nonstomatal factors as a result of progressive increase in the water stress. Thus, grain yield in chick pea and pigeon pea under terminal drought is largely influenced by remobilization of prestored carbon and nitrogen in the stems and leaves. Depending upon the cultivars, about 10–20% carbon and more than 60% nitrogen (N) in the seeds of water-stressed plants have been reported to be remobilized from stems and leaves of chick pea [107]. The soluble sugars including transportable sucrose and amino acids in leaves of water-stressed plants markedly increased as a result of starch and protein breakdown. The significant increase in the activation state of sucrose-phosphate synthase in leaves of water-stressed plants had been shown to faster conversion of sucrose in the leaves [108]. The increase in the low-molecular weight compounds like sugars, amino acids, organic acids, and sugar alcohols as a result of degradation of macromolecules, e.g. starch and proteins in water-stressed plants, also plays a significant role in enhancing low-molecular weight osmotic solutes which could likely to help in maintaining transient water balance during stress.

4.5 Role of pod wall to contribute photoassimilate under water stress

Increasing photosynthetic ability as a whole is essential for acquiring higher crop yields. Non-leaf green organs (NLGOs) make important contributions to photosynthate formation, especially under stress conditions [109]. The pod wall of pea (*P. sativum* L.) was shown to contain two distinct photosynthetic layers. The outer, comprising chlorenchyma of the mesocarp, captured CO₂ from the outside atmosphere; the inner, a chloroplast-containing epidermis lining the pod gas cavity, was involved in photoassimilation of the CO₂ released from respiring seeds [110]. The respiratory CO₂ released from the embryo of developing grains of legume pods is refixed by a layer of cells on the inner pod wall [111]. This refixation of respiratory CO₂ plays a significant role to gain carbon by developing seeds under drought when leaf photosynthesis is drastically declined. It has been reported that the excised embryo, seed coat, and pod wall in chick pea are all photosynthetically competent, but the pod wall alone is capable of net O₂ evolution over and above respiration. More than 80% of CO₂ is fixed by this tissue when provided to the pod interior. Moreover, seed coat cell turgor in chick pea is independent of changes in plant and pod water potential [112] which indicates that seed coat water status is less influenced under drought though photosynthesis of pod wall and leaves may be affected markedly but

seed coat photosynthesis maintains normal photosynthesis and significantly contributes photoassimilates to the growing seeds.

4.6 Remobilization of carbon and nitrogen from leaves and stems

The onset of pod filling of chick pea occurs when net photosynthesis and nitrogen fixation are low as a result of the onset of terminal drought. Remobilization of carbon (C) and nitrogen (N) from vegetative parts to developing seeds may be an important alternative source of C and N for seed filling. Genotypic variation in remobilization ability has been observed in desi and kabuli cultivars. The better drought tolerance in desi genotypes could be a consequence of better remobilization and higher pod number. Thus, C and N assimilated prior to podding can supplement the supply of current assimilates to the filling seed in both well-watered and water-stressed chick pea. Remobilization of pre-podding N is an essential source of N for seed filling irrespective of environmental stress. Terminal drought decreases the rate of net photosynthesis of leaves and N fixation during seed filling [41, 113]. A high demand for assimilate from filling seeds when the supply of current assimilate is decreasing often results in an assimilate shortfall [114]. Consequently, alternative sources of assimilate are required to maintain seed filling and seed size. In a number of species, the remobilization of pre-anthesis stored reserves of C and N can be an important assimilate source for seed filling, particularly when plants are subjected to water deficit [115–117]. In cereals, remobilization has been reported to contribute between 3% and 64% of seed dry matter (DM). The contribution of remobilized DM in pulses ranges from 2 to 42% [118, 119]. In chick pea, a decrease of DM in the stems, leaves, and pod walls of field-grown plants suggests that DM remobilization is important as an alternative assimilate source to current photosynthate [120]. Using this method, it was estimated that one-third of the pod DM was derived from the remobilization of DM from vegetative tissue in field-grown chick pea [120]. Chick pea has an indeterminate growth habit with flowers, pods, and seeds developing sequentially along branches [120]. Under terminal drought, pods and seeds that form later in the upper parts of the canopy are likely to be subject to a more severe water deficit during seed filling than pods formed early in the lower parts of the canopy. Consequently, the contribution of remobilized C and N is expected to be higher in seeds filling later when competition for assimilates is high and current C assimilation is very low. There have been no studies examining how remobilized assimilates are distributed among seeds of different ages and this requires investigation. Similar to other indeterminate species, chick pea responds to water deficit by reducing stem elongation, the rate of leaf emergence and expansion, and the establishment of new reproductive nodes [121, 122]. In a previous study by Davies et al. [107], terminal drought led to decreased rates of flower and pod production with a significant decrease in pod and seed number and seed yield in both desi and kabuli chick pea. However, desi chick pea tolerated drought better than kabuli chick pea and was better able to maintain yield relative to the irrigated plants. As there were no substantial genotypic differences in the decrease in photosynthetic rate with water deficit, this difference in drought tolerance may be accounted for by variation in remobilization of assimilates between desi and kabuli chick pea types.

4.7 Root characteristics

A wide genetic variability among root characters such as density and depth, total root biomass has been reported in chick pea genotypes (**Figure 6**). Chick pea lines

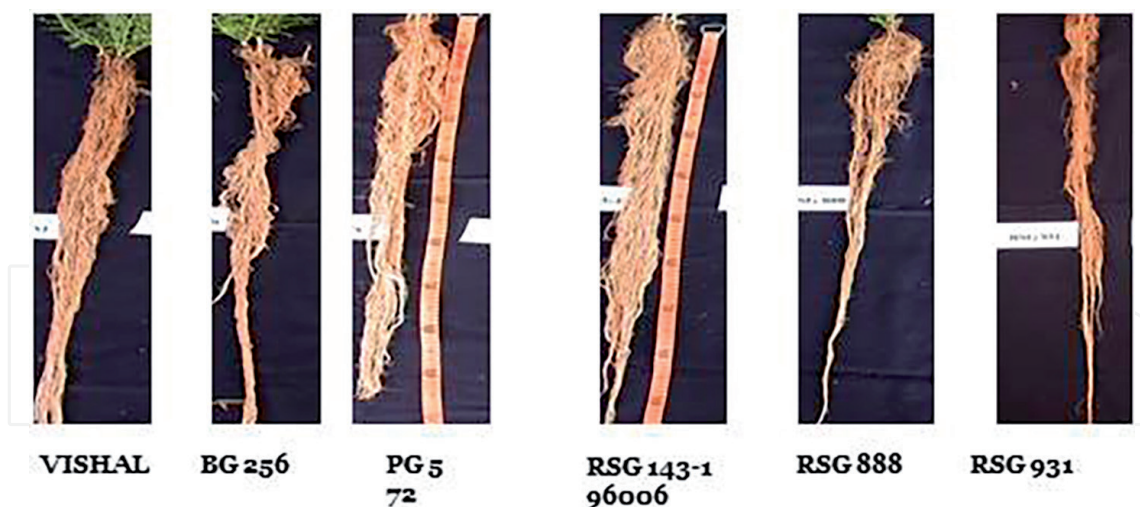


Figure 6.
Genotypic variability in root biomass in chick pea.

with increased drought tolerance through increased root biomass have identified by several workers [123]. A drought resistant genotype ICC 4958 had 30% higher root dry weight than the standard control cultivar “Annigeri” which is relatively more sensitive to drought stress [124].

Although vigorous root system plays a major role toward drought adaptation, however root architecture differs across the locations depending upon the drought situations. In a case study, majority of the chick pea grown under cool environment, root system tends to proliferate just 30 cm below the surface of ground allowing to trap surface moisture received by dew precipitation during winter as well as glandular leaf trichomes use to trap dew water quite heavily. As a result, root length density (RLD) at different depths of the soil profile varies in chick pea depending upon the environmental conditions. In chick pea cultivars adapted to warmer environment roots usually go into the deep soil for mining water efficiently due to lack of surface soil moisture as a result of high temperature-dependent faster evaporative water loss coupled with a very negligible amount of dew precipitation. Therefore, root architecture is very important to consider to make a breeding strategy in developing drought tolerant cultivars. Near infrared reflectance (NIR) pattern in an RIL (recombinant inbred lines) population derived from ICC 4958 (high root) × Annigeri (low root) cross revealed a significant NIR reflectance depicting different amount of water content in leaves (**Figure 7**).

4.8 Water-use efficiency, canopy temperature, and transpiration under stress

The specific leaf area is negatively associated with SPAD Chlorophyll meter reading (SCMR) and water-use efficiency measured by Carbon isotope discrimination ($^{13}\text{C}/^{12}\text{C}$ ratio). Therefore, SLA represents an indirect way of measuring water-use efficiency of plants, the low SLA indicated higher WUE and SCMR which could be useful to identify efficient genotypes with high water-use or transpiration-use efficiency (**Figure 8**) which is defined as more photosynthetic gain per unit loss of water through transpiration, or transpiration efficiency is a ratio between biomass and transpiration. The transpiration-use efficiency could be one of best strategies toward improved adaptation under stress environment. Improving water-use efficiency is associated with stomatal density, efficiency of RuBisco, and other physiological

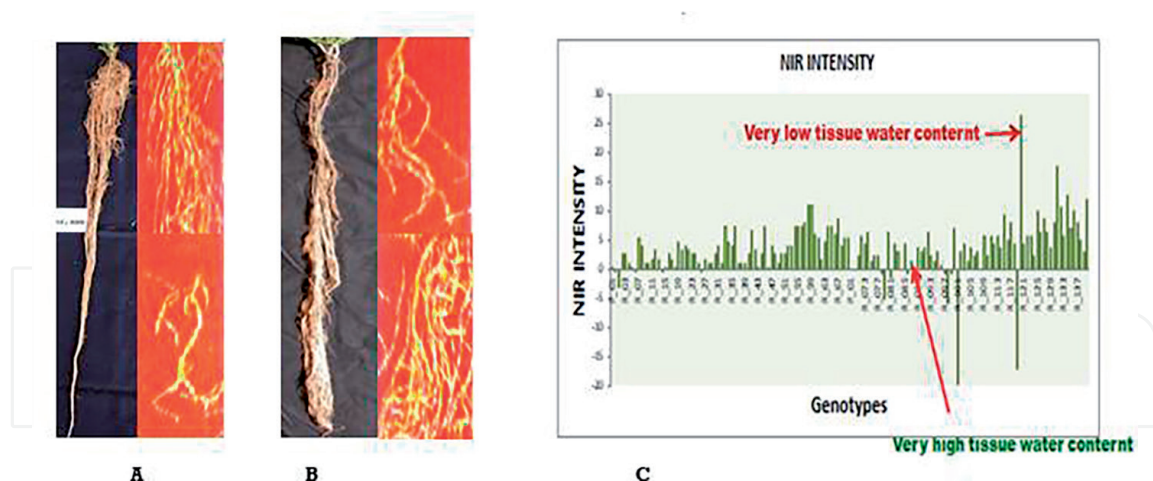


Figure 7. (A) Chick pea genotype with high root length density (RLD) at the top soil surface layer adapted to cooler environment. (B) Chick pea genotype with high root length density (RLD) at the bottom or deep soil layer, adapted to warmer environment. (C) Different NIR (near infrared reflectance) values shown by RIL population having different levels of tissue water content which is likely to be associated with different amounts and depths of root biomass.

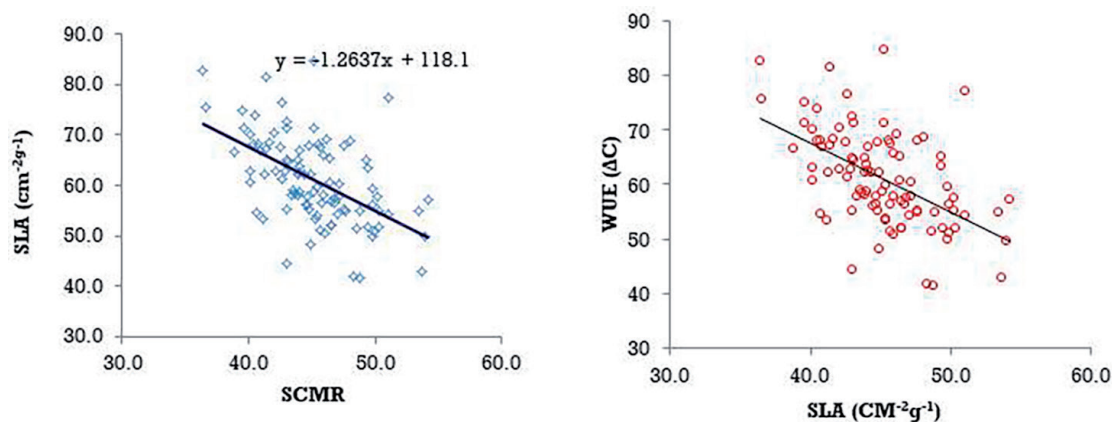


Figure 8. Associations of specific leaf area (SLA) and water-use efficiency, $^{13}\text{C}/^{12}\text{C}$ ratio (WUE).

parameters of mesophyll cells of leaves. Significant genotypic variation has been observed in chick pea and pigeon pea in water-use efficiency [125]. A decrease in transpiration rate due to drought may result in an increase of leaf internal temperature due to decreased evaporative cooling of leaf and therefore drought stressed plants show higher leaf or canopy temperatures than well-watered plants [126]. Cool canopies are associated with better yield output as a result of higher transpiration and photosynthesis [127]. To maintain canopy cool under drought and heat, plants should have attributed with deeper root system to access water from the deep soil layers. Key physiological traits like osmotic adjustments and root architecture need to be modified to make canopy cool under heat and drought stresses. Osmolyte accumulation also alters photoassimilate allocation between roots and shoots. Drought induced osmolyte accumulation tends to allocate more photosynthates toward roots; as a result, plants are able to adapt under drought by extracting more water from soil.

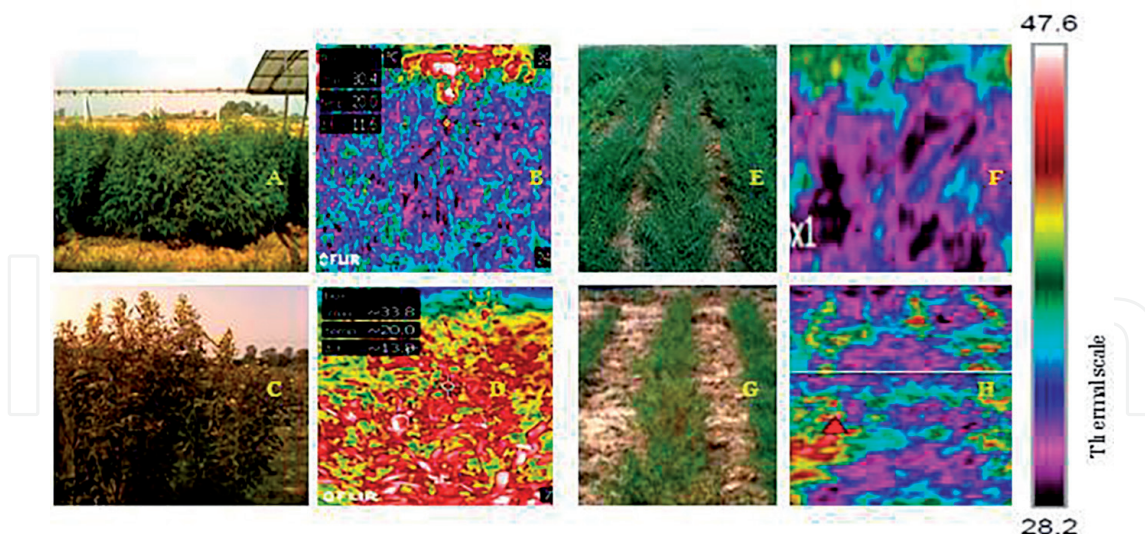


Figure 9. Plant microclimate under drought: A. Pigeon pea dwarf/closed canopy; B. Thermal image of A; C. Pigeon pea open canopy and D. Thermal image of C; E. Semi-erect dense chick pea canopy; F. Thermal image of E; G. Spreading open chick pea canopy; H. Thermal image of G. Canopy temperature can be assessed by different colors as shown by the thermal scale given at the right side.

4.9 Plant architecture for conserving moisture

Conserving moisture is one of the strategies of plants to withstand drought. The plant architecture plays an important role in configure plant microclimate for conserving moisture and to make the canopy cool. Evaluation of contrasting pigeon pea genotypes by a thermal imaging technique showed that dwarf and closed canopy of pigeon pea (**Figure 9A** and **B**) remained cooler as compared to tall and open canopy (**Figure 9C** and **D**). Similarly dense and semi-spreading chick pea (**Figure 9E** and **F**) may have the advantage to keep the canopy cooler than spreading and open chick pea plant type (**Figure 9G** and **H**). However, plant types with deeper root system maintain the canopy cool by means of extracting soil moisture efficiently from deeper soil layers which in turn allowing plant to transpire under drought conditions. The transpiration cooling under limiting soil moisture prevents stomatal closure to some extent and simultaneously restores photosynthesis to sustain dry matter production.

5. Dehydration postponement

The second mechanism is the postponement of drought by reducing water loss primarily by stomatal control of transpiration, by increasing water use through deep and vigorous root system, or by the accumulation of solutes to maintain turgor as water shortages develop (osmotic adjustment).

5.1 Stomatal mechanism

The open stomata result in transpirational cooling of leaf hence canopy of a particular genotype having higher stomatal conductance should show lower temperature

than those having close stomata. Techniques are now available to measure canopy temperature by infrared thermometry; hence, screening of pulse germplasm with varying stomatal responses to drought is possible. The reduction in the stomatal density and an increase in the leaf reflectance through production of glandular hairs in chick pea are considered to be adaptive traits through which leaves reduce water loss and intercepted non-photosynthetic radiation.

5.2 Osmotic adjustment

Osmotic adjustment (OA) is the process of active accumulation of solutes in leaves in response to increasing water deficits in the soil thereby maintaining turgor. Osmotic adjustment has been shown to maintain stomatal conductance and photosynthesis at low leaf water potential in many crops [128], delay leaf senescence, reduce flower abortion, and improve root growth and water extraction from the soil [129]. Intra and interspecies difference in osmotic adjustment and its range in grain legumes are given in **Table 1**. From the table it is clear that among pulses chick pea, pigeon pea, and peanut are tolerant to drought as compared to others. The genotypic variation in OA ranging from 0.45 to 1.25 MPa was significant at LWP (leaf water potential) below -2.0 MPa in chick pea and maximum was noticed in cultivar Tyson. The significant genetic variation in OA from 0 to 1.3 MPa has been reported earlier in chick pea at very low LWP. Comparative evaluation of two cultivars such as Tyson with high OA (1.25 MPa) and Kaniva with low OA (0.45) revealed that relative water content (RWC) varied periodically with progressive increase in water stress as crop growth advances toward maturity while RWC declined linearly in Kaniva with less OA (**Figure 10**). The expression of high OA in chick pea cultivars was usually observed in selective chick pea having inherent ability to osmotically adjust when crop was subjected to severe stress with decline in leaf water potential to -3.0 MPa and above, and this characteristic enables the cultivar

Species (pulses)	Range osmotic adjustment (MPa) in leaves	Degree of dehydration postponement	Species (cereals/vegetables)	Range in osmotic adjustment (MPa)	Degree of dehydration postponement
Groundnut	0.2–1.6	Very high	Sorghum	0.8–1.7	Very high
Pigeon pea	0.1–1.3	High	Wheat	0.2–1.5	High
Soybean	0.3–1.0	High	Barley	0.2–0.5	Moderate
Chickpea	0.0–1.3	High	Maize	0.1–0.4	Moderate
Lentil	0.0–0.6	Moderate	Potato	0.0–0.25	Low/sensitive
Green gram	0.3–0.4	Moderate			
Black gram	0.1–0.5	Moderate			
Cowpea	0.0–0.4	Moderate			
Lupin	0.1–0.5	Moderate			
Field pea	0.0–0.4	Moderate			
Faba bean	0.0–0.2	Low/sensitive			
Lathyrus	0.0–0.1	Low/sensitive			

Table 1.
Range of osmotic adjustment in grain legumes.

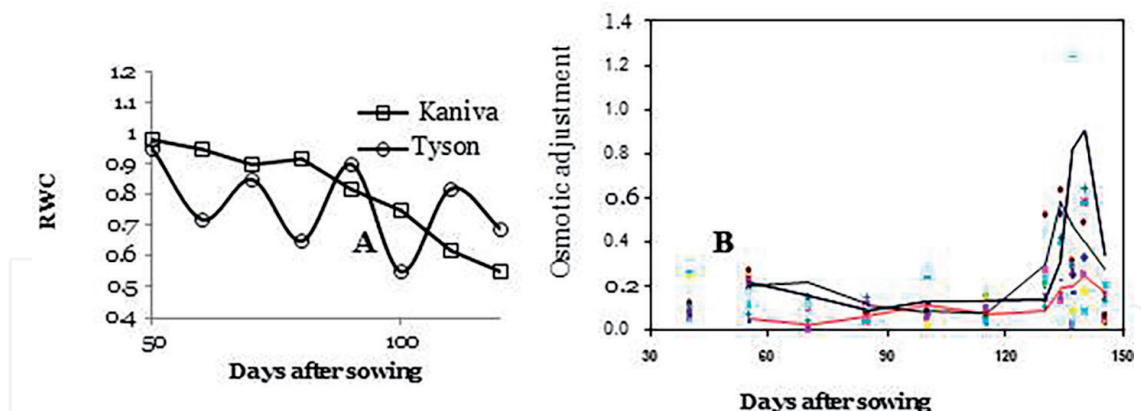


Figure 10. Linear decrease of RWC in chick pea cv Kaniva having low OA while periodical changes of RWC in chick pea cv Tyson having high OA were observed with progressive increase in drought as crop growth advances. (B) High expression of OA in different chick pea cultivars occurred when the drought level was intensified at the terminal end of crop growth and OA declined after reaching a threshold level.

to survive even under severe moisture limiting conditions. The mild water stress helps in conversion of starch into reducing sugars followed by increase in sucrose phosphate synthase (SPS) activity in leaves which led to transient accumulation of sucrose contributing osmotic solutes. The non-transportable carbohydrate, starch, is converted to transportable form of sugar such as sucrose in the process of osmotic adjustment, thereby facilitates remobilization of prestored photosynthates from leaf to various sinks. When sucrose accumulated a threshold level, it increases the water flux into the leaf cells to regain the turgidity and improve LWP or RWC. The leaf carbohydrates or sucrose and others as osmotic solutes started remobilizing as a consequence of regaining the leaf turgidity. Subsequently partial recovery of RWC (stress relief) led to decrease in the SPS activation state, partial restoration of photosynthesis, and reactivation of starch synthesis. Thus, it is evident that osmotic adjustment prevents lowering of RWC below a critical level by efficient water uptake, restores photosynthesis, and maintains positive carbon balance for longer stress periods. The increase in cellular osmolarity allows influx of water into cells and maintains the necessary turgor for cell expansion, maintains membrane integrity and prevents protein denaturation under adverse environmental conditions such as drought, high or low temperatures [130], and confers protection against oxidative damage [131]. The accumulation of mannitol in chloroplasts leads to increase resistance to oxidative stress in tobacco [132]. The accumulation of osmolyte in response to drought has a critical role in the mitigation or avoiding/ delaying the adverse effects of stress. The accumulation of osmoregulatory solutes has been considered as a unique biochemical trait which could be manipulated by breeding or transformation technologies.

5.3 Dehydration tolerance

5.3.1 Lethal leaf water potential

Sinclair and Ludlow [133] considered that the lethal leaf water potential, i.e. the lowest water potential experienced by the last viable leaf, was a key measure of dehydration tolerance. The lethal leaf water potentials in a range of grain legumes have been worked out, which shows that soybean has more dehydration tolerance than others.

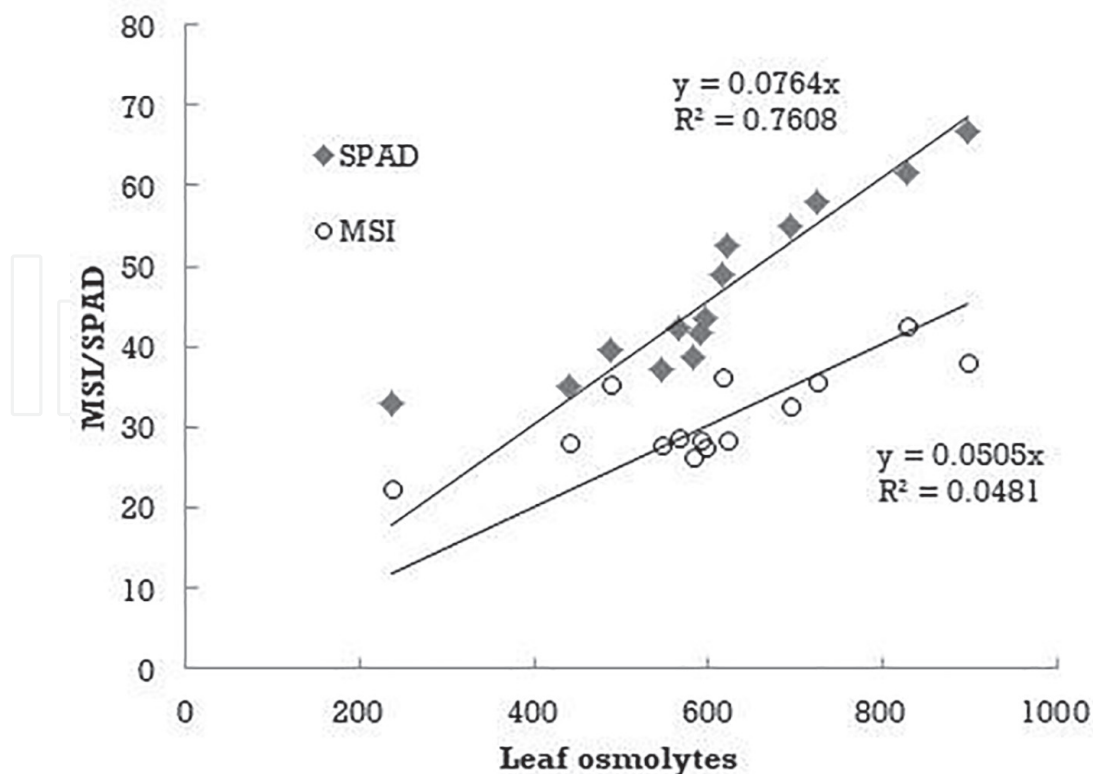


Figure 11. Significance of osmotic solutes in imparting drought tolerance by improving membrane stability (MSI) and chlorophyll content (SPAD).

5.3.2 Membrane stability

The drought tolerant mechanisms involve stability of the membrane, which could be assessed through electrolyte leakage from desiccated tissue (**Figure 11**). The ability of cells to continue metabolism at low leaf water status is termed dehydration tolerance. Membrane disorder is often measured as leakage of solutes from the cell [134]. Electrolyte leakage measured by a conductivity meter has been used as a screening technique for heat and dehydration tolerance.

5.3.3 Proline accumulation

Accumulation of proline in cell in response to water deficit is another mechanism protecting protein structures as cell dehydrate, and as an organic nitrogen source. Neither membrane injury index nor proline accumulation is being used as a screening technique against dehydration tolerance.

6. Pollen and ovule fertility at high temperature

Cool-season pulses such as chick pea, lentil, field pea, French beans, etc. are often exposed to very high day temperature during reproductive stages exceeding 40°C. The upper limit of cool-season legumes has been reported to be within the range of 30–35°C. The heat stress in cool-season legumes has been considered as major abiotic stress leading to substantial yield loss, reduction in seed size, flower abortion, leaf senescence, forced maturity, failure of pod setting, retarded pollen germination,

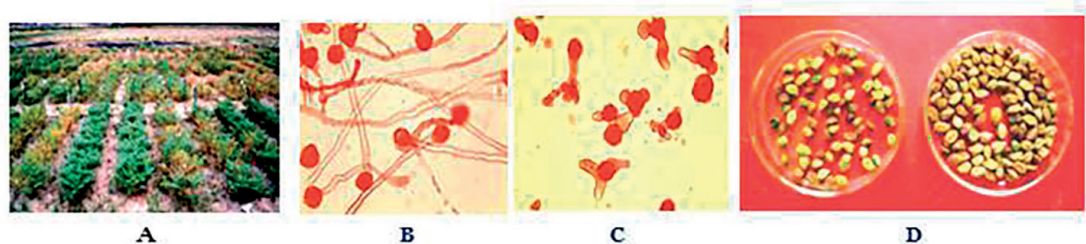


Figure 12. (A) Forced maturity of chick pea at high temperature with distinct genotypic variation; (B) normal pollen tube growth in chick pea at 25°; (C) reduced and abnormal pollen tube emergence in chick pea at high temperature 41°C; and (D) reduction in the seed size in chick pea when day temperature exceeding >40°C.

and ovule deformation (**Figure 12**) [135]. Though significant genotypic variation has been reported in all these reproductive traits. While warm-season pulses such as green gram, black gram, cowpea, and pigeon pea are less affected as their upper temperature limit of tolerance is relatively higher ranging between 35 and 45°C. Many legumes exhibit a high sensitivity to heat stress during flowering. One of the major yield determinants in food legumes is pollen fertility and flower shedding at high temperature. The pollen sap may be altered and becomes more viscous by progressive increase in the temperature beyond 37°C. The transformation of pollen sap into a dense and viscous fluid probably hinders the smooth movement of male gametes. A reduction in the pollen tube length was observed in the heat-tolerant chick pea ICCV 92944 and green gram genotype EC 398889 at 40°C and beyond. In contrast, multiple pollen abnormalities including emergence of multiple tubes, single or coiled forms, bursted pollen tubes were observed in heat-sensitive green gram LGG 460 at high temperatures. Earlier reports on rice have also indicated that an increase in temperature could limit yield by affecting pollen germination and grain formation [136]. The male gametophyte is particularly sensitive to high temperatures at all stages of development, while the pistil and the female gametophyte are considered to be more tolerant [137]. The pollens are most sensitive to high temperature; the crop yield is affected when temperature rises during pollen development [138]. High temperature decreases pollen viability and leads to sterile pollens and decrease of pod set and yield [139]. In legumes, heat stress during post-anthesis results in poor pollen germination on the stigma and reduced pollen tube growth in the style [140]. Under high temperatures (>30°C), flower sterility has been correlated with diminished anther dehiscence, poor shedding of pollens, and germination of pollens on stigma [6]. The reduction in photosynthesis under high temperature may also restrict supply of photoassimilates such as sucrose, hexoses, and starch in the developing pollens resulting in decrease in pollen fertility [49]. The role of sugars and invertase/sucrose synthase activity in anther development and pollen germination has been reported in several crops [141]. Some of the thermotolerant food legumes flowered and set pods at high temperature. Therefore, assessment of pollen viability and pollen germination at high temperature proved to be potential screening tools for heat tolerance.

6.1 Acquired thermotolerance

Acquired thermotolerance is a mechanism naturally occurring in plants and has been extensively used in thermotolerant line identification [142]. The cell viability after heat shock was tested using 2%Triphenyl tetrazolium chloride (TTC). Cells were considered viable if tissue turns purple color when treated with TTC; on the

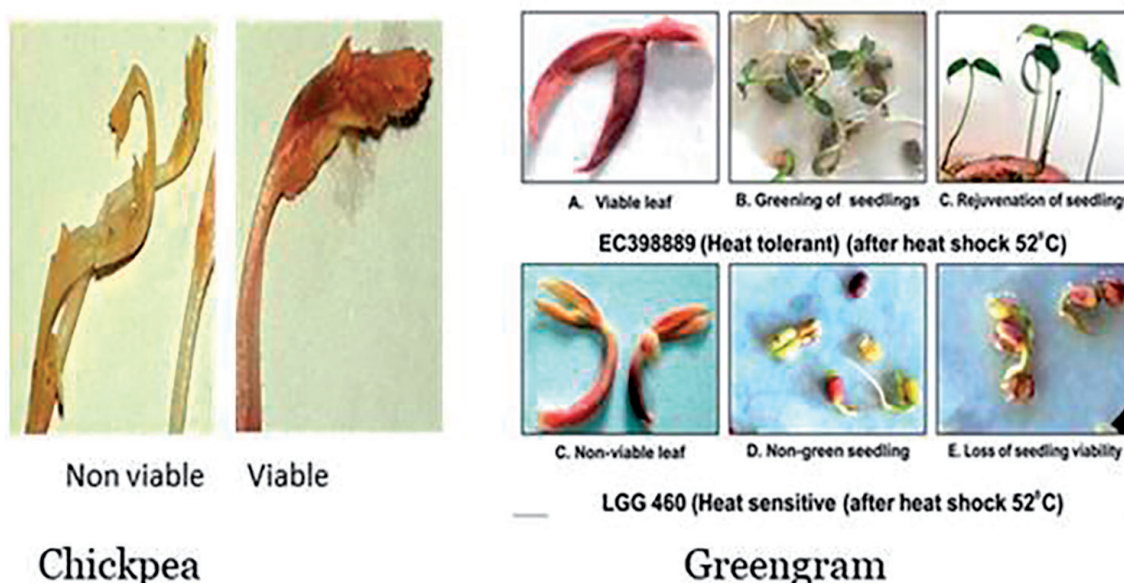


Figure 13. Non-viable (TTC negative) and viable seedlings (TTC positive) of two contrasting chick pea genotypes after heat shock at 52°C. Acquired thermotolerance (ATT) in green gram in HT line EC 398889 (A–C) top and lack of ATT in HS green gram LGG 460 (C–E).

other hand faint purple color or if tissue does not take stain, it is considered as dead. Thus, TTC (triphenyl tetrazolium chloride) test for tissue viability and chlorophyll accumulation after heat shock appeared to have some promise to identify thermotolerant genotypes having ability to acquire thermotolerance. Heat-sensitive green gram genotype LGG 460 lost cell viability after heat shock and thus identified as TTC negative. Thus, higher membrane thermostability and cell viability after heat stress could be monitored by the TTC test and the technique has been widely used for assessment of heat tolerance [143]. The TTC reduction assay measures the level of mitochondrial respiration activity, which serves as an indicator of cell viability [144]. Variability was detected among the 56 green gram genotypes for acquired thermotolerance ranging from 14.1% to 61.3% while it ranges from 20 to 40% in chick pea **Figure 13**.

6.2 Membrane stability (MSI)

Under stress conditions, a sustained function of cellular membranes is considered crucial for maintaining cellular processes such as photosynthesis and respiration [145]. The integrity and function of cell membranes are sensitive to high temperatures, as heat stress alters structures of membrane proteins leading to increased permeability of membranes resulting in increased loss of ions or solutes. The increased solute leakage is closely associated with cell membrane thermostability [146], and various attempts have been made to use this method as an indirect measure of heat tolerance in diverse plant species such as food legumes [147], soybean [81], potato, cotton, and tomato [148], and wheat [149]. Study conducted using green gram germplasm for assessing membrane stability index (MSI) and chlorophyll content or greenness index showed that both MSI and chlorophyll remained higher in heat-tolerant green gram line EC 398889 as compared to sensitive line LGG 460 when plants of these two contrasting genotypes grown under high thermal regimes 42/28°C maximum/minimum temperature [49].

6.3 Photosynthesis and chlorophyll fluorescence

Photosynthesis is the most thermosensitive plant function [150] which can occur optimally at wide temperature ranges between 15°C and 35°C, although adversely affected at temperatures ranging 35–40°C and above. The cultivars can be distinguished based on the photosynthetic performance under high temperatures. Photosynthesis at high temperatures can be assessed through gaseous exchange or the chlorophyll fluorescence imaging technique. The fluorescence imaging technique visualizes the activity or effects of stress on PSII, photosynthetic membrane system, and electron transport rates (ETR). The ETR in pretreated leaves (40°C) of heat-tolerant green gram EC 398889 was less affected at high irradiances whereas heat-sensitive genotype LGG 460 with similar treatment showed complete reduction of photosynthetic ETR (**Figure 14**). Reduced electron transport and damaged photosystems caused by high temperature have been reported in poplar [89]. Chloroplast stroma and thylakoid membranes are damaged by high temperatures [151]. Photosystem (PS) II in the light reaction [152] and Rubisco (ribulose1, 5-bisphosphate carboxylase/oxygenase) activase in the Calvin cycle [153] are both thermolabile. Heat stress thus impairs the electron transport chain and affects the activation and activity of the enzyme Rubisco [154]. Although PSI and PSII are both adversely affected by high temperatures, PSII is more sensitive to heat stress than is PSI [155]. Chlorophyll fluorescence is a rapid and non-invasive, high-resolution technique to determine changes in photochemistry through monitoring the fluorescence emission of photosystem II (PSII) *in situ* [156]. High temperature affects membrane stability, cell viability, and the quantum efficiency of photosystem II, as measured by chlorophyll fluorescence [157]. Chlorophyll fluorescence as affected by heat stress causes a decrease of F_v/F_m ratio in susceptible wheat compared with tolerant lines [158]. The quantum yield is one of the powerful non-destructive parameters to differentiate

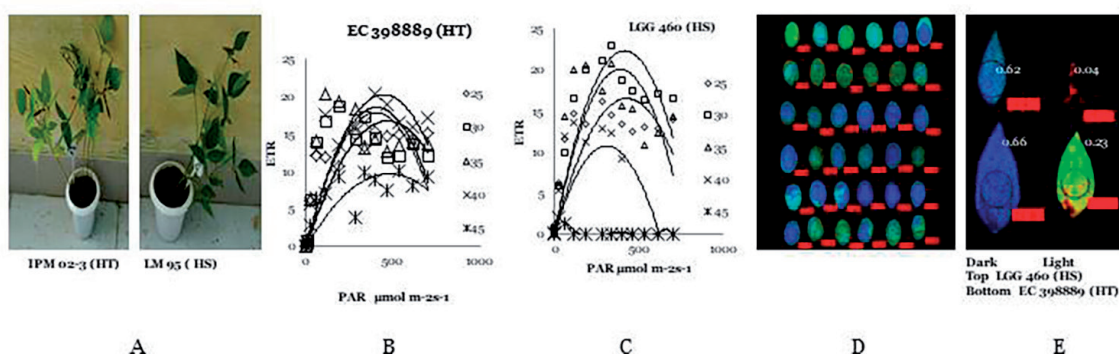


Figure 14. A. Heat-tolerant green gram genotype IPM 02-3 abled to set pods at high temperature 43/28°C whereas heat-sensitive genotype LM 95 failed to set pods or flower at the same temperature regime. B. Light response of photosynthetic electron transport rate (ETR) at different temperatures in heat-tolerant (HT) green gram exotic accession EC 398889. High photosynthesis (ETR) detected even at 40°C coupled with high irradiance levels; however, ETR was inhibited beyond 40°C. C. Light response of photosynthetic electron transport rate (ETR) at different temperatures in heat-sensitive (HS) green gram exotic accession LGG 460. Photosynthesis (ETR) inhibited even at 40°C coupled with high irradiance levels; however, ETR was inhibited completely at 45°C at all irradiances. D. Large-scale phenotype of heat tolerance in green gram genotypes based on heat treatment of leaves at 40°C for 1 h followed by capturing quantum yield images. Deep blue color represents high values of quantum yield (F_v/F_m) and indicated tolerant lines. Whereas color deviated to green or pale green represented reduction in the quantum yield or heat-sensitive lines. E. Fluorescence imaging (quantum yield; F_v/F_m) of high temperature treated (40°C for 1 h) and light-adapted leaves distinguished HT (EC 398889) and HS (LGG 460) green gram accessions.

tolerance levels of a large number of genotypes with respect to particular abiotic stress. QTLs have been reported for chlorophyll fluorescence in drought- or heat-stressed wheat. The fluorescence parameters such as minimal F_0 , maximal fluorescence, F_m , and variable fluorescence F_v change when plants are subjected to various abiotic stresses and eventually quantum yield of PSII (ratio of variable to maximum fluorescence, F_v/F_m) is affected. Using a large number of different fluorescence data, modifications of photosynthetic process under stresses can be assessed precisely, which includes thylakoid membrane organization, electron transport, and carbon assimilation [159]. The images captured for effective PSII quantum yield (YII) in high temperature treated leaves under high irradiances would be able to distinguish heat-tolerant and susceptible genotypes. The numerical values of different fluorescence parameters such as F_0 , F_m , and F_v/F_m were converted to image format to visualize the adverse effects of heat on photosynthetic machinery at the chloroplast level. The image transformation with specific color code was shown in **Figure 7**. The intensity of the color depicts increase or decrease in the numerical values of fluorescence parameters. Similarly, the light response of electron transport rate (ETR) based on calculation using quantum yield (F_v/F_m) and PAR was also able to distinguish the genotypes based on their sensitivity to heat stress. Overall, this technique involving chlorophyll fluorescence imaging has proved to be effective and a precise phenotyping method for screening germplasm of pulses in a big way for stress tolerance. One of the mungbean line EC 398889 has been identified as highly heat tolerant based on chlorophyll fluorescence imaging and pollen fertility, and this line was used as one of the donor parents for developing short duration mungbean variety 'Virat'. The first distinct change in both the structure and function of photosystem II (PSII) reported to be occurred at 40–50°C in barley [160]. The first temperature induced transient changes had been shown at 42–48°C with a disruption of the PSII donor side and corresponding loss of oxygen evolution [161] followed by changes in thylakoid membranes at about 60°C and loss of electron transport through PSII [162] representing a denaturation of the PSII reaction centers. At about 75°C, a denaturation of light-harvesting complex of PSII (LHCII) has been observed [162]. The modification of chlorophyll fluorescence in response to heat stress has been reported in numerous crops, and heat tolerance of plant species can be quantified by measuring chlorophyll fluorescence [163]. When leaves are exposed to high temperatures and high light intensity simultaneously, the combined effects are more detrimental to photosynthesis. The relative assessment of fluorescence images for quantum yield (F_v/F_m) in high temperature treated in several green gram genotypes revealed that light-adapted leaves of the heat-tolerant green gram genotype EC 398889 exhibited higher quantum yield than the heat-sensitive genotype, LGG 460. The photosynthetic system partially or completely collapsed in light-adapted leaves of LGG 460. The fluorescence images combined with the light curve of ETR strongly could precisely differentiate varying sensitivity of photosynthesis to heat stress in the two contrasting genotypes, e.g. heat-tolerant green gram EC 398889 and sensitive ones LGG 460 [49]. The differential degree of membrane thermostability may distinguish the genotypes toward different sensitivity to heat stress. Chloroplast-targeted AtFtsH11 protease plays critical roles for maintaining the thermostability and structural integrity of photosystems under high temperatures [164]. Therefore, the photosynthetic efficiency may be modified under heat stress by improving FtsH11 protease in photosystems, hence, to improve plant productivity. Molecular characterization of heat tolerance in green gram using specific marker CEDG 147 could also be able to distinguish heat-tolerant green gram genotypes from sensitive ones (**Figure 15**).

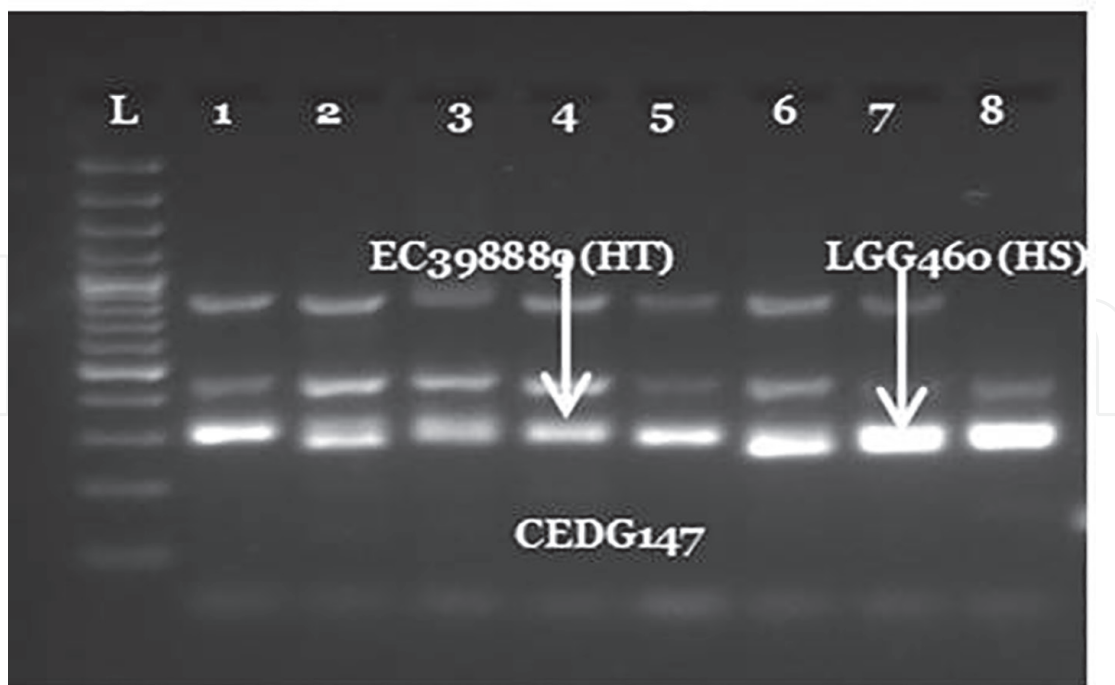


Figure 15.
 Molecular characterization of heat tolerance in green gram. Marker CEDG147 (C) differentiated heat-tolerant (HT) and heat-sensitive (HS) green gram genotypes, L- 100 bp ladder, 1 (HUM12), 2 (Ganga-8), 3 (EC398889), 4 (IPM-02-3), 5 (IPM-02-14), 6 (LGG460), 7 (Kopergaon), 8 (NSB 007).

6.4 Oxidative stress

The plants produce antioxidant enzyme systems as a defensive mechanism which involve superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) for scavenging ROS under stressed conditions [165]. Heat-sensitive chick pea and black gram genotypes were induced to express more SOD and POX under heat treatment as a defensive mechanism of protection from ROS; however, heat-tolerant genotype is inherently tolerant to stress and therefore producing less ROS (**Figure 16**). During prolonged stress exposure, photosynthetic activity is further inhibited by excessive accumulation of reactive oxygen species (ROS), causing damage to the membranes, proteins, and chlorophyll molecules of the photosynthetic apparatus [2, 166]. Plants use a complex antioxidant system to regulate ROS levels and avoid toxicity, but



Figure 16.
 Superoxide radical SOD in heat-tolerant (HT) and sensitive (HS) chick pea (A) and black gram (B) and peroxidase (POX) in black gram (C) when both HT and HS grown under high temperature regimes 43/25°C max/min day/night.

changes in redox status are also perceived by plants as a signature of a specific stress that will result in a corresponding acclimation response [167]. ROS scavenging is commonly induced under drought and heat stresses through enhancing antioxidant activities, and this is correlated with tolerance to stress [168]. In some wheat genotypes, tolerance to drought or heat stress was associated with increased antioxidant capacity and reduced oxidative damage in some wheat genotypes [169]. Under prolonged stress exposure, photosynthetic activity is further inhibited by excessive accumulation of ROS, causing damage to the membranes, proteins, and chlorophyll molecules of the photosynthetic apparatus [166].

6.5 Trait introgression for combined tolerance: Use of wild accessions

The pulses have narrow genetic diversity to accept the challenges of global warming and associated changes in the water availability [170]. Therefore, it is necessary to exploit wild species and land races for extensive gene mining for useful adaptive traits/genes to incorporate into our present cultivars. The wild species are the rich sources of many useful genes [171] as they have evolved under natural selection to survive climatic extremes and can potentially provide further genetic gains [172]. Therefore, wild species need to be exploited in genetic improvement programs to alleviate the challenges of global warming and its related effects in pulses. Two wild accessions of *Vigna* were identified as photo-thermo insensitive. These include one accession each of *V. glabrescens* (IC 251372) and *Vigna umbellata* (IC 251442) based upon viable pollen and normal pollen tube formation, podding, and seed set at high temperature up to 44°C and low temperature up to 4.4°C. Distant hybridization programme for climate resilience in mungbean was initiated using these wild *Vigna* species. Wild relatives of pigeon pea are known to have many useful traits for tolerance to various abiotic stresses. The wild species of pigeon pea like *Cajanus sericeus*, *C. scarabaeoides*, and *Cajanus acutifolius* showed a high degree of osmotic adjustment, OA (−2.5 to −5.0 MPa) imparting drought and heat tolerance based on the chlorophyll fluorescence imaging and pollen fertility test. These wild species showed fertile pollens and pod setting under severe drought. The photo-thermo insensitive accession of wild *C. scarabaeoides* ICP 15671 demonstrated high OA and normal pollen germination at temperature as high as 47°C. The heat-tolerant ICP 15671 showed normal pollen fertility and ability to set pods even at 47°C (**Figure 17**). The accumulation of osmolytes with higher order plays a major role as thermo and desiccation protectant preventing damage of membrane and vital macromolecules. This wild species is photo-thermo insensitive as well as heat and drought tolerant, and therefore, this wild *Cajanus sps* (ICP 15671) appeared to be a potential reservoir of genes for multiple abiotic stress tolerance. Many wild derivatives developed from crosses *C. cajan cajan* × *C. scarabaeoides* (ICP 15671) showed significant genetic variations in the combined

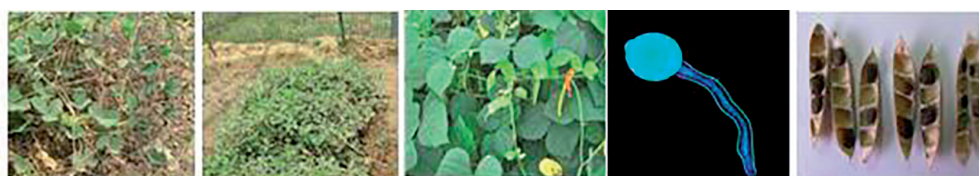


Figure 17. Combined tolerance (heat and drought) in pigeon pea wild accession *Cajanus scarabaeoides* (L.). One of the accessions of *C. scarabaeoides* ICP 15671 flowered and set pods even temperature as high as 47°C with normal pollen germination.

tolerance to both drought and heat stresses. The pre-breeding line ICP 711 developed from a cross between cultivated vs. wild chick pea *C. arietinum* × *C. judaicum* showed an increased number of primary branches, pods per plant, and green seeds for further use in chick pea improvement program [173].

7. Conclusion

Drought and heat stresses or combined effects of both are the major challenges for pulses which adversely affect grain yield to the extent of about 60%. Underlying mechanisms of drought tolerance in major pulses involve extensive and deep root systems, osmotic adjustment, high water-use efficiency, remobilization of prestored photosynthates, stomatal control for regulated water loss, and internal moisture conservation, etc. While stable photosynthetic system, membrane stability, and high pollen fertility have been considered as potential physiological considerations for heat tolerance. However, the fact is that very little success has been achieved so far to improve grain yield through introgression of these traits. The major yield limiting factors for low yield in pulses under these stresses could be due to poor biomass accumulation which is the most sensitive component as affected by stresses. No potential traits have so far been identified by which biomass enhancement can be achieved, if biomass accumulation is adequate at initial stages of growth, the adverse effects of these stresses can be minimized. Therefore, plant type concept has been emerged as a potential strategy to improve yield under abiotic stresses. At the initial growth stage, plants must be configured to achieve more branches and pod bearing nodes to store more moisture in the vegetative parts as it is an inherent character of pulses to retain water for longer time. Pods are semi-autonomous organs to photosynthesize and gaining carbon and capable of refixing respiratory release of CO₂ internally, and moreover the water status of pod wall/seed coat is partially independent of water status of plants. High biomass also contributes proportionately higher carbon and nitrogen mobilization to developing sinks. The early, phenology, quick biomass accumulation with profuse branching and podding nodes are considered to be important in determining yield under drought and heat. The physiological trait introgression needs to be considered important on the background of high yielding plant types. Extensive efforts have been made to identify genes/QTLs in chick pea, pigeon pea, and other pulse crops [174]. Recently, genomics tools are becoming an integral part of the current conventional breeding which could be applied for genetic improvement for climate-smart pulses [175]. Genome sequences of major pulses including pigeon pea and chick pea are now available [176].

Acknowledgements

Authors are grateful to the Indian Council of Agricultural Research, New Delhi, India for funding this work under the project National Innovations on Climate resilient Agriculture (NICRA). The facilities provided by Director, ICAR-Indian Institute of Pulses Research, Kanpur, India to carry out this investigation are thankfully acknowledged.

IntechOpen

Author details

Partha S. Basu^{1*}, Sushil Kumar Chaturvedi², Pooran Mall Gaur³, Biswajit Mondal¹, Surendra Kumar Meena⁴, Krishnashis Das¹, Vaibhav Kumar¹, Kalpana Tewari¹ and Kusum Sharma¹

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


2 Rani Lakshmi Bai Central Agriculture University, Jhansi, Uttar Pradesh, India

3 International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India

4 ICAR-IIPR, Arid Pulses Research Centre, Bikaner, Rajasthan, India

*Address all correspondence to: psbsu59@gmail.com

IntechOpen

© 2022 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/3.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. 

References

- [1] Barnabás B, Jager K, Feher A. The effect of drought and heat stress on reproductive processes in cereals. *Plant Cell and Environment*. 2008;**31**:11-38
- [2] Awasthi R, Kaushal N, Vadez V, Turner NC, Berger J, Siddique KHM, et al. Individual and combined effects of transient drought and heat stress on carbon assimilation and seed filling in chick pea. *Functional Plant Biology*. 2014;**41**:1148-1167
- [3] Zandalinas SI, Mittler R, Balfagon D, Arbona V, Gomez-Cadenaz A. Plant adaptations to the combination of drought and high temperatures. *Physiologia Plantarum*. 2018;**162**:2-12
- [4] Singh J, Kanaujia R, Singh NP. Pulse phytonutrients: Nutritional and medicinal importance. *Journal of Pharmacy and Nutrition Sciences*. 2016;**6**:160-160. DOI: 10.6000/1927-5951.2016.06.04.5
- [5] Daryanto S, Wang L, Jacinthe PA. Global synthesis of drought effects on food legume production. *PLoS ONE*. 2015;**10**:e0127401. DOI: 10.1371/journal.pone.0127401
- [6] Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A, et al. Crop production under drought and heat stress: Plant responses and management options. *Frontiers in Plant Science*. 2017;**8**:1147. DOI: 10.3389/fpls.2017.01147
- [7] Summerfield RJ, Hadley R, Minchin EH, Awsthorpe FRS. Sensitivity of chick pea (*Cicer arietinum*) to hot temperatures during the reproductive period. *Experimental Agriculture*. 1984;**20**:77-93
- [8] Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: An overview. *Environment and Experimental Botany*. 2007;**61**:199-223. DOI: 10.1016/j.envexpbot.2007.05.011
- [9] Morison JI, Baker NR, Mullineaux PM, Davies WJ. Improving water use in crop production. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences*. 2008;**363**:639-658. DOI: 10.1098/rstb.2007.2175
- [10] Acevedo M, Pixley K, Zinyengere N, Meng S, Tufan H, KarenCichy K, et al. A scoping review of adoption of climate-resilient crops by small-scale producers in low-and middle-income countries. *Nature Plants*. 2020;**6**:1231-1241. DOI: 10.1038/s41477-020-00783-z
- [11] FAO. *The Future of Food and Agriculture—Trends and Challenges*. Rome; 2017
- [12] Nam NH, Chauhan YS, Johansen C. Effect of timing of drought stress on growth and grain yield of extra-short duration pigeon pea lines. *Journal of Agricultural Science*. 2001;**136**:179-189. DOI: 10.1017/S0021859601008607
- [13] Lopez FB, Johansen C, Chauhan YS. Effects of timing of drought stress on phenology, yield and yield components of short duration pigeon pea. *Journal of Agronomy and Crop Science*. 1996;**177**:311-320
- [14] Sayan S. Adaptive mechanisms of Black gram (*Vigna mungo* (L.) Hepper) and pigeon pea (*Cajanus cajan* (L.) Millsp.) to water stress at different growth states [PhD thesis]. The University of Queensland: School of Land, Crop and Food Sciences; 1991. DOI: 10.14264/uql.2017.579
- [15] Turner NC, Wright G, Siddique KHM. Adaptation of grain

legumes (pulses) to water-limited environments. *Advances in Agronomy*. 2001;**71**:193-231. DOI: 10.1016/S0065-2113(01)71015-2

[16] Leopold AC, Musgrave ME, Williams KM. Solute leakage resulting from leaf desiccation. *Plant Physiology*. 1981;**68**:1222-1225

[17] Kimani PM, Benzioni A, Ventura M. Genetic variation in pigeon pea (*Cajanus cajan* (L.) Mill sp.) in response to successive cycles of water stress. *Plant and Soil*. 1994;**158**:193-201. DOI: 10.1007/BF00009494

[18] Incrocci L, Pardossi A, Vernieri P, Tognoni F, Serra. Effects of heat stress and hypoxia on growth, water relations and ABA levels in bean (*Phaseolus vulgaris* L.) seedlings. *Acta Horticulturae*. 2000;**516**:31-39. DOI: 10.17660/ActaHortic.2000.516.3

[19] Mishra B. Challenges and preparedness for increasing wheat production in India. *Journal of Wheat Research*. 2007;**I**(1 and 2):1-12

[20] Kumar S. Climate change and crop breeding objectives in the twenty first century. *Current Science*. 2006;**90**:1053-1154

[21] Van Der Maesen LJG. *Cicer L.: A monograph of the genus, with special reference to the chickpea (Cicer arietinum L.) its ecology and cultivation*. Mededelingen Landbouwhogeschool Wageningen; 1972

[22] Hall AE. Breeding for heat tolerance. *Plant Breeding Review*. 1992;**10**:129-168

[23] Prasad PVV, Craufurd PQ, Summerfield RJ. Fruit number in relation to pollen production and viability in groundnut exposed to short episodes of heat stress. *Annals of*

Botany. 1999;**84**:381-386. DOI: 10.1006/anbo.1999.0926

[24] Rainey K, Griffiths PD. Evaluation of *Phaseolus acutifolius* A. Gray plant introductions under high temperatures in a controlled environment. *Genetic Resource and Crop Evolution*. 2005;**52**:117-120. DOI: 10.1007/s10722-004-1811-2

[25] Barghi SS, Mostafaii H, Peighami F, Zakaria RA. Path analysis of yield and its components in lentil under end season heat condition. *International Journal of Agriculture Research Review*. 2012;**2**:969-974

[26] Gaur PM, Kumar J, Gowda CLL, Pande S, Siddique KHM, Khan TN, et al. Breeding chick pea for early phenology: Perspectives, progress and prospects. In: Kharkwal MC, editor. *Food Legumes for Nutritional Security and Sustainable Agriculture*. Vol. 2. New Delhi, India: Indian Society of genetics and Plant Breeding; 2008. pp. 39-48

[27] Devasirvatham V, Gaur PM, Mllikarjuna N, Tokachichu RN, Trethowan RM, Tan DKY. Effect of high temperature on reproductive development of chick pea genotypes under controlled environments. *Functional Plant Biology*. 2012;**39**:1009-1018. DOI: 10.1071/FP12033

[28] Giaveno C, Ferrero J. Introduction of tropical maize genotypes to increase silage production in the central area of Santa Fe, Argentina. *Crop Breeding and Applied Biotechnology*. 2003;**3**:89-94

[29] Boote KJ, Allen LH, Prasad PVV, Baker JT, Gesch RW, Snyder AM, et al. Elevated temperature and CO₂ impacts on pollination, reproductive growth, and yield of several globally important crops. *Journal of Agricultural Meteorology*. 2005;**60**:469-474

- [30] Horváth I, Glatz A, Nakamoto H, Mishkind ML, Munnik T, Saidi Y. Heat shock response in photosynthetic organisms: Membrane and lipid connections. *Progress in Lipid Research*. 2012;**51**:208-220. DOI: 10.1016/j.plipres.2012.02.002
- [31] Rakavi B, Sritharan N. Physiological response of green gram under heat stress. *Journal of Pharmacognosy and Phytochemistry*. 2019;**SP1**:181-185
- [32] Reynolds MP, Pierre CS, Saad ASI, Vargas M, Condon AG. Evaluating potential genetic gains in wheat associated with stress-adaptive trait expression in elite genetic resources under drought and heat stress. *Crop Science*. 2007;**47**:S-172-S-189. DOI: 10.2135/cropsci.2007.10.0022 IPBS
- [33] Wang Q-L, Chen J-H, He N-Y, Guo F-Q. Metabolic reprogramming in chloroplasts under heat stress in plants. *International Journal of Molecular Sciences*. 2018;**19**:849. DOI: 10.3390/ijms19030849
- [34] Langjun C, Jianlong L, Yamin F, Sheng X, Zhen Z. High temperature effects on photosynthesis, PSII functionality and antioxidant activity of two *Festuca arundinacea* cultivars with different heat susceptibility. *Botanical Studies*. 2006;**47**:61-69
- [35] Zhao FC. Effects of heat stress during grain filling on sugar accumulation and enzyme activity associated with sucrose metabolism in sweet corn. *Acta Agronomica Sinica*. 2013;**39**:1644-1651. DOI: 10.3724/SPJ.1006.2013.01644
- [36] Suzuki N, Koussevitzky S, Mittler R, Miller G. ROS and redox signalling in the response of plants to abiotic stress. *Plant Cell Environment*. 2012;**35**:259-270. DOI: 10.1111/j.1365-3040.2011.02336.x
- [37] Meriga B, Krishna Reddy B, Rajender Rao K, Ananda Reddy L, Kavi Kishor PB. Aluminium-induced production of oxygen radicals, lipid peroxidation and DNA damage in seedlings of rice (*Oryza sativa*). *Journal of Plant Physiology*. 2004;**161**:63-68. DOI: 10.1078/0176-1617-01156
- [38] Vadez V, Soltani A, Krishnamurthy L, Sinclair TR. Modelling possible benefit of root related traits to enhance terminal drought adaption of chick pea. *Field Crops Research*. 2012;**137**:108-115. DOI: 10.1016/j.fcr.2012.07.022
- [39] Hassan M, Mansoor S. Oxidative stress and antioxidant defense mechanism in mung bean seedlings after lead and cadmium treatments. © TÜBİTAK. *Turkish Journal of Agriculture and Forestry*. 2014;**38**:55-61. DOI: 10.3906/tar-1212-4
- [40] Rodrigues CS, Laranjo M, Oliveira S. Effect of heat and pH stress in the growth of chick pea *Mesorhizobia*. *Current Microbiology*. 2006;**2006**(53):1-7
- [41] Kurdali F. Nitrogen and phosphorus assimilation, mobilization and partitioning in rainfed chick pea (*Cicer arietinum* L.). *Field Crops Research*. 1996;**47**:81-92
- [42] Minchin FR, Summerfield RJ, Hadley P, Roberts EH, Rawsthorne S. Carbon and nitrogen nutrition of nodulated roots of grain legumes. *Plant, Cell & Environment*. 1981;**4**:5-26
- [43] Rawsthorne S, Hadley P, Roberts EH, Summerfield RJ. Effects of supplemental nitrate and thermal regime on the nitrogen nutrition of chick pea (*Cicer arietinum* L.) II: Symbiotic development and nitrogen assimilation. *Plant and Soil*. 1985;**83**:279-293
- [44] Hedhly A, Hormaza JI, Herrero M. Global warming and plant sexual

reproduction. Trends Plant Science. 2008;**14**:30-36

[45] Kaushal N, Bhandari K, Siddique KHM, Nayyar H. Food crops face rising temperatures: An overview of responses, adaptive mechanisms, and approaches to improve heat tolerance. Cogent Food and Agriculture. 2016;**2**:1134380. DOI: 10.1080/23311932.2015.1134380

[46] Omae H, Kumar A, Egawa Y, Kashiwaba K, Shono M. Genotypic differences in plant water status and relationship with reproductive responses in snap bean (*Phaseolus vulgaris* L.) during water stress. Japanese Journal of Tropical Agriculture. 2005;**49**:1-7

[47] Sita K, Sehgal A, Bindumadhava HR, Nair RM, Prasad PVV, Kumar S, et al. Food legumes and rising temperatures: Effects, adaptive functional mechanisms specific to reproductive growth stage and strategies to improve heat tolerance. Frontiers in Plant Science. 2017;**8**:1658. DOI: 10.3389/fpls.2017.01658

[48] Suzuki K, Takeda H, Tsukaguchi T, Egawa Y. Ultrastructural study on degeneration of tapetum in anther of snap bean (*Phaseolus vulgaris* L.) under heat stress. Sexual Plant Reproduction. 2001;**13**:293-299. DOI: 10.1007/s004970100071

[49] Basu PS, Pratap A, Gupta S, Sharma K, Tomar R, Singh NP. Physiological traits for shortening crop duration and improving productivity of green gram (*Vigna radiata* L. Wilczek) under high temperature. Frontiers in Plant Science. 2019;**10**:1508. DOI: 10.3389/fpls.2019.01508

[50] Sung D-Y, Kaplan F, Lee K-J, Guy CL. Acquired tolerance to temperature

extremes. Trends in Plant Science. 2003;**8**:179-187

[51] Omae H, Kumar A, Kashiwaba K, Shono M. Influence of temperature shift after flowering on dry matter partitioning in two cultivars of snap bean (*Phaseolus vulgaris*) that differ in heat tolerance. Plant Production Science. 2007;**10**:14-19

[52] Omae H, Kumar A, Kashiwaba K, Shono M. Influence of high temperature on morphological characters, biomass allocation, and yield components in snap bean (*Phaseolus vulgaris* L.). Plant Production Science. 2006;**9**:200-205. DOI: 10.1626/pp.9.200

[53] Board JE, Kahlon CS. Soybean yield formation: What controls it and how it can be improved? In: ElShemy HA, editor. Soybean Physiology and Biochemistry. Rijeka: InTech Open Access; 2011. pp. 1-36

[54] Tsukaguchi T, Kawamitsu Y, Takeda H, Suzuki K, Egawa Y. Water status of flower buds and leaves as affected by high temperature in heat-tolerant and heat-sensitive cultivars of snap bean (*Phaseolus vulgaris* L.). Plant Production Science. 2003;**6**:4-27

[55] Barghi SS, Mostafaii H, Peighami F, Zakaria RA, Nejhad RF. Response of in vitro pollen germination and cell membrane thermostability of lentil genotypes to high temperature. International Journal of Agriculture Research Review. 2013;**3**:13-20

[56] Kumar U, Joshi AK, Kumari M, Paliwal R, Kumar S, Roder MS. Identification of QTLs for stay green trait in wheat (*T. aestivum* L.) in the Chirya 3'9 Sonalika' population. Euphytica. 2010;**174**:437-445. DOI: 10.1007/s10681-010-0155-6

- [57] Porch TG, Jahn M. Effects of high-temperature stress on microsporogenesis in heat-sensitive and heat-tolerant genotypes of *Phaseolus vulgaris*. *Plant Cell Environment*. 2001;**24**:723-731. DOI: 10.1046/j.1365-3040.2001.00716.x
- [58] Kumar S, Thakur P, Kaushal N, Malik JA, Gaur PM, Nayyar H. Effect of varying high temperatures during reproductive growth on reproductive function, oxidative stress and seed yield in chick pea genotypes differing in heat sensitivity. *Archives of Agronomy and Soil Science*. 2013;**59**:823-843. DOI: 10.1080/03650340.2012.683424
- [59] Kakani VG, Reddy KR, Koti S, Wallace TP, Prasad PVV, Reddy VR, et al. Differences in *in vitro* pollen germination and pollen tube growth of cotton cultivars in response to high temperature. *Annals of Botany*. 2005;**96**:59-67. DOI: 10.1093/aob/mci149
- [60] Clarke HJ, Siddique KHM. Response of chick pea genotypes to low temperature stress during reproductive development. *Field Crops Research*. 2004;**90**:323-334. DOI: 10.1016/j.fcr.2004.04.001
- [61] Ohnishi S, Miyoshi T, Shirai S. Low temperature stress at different flower developmental stages affects pollen development, pollination, and pod set in soybean. *Environment and Experimental Botany*. 2010;**69**:56-62
- [62] Pang J, Turner NC, Khan T, Du YL, Xiong JL, Colmer TD, et al. Response of chick pea (*Cicer arietinum* L.) to terminal drought: Leaf stomatal conductance, pod abscisic acid concentration, and seed set. *Journal of Experimental Botany*. 2017;**68**:1973-1985. DOI: 10.1093/jxb/erw153
- [63] Thiaw S, Hall AE. Comparison of selection for either leaf-electrolyte-leakage or pod set in enhancing heat tolerance and grain yield of cowpea. *Field Crops Research*. 2004;**86**:239-253. DOI: 10.1016/j.fcr.2003.08.011
- [64] Priya M, Dhanker OP, Siddique KHM, Bindumadhava H, Nair R, Pandey S, et al. Drought and heat stress-related proteins: An update about their functional relevance in imparting stress tolerance in agricultural crops. *Theoretical and Applied Genetics*. 2019;**132**. DOI: 10.1007/s00122-019-03331-2
- [65] Perdomo JA, Capó-Bauçà S, Carmo-Silva E, Galmés J. Rubisco and Rubisco activase play an important role in the biochemical limitations of photosynthesis in rice, wheat, and maize under high temperature and water deficit. *Frontiers in Plant Science*. 2017;**8**:490
- [66] Pradhan GP, Prasad PVV, Fritz AK, Kirkham MB, Gill BS. Effects of drought and high temperature stress on synthetic hexaploid wheat. *Functional Plant Biology*. 2012;**39**:190-198
- [67] Farooq M, Hussain M, Ul-Allah S, Siddique KHM. Physiological and agronomic approaches for improving water-use efficiency in crop plants. *Agricultural Water Management*. 2019;**219**:95-108
- [68] Lamaoui M, Jemo M, Datla R, Bekkaoui F. Heat and drought stresses in crops and approaches for their mitigation. *Frontiers in Chemistry*. 2018;**6**:26-30
- [69] Rivero RM, Mestre TC, Mittler R, Rubio F, Garcia-Sanchez F, Martinez V. The combined effect of salinity and heat reveals a specific physiological, biochemical and molecular response in tomato plants. *Plant Cell and Environment*. 2014;**37**:1059-1073

- [70] FAO. Statistical Database. Rome, Italy: Food and Agriculture Organization of the United Nations; 2016. Available from: <http://www.apps.fao.org>
- [71] Jukanti A, Gaur PM, Gowda CLL, Chibbar R. Nutritional quality and health benefits of chick pea (*Cicer arietinum* L.): A review. *The British Journal of Nutrition*. 2012;**108**(Suppl. 1):S11-S26. DOI: 10.1017/S0007114512000797
- [72] Ryan JG. A global perspective on pigeon pea and chick pea sustainable production systems: Present status and future potential. In: Asthana AN, Ali M, editors. *Recent Advances in Pulses Research*. Kanpur: Indian Institute of Pulses Research; 1977. pp. 1-31
- [73] Gaur PM, Gowda CLL, Knights EJ, Warkentin TD, Acikgoj N, Yadav SS, et al. Breeding achievements. In: Yadav SS, Redden B, Chen W, Sharma B, editors. *Chick Pea Breeding and Management*. Wallingford: CABI; 2007. pp. 391-416
- [74] Wang J, Gan YT, Clarke F, McDonald CL. Response of chick pea yield to high temperature stress during reproductive development. *Crop Science*. 2006;**46**:2171-2178. DOI: 10.2135/cropsci2006.02.0092
- [75] Fowden I, Manstield T, Stoddart J, editors. *Plant adaptation to environmental stress*. Landan. Edition I. Netherlands: Springer, Chapman and Hall; 1993:109-132
- [76] Kalra N, Chakraborty D, Sharma A, Rai HK, Jolly M, Cher S, et al. Effect of increasing temperature on yield of some winter crops in Northwest India. *Current Science*. 2008;**94**:82-88
- [77] Delahunty A, Nuttall J, Nicolas M, Brand J. Genotypic heat tolerance in lentil. In: *Proceedings of the 17th ASA Conference*, Hobart, Australia. 2015. pp. 20-24
- [78] Subbarao GV, KumarRao JVDK, Kumar J, Johansen C, Deb UK, Ahmed I, et al. *Spatial Distribution and Quantification of Rice-Fallows in South Asia-Potential for Legumes*. Patancheru, India: ICRISAT; 2001
- [79] Kaur R, Bains TS, Bindumadhava H, Nayyar H. Responses of mungbean (*Vigna radiata* L.) genotypes to heat stress. Effects on reproductive biology, leaf function and yield traits. *Scientia Horticulturae*. 2015;**197**:527-541. DOI: 10.1016/j.scienta.2015.10.015
- [80] Gaur P, Saminen S, Krishnamurthy L, Kumar S, Ghane M, Beebe S, et al. High temperature tolerance in grain legumes. *Legume Perspectives*. 2015;**7**:23-24
- [81] Scafaro AP, Haynes PA, Atwell BJ. Physiological and molecular changes in *Oryza meridionalis* Ng., a heat-tolerant species of wild rice. *Journal of Experimental Botany*. 2010;**61**:191-202. DOI: 10.1093/jxb/erp294
- [82] Murata N, Takahashi S, Nishiyama Y, Allakhverdiev SI. Photoinhibition of photosystem II under environmental stress. *Biochimica et Biophysica Acta (BBA)—Bioenergetics*. 2007;**1767**:414-421. DOI: 10.1016/j.bbabi.2006.11.019
- [83] Allakhverdiev SI, Murata N. Environmental stress inhibits the synthesis de novo of proteins involved in the photodamage–repair cycle of photosystem II in *Synechocystis* sp. PCC 6803. *Biochimica et Biophysica Acta (BBA)—Bioenergetics*. 2004;**1657**:23-32. DOI: 10.1016/j.bbabi.2004.03.003
- [84] Allakhverdiev SI, Klimov VV, Carpentier R. Evidence for 55 the involvement of cyclic electron transport in the protection of photosystem II against photoinhibition: Influence of a new phenolic compound. *Biochemistry*. 1997;**36**:4149-4154. DOI: 10.1021/bi962170

- [85] Nene YL, Sheila VK. c. In: Nene YL, Hall SD, Sheila VK, editors. Pigeon Pea. Wallingford, UK: CAB Intl; 1990. pp. 1-14
- [86] Upadhyaya HD, Kashiwagi J, Varshney R, Gaur PM, Saxena K, Krishnamurthy L, et al. Phenotyping chick peas and pigeonpeas for adaptation to drought. *Frontiers in Physiology*. 2012;**3**:179. DOI: 10.3389/fphys.2012.00179
- [87] Basu PS, Singh U, Kumar A, Praharaj CS, Shivran RK. Climate change and its mitigation strategies in pulses production. *Indian Journal of Agronomy*. 2016;**61**:S71-S82
- [88] Smertenko A, Draber P, Viklicky V, Opatrny Z. Heat stress affects the organization of microtubules and cell division in *Nicotiana tabacum* cells. *Plant Cell Environment*. 1997;**20**:1534-1542. DOI: 10.1046/j.1365-3040.1997.d01-44.x
- [89] Song Y, Chen Q, Ci D, Shao X, Zhang D. Effects of high temperature on photosynthesis and related gene expression in poplar. *BMC Plant Biology*. 2014;**14**:111. DOI: 10.1186/1471-2229-14-111
- [90] Valenzuela H, Smith J. Pigeon pea: Sustainable Agriculture Green Manure Crops Aug. 2002, SA-GM-8 Cooperative State Research, Education, and Extension Service, U.S. Department of Agriculture, and the Agricultural Experiment Station, Utah State University, under Cooperative Agreement 98-ESAG-1-0340. Portions of this text were adapted from the USDA. Natural Resources Conservation Service Hawaii Field. 2002
- [91] Zhang L, Li FG, Liu CL, Zhang CJ, Zhang XY. Construction and analysis of cotton (*Gossypium arboreum* L.) water-related cDNA library. *BMC Research Note*. 2009;**2**:120
- [92] Sekhar K, Priyanka B, Reddy VD, Rao KV. Isolation and characterization of a pigeon pea cyclophilin (*CcCYP*) gene, and its over-expression in *Arabidopsis* confers multiple abiotic stress tolerance. *Plant, Cell and Environment*. 2010;**33**:1324-1338. DOI: 10.1111/j.1365-3040.2010.02151.x
- [93] Mazars C, Thuleau P, Lamotte O, Bourque S. Cross-talk between ROS and calcium in regulation of nuclear activities. *Molecular Plant*. 2010;**3**:706-718
- [94] Sen Gupta D, Singh U, Kumar J, Shivay YS, Dutta A, Sharanagat VS, et al. Estimation and multi-variate analysis of iron and zinc concentration in a diverse panel of urdbean (*Vigna mungo* L. Hepper) genotypes grown under differing soil conditions. *Journal of Food Composition and Analysis*. 2020;**93**:103605. DOI: 10.1016/j.jfca.2020.103605
- [95] Roy SJ, Tucker EJ, Tester M. Genetic analysis of abiotic stress tolerance in crops. *Current Opinion in Plant Biology*. 2011;**14**:232-239. DOI: 10.1016/j.pbi.2011.03.002
- [96] Sinha SK. Food legumes: Distribution adaptability and biology of yield. In: Food and Agriculture Organisation of the United Nations, Plant Production and Protection Paper No. 3. Rome: FAO; 1977. p. 124
- [97] Siddique KHM, Loss SP, Regan KL, Jettner RL. Adaptation and seed yield of cool season grain legumes in Mediterranean environments of 5 South-Western Australia. *Australian Journal of Agricultural Research*. 1999;**50**:375-387. DOI: 10.1071/A98096
- [98] Landi S, Hausman JF, Guerriero G, Esposito S. Poaceae vs. abiotic stress: Focus on drought and salt stress, recent insights and perspectives. *Frontiers in Plant Science*. 2017;**8**:1214. DOI: 10.3389/fpls.2017.01214

- [99] Bindumadhava HR, Nair RM, Nayyar H. Salinity and high temperature tolerance in mungbean [*Vigna radiata* (L.) Wilczek] from a physiological perspective. *Frontiers in Plant Science*. 2016;7:957. DOI: 10.3389/fpls.2016.00957
- [100] Gaur PM, Samineni S, Thudi M, Tripathi S, Sajja SB, Jayalakshmi V, et al. Integrated breeding approaches for improving drought and heat adaptation in chick pea (*Cicer arietinum* L.). *Plant Breeding*. 2019;138:389-400. DOI: 10.1111/pbr.12641
- [101] Asseng S, Ewert F, Martre P, Rötter RP, Lobell DB, Cammarano D, et al. Rising temperatures reduce global wheat production. *Nature Climate Change*. 2015;5:143-147. DOI: 10.1038/nclimate2470
- [102] Challinor A, Wheeler T, Garforth C, Craufurd P, Kassam A. Assessing the vulnerability of food crop systems in Africa to climate change. *Climate Change*. 2007;83:381-399. DOI: 10.1007/s10584-007-9249-0
- [103] Passioura JB. Grain yield, harvest index, and water use of wheat. *Journal of the Australian Institute of Agricultural Science*. 1977;43:117-121
- [104] Turner NC. Further progress in crop water relations. *Advances in Agronomy*. 1997;528:293-338
- [105] Yadav S, Sharma KD. Molecular and morphophysiological analysis of drought stress in plants. In: Rigobelo EC, editor. *Plant Growth*. London: IntechOpen; 2016. DOI: 10.5772/65246
- [106] Subbarao G, Johansen C, Slinkard AE, Rao N, Saxena NP, Chauhan Y. Strategies for improving drought resistance in grain legumes. *Critical Reviews in Plant Sciences*. 1995;14:469. DOI: 10.1080/713608125
- [107] Davies S, Turner NC, Palta J, Siddique K, Plummer JA. Remobilisation of carbon and nitrogen supports seed filling in chick pea subjected to water deficit. *Australian Journal of Agricultural Research*. 2000;51:855-866. DOI: 10.1071/Ar00018
- [108] Basu PS, Ali M, Chaturvedi SK. Osmotic adjustment increases water uptake, remobilization of assimilates and maintains photosynthesis in chick pea under drought. *Indian Journal of Experimental Biology*. 2007;45:261-267
- [109] Wang H, Zhou Q, Mao P. Ultrastructural and photosynthetic responses of pod walls in alfalfa to drought stress. *International Journal of Molecular Sciences*. 2020;21:4457. DOI: 10.3390/ijms21124457
- [110] Atkins CA, Kuo J, Pate JS. Photosynthetic pod wall of pea (*Pisum sativum* L.): Distribution of carbon dioxide-fixing enzymes in relation to pod structure. *Plant Physiology*. 1977;60:779-786. DOI: 10.1104/pp.60.5.779
- [111] Furbank R, White R, Palta J, Turner NC. Internal recycling of respiratory CO₂ in pods of chick pea (*Cicer arietinum* L.): The role of pod wall, seed coat, and embryo. *Journal of Experimental Botany*. 2004;55:1687-1696. DOI: 10.1093/jxb/erh190
- [112] Kenneth A, Shackel TNC. Seed coat cell turgor in chick pea is independent of changes in plant and pod water potential. *Journal of Experimental Botany*. 2000;51:895-900. DOI: 10.1093/jexbot/51.346.895
- [113] Hooda RS, Rao AS, Luthra YP, Sheoran IS, Singh R. Partitioning and utilization of carbon and nitrogen for dry matter and protein production in chick pea (*Cicer arietinum* L.). *Journal of Experimental Botany*. 1986;37:1492-1502

- [114] Egli DB, Crafts-Brandner SJ. Soybean. In: Zamski E, Schaffer AA, editors. Photoassimilate Distribution in Plants and Crops. Source-sink Relationships. New York: Marcel Dekker, Inc.; 1996. pp. 595-623
- [115] Bidinger F, Musgrave RB, Fischer RA. Contribution of stored pre-anthesis assimilates to grain yield in wheat and barley. *Nature*. 1977;**270**:431-433. DOI: 10.1038/270431a0
- [116] Palta JA, Kobata T, Turner NC, Fillery IR. Remobilization of carbon and nitrogen in wheat as influenced by postanthesis water deficits. *Crop Science*. 1994;**34**:118-124. DOI: 10.2135/cropsci1994.0011183X003400010021x
- [117] Foster EF, Pajarito A, Acosta-Gallegos J. Moisture stress impact on N partitioning, N remobilization and N-use efficiency in beans (*Phaseolus vulgaris*). *Journal of Agricultural Science (Cambridge)*. 1995;**124**:27-37
- [118] Rawson HM, Evans LT. The contribution of stem reserves to grain development in a range of wheat cultivars of different height. *Australian Journal of Agricultural Research*. 1971;**22**:851-863. DOI: 10.1071/AR9710851
- [119] Bushby HVA, Lawn RJ. Accumulation and partitioning of nitrogen and dry matter by contrasting genotypes of mungbean (*Vigna radiata* (L.) Wilczek). *Australian Journal of Agricultural Research*. 1992;**43**:1609-1628
- [120] Khanna-Chopra R, Sinha SK. The chickpea book chapter: Physiological aspects of growth and yield. In: Saxena MC, Singh KB, editors. *The Chick Pea*. Wallingford, UK: CAB International; 1987:163-187. ISBN: 9780851985718
- [121] Muchow R, Sinclair T, Bennett J, Hammond L. Response of leaf growth, leaf nitrogen, and stomatal conductance to water deficits during vegetative growth of field-grown Soybean. *Crop Science*. 1986;**26**:1190-1195. DOI: 10.2135/cropsci1986.0011183X002600060024x
- [122] Mwanamwenge J, Loss SP, Siddique KHM, Cocks PS. Effect of water stress during floral initiation, flowering and podding on the growth and yield of faba bean (*Vicia faba* L.). *European Journal of Agronomy*. 1999;**11**:1-11
- [123] Krishnamurthy L, Johansen C, Ito O. Genotypic variation in root system development and its implications for drought resistance in chick pea. In: Conference Paper presented in Dynamics of roots and nitrogen in cropping systems of semi-arid tropics held at ICRISAT. Patancheru, India. January 1996. pp. 236-250
- [124] Saxena NP, Krishnamurthy L, Johansen C. Registration of a drought resistant chick pea germplasm. *Crop Science*. 1994;**33**:1424
- [125] Kashiwagi J, Krishnamurthy L, Crouch JH, Serraj R. Variability of root length density and its contributions to seed yield in chick pea (*Cicer arietinum* L.) under terminal drought stress. *Field Crops Research*. 2006;**95**:171-181
- [126] Reynolds MP, Manes Y, Izanloo A, Langridge P. Phenotyping for physiological breeding and gene discovery in wheat. *Annals of Applied Biology*. 2009;**155**:309-320
- [127] Pinto RS, Reynolds MP. Common genetic basis for canopy temperature depression under heat and drought stress associated with optimized root distribution in bread wheat. *Theoretical and Applied Genetics*. 2015;**128**:575-585. DOI: 10.1007/s00122-015-2453-9
- [128] Ludlow MM, Santamaria JM, Fukai S. Contribution of osmotic

- adjustment to grain yield in *Sorghum bicolor* (L.) Moench under water-limited conditions. II. Water stress after anthesis. *Australian Journal of Agricultural Research*. 1990;**41**:67-78
- [129] Morgan JM, Condon AG. Water use, grain yield and osmoregulation in wheat. *Australian Journal of Plant Physiology*. 1986;**13**:523-532
- [130] Crowe JH, Hoekstra FA, Crowe LM. Anhydrobiosis. *Annual Review of Physiology*. 1992;**54**:579-599
- [131] Rhodes D, Hanson AD. Quaternary ammonium and tertiary sulfonium compounds in higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology*. 1993;**44**:357-384
- [132] Shen B, Jensen RG, Bohnert HJ. Increased resistance to oxidative stress in transgenic plants by targeting mannitol biosynthesis to chloroplasts. *Plant Physiology*. 1997;**113**:1177-1183
- [133] Sinclair TR, Ludlow MM. Influence of soil water supply on the plant water balance of four tropical grain legumes. *Australian Journal of Plant Physiology*. 1986;**13**:329-341. DOI: 10.1071/PP9860329
- [134] Blum A. *Plant Breeding for Stress Environments*. Boca Raton, FL: CRC Press; 1988
- [135] Prasad PVV, Craufurd PQ, Kakani VG, Wheeler TR, Boote KJ. Influence of high temperature during pre- and post-anthesis stages of floral development on fruit-set and pollen germination in peanut. *Australian Journal of Plant Physiology*. 2001;**28**:233-240
- [136] Wassmann R, Jagadish SVK, Heuer S, Ismail A, Redoña E, Serraj R, et al. Climate change affecting rice production: The physiological and agronomic basis for possible adaptation strategies. *Advances in Agronomy*. 2009;**101**:59-122
- [137] Hedhly A. Sensitivity of flowering plant gametophytes to temperature fluctuations. *Environmental and Experimental Botany*. 2011;**74**:9-16. DOI: 10.1016/j.envexpbot. 2011.03.016
- [138] Ploeg Van der A, Heuvelink E. Influence of sub-optimal temperature on tomato growth and yield: A review. *The Journal of Horticultural Science and Biotechnology*. 2005;**80**:652-659. DOI: 10.1080/14620316.2005.11511994
- [139] Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. *International Journal of Molecular Science*. 2013;**14**:9643-9684. DOI: 10.3390/ijms14059643
- [140] Talwar HS, Yanagahira S. Physiological basis of heat tolerance during flowering and pod setting stages in groundnut *Arachis hypogaea* L. In: JIRCAS Working Report, No. 14. Tsukuba, Japan: JJRCAS; 1999. pp. 47-65
- [141] García CC, Guarnieri M, Pacini E. Inter-conversion of carbohydrate reserves from pollen maturation to rehydration in a chili pepper. *American Journal of Plant Science*. 2013;**4**:1181-1186. DOI: 10.4236/ajps.2013.46146
- [142] Song L, Jiang Y, Zhao H, Hou M. Acquired thermotolerance in plants. *Plant Cell, Tissue and Organ Culture (PCTOC)*. 2012;**111**:265-276. DOI: 10.1007/s11240-012-0198-6
- [143] Gupta S, Kaur S, Sehgal S, Sharma A, Chhuneja P, Bains NS. Genotypic variation for cellular thermotolerance in *Aegilops tauschii* Coss., the D genome progenitor of

wheat. *Euphytica*. 2010;**175**:373-381.
DOI: 10.1007/s10681-010-0185-0

[144] Berridge M, Herst P, Tan A. Tetrazolium dyes as tools in cell biology: New insights into their cellular reduction. *Biotechnology Annual Review*. 2005;**11**:127-152. DOI: 10.1016/S1387-2656(05)11004-7

[145] Blum A. Drought resistance, water-use efficiency, and yield potential—Are they compatible, dissonant, or mutually exclusive? *Australian Journal of Agricultural Research*. 1998;**56**:1159-1168. DOI: 10.1071/AR05069

[146] Ilík P, Špundová M, Šicner M, Melkovičová H, Kučerová Z, Krchňák P, et al. Estimating heat tolerance of plants by ion leakage: A new method based on gradual heating. *The New Phytologist*. 2018;**218**(3):1278-1287. DOI: 10.1111/nph.15097. Epub 2018 Mar 24

[147] Srinivasan A, Takeda H, Senboku T. Heat tolerance in food legumes as evaluated by cell membrane thermostability and chlorophyll fluorescence techniques. *Euphytica*. 1996;**88**:35-45. DOI: 10.1007/BF00029263

[148] Hu X, Li Y, Li C, Yang H, Wang W, Lu M. Characterization of small heat shock proteins associated with maize tolerance to combined drought and heat stress. *Journal of Plant Growth Regulation*. 2010;**29**:455-464. DOI: 10.1007/s00344-010-9157-9

[149] Blum A, Klueva N, Nguyen HT. Wheat cellular thermotolerance is related to yield under heat stress. *Euphytica*. 2001;**117**:117-123. DOI: 10.1023/A:100408330 5905

[150] Kim K, Portis AR. Temperature dependence of photosynthesis in *Arabidopsis* plants with modifications in Rubisco activase and membrane fluidity.

Plant & Cell Physiology. 2005;**46**:522-530. DOI: 10.1093/pcp/pci052

[151] Wang GP, Zhang XY, Li F, Luo Y, Wang W. Overaccumulation of glycine betaine enhances tolerance to drought and heat stress in wheat leaves in the protection of photosynthesis. *Photosynthetica*. 2010;**48**:117-126. DOI: 10.1007/s11099-010-0016-5

[152] Heckathorn SA, Ryan SA, Baylis JA, Wang D, Hamilton EW, Cundiff L. In vivo evidence from an *Agrostis stolonifera* selection genotype that chloroplast small heat-shock proteins can protect photosystem II during heat stress. *Functional Plant Biology*. 2002;**29**:935-946. DOI: 10.1071/PP01191

[153] Crafts-Brandner SJ, Salvucci ME. Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO₂. *Proceedings of the National Academy of Sciences*. 2000;**97**:13430-13435. DOI: 10.1073/pnas.230451497

[154] Ahmad A, Diwan H, Abrol YP. Global climate change, stress and plant productivity. In: Pareek A, Sopory SK, Bohnert HJ, Govindjee, editors. *Abiotic Stress Adaptation in Plants: Physiological, Molecular and Genome Foundation*. Dordrecht: Springer Science Business Media BV; 2010. pp. 503-521. DOI: 10.1007/978-90-481-3112-9_23

[155] Moustaka J, Ouzounidou G, Sperdouli I, Moustakas M. Photosystem II is more sensitive than photosystem I to Al³⁺-induced Phytotoxicity. *Materials*. 2018;**11**:1772. DOI: 10.3390/ma11091772

[156] Murchie EH, Lawson T. Chlorophyll fluorescence analysis: A guide to good practice and understanding some new applications. *Journal of Experimental*

Botany. 2013;**64**:3983-3998.
DOI: 10.1093/jxb/ert208

[157] Mohammed A-R, Tarpley L. Impact of high night time temperature on respiration, membrane stability, antioxidant capacity, and yield of rice plants. *Crop Science*. 2009;**49**:313-322

[158] Izanloo A, Condon AG, Langridge P, Tester M, Schnurbusch T. Different mechanisms of adaptation to cyclic water stress in two south Australian bread wheat cultivars. *Journal of Experimental Botany*. 2008;**59**:3327-3346

[159] Kalaji HM, Rastogi A, Živčák M, Brestic M, Daszkowska-Golec A, Sitko K, et al. Prompt chlorophyll fluorescence as a tool for crop phenotyping: An example of barley landraces exposed to various abiotic stress factors. *Photosynthetica*. 2018;**56**:953-961. DOI: 10.1007/s11099-018-0766-z

[160] Lípová L, Krchňák P, Josef KJ, Ilík P. Heat-induced disassembly and degradation of chlorophyll-containing protein complexes in vivo. *Biochimica et Biophysica Acta*. 2010;**1797**:63-70. DOI: 10.1016/j.bbabi.2009.08.001

[161] Cramer WA, Whitmarsh J, Low PS. Differential scanning calorimetry of chloroplast membranes: Identification of endothermic transition associated with the water-splitting complex of photosystem II. *Biochemistry*. 1981;**20**:157-162. DOI: 10.1021/bi00504a026

[162] Smith KA, Ardelit BK, Huner NPA, Krol M, Myscich E, Low PS. Identification and partial characterization of the denaturation transition of the light harvesting complex II of spinach chloroplast membranes. *Plant Physiology*. 1989;**90**:492-499

[163] Willits DH, Peet MM. Measurement of chlorophyll fluorescence as a heat

stress indicator in tomato: Laboratory and greenhouse comparisons. *Journal of American Society of Horticultural Science*. 2001;**126**:188-194. DOI: 10.21273/JASHS.126.2.188

[164] Chen J, Burke JJ, Xin Z. Chlorophyll fluorescence analysis revealed essential roles of FtsH11 protease in regulation of the adaptive responses of photosynthetic systems to high temperature. *BMC Plant Biology*. 2018;**18**:11. DOI: 10.1186/s12870-018-1228-2

[165] Chen J, Xu W, Velten J, Xin Z, Stout J. Characterization of maize inbred lines for drought and heat tolerance. *Journal of Soil and Water Conservation*. 2012;**2012**(67):354-364

[166] Redondo-Gómez S. Abiotic and biotic stress tolerance in plants. In: Rout GR, Das AB, editors. *Molecular Stress Physiology of Plants*. New Delhi: Springer India; 2013. pp. 1-20

[167] Choudhury FK, Rivero RM, Blumwald E, Mittler R. Reactive oxygen species, abiotic stress and stress combination. *The Plant Journal*. 2017;**90**:856-867

[168] Suzuki N, Rivero RM, Shulaev V, Blumwald E, Mittler R. Abiotic and biotic stress combinations. *New Phytology*. 2014;**203**:32-43. DOI: 10.1111/nph.12797

[169] Kiani R, Arzani A, Mirmohammady Maibody SA, Rahimmalek M, Razavi K. Morpho-physiological and gene expression responses of wheat by *Aegilops cylindrica* amphidiploids to salt stress. *Plant Cell, Tissue and Organ Culture (PCTOC)*. 2021;**144**:619-639

[170] Rana JC, Gautam NK, Gayacharan MS, Yadav R, Tripathi K, Yadav SK, et al. Genetic resources of pulse crops in India: An overview. *Indian Journal of Genetics and Plant Breeding*. 2016;**76**:420-436

[171] Choudhary AK, Sultana R, Vales MI, Saxena KB, Kumar RR, Ratnakumar P. Integrated physiological and molecular approaches to improvement of abiotic stress tolerance in two pulse crops of the semi-arid tropics. *Crop Journal*;6:99-114

[172] Maxted N, Kell SP. Establishment of a Global Network for the *in Situ* Conservation of Crop Wild Relatives: Status and Needs. FAO Commission on Genetic Resources for Food and Agriculture: Roman, Italy; 2009

[173] Brumlop S, Reichenbecher W, Tappeser B, Finckh M. What is the SMARTest way to breed plants and increase agrobiodiversity? *Euphytica*. 2013;194. DOI: 10.1007/s10681-013-0960-9

[174] Kumar J, Choudhary A, Gupta DS, Kumar S. Towards exploitation of adaptive traits for climate-resilient smart pulses. *International Journal of Molecular Sciences*. 2019;20:10.3390/ijms20122971

[175] Kole C, Muthamilarasan M, Henry R, Edwards D, Sharma R, Abberton M, et al. Application of genomics-assisted breeding for generation of climate resilient crops: Progress and prospects. *Frontiers in Plant Science*. 2015;6. Available from: <https://www.frontiersin.org/article/10.3389/fpls.00563DOI=10.3389/fpls.2015.00563>

[176] Varshney RK, Pandey MK, Bohra A, Singh VK, Thudi M, Saxena RK. Toward the sequence -based breeding in legumes in the post-genome sequencing era. *Theoretical and Applied Genetics*. 2019;132:797-816