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



122,000

135M



Our authors are among the

TOP 1%





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

Chickpea Abiotic Stresses: Combating Drought, Heat and Cold

Peter Kaloki, Viola Devasirvatham and Daniel K.Y. Tan

Abstract

Chickpea is an important legume providing dietary proteins to both humans and animals. It also ameliorates soil nitrogen through biological nitrogen fixation. Drought, heat and cold are important factors among abiotic stresses limiting production in chickpea. Identification, validation and integration of agronomic, physiological and biochemical traits into breeding programs could lead to increased rates of genetic gain and the development of better adapted cultivars to abiotic stress conditions. This chapter illustrates the effects of stresses on chickpea growth and development. It also reviews the various traits and their relationship with grain yield under stress and proposes recommendation for future breeding.

Keywords: abiotic stresses, chickpea, cold, drought, genomic regions, heat, phenotyping, quantitative trait loci (QTL) and traits

1. Introduction

Chickpea is the third most important food legume globally after dry beans and dry peas [1]. It is grown on 12.4 million hectares (mean of 2010–2012, FAOSTAT) producing 11.3 million tonnes at an average yield of 910 kg/ha (mean of 2010–2012, FAOSTAT) [2]. Chickpea is an important legume in many farming systems and provides biological N fixation which benefits the entire farming system.

However, chickpea production is hampered by biotic and abiotic constraints depending on the ecological region. Among abiotic stresses, drought, heat and cold stresses are the most important yield limiting factors [3, 4]; accounting for up to 50% of chickpea production losses for drought, and 15–20% of yield losses for low and high temperatures [5]. This situation is exacerbated by climate change which may cause higher intensity and frequency of droughts, heat waves and cold spills in the arid and semi-arid areas [6] where chickpea is traditionally cultivated.

Improvements in chickpea abiotic stresses responses have been slowed by the complex inheritance of tolerance, the multi-dimensional nature of stress and the fact that various agronomic, physiological and biochemical changes occur in plants that are difficult to predict [3]. Jha et al. [7] suggest that abiotic stresses are limited by quantitative inheritance and large genotype x environment interaction.

It is important to integrate physiological traits into crop improvement; however, plant breeders have largely focused on empirical selection for yield [8, 9]. This may be a result of the challenges associated with measuring physiological traits

compared with other easily measured traits such as photosynthetic rate or carbon isotopic discrimination as well as lack of proper multidisciplinary training [10]. Although traditional plant breeding contributed to increased yields [11], largely attributed to environmental adjustments, genotype and their interaction [12], recent rates of yield increase have started to plateau [13]. However, agronomic, physiological and biochemical traits and their correlation with grain yield under stressed and non-stressed conditions are important to select genotypes by screening [14]. Tolerance to abiotic stresses is influenced by polygenes. Under abiotic stress conditions, many factors and their interaction are involved at a particular time which affects crop growth and yield. To define abiotic stresses in a target environment, the above-mentioned should be considered [15]. This chapter explains the background of major abiotic stresses such as drought, heat and cold and breeding strategies to improve tolerance in chickpea along with present molecular breeding approaches.

2. Drought stress

2.1 The concept of physiological breeding and its current status

Physiological breeding relies on the identification of traits which are later used as indirect selection criteria in core breeding or in introgression programs [8]. Fischer [16] proposed two approaches which can be used for trait identification namely, the black box and the ideotype approaches. The black box approach entails evaluation of genotypes in a specified limiting factor (e.g. drought) and measuring trait associations with economic performance. This method aims to identify and characterise the underlying factors that contribute to the target trait. In contrast, the ideotype approach predicts the desired genotype in the target environment and this is used as a blueprint for cultivar development. The target environment should be as homogeneous as possible and the selection process well managed to reduce confounding factors which may affect trait expression [9]. Nevertheless, most target environment type, based on long-term environmental records, should be targeted [17].

Target physiological traits for drought response should be easy to measure, highly heritable and correlated with yield. They should not limit yield when conditions are conducive nor have negative pleiotropic effects on other traits of economic importance [18]. As such, developing high yielding cultivars which show plasticity is vital since they can maintain yield in water limited environments and at the same time take advantage of excess moisture during wet years [18]. These physiological traits influence yield through additive gene action [19].

There are several traits that can be targeted in physiological breeding which may help increase yield either directly or indirectly. Some examples include selection for optimised plant height, especially in temperate crops to reduce lodging and to increase harvest index under favourable conditions [18]. Genes that govern plant height have contributed to higher yields by ensuring that more assimilates are partitioned to the grains and the reproductive organs instead of the stem [20]. This reduction in plant height was the key driver of the Green Revolution which saw a quadrupling of wheat and rice yields across much of Asia [21]. Selection for flowering time is also very important, especially in water limited environments since it may have a direct effect on yield [22].

Some research organisations including CIMMYT Mexico are practicing physiological breeding but generally the research arena is still in its infancy. There have been several success stories recently in physiological breeding in wheat, soybean,

sunflower, sorghum and maize. These examples are summarised by Richards [18] and include increased axial resistance in wheat whereby reduced xylem vessel diameter in the seminal roots increased hydraulic resistance and thus decreased extraction of water from the subsoil, reduced anthesis to silking interval in maize leading to increased yields, increased ability of soybean to fix nitrogen under drought environments, improved transpiration efficiency in wheat and sunflower via selection for low carbon discrimination, stay green trait in sorghum where plants delay senescence and sanction further uptake of soil water and nitrogen (**Figure 1**).

Step 1: Trait identification based on association with vield

- Select experimental conditions to match target environment
- Selection of traits with high variability and heritability
- Selection of experimental material with similar phenology but contrasting genetic potential
- •Selection of an experimental site similar to target environment
- Design and implement proper protocols for data capture
- •Measure the association of the trait with yield

Step 2: Quantifying heritability and gains from selecion

Develop populations from contrasting parents with respect to traits of interest
Measure heritability and gains obtained from selection
Integrate selected traits into breeding program

Figure 1.

Schematic illustration of physiological breeding compiled from Reynolds and Trethowan [9].

2.2 Phenotyping target physiological traits in chickpea

Over the last century, breeders have made progress in drought tolerance by selecting constitutive traits that affect dehydration avoidance rather than drought responsive traits because of fewer yield penalties [23]. Target traits in water limited environments should be correlated with yield and should have higher heritability than yield [24]. Phenotyping these traits should also be non-destructive, accurate, cheap and inexpensive [25]. The phenotypic performance needs to be associated with genotypic data to understand the genetic basis of complex these traits [26]. For phenotyping to be successful and relevant, environmental characterisation [25, 27] is vital so that genotype by environment interactions can be exploited [17].

Phenotyping of large plant populations for various traits in the field can be labour intensive and expensive. However, the emergence of high-throughput genotyping platforms such as near infra-red spectroscopy and multi-spectral reflectance makes it possible to phenotype large populations in multi-locations [26]. Chickpea phenotyping for drought tolerance has focused on selection for early maturity to avoid drought and root traits to confer water-use-efficiency under drought [28]. Phenotyping for water use efficiency in chickpea has been conducted using gravimetric methods in a pot culture [28]; however these methods do not generally correlate well with field conditions.

Near infrared spectroscopy has been used to capture differences in dry matter, starch and crude proteins [26]. Spectral reflectance allows monitoring of various dynamic complex traits using high temporal resolution without interfering with the plant [26]. It can be used to measure canopy architecture, nitrogen concentration and water status [26]. Other measurements can be taken on individual plants including plant photosynthesis pigment composition and water status (**Figure 2**) [29].



Figure 2. Some target traits for chickpea physiological breeding.

2.2.1 Canopy temperature

Canopy temperature is an indirect indicator of crop water status since water deficit results in partial stomatal closure, thus reducing transpiration and in effect causing sunlit leaves to become warmer than the ambient temperature [30]. Since transpiration has a cooling effect on canopies, cooler plant canopies indicate higher transpiration rates. This is one of the many factors that affect plant canopy temperature. Others include incident radiation, wind and relative humidity [31]. Under water limited conditions, cooler canopy temperatures are related to the capacity of plants to extract soil water from deep in the subsoil, whereas under well-watered conditions sink strength and photosynthetic capacity are more important [32]. The hand-held canopy temperature gun is a simple and rapid method of determining canopy temperatures. However, in very large populations it may be limiting. Thermal imagery systems are more amenable to high throughput phenotyping for canopy temperature in large populations [33]. Canopy temperature is quite sensitive to environmental conditions and caution should be taken while taking the measurements. Good results are achieved when the conditions are ideal for high vapour pressure deficit (VPD), in conditions of warm air, generally above 15°C and relative humidity of less than 60% with clear sunny skies and low wind speeds [32].

2.2.2 Plant vigour and plant green biomass

Over the years remote sensing imagery has gained popularity because it is not limited by sampling interval or geostatistical interpolation [34], does not involve destructive sampling and it is amenable to high throughput. The premise for using optical remote sensing for crop assessment is that crop canopy multispectral reflectance and temperature is associated with photosynthesis and evaporation whereby leaf area index (LAI) and crop development stage are central [35].

Several indices have been developed which are used to analyse aerial imagery [36] including the Normalised Difference Vegetation Index (NDVI). The NDVI links reflectance in the red region and the NIR to vegetation parameters such as canopy cover, leaf area index and the concentration of total chlorophyll [36]. Korobov and Railyan [37] concluded that the NIR and red areas of the spectrum correlated highly with plant parameters such as plant height, plant density and percent plant cover.

Initially, NDVI was used for estimating green biomass [38]; however, it was subsequently used to assess crop health [39, 40].

2.2.3 Photosynthetically active radiation (PAR)

The photosynthetic active radiation spectrum (PAR), which consists of 50% of total global radiation [41], lies in the wavelength $0.4-0.7 \mu m$ [42]. The crop canopy absorbs PAR, referred to as intercepted photosynthetically active radiation (IPAR) to aid photosynthesis, eventually producing biomass [43]. The radiation intercepted during the growing period is determined by the canopy radiation extinction coefficient (k) and is influenced by leaf orientation and the green leaf area [44]. Research has shown that lower k values are associated with narrow and erect leaves compared to plant genotypes with more horizontal leaf arrangements [45]. Lower k values allow more light to penetrate the canopy and illuminate more leaf area in conditions of low light intensity, thus increasing carbon exchange rates and consequently, radiation use efficiency [45].

The fraction of intercepted photosynthetically active radiation can be used to estimate the leaf area index (LAI) by relationship with the plant canopy [43]. This provides an easy and non-destructive way of estimating the leaf area index. IPAR can be accurately determined using a ceptometer, though care should be taken to avoid confounding factors such as the soil albedo, row spacing and lack of canopy uniformity [46].

2.2.4 Chlorophyll content

There is a close relationship between chlorophyll concentration, leaf nitrogen content and crop yield [47]. This relationship arises because the majority of leaf nitrogen is usually contained in the chlorophyll [47]. Since chlorophyll absorbs PAR, which aids in photosynthesis, it indicates the strength of the internal leaf apparatus during photosynthesis [48].

Leaf chlorophyll content can be determined by extraction with organic solvents including acetone [49] and methanol [50] and subsequent quantification using a spectrometer; however this method is expensive and time consuming [51]. A higher throughput non-destructive method is the SPAD chlorophyll meter which allows rapid and inexpensive assessment of leaf greenness [52]. SPAD measures leaf absorbance in the red (650 nm) and infrared (940 nm) regions [53] and gives readings that have been correlated with chlorophyll content under different moisture regimes in many crops [51].

2.2.5 Root traits

Plants extract water from the soil through the roots and the spatial distribution of the root system influences water and nutrient intake capacity [54]. Dense root systems are more efficient at extracting water from the top soil horizon whereas deeper rooting systems better extract water from the lower soil horizons. These contrasting traits are important influences on yield under water deficit conditions during the reproductive stage in many crops [55]. Kashiwagi, Krishnamurthy [56] showed that root architecture affects transpiration by influencing soil moisture use and subsequent harvest index in terminal drought. However, the heritability of these root characteristics will determine their utility in plant breeding. Varshney et al. [57] reported genetic variation for both root length density and root depth in chickpea and found heritabilities ranging from medium to low. Root hydraulic conductivity impacts the amount of water taken up by the plant and is determined by the anatomy and morphology of the roots and their aquaporin activity [58]. In legumes, root hydraulic conductivity is influenced by the total root length since water is absorbed along the full root length [58].

Root phenotyping is difficult and for this reason the literature on chickpea is not extensive. However, Kashiwagi et al. [56] and Zaman-Allah et al. [59] used polyvinyl chloride (PVC) cylinders (lysimeters) to grow chickpeas for assessment. The soil was subsequently washed off from sampled plants to measure total rooting depth. Image analysis software (WinRhizo, Regent Instruments INC., Canada) was then used to estimate the root length at various sections of the lysimeters and divided by the specific volume of that section to determine the root length density.

2.2.6 Transpiration efficiency

Transpiration efficiency is an important yield determinant under drought [60] and as such can be targeted in a breeding program. Carbon isotope discrimination (CID) can be used as a surrogate to measure transpiration efficiency compared with the more tedious gravimetric methods [61].

Carbon isotope composition of plant dry matter was used to evaluate the relative differences of Ci/Ca in C3 species [62]. The stable carbon isotope (¹³C), which constitutes 1% of total atmospheric CO₂, is usually lower in plant dry matter than in the atmosphere since C3 plants discriminate against ¹³C during photosynthesis. Carbon isotope discrimination (Δ^{13} C), is the value of the ratio of ¹³C/¹²C in plant material in relation to the same value of the ratio of the air that plants use [63]. However, transpiration efficiency is a conservative trait that both limits water loss through reduced transpiration and photosynthesis through stomatal closure. While selection for CID will optimise survival under drought stress, yield will be limited under more favourable conditions due to lower stomatal conductance.

2.2.7 Water use efficiency (WUE)

WUE in agriculture can be considered at the whole plant (ratio of total dry matter produced to total water used), economic yield (ratio of crop grain per unit area to transpiration) and leaf (ratio of instantaneous carbon dioxide assimilation rate to transpiration rate at the stomata) levels [64].

At the leaf level, crop water loss is as a result of differences in water vapour concentration between the crop canopy and the atmosphere and is least during cool humid periods of the season. Thus, the rates of CO_2 assimilation (A) and transpiration (T) are a product of stomatal conductance, either of CO_2 (g_c) and water vapour (g_w) or the gradient of either CO_2 ($C_a - C_i$) or water vapour ($W_i - W_a$) between the air outside and

inside the leaf [65]. Theoretically, W_T can be improved by lowering the value of C_i/C_a , albeit trade-offs are likely to occur [65]. However, breeders have successfully selected for lower C_i/C_a to produce materials with low stomatal conductance in wheat, higher photosynthetic capacity or a combination of both [62]. There is substantial genetic variation for C_i/C_a determined through $\Delta^{13}C$ which is large enough to cause variation in A/T and consequently WUE for dry matter production [63]. Rebetzke et al. [66] showed that $\Delta^{13}C$ is a highly heritable trait that can be manipulated through plant breeding. Thus increasing intrinsic WUE has been an attractive crop breeding target for many years [16]. By exploiting genetic variation associated with intrinsic earliness and response to photoperiod, breeders have developed genotypes that can grow when the evaporative demand is low, which in turn raises the ratio of A/T and increases yield [67].

Traits associated with water use efficiency have been identified including CID, where low CID implies higher transpiration efficiency resulting from low stomatal conductance, delayed leaf senescence or stay green, spike photosynthesis which results in high water use efficiency due to partial re-fixation of respiratory carbon dioxide, and subcellular processes such as photo-protective mechanisms [68]. These traits can be used as surrogates if yield penalties are not very high.

2.3 Biochemical traits and their relationship with drought tolerance

Production of various secondary metabolites through alteration of plant biochemical tissue profile is one of the ways plants respond to abiotic stresses [69]. The production of the secondary metabolites may be initiated by lipid peroxidation [70] and they help in the protection of membrane lipids from oxidative stress [71]. In order to prevent oxidative damage in plant tissue under water stress conditions, both enzymatic and non-enzymatic antioxidant systems are involved [69]. These include ascorbate, reduced glutathione, β -carotenes, carotenoids, α -tocopherol, peroxidase, catalase, superoxide dismutase, glutathione reductase, polyphenol oxidase and ascorbate peroxidase [69]. The activity levels of the enzymes in the antioxidant system have been used to indicate stress tolerance capabilities for plants exposed to stress conditions [72].

Water stress results in an increase in the production of reactive oxygen species which causes a risk to the plant since it causes the peroxidation of membrane lipids, damage to nucleic acids and the denaturation of proteins [73, 74]. Plants exposed to water stress over a prolonged period of time suffer from extensive cellular damage and eventual death as a result of reactive oxygen species overpowering the scavenging action of the antioxidant system [69].

Hydrogen peroxide plays two roles in plants depending on its concentration. At low levels, it acts as a signal molecule that triggers tolerance to many biotic and abiotic stresses whereas at high levels it causes programmed cell death [69]. Many studies have shown hydrogen peroxide to be an important regulator in many physiological processes including stomatal movement [75], photorespiration and photosynthesis [76], senescence [77], cell division cycle [73] and growth and development [78].

Soluble sugar (fructose, glucose and sucrose) accumulation in plants is closely linked to drought tolerance [69]. Soluble sugars protect plant cells under drought conditions by interacting with proteins and membranes through hydrogen bonding thus inhibiting protein denaturation and secondly, by maintaining structural and functional integrity of macromolecules through vitrification [69].

2.4 Identifying genomic regions linked to physiological traits through association analysis

Genetic association analysis (linkage disequilibrium analysis) is used to identify quantitative trait loci (QTL) by linking the phenotype to the genotype. It exploits

historical and evolutionary recombination events at the population level to resolve complex variation up to the sequence level [79]. Phenotypic variation of complex traits in plant species is influenced by multiple QTLs and their interaction with themselves (epistasis) and the environment [80]. Association analysis frequently used [80] because of increased mapping resolution, greater allele number and efficiency [81]. The technique can be applied to a wide array of germplasm from natural populations to study complex trait variation whereas traditional linkage analysis provides information on specific parents [80]. Recent association studies include disease resistance in potato [82], flowering time in maize [83] and iron deficiency chlorosis in soybean [84].

Many QTLs in chickpea for various traits including plant height, plant canopy cover, number of branches per plant, number of pods per plant, 1000 seed weight and days to maturity have been identified using linkage mapping. Gowda et al. [85] identified 41 and 65 QTLs for these traits using single locus QTL analysis from two intraspecific chickpea mapping populations, JG 62 X Vijay and Vijay X ICC 4958, respectively. Rehman et al. [86] found multiple QTLs from a kabuli biparental population of ILC 588 X ILC 3279 for grain yield, harvest index, drought tolerance score, days to flowering, days to maturity and plant height. They also identified two QTLs for stomatal conductance in linkage group (LG) 7 and 3 and six for canopy temperature differential in LG 1, LG 3, LG 4, LG 6 and LG 7. These genomic regions were associated with traits that confer higher productivity under drought stress. The studies of Rehman et al. [86] identified 15 genomic regions associated with drought tolerance traits. Genomic regions on LG 1 and LG 3 were strongly associated with days to flowering, days to maturity, harvest index, reproductive period, canopy temperature differential, plant height and grain yield under drought. Of particular interest was Q3-1 on LG 3 which explained most of the important drought traits. These traits included enhanced stomatal conductance (Q3-3) in LG 3 and cooler canopies (Q1-1 and Q3-2). Hamwieh et al. [87] reported 93 significant QTLs in an intraspecific mapping population developed between ILC 588 and ILC 3279. However, only 8 of these QTLs were expressed in more than one environment. Nevertheless, these authors found a significant QTL region measuring 12.1 cM for days to flowering, drought resistance score, grain yield, days to maturity, harvest index, number of seeds per plant, biological yield and number of pods per plant on LG 3. A second QTL spanning 0.68 cM was detected in the same linkage group which influenced 1000 seed weight, number of pods per plant, percent empty pods, number of seeds plant and biological yield [87]. Clearly, the LG 3 and LG 4 regions appear to have a strong effect on yield under stress. These QTLs appear to be pleiotropic for a number of traits and selection for those with the highest heritability should assist crop improvement for drought stress response [87]. Furthermore, one genomic region concealing QTL for selected drought tolerant traits has been identified and introgressed into three popular chickpea varieties by using a markerassisted back crossing approach [88]. This attempt will lead to develop improved lines with greater drought tolerance.

3. Heat stress

3.1 Context of heat stress

Adverse effect of heat stress on grain legumes is increasing due to global warming. Chickpea is an important grain legume mostly grown in semi-arid regions which frequently encounters of heat waves that affects crop growth and yield [89]. High temperatures stress in chickpea production is mainly associated with climate

change (e.g. summer dominant rainfall zone in Australia) and changes in cropping systems that have shifting chickpea production from cooler region to warmer region (e.g. India) [90, 91]. Both situations, the crop is experiencing high temperature during reproductive stage. Therefore, the effects of heat stress on chickpea growth, development and yield are important to understand by observing agronomic, physiological and biochemical traits to develop high temperature tolerant cultivars.

3.2 Agronomic traits and their relationship with grain yield

Generally, temperature (>30°C) limited yield in cool season legumes such as chickpea, lentil, faba bean and field peas [92–95]. Plant growth, phenology, biomass accumulation and yield are important agronomic traits which depends on the crop ability to withstand or acclimate under abiotic stress [96]. Phenological traits such as days to first flowering, days to 50% flowering and days to crop maturity plays a major role under high temperature. Under stress plants forced to maturity i.e. escaping from heat. Therefore, earliness can be observed through phenological traits. Significant variation in phenology in chickpea under heat stress was observed. Particularly, days to 50% flowering was delayed and days to crop maturity was hastened due to requirement of thermal time (growing degree days °C) to attain any developmental stage [92]. Furthermore, grain yield under heat stress was negatively associated with phenology. To eliminate heat escape, classification of genotypes based on maturity (short, medium and long duration) and stress tolerance index would helpful to identify the genotypes that could be used for future breeding [92, 97].

Plant height, plant width, biomass accumulation, pod number, filled pod number, seed number per plant and grain yield are also plays significant role under high temperature. Plant height and width was affected under heat stress as well as biomass accumulation, pod number and seed weight [92, 98]. Generally, high temperature reduces the duration of plant developmental stages and carbon assimilation process within the plant, resulting low biomass production and reduces source-sink activity (yield) [99]. The most affected yield traits in chickpea are pod number per plant and harvest index. Similar findings have been found in lentil [100].

3.3 Physiological traits and their relationship with grain yield

The difference between heat tolerant and sensitive genotypes of legumes can be identified on the basis of physiological traits such as photosynthetic activity, canopy temperature, CO₂ uptake and membrane thermostability. There are limited research findings available in cool season grain legumes for physiological traits and their relationship with heat stress. Generally, high temperature can negatively affect photosynthesis. The sensitive chickpea genotype at 40/30°C reduced chlorophyll content with a symptom of chlorosis leaves. The symptom of chlorosis in heat stressed plants is common and it was evident in mung bean [101]. Due to inhibition of chlorophyll synthesis, the chlorophyll content may be affected under stress. However, the tolerant chickpea genotype maintained greater chlorophyll content and photochemical efficiency than sensitive genotypes [101] which correlated with yield reduction in sensitive genotypes [102]. This is a clear example to screen genetic material based on photosynthetic activity for heat tolerance.

High temperature affects membrane structure and function. Stress injury can be regulated by loss of membrane integrity and leakage of ions from cells [103]. Therefore, monitoring the function of membrane through electrolyte leakage has been used to screen thermostability under high temperature. The effects of heat stress on the function of membrane has been studied in legumes. Cell membrane thermostability and its correlation with sensitivity was observed by Srinivasan, Takeda [104] and chickpea is the most sensitive crop to high temperature. Similarly, membrane thermostability had linked with sensitivity in chickpea, lentil and faba bean [105]. In lentil, high temperature increased electrolyte leakage due to membrane damage [106]. Thus, membrane damage can be considered as an indicator of heat stress tolerance in legumes and can be used as a physiological trait for screening. Furthermore, Awasthi et al., [107] suggested that drought or heat and combined stresses decreased cellular oxidising ability, stomatal conductance, PSII function and leaf chlorophyll content in chickpea.

Transpiration is the main reason of changes in leaf temperature due to abiotic stresses [105, 108]. Canopy temperature can be sustained through transpiration by open stomata and maintained cool canopy. It was confirmed as an important physiological trait in wheat for high temperature tolerance [109]. In addition to that, canopy temperature depression (CTD) is an indicator of the difference between plant canopy and air temperature. Since the plant closes stomata for certain period due to stress, this will change canopy temperature [33]. Canopy temperature was observed and CTD was calculated using a large set of chickpea genotypes in the field for heat tolerance [97]. Therefore, CTD can be used as a screening method in legumes [97] as it is widely used in cereals [110].

3.4 Biochemical traits and their relationship with grain yield

Soluble sugars play an essential role in plant metabolism, energy production, sugar sensing and signalling in the plant. Generally, biochemical responses in plants observe in the reproductive stage i.e. final stage of grain legumes which involves synthesis of carbohydrates, proteins and lipids in seeds [111]. A positive correlation was found between seed dry weight and sucrose synthase activity under water stress in chickpea [112]. In chickpea, starch metabolism in the leaves affects sucrose availability in the developing seeds and the activities of enzymes related to these metabolic pathways were assessed by Awasthi et al. [107]. Starch concentration, the starch synthesising enzyme were increased under heat-stressed chickpea plants than non-stressed plants. In the seed, the activity of enzyme was inhibited under heat stress. Sucrose in leaves and seeds, sucrose synthase in leaves and seeds and starch phosphorylase in seeds had strong correlation with seed weight per plant and biomass production under heat stress [107]. In lentil, sucrose concentration, sucrose phosphate synthase activity in leaves was significantly low under stressed condition compared non-stressed conditions, finally which influenced seed yield. Similar results were found in wheat under stress and furthermore wheat flour quality was affected [113]. This research confirms that biochemical traits are also plays a role in grain yield under heat stress.

3.5 Pollen as a trait and its relationship with pod set

In legumes, reproductive stage is known to be more sensitive to high temperature than vegetative stage. In reproductive stage, pre-anthesis, anthesis and post-anthesis are important developmental stages which are considered to be sensitive stages among flowering. Heat stress affects reproductive development in chickpea [114], lentil [115], common bean [116] and soybean [117]. Male (anther, pollen) and female organs (stigma-style, ovary) of flowers are severally affected by heat stress (\geq 30°C) associated with abscission of flower buds, flowers and pods, leading to significant yield loss [118, 119]. Recent findings in legumes revealed that pollen grains are more susceptible to high temperature, thus; chickpea (35/20°C) [114], lentil (35/25°C) [115], soybean (34/24°C) [117]. The effects of high temperature stress

in cereals such as wheat, maize and barley also suggested that male reproductive organs might be more sensitive than female organs [120]. Pollen sterility depends on tapetum (anther tissue) and pollen mother cell for pollen formation [121]. Under heat stress, pollen grain fertility is also associated with sucrose content in leaves and anthers [102, 122]. Under stress, pollen tube growth rate also plays an important role [123]. Pollen sterility due to heat stress in cool season legumes such as chickpea and lentil affects pod set and yield [124, 125]. Generally, pollen morphology, in vitro pollen germination and stigma length is a good predictor for hybridization success in lentil [126]. Therefore, analysis of pollen viability and pod set under high temperature is a trait for the study of high temperature tolerance in chickpea.

3.6 Genomic regions linked to heat tolerance

In the recent years, molecular markers have been used to understand quantitatively important traits and markers linked to genomic regions (Quantitative Trait Loci—QTL/genes). Through association analysis, markers have been used to identify the QTLs/genes linked with economically important traits [85]. Association analysis has been clearly comprehended in cereals such as wheat [127, 128], maize [129], barley [130], and sorghum [131]. In winter wheat, QTLs and markers associated with seedling heat tolerance was studied which is useful for early planting and dual-purpose wheat breeding in United States [128]. In legumes, very limited reports are available for association studies particularly under abiotic stress. Association analysis was conducted to identify genomic regions linked to heat tolerance in chickpea. In this study, 107 DArT markers were linked with 11 traits under heat stressed and non-stressed conditions. Four agronomic traits such as total number of pods, filled pods, number of seeds and grain yield were linked to DArT markers under heat stressed and non-stressed conditions. Many significant mapped markers associated in genomic regions in the current study align with previously reported QTLs that influence traits such as plant height, plant width, pod number and grain yield. Therefore, this study identified genomic regions associated with heat tolerance in chickpea and identification of the genes or QTLs linked to this response is the obvious next step [124]. Thudi et al., [88] suggested that 100-seed weight is an important trait linked with 70 significant markers under drought and heat stresses. Other traits such as transpiration efficiency, plant height, root dry weight, pods per plant and yield had significant association under stress. This information can be used for further validation and provide base knowledge to develop tolerant chickpea varieties for drought and heat. Recently, QTLs responsible for traits such as number of filled pods per plot, total number of seeds per plot, grain yield per plot and % pod set were found [132]. The markers linked to QTLs under heat stress will enable marker assisted breeding in the future and assist to understand the mechanism of heat tolerance.

4. Cold stress

4.1 Context of cold stress

Chickpea experiences low temperature $(0-12^{\circ}C)$ in north India and Australia as a spring crop. It is grown in Western Asia and North Africa and Europe as a winter crop which experiences freezing temperature (down to $-10^{\circ}C$) [133, 134]. Low temperature has negative impact on yield and 15–20% of yield loss was estimated [15]. Temperature below 15°C during flowering leads to flower and pod abortion then poor yield [135, 136]. Therefore, the effects of low and freezing temperatures in vegetative and reproductive stages need to study by observing agronomic, physiological and biochemical traits to develop cold temperature tolerant cultivars.

4.2 Agronomic traits and their relationship with grain yield

Chickpea crop is affected by low temperature during flowering (<10°C) in India and Australia. Therefore, low temperature tolerant cultivars or varieties having ability to set pod at <8°C is needed [15]. Low temperature during vegetative stage produced poor vegetative growth, biomass production and yield in north India. While in middle-eastern regions needs chilling tolerance from vegetative to reproductive stage. Germination and early vegetative period are important growth stages under low temperature tolerance [137]. Screening methods for chilling temperatures ranges—1–7°C with pod set developed by ICRISAT [138]. For freezing temperature during early vegetative stage or seedling stage plants were scored using scale 1–9 [139]. Toker [140] found that selected wild *Cicer* species had more freezing tolerance than well-known cold tolerant cultivars.

The effect of chilling range of temperature depends on the phenological stage of the crop. At germination, it causes poor crop establishment and vegetative stage, it results poor crop growth and dry matter accumulation which leads to reduced source-sink production and potential yield [141]. Generally, winter sown chickpea produces more vegetative structure and intercepts with photosynthetically active radiation (PAR) with sufficient dry matter production [142]. Improved exploitation of PAR increases total biomass production and sustains the harvest index similar to spring sown crop [143]. At low temperature, pod set was observed however, seed development was affected. Day and night temperatures play an important role in seed development for cold tolerance [144]. Kanouni et al. [134] suggested that seed yield and had significant correlation with number of secondary branches for freezing temperature tolerance. Correlation between 100 seed weight and cold tolerance rate was also significant. Those traits are important agronomic traits for cold and freezing tolerance.

4.3 Physiological and biochemical traits and their relationship with grain yield

Generally, cold stress causes damage to photosystem II and reduces the stability of chloroplast membranes and photosynthesis. It is confirmed in soybean [145]. Cold stress also results in membrane integrity leading to solute leakage. Under freezing temperature, ice formation in plant tissues is a major injury leads to dehydration [146]. Studies at biochemical level have been reported different changes in crops such as soluble carbohydrate content, soluble protein content and degree of fatty acid content in the shoot cells that perform to complement cold acclimation [147–149]. Elevation of abscisic acid (ABA) and calcium is also associated with cold acclimation [150, 151]. Effect of cold acclimation (1–7°C) on chickpea early vegetative stage was observed by [152]. At 4°C, the electrolyte leakage increased and triphenyl tetrazolium (TTC) content was decreased, finally relative growth rate of root also stopped. ABA content increased in cold acclimated seedling than nonacclimated. The non-acclimated seedlings exposed to 4°C with ABA application showed cold acclimation like response by increasing soluble carbohydrate content. This is an evidence for cold tolerance influenced by ABA content [153]. Later, the influence of ABA application on 40 days old plants and its biomass production and yield was observed in the field [154]. The application of ABA reduces the lowtemperature induced biomass production and responsible for yield improvements due to additional photosynthesis [154]. Therefore, ABA application confers cold tolerance in chickpea. Similar effects have been reported in soybean and other grain crops such as rice and maize [155].

4.4 Pollen as a trait and its relationship with pod set

The failure of pod set at low temperature (15–20°C for day and <8°C for night) was observed in chickpea [156] which shows the sensitivity of reproductive organs to cold. At low temperature (15/0°C; 15/5°C) pollen viability and pollen tube growth was affected and pod set was reduced [157]. Clarke and Siddique [158] confirmed the results of Srinivasan, Saxena [157] and justified that low temperature stress during pollen development caused changes in pollen viability and following seed set. It shows the sensitivity of meiosis in the male gametophyte under cold stress. Therefore, pollen viability and its relationship with pod set, seed development and yield are an indirect trait for cold tolerance in chickpea.

4.5 Genomic regions linked to cold tolerance

Limited information is available on the chromosomal locations on the genes and QTLs for cold tolerance in cool season legumes. A study on QTL mapping for winter hardiness in lentil found that cold tolerance is a multi-genic trait. Seven QTLs were identified for winter hardiness in lentil [159]. Recently association analysis of cold and drought stresses along with Ascochyta blight in chickpea was studied using amplified fragment length polymorphism (AFLP) markers [160]. The AFLP markers linked to genes controlling stem number, first effective raining after sowing to 50% flowering, maturity, partial tolerance to Ascochyta blight, 100 seed weight and yield were identified. Identified markers for cold and drought tolerance were not significant. Furthermore, there is no evidence for QTLs reported for cold tolerance in chickpea. Therefore, finding of molecular markers associated with genes controlling different traits under stress could increase the efficiency of marker assisted breeding for abiotic stresses [160].

5. Conclusion and recommendation

Abiotic stresses limit chickpea productivity by affecting its growth and development. Drought, high and low temperatures generally have negative effects on reproductive stage. Freezing temperatures have a negative impact on crop establishment. High and low temperatures affect pollen viability, pollen tube growth and pod set where as in drought more field-based research is needed to confirm effect of stress on male and female organs. Therefore, pollen can be used as a trait under temperature stress. But, correlation between pollen viability and grain yield needs to be comprehended. Physiological and biochemical traits are also affected by abiotic stresses. The effects of combined stresses on physiological and biochemical traits should also be explored. However, more studies are required in chickpea to better understand the relationships among economically important traits and yield and their influence on grain quality under stress conditions. In addition, QTLs for several drought tolerance traits have been identified that can be targeted for molecular breeding. In this context, QTLs for heat and cold tolerance traits have limited information. In future identifying QTLs that explains significant variation in pollen viability under stress and linked markers would accelerate the breeder's interest.

Intechopen

Author details

Peter Kaloki^{*}, Viola Devasirvatham and Daniel K.Y. Tan Faculty of Science, School of Life and Environmental Sciences, Plant Breeding Institute, Sydney Institute of Agriculture, The University of Sydney, Cobbitty, NSW, Australia

*Address all correspondence to: p.kaloki@ymail.com

IntechOpen

© 2019 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] Parthasarathy Rao P, Birthal PS, Bhagavatula S, Bantilan MCS. Chickpea and Pigeonpea Economies in Asia: Facts, Trends and Outlook. Andhra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics; 2010

[2] FAOSTAT. In: Kashiwagi J, Krishnamurthy L, Gaur PM, Upadhyaya HD, Varshney RK, Tobita S, editors. Traits of Relevance to Improve Yield Under Terminal Drought Stress in Chickpea (*C. arietinum* L): Field Crops Research; 2012. pp. 88-95

[3] Gunes A, Inal A, Adak MS, Bagci EG, Cicek N, Araslan F. Effect of drought stress implemented at pre- or postanthesis stage on some physiological parameters as screening criteria in chickpea cultivars. Journal of Plant Physiology. 2008;55(1):59-67

[4] Boyer JS. Plant productivity and environment. Science. 1982;**218**:443-448

[5] Varshney R, Thudi M, Nayak S,
Gaur P, Kashiwagi J, Krishnamurthy L,
et al. Genetic dissection of drought
tolerance in chickpea (*Cicer arietinum*L.). Theoretical and Applied Genetics.
2013;127:1-18

[6] IPCC. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, editors. Climate Change 2007: The Physical Science Basis. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press; 2007

[7] Jha UC, Chaturvedi SK, Bohra A, Basu PS, Khan MS, Barh D. Abiotic stresses, constraints and improvement strategies in chickpea. Plant Breeding. 2014;**133**(2):163-178

[8] Jackson P, Robertson M, Cooper M, Hammer G. The role of physiological understanding in plant breeding: From a breeding perspective. Field Crops Research. 1996;**49**(1):11-37

[9] Reynolds M, Trethowan R, van Ginkel M, Rajaran S. Application of physiology in wheat breeding. In: Reynolds M, Ortiz-Monasterio JI, McNab A, editors. Application of Physiology in Wheat Breeding. Mexico: CIMMYT; 2001

[10] Quisenberry JE. The interface between plant physiology and genetics.In: Mauney JR, Stewart JM, editors.Cotton Physiology. Vol. 1. Memphis, Tennessee: The Cotton Foundation; 1986. pp. 633-639

[11] Innes NL. The contribution from conventional plant-breeding. Proceedings of the Royal Society of Edinburgh Section B—Biological Sciences. 1992;**99**:1-10

[12] Simmonds NW. Genotype (G), environment (E) and GE components of crop yields. Experimental Agriculture.1981;17(4):355-362

[13] Araus JL, Slafer GA, Royo C, Serret MD. Breeding for yield potential and stress adaptation in cereals.Critical Reviews in Plant Sciences.2008;27(6):377-412

[14] Porch TG. Application of stress indices for heat tolerance screening of common bean. Journal of Agronomy and Crop Science. 2006;**192**(5):390-394

[15] Chaturvedi S, Mishra D, Vyas P,Mishra N. Breeding for cold tolerance in chickpea. Trends in Biosciences.2009;2(2):1-4

[16] Fischer RA. Optimizing the use of water and nitrogen through breeding of crops. Plant and Soil. 1981;**58**(1-3):249-278 [17] Trethowan RM. Defining a genetic ideotype for crop improvement. In: Fleury D, Whitford R, editors. Crop Breeding: Methods and Protocols. New York, NY: Springer; 2014. pp. 1-20

[18] Richards RA. Physiological traits used in the breeding of new cultivars for water-scarce environments. Agricultural Water Management.
2006;80(1-3):197-211

[19] Topal A, Aydın C, Akgün N, Babaoglu M. Diallel cross analysis in durum wheat (*Triticum durum* Desf.): Identification of best parents for some kernel physical features. Field Crops Research. 2004;**87**(1):1-12

[20] Richards RA. The effect of dwarfing genes in spring wheat in dry environments. 1. Agronomic characteristics. Australian Journal of Agricultural Research. 1992;**43**(3):517-527

[21] Trethowan R, Reynolds M. Drought resistance: Genetic approaches for improving productivity under stress.In: Wheat Production in Stressed Environments. Dordrecht: Springer;2007. pp. 289-299

[22] Siddique KHM, Tennant D, Perry MW, Belford RK. Water-use and water-use efficiency of old and modern wheat cultivars in a Mediterraneantype environment. Austalian Journal of Agricultural Research. 1990;**41**(3):431-447

[23] Blum A. Drought adaptation in cereal crops. In: Ribaut J, editor. Drought Adaptation in Cereals. New York: Food Products Press; 2006

[24] Monneveux P, Ribaut J-M. Secondary traits for drought tolerance improvement in cereals. In: Ribaut J-M, editor. Drought Adaptation in Cereals. New York: Food Products Press; 2006

[25] Tuberosa R. Phenotyping droughtstressed crops: Key concepts, issues, and approaches. In: Monneveux P, Ribaut J, editors. Drought Phenotyping in Crops: From Theory to Practice. Mexico: CGIAR Generation Challenge Programme; 2011. pp. 3-24

[26] Montes JM, Melchinger AE, Reif JC. Novel throughput phenotyping platforms in plant genetic studies. Trends in Plant Science. 2007;**12**(10):433-436

[27] Chenu K, Cooper M, Hammer GL, Mathews KL, Dreccer MF, Chapman SC. Environment characterization as an aid to wheat improvement: Interpreting genotype-environment interactions by modelling water-deficit patterns in North-Eastern Australia. Journal of Experimental Botany. 2011;**62**(6):1743-1755

[28] Upadhyaya HD, Kashiwagi J, Varshney RK, Gaur PM, Saxena KB, Krishnamurthy L, et al. Phenotyping chickpeas and pigeonpeas for adaptation to drought. In: Monneveu P, Ribau J-M, editors. Drought Phenotyping in Crops: From Theory to Practice: Generation Challenge Program (GCP); 2011

[29] Peñuelas J, Filella I. Visible and near-infrared reflectance techniques for diagnosing plant physiological status. Trends in Plant Science. 1998;**3**(4):151-156

[30] Jackson RD, Reginato RJ, Idso SB. Wheat canopy temperature: A practical tool for evaluating water requirements. Water Resources Research. 1977;**13**(3):651

[31] Mariano CC, Pietragalla J, Reynolds M. Canopy temperature and plant water relations traits. In: Reynolds M, Pask A, Mullan D, editors. Physiological Breeding I: Interdisciplinary Approaches to Improve Crop Adaptation. Mexico: CIMMYT; 2012. pp. 60-68

[32] Pietragalla J. Canopy temperature. In: Pask AJD, Pietragalla J, Mullan DM,

Reynolds MP, editors. Physiological Breeding II: A Field Guide to Wheat Phenotyping. Mexico: CIMMYT; 2012

[33] Kashiwagi J, Krishnamurthy L, Upadhyaya HD, Gaur PM. Rapid screening technique for canopy temperature status and its relevance to drought tolerance improvement in chickpea. Journal of SAT Agricultural Research. 2008;**6**:1-4

[34] Moran MS, Inoue Y, Barnes EM. Opportunities and limitations for image-based remote sensing in precision crop management. Remote Sensing of Environment. 1997;**61**(3):319-346

[35] Bauer ME. Spectral inputs to crop identification and condition assessment. Proceedings of the IEEE. 1985;**73**(6):1071-1085

[36] Shanahan JF, Schepers JS, Francis DD, Varvel GE, Wilhelm WW, Tringe JM, et al. Use of remote-sensing imagery to estimate corn grain yield. Agronomy Journal. 2001;**93**(3):583-589

[37] Korobov RM, Railyan VY. Canonical correlation relationships among spectral and phytometric variables for 20 winter-wheat fields. Remote Sensing of Environment. 1993;**43**(1):1-10

[38] Tucker CJ. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing of Environment. 1979;8(2):127-150

[39] Douglas Ramsey R, Falconer A, Jensen JR. The relationship between NOAA-AVHRR NDVI and ecoregions in Utah. Remote Sensing of Environment. 1995;**53**(3):188-198

[40] Teillet PM. An algorithm for the radiometric and atmospheric correction of AVHRR data in the solar reflective channels. Remote Sensing of Environment. 1992;**41**(2):185-195

[41] Bonhomme R. Beware of comparing RUE values calculated from PAR vs solar

radiation or absorbed vs intercepted radiation. Field Crops Research. 2000;**68**(3):247-252

[42] Zhang L, Zhang S, van der Werf W, Bastiaans L, Li B, Spiertz JHJ. Light interception and utilization in relay intercrops of wheat and cotton. Field Crops Research. 2008;**107**(1):29-42

[43] Johnson MVV, Kiniry JR, Burson BL. Ceptometer deployment method affects measurement of fraction of intercepted photosynthetically active radiation. Agronomy Journal. 2010;**102**(4):1132-1137

[44] Thomson BD, Siddique KHM. Grain legume species in low rainfall Mediterranean-type environments
II. Canopy development, radiation interception, and dry-matter production. Field Crops Research.
1997;54(2):189-199

[45] Kiniry JR, Simpson CE, Schubert AM, Reed JD. Peanut leaf area index, light interception, radiation use efficiency, and harvest index at three sites in Texas. Field Crops Research. 2005;**91**(2):297-306

[46] Andrade FH, Calviño P, Cirilo A, Barbieri P. Yield responses to narrow rows depend on increased radiation interception. Agronomy Journal. 2002;**94**(5):975-980

[47] Cartelat A, Agati G, Moya I, Cerovic ZG, Goulas Y, Meyer S, et al. Optically assessed contents of leaf polyphenolics and chlorophyll as indicators of nitrogen deficiency in wheat (*Triticum aestivum* L.). Field Crops Research. 2005;**91**(1):35-49

[48] Li R-h, P-g G, Michael B, Stefania G, Salvatore C. Evaluation of chlorophyll content and fluorescence parameters as indicators of drought tolerance in barley. Agricultural Sciences in China. 2006;5(10): 751-757 [49] Liu YB, Zhang TG, Wang J.
Photosynthesis and metabolite
levels in dehydrating leaves of
Reaumuria soongorica. Acta Biologica
Cracoviensia Series Botanica.
2008;50(1):19-26

[50] Cenkci S, Ciğerci İH, Yıldız M, Özay C, Bozdağ A, Terzi H. Lead contamination reduces chlorophyll biosynthesis and genomic template stability in *Brassica rapa* L. Environmental and Experimental Botany. 2010;**67**(3):467-473

[51] Jangpromma N, Songsri P, Thammasirirak S, Jaisil P. Rapid assessment of chlorophyll content in sugarcane using a SPAD chlorophyll meter across different water stress conditions. Asian Journal of Plant Sciences. 2010;**9**(6):368-374

[52] Ahmed SU. Effects of soil water deficit on leaf nitrogen, chlorophylls and spad chlorophyll meter reading on growth stages of soybean. Bangladesh Journal of Botany. 2011;**40**(2):171-175

[53] Markwell J, Osterman JC, Mitchell JL. Calibration of the Minolta SPAD-502 leaf chlorophyll meter. Photosynthesis Research. 1995;**46**(3):467-472

[54] Lynch J. Root architecture and plant productivity. Plant Physiology. 1995;**109**(1):7-13

[55] Ludlow MM, Muchow RC. A critical evaluation of traits for improving crop yields in water-limited environments. Advances in Agronomy. 1990;**43**(C):107-153

[56] Kashiwagi J, Krishnamurthy L, Crouch JH, Serraj R. Variability of root length density and its contributions to seed yield in chickpea (*Cicer arietinum* L.) under terminal drought stress. Field Crops Research. 2006;**95**(2):171-181

[57] Varshney RK, Tripathi S, Rathore A, Jukanti AK, Jayalakshmi V, Vemula A, et al. Genetic dissection of drought tolerance in chickpea (*Cicer arietinum* L.). Theoretical and Applied Genetics. 2014;**127**(2):445-462

[58] Bramley H, Turner NC,
Turner DW, Tyerman SD. Roles of morphology, anatomy, and aquaporins in determining contrasting hydraulic behavior of roots. Plant Physiology.
2009;150(1):348-364

[59] Zaman-Allah M, Jenkinson DM,
Vadez V. A conservative pattern of
water use, rather than deep or profuse
rooting, is critical for the terminal
drought tolerance of chickpea.
Journal of Experimental Botany.
2011;62(12):4239-4252

[60] Passioura JB. Grain yield, harvest index, and water use of wheat. Journal of the Australian Institute of Agricultural Science. 1977;**43**:117-120

[61] Krishnamurthy L, Vadez V, Varshney RK, Kashiwagi J, Tobita S, Ito O, et al. Variation in carbon isotope discrimination and its relationship with harvest index in the reference collection of chickpea germplasm. Functional Plant Biology. 2013;**40**(12):1350-1361

[62] Farquhar GD, Ehleringer
JR, Hubick KT. Carbon isotope
discrimination and photosynthesis.
Annual Review of Plant Biology.
1989;40(1):503-537

[63] Farquhar GD, Richards RA. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Australian Journal of Plant Physiology. 1984;**11**(6):539

[64] Ali MH, Talukder MSU.Increasing water productivity in crop production—A synthesis.Agricultural Water Management.2008;95(11):1201-1213

[65] Condon AG, Richards RA, Rebetzke GJ, Farquhar GD. Improving intrinsic water-use efficiency and crop yield. Crop Science. 2002;**42**(1):122-131

[66] Rebetzke GJ, Condon AG, Richards RA, Farquhar GD. Selection for reduced carbon isotope discrimination increases aerial biomass and grain yield of rainfed bread wheat. Crop Science. 2002;**42**(3):739-745

[67] Condon AG, Richards RA, Rebetzke GJ, Farquhar GD. Breeding for high water-use efficiency. Journal of Experimental Botany. 2004;55(407):2447-2460

[68] Reynolds M, Tuberosa R. Translational research impacting on crop productivity in drought-prone environments. Current Opinion in Plant Biology. 2008;**11**(2):171-179

[69] Bahadur A, Chatterjee A, Kumar R, Singh M, Naik PS. Physiological and biochemical basis of drought tolerance in vegetables. Vegetable Science. 2011;**38**(1):1-16

[70] Shohael AM, Ali MB, Yu KW, Hahn EJ, Islam R, Paek KY. Effect of light on oxidative stress, secondary metabolites and induction of antioxidant enzymes in *Eleutherococcus senticosus* somatic embryos in bioreactor. Process Biochemistry. 2006;**41**(5):1179-1185

[71] Zhu Z, Liang Z, Han R. Saikosaponin accumulation and antioxidative protection in droughtstressed *Bupleurum chinense* DC. Plants. Environmental and Experimental Botany. 2009;**66**(2):326-333

[72] Iturbe-Ormaetxe I, Becana M. Oxidative damage in pea plants exposed to water deficit or paraquat. Plant Physiology. 1998;**116**(1):173-181

[73] Mittler R. Oxidative stress, antioxidants and stress tolerance.Trends in Plant Science.2002;7(9):405-410

[74] Smirnoff N. The role of active oxygen in the response of plants to water-deficit and desiccation. New Phytologist. 1993;**125**(1):27-58 [75] Bright J, Desikan R, Hancock JT, Weir IS, Neill SJ. ABA-induced NO generation and stomatal closure in arabidopsis are dependent on H_2O_2 synthesis. The Plant Journal. 2006;**45**(1):113-122

[76] Noctor G, Foyer CH. A re-evaluation of the ATP : NADPH budget during C-3 photosynthesis: A contribution from nitrate assimilation and its associated respiratory activity. Journal of Experimental Botany. 1998;**49**(329):1895-1908

[77] Quan LJ, Zhang B, Shi WW, Li HY. Hydrogen peroxide in plants: A versatile molecule of the reactive oxygen species network. Journal of Integrative Plant Biology. 2008;**50**(1):2-18

[78] Foreman J, Jones JDG, Davies JM, Dolan L, Demidchik V, Bothwell JHF, et al. Reactive oxygen species produced by NADPH oxidase regulate plant cell growth. Nature. 2003;**422**(6930):442-446

[79] Nordborg M, Tavaré S. Linkage disequilibrium: What history has to tell us. Trends in Genetics: TIG. 2002;**18**(2):83-90

[80] Zhu C, Gore M, Buckler E, Yu J. Status and prospects of association mapping in plants. Plant Genome. 2008;**1**:5-20

[81] Yu J, Buckler ES. Genetic association mapping and genome organization of maize. Current Opinion in Biotechnology. 2006;**17**(2):155-160

[82] Malosetti M, van der Linden CG, Vosman B, van Eeuwijk FA. A mixedmodel approach to association mapping using pedigree information with an illustration of resistance to *Phytophthora infestans* in potato. Genetics. 2007;**175**(2):879-889

[83] Thornsberry JM, Goodman MM, Doebley J, Kresovich S, Nielsen D, Buckler ES. Dwarf8 polymorphisms associate with variation in flowering time. Nature Genetics. 2001;**28**(3):286-289

[84] Wang J, McClean PE, Lee R,
Goos RJ, Helms T. Association mapping of iron deficiency chlorosis loci in soybean (*Glycine max*L. Merr.) advanced breeding lines.
Theoretical and Applied Genetics.
2008;**116**(6):777-787

[85] Gowda SJM, Radhika P, Mhase LB, Jamadagni BM, Gupta VS, Kadoo NY. Mapping of QTLs governing agronomic and yield traits in chickpea. Journal of Applied Genetics. 2011;**52**:9-21

[86] Rehman AU, Malhotra RS, Bett K, Tar'an B, Bueckert R, Warkentin TD. Mapping QTL associated with traits affecting grain yield in Chickpea (*Cicer arietinum* L.) under terminal drought stress. Crop Science. 2011;**51**(2):450-463

[87] Hamwieh A, Imtiaz M, Malhotra RS. Multi-environment QTL analyses for drought-related traits in a recombinant inbred population of chickpea (*Cicer arietinum* L.). Theoretical and Applied Genetics. 2013;**126**(4):1025-1038

[88] Thudi M, Upadhyaya HD, Rathore A, Gaur PM, Krishnamurthy L, Roorkiwal M, et al. Genetic dissection of drought and heat tolerance in chickpea through genome-wide and candidate gene-based association mapping approaches. PLoS One. 2014;**9**(5):e96758

[89] Jumrani K, Bhatia VS. Impact of elevated temperatures on growth and yield of chickpea (*Cicer arietinum* L.). Field Crops Research. 2014;**164**:90-97

[90] Gowda CLL, Rao PP, Tripathi S, Gaur PM, Deshmukh RB. Regional shift in chickpea production in India. In: Milestones in Food Legumes Research. Kanpur, India: Indian Institute of Pulses Research; 2009. pp. 21-35

[91] Anwar MR, O'Leary G, Brand J, Redden RJ. Crop simulation model for yield prediction. In: Yadav SS, Redden RJ, Chen W, Sharma B, editors. Chickpea Breeding and Management. UK: CABI; 2007. pp. 575-597

[92] Krishnamurthy L, Gaur P, Basu P, Chaturvedi S, Tripathi S, Vadez V, et al. Large genetic variation for heat tolerance in the reference collection of chickpea (*Cicer arietinum* L.) germplasm. Plant Genetic Resources. 2011;**9**(1):59-69

[93] Bhandari K, Sharma KD, Rao BH, Siddique KH, Gaur P, Agrawal SK, et al. Temperature sensitivity of food legumes: A physiological insight. Acta Physiologiae Plantarum. 2017;**39**(3):68

[94] Bishop J, Potts SG, Jones HE. Susceptibility of faba bean (*Vicia faba* L.) to heat stress during floral development and anthesis. Journal of Agronomy and Crop Science. 2016;**202**(6):508-517

[95] Jiang Y, Lahlali R, Karunakaran C, Kumar S, Davis AR, Bueckert RA. Seed set, pollen morphology and pollen surface composition response to heat stress in field pea. Plant, Cell & Environment. 2015;**38**(11):2387-2397

[96] Prasad P, Staggenborg S, Ristic Z. Impacts of drought and/or heat stress on physiological, developmental, growth, and yield processes of crop plants. In: Response of Crops to Limited Water: Understanding and Modeling Water Stress Effects on Plant Growth Processes. American Society of Agronomy, Crop Science Society of America and Soil Science Society of America; 2008 (response of crops). pp. 301-355

[97] Devasirvatham V, Gaur P, Raju T, Trethowan R, Tan D. Field response of chickpea (*Cicer arietinum* L.) to high temperature. Field Crops Research. 2015;**172**:59-71

[98] Upadhyaya HD, Dronavalli N, Gowda C, Singh S. Identification and evaluation of chickpea germplasm for

tolerance to heat stress. Crop Science. 2011;**51**(5):2079-2094

[99] Harding SA, Guikema JA, Paulsen GM. Photosynthetic decline from high temperature stress during maturation of wheat: II. Interaction with source and sink processes. Plant Physiology. 1990;**92**(3):654-658

[100] Kumar J, Kant R, Kumar S, Basu P, Sarker A, Singh N. Heat tolerance in lentil under field conditions. Legume Genomics and Genetics. 2016;7:1-11

[101] Kumar S, Kaur R, Kaur N, Bhandhari K, Kaushal N, Gupta K, et al. Heat-stress induced inhibition in growth and chlorosis in mungbean (*Phaseolus aureus* Roxb.) is partly mitigated by ascorbic acid application and is related to reduction in oxidative stress. Acta Physiologiae Plantarum. 2011;**33**(6):2091

[102] Kaushal N, Awasthi R, Gupta K, Gaur P, Siddique KHM, Nayyar H. Heat-stress-induced reproductive failures in chickpea (*Cicer arietinum*) are associated with impaired sucrose metabolism in leaves and anthers. Functional Plant Biology. 2013;**40**(12):1334

[103] Salvucci ME, Crafts-Brandner SJ. Mechanism for deactivation of Rubisco under moderate heat stress. Physiologia Plantarum. 2004;**122**(4):513-519

[104] Srinivasan A, Takeda H, Senboku T. Heat tolerance in food legumes as evaluated by cell membrane thermostability and chlorophyll fluorescence techniques. Euphytica. 1996;**88**(1):35-45

[105] Ibrahim HM. Heat stress in food legumes: Evaluation of membrane thermostability methodology and use of infra-red thermometry. Euphytica. 2011;**180**(1):99-105

[106] 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. 2013;**3**(1):13

[107] Awasthi R, Kaushal N, Vadez V, Turner NC, Berger J, Siddique KH, et al. Individual and combined effects of transient drought and heat stress on carbon assimilation and seed filling in chickpea. Functional Plant Biology. 2014;**41**(11):1148-1167

[108] Blum A. Plant Breeding for Stress Environments. Boca Raton, FL: CRC Press; 1988

[109] Munjal R, Rana R. Evaluation
of physiological traits in wheat
(*Triticum aestivum* L.) for terminal high
temperature tolerance. In: Proceedings
of the Tenth International Wheat
Genetics Symposium, Poestum, Italy.
2003

[110] Rosyara UR, Subedi S, Duveiller E, Sharma RC. The effect of spot blotch and heat stress on variation of canopy temperature depression, chlorophyll fluorescence and chlorophyll content of hexaploid wheat genotypes. Euphytica. 2010;**174**(3):377-390

[111] Weschke W, Panitz R, Sauer N, Wang Q, Neubohn B, Weber H, et al. Sucrose transport into barley seeds: Molecular characterization of two transporters and implications for seed development and starch accumulation. The Plant Journal. 2000;**21**(5):455-467

[112] Turner NC, Furbank RT, Berger JD, Gremigni P, Abbo S, Leport L. Seed size is associated with sucrose synthase activity in developing cotyledons of chickpea. Crop Science. 2009;**49**(2):621-627

[113] Dias AS, Bagulho AS, Lidon FC. Ultrastructure and biochemical traits of bread and durum wheat grains under heat stress. Brazilian Journal of Plant Physiology. 2008;**20**(4):323-333 [114] Devasirvatham V, Gaur PM, Mallikarjuna N, Tokachichu RN, Trethowan RM, Tan DK. Effect of high temperature on the reproductive development of chickpea genotypes under controlled environments. Functional Plant Biology. 2012;**39**(12):1009-1018

[115] Sita K, Sehgal A, Kumar J, Kumar S, Singh S, Siddique KH, et al. Identification of high-temperature tolerant lentil (*Lens culinaris* Medik.) genotypes through leaf and pollen traits. Frontiers in Plant Science. 2017;**8**:744

[116] Gross Y, Kigel J. Differential sensitivity to high temperature of stages in the reproductive development of common bean (*Phaseolus vulgaris* L.). Field Crops Research. 1994;**36**(3):201-212

[117] Jumrani K, Bhatia VS, Pandey GP. Screening soybean genotypes for high temperature tolerance by in vitro pollen germination, pollen tube length, reproductive efficiency and seed yield. Indian Journal of Plant Physiology. 2018;**23**(1):77-90

[118] Nakano H, Kobayashi M, Terauchi T. Sensitive stages to heat stress in pod setting of common bean (*Phaseolus vulgaris* L.). Japanese Journal of Tropical Agriculture. 1998;**42**(2):78-84

[119] Duthion C, Pigeaire A. Seed lengths corresponding to the final stage in seed abortion of three grain legumes. Crop Science. 1991;**31**(6):1579-1583

[120] Sakata T, Higashitani A. Male sterility accompanied with abnormal anther development in plants—Genes and environmental stresses with special reference to high temperature injury. International Journal of Plant Developmental Biology. 2008;**2**(4):42-51

[121] Zinn KE, Tunc-Ozdemir M, Harper JF. Temperature stress and plant sexual reproduction: Uncovering the weakest links. Journal of Experimental Botany. 2010;**61**(7):1959-1968

[122] Kumar S, Thakur P, Kaushal N, Malik JA, Gaur P, Nayyar H. Effect of varying high temperatures during reproductive growth on reproductive function, oxidative stress and seed yield in chickpea genotypes differing in heat sensitivity. Archives of Agronomy and Soil Science. 2013;**59**(6):823-843

[123] Hedhly A, Hormaza JI, Herrero M. Global warming and sexual plant reproduction. Trends in Plant Science. 2009;**14**(1):30-36

[124] Devasirvatham V, Gaur PM, Mallikarjuna N, Raju TN, Trethowan RM, Tan DK. Reproductive biology of chickpea response to heat stress in the field is associated with the performance in controlled environments. Field Crops Research. 2013;**142**:9-19

[125] Sita K, Sehgal A, HanumanthaRao B, Nair RM, Vara Prasad P, 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

[126] Fratini R, Ruiz ML. Interspecific hybridization in the genus Lens applying in vitro embryo rescue. Euphytica. 2006;**150**(1-2):271-280

[127] Neumann K, Kobiljski B, Denčić S, Varshney R, Börner A. Genome-wide association mapping: A case study in bread wheat (*Triticum aestivum* L.). Molecular Breeding. 2011;**27**(1): 37-58

[128] Maulana F, Ayalew H, Anderson JD, Kumssa TT, Huang W, Ma X-F. Genome-wide association mapping of seedling heat tolerance in winter wheat. Frontiers in Plant Science. 2018;**9**:1-16

[129] Lu Y, Yan J, Guimaraes CT, Taba S, Hao Z, Gao S, et al. Molecular

characterization of global maize breeding germplasm based on genomewide single nucleotide polymorphisms. Theoretical and Applied Genetics. 2009;**120**(1):93-115

[130] Cockram J, White J, Leigh FJ, Lea VJ, Chiapparino E, Laurie DA, et al. Association mapping of partitioning loci in barley. BMC Genetics. 2008;**9**(1):16

[131] Shehzad T, Iwata H, Okuno K. Genome-wide association mapping of quantitative traits in sorghum (*Sorghum bicolor* (L.) Moench) by using multiple models. Breeding Science. 2009;**59**(3):217-227

[132] Paul PJ, Samineni S, Thudi M, Sajja SB, Rathore A, Das RR, et al. Molecular mapping of QTLs for heat tolerance in chickpea. International Journal of Molecular Sciences. 2018;**19**(8):2166

[133] Toker C, Lluch C, Tejera NA, Serraj R, Siddique KHM. Abiotic stresses. In: Yadav SS, Redden RJ, Chen W, Sharma B, editors. Chickpea Breeding and Management. UK: CABI; 2007

[134] Kanouni H, Farayedi Y, Saeid A,
Sabaghpour SH. Stability analyses for seed yield of chickpea (*Cicer arietinum* L.) genotypes in the western cold zone of Iran. Journal of Agricultural Science.
2015;7(5):219

[135] Sharma P, Shekhon HS, JS S, editors. Cold tolerance studies in chickpea (*Cicer arietinum*). In: 4th International Food Legume Research Conference (IFLRC-IV). New Delhi, India: Consultative Group on International Agricultural Research (CGIAR); 2005

[136] Ali M, Kumar S. Chickpea(*Cicer arietinum* L.) research in India: Accomplishments and future strategies.Indian Journal of Agricultural Sciences.2005;**75**:125-133 [137] Singh KB, Malhotra RS, Halila MH, Knights EJ, Verma MM. Current status and future strategy in breeding chickpea for resistance to biotic and abiotic stresses. Euphytica. 1993;**73**(1): 137-149

[138] ICRISAT. Chickpea kabuli varietyICCV6. In: ICRISAT, editor. PlantMaterial Description ICRISAT No. 124.1989

[139] Singh KB, Malhotra RS, Saxena MC. Chickpea evaluation for cold tolerance under field conditions. Crop Science. 1989;**29**(2):282-285

[140] Toker C. Preliminary screening and selection for cold tolerance in annual wild Cicer species. Genetic Resources and Crop Evolution. 2005;**52**(1):1-5

[141] Croser JS, Clarke HJ, Siddique KHM, Khan TN. Low-temperature stress: Implications for chickpea (*Cicer arietinum* L.) improvement. Critical Reviews in Plant Sciences. 2003;**22**(2):185-219

[142] Singh KB, Omar M, Saxena MC, Johansen C. Screening for drought resistance in spring chickpea in the Mediterranean Region^{*}. Journal of Agronomy and Crop Science. 1997;**178**(4):227-235

[143] Siddique K, Sedgley R. Chickpea
(*Cicer arietinum* L.), a potential grain
legume for South-Western Australia:
Seasonal growth and yield. Australian
Journal of Agricultural Research.
1986;37(3):245-261

[144] Srinivasan A, Johansen C, Saxena NP. Cold tolerance during early reproductive growth of chickpea (*Cicer arietinum* L.): Characterization of stress and genetic variation in pod set. Field Crops Research. 1998;**57**(2):181-193

[145] Heerden PDRV, Krüger GHJ. Photosynthetic limitation in soybean during cold stress. South African Journal of Science. 2000;**96**(4):201-206

[146] Yadav SK. Cold stress tolerance mechanisms in plants. A review. Agronomy for Sustainable Development. 2010;**30**(3):515-527

[147] Thakur P, Kumar S, Malik JA, Berger JD, Nayyar H. Cold stress effects on reproductive development in grain crops: An overview. Environmental and Experimental Botany. 2010;**67**(3):429-443

[148] Lee T-M, Lur H-S, Chu C. Role of abscisic acid in chilling tolerance of rice (*Oryza sativa* L.) seedlings:
II. Modulation of free polyamine levels. Plant Science. 1997;126(1):1-10

[149] Bakht J, Bano A, Dominy P. The role of abscisic acid and low temperature in chickpea (*Cicer arietinum*) cold tolerance. II. Effects on plasma membrane structure and function. Journal of Experimental Botany. 2006;**57**(14):3707-3715

[150] Lang V, Mantyla E, Welin B, Sundberg B, Palva ET. Alterations in water status, endogenous abscisic acid content, and expression of rab18 gene during the development of freezing tolerance in *Arabidopsis thaliana*. Plant Physiology. 1994;**104**(4):1341-1349

[151] Knight H, Trewavas AJ, Knight MR. Cold calcium signaling in Arabidopsis involves two cellular pools and a change in calcium signature after acclimation. The Plant Cell. 1996;**8**(3):489-503

[152] Nayyar H, Bains TS, Kumar S. Chilling stressed chickpea seedlings: Effect of cold acclimation, calcium and abscisic acid on cryoprotective solutes and oxidative damage. Environmental and Experimental Botany. 2005;**54**(3):275-285

[153] Nayyar H, Bains T, Kumar S. Low temperature induced floral abortion in

chickpea: Relationship to abscisic acid and cryoprotectants in reproductive organs. Environmental and Experimental Botany. 2005;**53**(1):39-47

[154] Bakht J, Bano A, Shafi M, Dominy P. Effect of abscisic acid applications on cold tolerance in chickpea (*Cicer arietinum* L.). European Journal of Agronomy. 2013;**44**:10-21

[155] Frascaroli E, Tuberosa R. Effect of abscisic acid on pollen germination and tube growth of maize genotypes 1. Plant Breeding. 1993;**110**(3):250-254

[156] Saxena NP, Johansen C, editors. Realised yield potential in chickpea and physiological considerations for further genetic improvement. In: Int Congress Plant Physiology. New Delhi: Society for Plant Physiology and Biochemistry; 1990

[157] Srinivasan A, Saxena NP, Johansen C. Cold tolerance during early reproductive growth of chickpea (*Cicer arietinum* L.): Genetic variation in gamete development and function. Field Crops Research. 1999;60(3):209-222

[158] Clarke HJ, Siddique KHM. Response of chickpea genotypes to low temperature stress during reproductive development. Field Crops Research. 2004;**90**(2):323-334

[159] Kahraman A, Kusmenoglu I,
Aydin N, Aydogan A, Erskine W,
Muehlbauer FJ. QTL mapping of winter hardiness genes in lentil. Crop Science.
2004;44(1):13

[160] Saeed A, Darvishzadeh R. Association analysis of biotic and abiotic stresses resistance in chickpea (Cicer spp.) using AFLP markers. Biotechnology & Biotechnological Equipment. 2017;**31**(4):698-708