Breeding, genetics, and genomics for tolerance against terminal heat in lentil: Current status and future directions

Jitendra Kumar¹ | Debjyoti Sen Gupta¹ | Ivica Djalovic²

¹Division of Crop Improvement, ICAR-Indian Institute of Pulses Research, Kanpur, India
²Institute of Field and Vegetable Crops, Novi Sad, Serbia

Correspondence
Jitendra Kumar, Division of Crop Improvement, ICAR-Indian Institute of Pulses Research, Kanpur 208024, India. Email: jitendra.kumar@icar.gov.in

Funding Information
National Innovations in Climate Resilient Agriculture (NICRA) funded by ICAR (Indian Council of Agricultural Research), New Delhi

Abstract
Heat stress at terminal stage in lentil is one of the major factors causing drastic yield loss. Development of heat tolerant cultivars is one of the ways to tackle this problem. However, heat stress tolerance is a complex trait in nature and many morphological, physiological, biochemical, and metabolic changes are responsible for heat stress tolerance in lentil. Therefore, in the past years, efforts have been made to know genetics and genomics of heat stress tolerance in lentil. In this review, we discussed current progress on breeding, genetics, and genomics including quantitative trait locus (QTL) mapping, transcriptomics, proteomics, and network of metabolic pathways for heat tolerance and future directions for developing heat tolerant cultivars in lentil.

KEYWORDS
high temperature, lentil, mapping, molecular markers, pathways' network, traits, transcriptome

1 | INTRODUCTION

Lentil (Lens culinaris Medikus) is cultivated globally as a rainfed crop during the winter season. It is mainly cultivated in Indian subcontinent, West-Asia, and Australia where it faces heat stress. Heat stress is a period of hot temperature that causes irreversible damage during growth and development of crop plants (Delahunty, Nuttall, Nicolas, & Brand, 2018). In major growing areas, lentil crop is exposed to temperature >35°C at flowering and pod filling stages during maturity (Delahunty, Nuttall, Nicolas, & Brand, 2015). In rice-lentil crop rotations, the problem is even more serious as late harvesting of the rice crop delays sowing of lentil crop, which may place the reproductive phase of lentil under high temperature stress (Subbarao, Rao, Kumar, Johansen, & Deb, 2001). Therefore, high temperature causes drastic losses of yields due to poor grain filling in lentil. Several days' exposure of the lentil crop to high temperature affects many physiological processes leading to forced grain maturity (Redden et al., 2014). For example, in Australia, a continuous heat wave with a temperature of ≥35°C for 6 days resulted in a yield loss of ~70% in lentil (Delahunty et al., 2015). In another study, an 87% yield reduction was observed when lentil plants were grown in the pots under field conditions at temperature of >38/23°C (average day/night temperature) during the reproductive phase (Bhandari et al., 2016). In coming years, higher temperatures due to global warming can be more challenging for the production and productivity of lentil (Kaur, Bains, Bindumadhava, & Nayyar, 2015).

Development of heat tolerant cultivars is one of the ways to tackle the problem of high temperature in lentil under present climatic conditions. However, heat stress tolerance is a complex trait in nature because many morphological, physiological, biochemical, and metabolic changes are responsible as discussed earlier in different crop plants (Abdelrahman, Burritt, Gupta, Tsujimoto, & Tran, 2019; Duan, Liu, Zhang, Li, & Guo, 2019; El Hassouni et al., 2019; Kaur, Sinha, & Bhunia, 2019). Moreover, recent reviews have also discussed different aspects of heat stress tolerance either on food legume crops (Sita, Sehgal, Kumar, et al., 2017; Liu et al., 2019) or on a specific pulse crop like chickpea (Kaloki, Devasirvatham, & Tan, 2019). However, during the past years, continuous efforts have been made to study the heat stress tolerance in lentil. These studies identified the heat tolerant genotypes and the associated morpho-physio-biochemical traits,
characterized the heat tolerance at molecular level, and deciphered the genetics and pathways underlying the heat stress tolerance in lentil (Kumar et al., 2016; Singh et al., 2016; Kumar, Basu, et al., 2018; Singh, Singh, Singh, & Pal, 2017; Delahunty et al., 2018; Singh et al., 2019). Also, knowledge of heat stress in lentil is enriching day by day and is becoming available in the public domain. Therefore, this review is aimed to know the current progress on breeding, genetics, and genomics including quantitative trait locus (QTL) mapping, transcriptomics, proteomics, and network of metabolic pathways for heat tolerance and future strategies of using this knowledge in breeding programs for developing high temperature tolerant lentil cultivars in order to sustain the production and productivity of lentil under changing climatic conditions.

2 | BREEDING FOR HEAT TOLERANCE

2.1 | Selection and screening for heat tolerance

2.1.1 | Critical temperature for screening of heat tolerant genotypes

The average day and night temperature between 15°C to 25°C and 8°C to 10°C, respectively, during reproductive phase is generally required for normal pods and seeds setting in lentil, and it showed high sensitivity to heat stress when day/night temperatures exceeded from 32/20°C (Ibrahim, 2011). A day/night temperature at or above 35/20°C causes pod abortion, reduction in the number of flowers, pollen viability, pollen germination, stigmatic function, ovular viability, pollen tube elongation, and shortening of flowering time in lentil (Bhandari et al., 2016; Sita et al., 2017). Therefore, for this crop, temperatures >35/25°C is identified as harmful for growth and yield (Sita, Sehgal, Kumar, et al., 2017) and >35/25°C can be used as critical temperature for differentiating the heat tolerant and sensitive lentil genotypes (Gaur et al., 2015). However, heat tolerant genotypes can even produce fewer pods up to 40/30°C temperature (Sita, Sehgal, Kumar, et al., 2017). In other legume crops such as mung bean and common bean, flowering or just prior to flowering stage has been shown to be highly affected by heat stress (Patriyawaty, Rachaputi, & George, 2018), whereas the post-fertilization stages like early pod development has been identified more tolerant to heat stress (Gross & Kigel, 1994). Studies demonstrated that high temperature stress, that is, even a few days exposure to high temperature (30–35°C) affects physiological, metabolic, and molecular function of reproductive organs leading to poor seed set or yield (Gaur et al., 2015; Jiang et al., 2015; Sage et al., 2015).

2.1.2 | Phenomics for identification of heat tolerant genotypes

Heat tolerant genotype can survive/reproduce at/above the critical temperature (>35/25°C; Figure 1). Therefore, screening methods have been developed for identifying heat tolerant genotypes under natural (field or pot) and controlled (hydroponic and pot assay) conditions in lentil (Kumar et al., 2016; Singh et al., 2017). Naturally, lentil genotypes are grown either in earthen pots or fields under late-sown conditions in order to coincide the reproductive stage of plants with high temperature (>35°C), and then, traits like pod setting (seed set) and grain yield are used to identify heat tolerant genotypes (Delahunty et al., 2015; Kumar et al., 2016; Singh et al., 2019; Sita, Sehgal, HanumanthaRao, et al., 2017). However, under field conditions, fluctuating day temperature limits to give uniform temperature during reproductive period across the genotypes when they differ in flowering times (Kumar et al., 2016). As a result, it is difficult to identify early flowering heat tolerant genotypes due to their maturity before onset of the heat stress. Also, it is a challenging task to measure traits imparting heat tolerance with more accuracy and precision under field conditions. However, use of advance phenomic platforms can help in measuring of several physiological traits with more accuracy and precision directly in the field (Basu et al., 2015). In lentil, high-precision laboratory techniques have been used in measuring the several physiological traits such as photosynthetic rate, pollen viability, and membrane stability taken from field grown samples, and these traits have been used to differentiate heat tolerant and sensitive genotypes (Kumar, Gupta, Gupta, & Singh, 2018).

The controlled conditions give precise monitoring of the traits imparting heat tolerance due to availability of uniform and stable high

![FIGURE 1](image-url) Sensitivity of lentil plants during reproductive period under the high temperature (>35°C) (a) sensitive, (b) highly sensitive, (c) tolerant, and (d) highly tolerant (Source: Kumar et al., 2016)
temperature across the growth and development of crop plants (Basu et al., 2015). In lentil, heat tolerant genotypes have been identified on the basis of growth and development of germinating seeds under high temperature in laboratory or hydroponic conditions (Roy, Tucker, & Tester, 2011; Singh et al., 2016, 2019). However, a heat tolerant genotype identified at seedling stage requires its further validation at reproductive stage as heat stress occurs at terminal stage in lentil. Studies showed that heat tolerant genotypes identified under controlled conditions do not have their reproducibility under field conditions (Singh et al., 2016). Therefore, a potential heat tolerant genotype can be identified with more confidence by the use of natural and controlled conditions together. The use of screening methods based on controlled conditions can help to screen the large number of genotypes cost-effectively, which is not possible by using the field screening methods alone. Moreover, controlled conditions are used to provide relevant temperature during targeted stages or for a period of time. In lentil heat stress (35/20°C) applied for 4 h for 7 days from the first day of anthesis under controlled conditions and after that, the normal temperature (27/16°C) was given for pods development (Singh et al., 2017). In another study, plants were first grown in pots under natural conditions, and after that, at the flower initiation stage, these pots were moved into the controlled conditions in order to provide relevant temperature during anthesis (Chen et al., 2019; Sita, Sehgal, Kumar, et al., 2017).

The focused identification of germplasm strategy (FIGS) is one of the approaches for identifying heat tolerant genotypes in lentil. It works on the concept that environmental conditions strongly help natural selection towards the growing habitat and hence use of lentil accessions from regions exposed to high temperature stress in the screening can have a higher probability of containing traits and genes imparting heat tolerance (Delahunty et al., 2015; Gaur et al., 2015).

### 2.2 Trait discovery

Phenotypic and physio-biochemical traits have been used to identify the heat tolerant genotypes in lentil (Table 1). As heat stress has the most devastating effects on just before/during flowering in legumes (Patrivyavaty et al., 2018), the number of filled pods per plant and seed size under heat stress has been used as a key indicator trait to assess heat tolerance among genotypes (Kumar et al., 2016; Singh et al., 2017; Sehgal et al., 2019; Kumar, Gupta, et al., 2018). In addition to this, different physio-biochemical traits had been examined to differentiate heat tolerant and heat sensitive genotypes that led to identification of key physiological traits in lentil (Kumar, Gupta, et al., 2018; Sita, Sehgal, HanumanthaRao, et al., 2017). These traits listed in Table 1 and also reviewed earlier (Liu et al., 2019; Sita, Sehgal, Kumar, et al., 2017) are important because they directly help plants for sustaining against heat stress. Therefore, they can be used as indicator traits to identify heat tolerant genotypes in lentil. For example, higher membrane stability and photosynthetic electron transport rate played an important role to tolerate plants against heat stress at vegetative stage in lentil (Kumar, Gupta, et al., 2018). In lentil, high temperature stress limits the availability of carbohydrates during reproductive development leading to poor seed filling and grain yield (Baghi, Mostafalizadeh, & Reinecke, 2017; Tao, Paponov, & Palme, 2006; Todaka, Nakashima, Shinozaki, & Yamaguchi-Shinozaki, 2012). Therefore, above physiological and biochemical traits can be used for identification of heat tolerant genotypes in breeding program.

### 2.3 Genetics and exploitation of genetic diversity through conventional breeding

Knowledge of the genetics underlying the traits imparting heat tolerance helps plant breeders for making genetic improvement using either conventional or modern breeding approaches. Considerably large genetic variation has been observed among the lentil germplasm for the traits listed in Table 1 (Delahunty et al., 2015; Kumar, Gupta, et al., 2018; Sita, Sehgal, Kumar, et al., 2017; Sita, Sehgal, HanumanthaRao, et al., 2017; Bhandari et al., 2016; Kumar, Gupta, et al., 2018; Chakraborty & Pradhan, 2011; Delahunty et al., 2015; Kumar et al., 2016; Singh et al., 2017, 2019).

Peighami, & Zakaria, 2012; Bhandari et al., 2016; Sita, Sehgal, HanumanthaRao, et al., 2017). Therefore, activities of sucrose synthase, sucrose phosphate synthase, and acid invertase enzymes can be used as key biochemical traits because activities of these enzymes have been found slow in developing pollen grains leading to poor accumulation of soluble carbohydrates compared with heat tolerant genotypes (Bhandari et al., 2016; Sita, Sehgal, HanumanthaRao, et al., 2017). In other crop plants, heat stress suppressed auxin biosynthesis leading to pollen abnormalities because auxin regulates reproductive process in plants, and hence, its role can be studied in lentil (Ozga, Kaur, Savada, & Reinecke, 2017; Tao, Paponov, & Palme, 2006; Todaka, Nakashima, Shinozaki, & Yamaguchi-Shinozaki, 2012). Therefore, above physiological and biochemical traits can be used for identification of heat tolerant genotypes in breeding program.

### TABLE 1 Phenotypic, physiological, and biochemical traits used for differentiating heat sensitive and tolerant genotypes in lentil

| Phenotypic trait | Physiological trait | Biochemical trait |
|------------------|--------------------|-------------------|
| Seedling survival, pod setting, pod setting at terminal of branches, yield, number of flowers, and biomass | Anther morphology, pollen morphology, pollen viability, pollen load and pollen germination, pollen germination (in vivo) and fate of pollen tube, stigma receptivity, ovule viability, stomatal conductance and leaf temperature, photosynthetic electron transport rate, membrane damage (as electrolyte leakage), leaf photosynthetic function, stress injury to leaves, cellular oxidizing ability, chlorophyll concentration, and relative leaf water content (RLWC) | Soluble protein, reducing sugars, sucrose, sucrose phosphate synthase, malondialdehyde, hydrogen peroxide ($\text{H}_2\text{O}_2$), superoxide dismutase, catalase, ascorbate peroxidase, glutathione reductase, ascorbic acid, glutathione, effect of sucrose on pollen germination (in vitro), cellular oxidizing ability of leaves, acid invertase, sucrose synthase, lipid peroxidation, ascorbate, and carotenoids |

Source: Sita, Sehgal, HanumanthaRao, et al., 2017; Sita, Sehgal, Kumar, et al., 2017; Bhandari et al., 2016; Kumar, Gupta, et al., 2018; Chakraborty & Pradhan, 2011; Delahunty et al., 2015; Kumar et al., 2016; Singh et al., 2017, 2019.
et al., 2016; Singh et al., 2016). However, genetics of few traits responsible for heat stress tolerance has been studied in lentil. In one of the studies, monogenic inheritance has been reported for seedling survival and pod setting under heat stress condition (Singh et al., 2017). In this study, a simple inheritance has been reported for a complex trait like pod setting under heat stress condition. However, in snap beans, the pods number per plant under heat stress condition has been controlled by major genes (Rainey & Griffiths, 2005), whereas a quantitative inheritance has been reported for heat stress tolerance in wheat (Barakat, Al-Doss, Elshafei, & Moustafa, 2011; Talukder et al., 2014). Therefore, more studies are required to understand the genetics of many traits imparting heat tolerance in lentil.

Exploiting the genetic diversity in conventional breeding programs is one of the ways to reduce yield losses caused by high-temperature (Krishnamurthy et al., 2011). Donors for the morpho-physiological traits imparting heat tolerance have been identified (i.e., IG 2507, IG 3263, IG 3745, IG4258, FLIP 2009, PDL-1, and PDL-2) during the past years in lentil (Kumar et al., 2016; Singh et al., 2016; Sita, Sehgal, HanumanthaRao, et al., 2017). However, there is a need to use these donors in a breeding program, which is otherwise still limited so far. The complex genetics and low heritability of yield trait under heat stress conditions restricts their direct use as heat tolerant cultivars (Manavalan, Guttikonda, Tran, & Nguyen, 2009). However, screening of the breeding lines, which are developed by using heat tolerant donors, under hot climatic conditions increases the chance of developing the heat tolerant cultivars because crops grown in warmer regions are often more tolerant to high temperatures than those grown in cooler regions (Gaur et al., 2015; Kublenu et al., 2013). This breeding strategy has facilitated the identification of a heat tolerant chickpea breeding line (ICCV 92944), which subsequently released as a heat tolerant cultivar in different countries (Gaur et al., 2015). Exploitation of physiological traits in breeding programs can accelerate the development of heat tolerant cultivars as several physiological traits, including cooler canopy temperature, light interception, and radiation use efficiency used successfully for the development of heat tolerant cultivars in wheat (Cossani & Reynolds, 2012; Reynolds, Manes, Izanloo, & Langridge, 2009). The genotypic variation observed for several physiological traits in lentil earlier (Kumar, Gupta, et al., 2018; Sita, Sehgal, HanumanthaRao, et al., 2017) that can be exploited in breeding programs. Currently, genetic diversity for heat tolerance in lentil (Kumar et al., 2016) is being exploited in breeding programs for improving the lentil production and productivity under global warming conditions.

3 | GENOMICS FOR HEAT STRESS TOLERANCE

3.1 | QTL mapping and genomic-assisted breeding for heat tolerance

Molecular markers help to decipher the genetics of complex traits in food legumes (Kumar, Choudhary, Solanki, & Pratap, 2011). In lentil, a number of molecular markers have been developed in the past years (Hamwieh, Udupa, Sarkar, Jung, & Baum, 2009; Kaur et al., 2011, 2014; Verma, Sharma, Srivastava, Abdin, & Bhatia, 2014; Kumar, Rajendran, Kumar, Hamwieh, & Baum, 2015; Gupta et al., 2018; Singh et al., 2019) and used to map genes governing resistance/tolerance to biotic and abiotic stresses (Kumar, Basu, et al., 2018; Kumar, Gupta, et al., 2018; Kumar, Rajendran, et al., 2015; Sita, Sehgal, HanumanthaRao, et al., 2017). However, limited studies have been conducted for either differentiating the heat sensitive and tolerant genotypes on the basis of genetic markers (Kumar, Gupta, et al., 2018) or mapping a major QTL controlling the seedling survival and pod setting traits under heat stress in lentil (Singh et al., 2017). Therefore, in lentil, more efforts are needed to develop the mapping populations for key traits imparting tolerance to heat stress and use of these populations for mapping of genes/QTLs controlling these traits. These markers can be used in marker-assisted breeding. However use of functional markers in the QTL mapping for heat stress can be more useful because identified linked functional markers can be used directly in marker assisted-breeding programs without any validation (Kalendar et al., 2011). For other traits, use of closely linked molecular markers with genes/QTLs governing wilt resistance and root traits in a breeding program led to the development of two wilt resistant cultivars in chickpea, (Super Annigeri 1 and improved JG 74) and two drought tolerant (Pusa 10,216 and Geletu). These varieties have been released for cultivation in India and Ethiopia (Economic Times, 2019; Mannur, et al., 2019).

3.2 | Transcriptome analysis for identification of candidate genes responsible for heat tolerance

In lentil, heat and drought stresses occur together during seed filling due to rapid water loss from soil and plant. These two stresses affect different physiological process (Sehgal et al. 2017). For example, activity of RuBisCo and stomatal conductance increases under heat stress but is decreased under drought condition (Sehgal et al. 2017). In another case, hydrolysis of sucrose has been observed to increase under heat and drought stresses, but it has been inhibited due to combination of stresses (Sehgal et al. 2017). Effects of heat and drought also observed differently in different parts of lentil plant as starch tends to increase under heat stress in leaves but decreased in seeds. Whereas it is drastically declined in seeds under drought alone or in combination with heat stress (Sehgal et al. 2017). The effect of heat stress has been observed more on yield traits than drought, whereas drought stress reduced individual seed weights more than heat stress (Sehgal et al. 2017). Therefore, there is a need to identify the candidate genes separately for heat and drought stress. Next generation sequencing (NGS) platforms have opened up the new opportunity for obtaining the genome sequences and transcriptomes. In lentil, NGS based transcriptome analysis provided opportunity to identify candidate genes expressed under biotic and abiotic stress conditions, including heat stress (Singh et al., 2017; Singh et al., 2019). The transcriptome analysis of heat sensitive and tolerant genotypes led to the identification of candidate genes related to physiological and pollen...
phenotypes, cell wall, and secondary metabolism in lentil (Singh et al., 2019). This study identified the genes for plasmodesmata callose-binding protein 3 (PDCB), phosphatidylinositol/phosphatidylcholine transfer protein SFH13, CDP-diacylglycerol-glycerol-3-phosphate 3-phosphatidylinositol transferase 1 chloroplastic, probable glycerol-3-phosphate acyltransferase 2 (GPAT2), O-acyltransferase, and phosphatidylcholine diacylglycerol choline phosphotransferase. Those were up-regulated in tolerant genotype under heat stress. A gene encoding pyruvate phosphate dikinase identified under heat stress conditions has been found to be responsible for producing the phosphoenolpyruvate (PEP). This metabolite is an essential compound of shikimate pathway that is responsible for production of secondary metabolites involved in heat tolerance. These genes are involved in different pathways in cell wall formation and secondary metabolites production that are affected under heat stress (Singh et al., 2019). These candidate genes can be utilized after validation of their role in breeding programs for developing the heat tolerant genotypes.

3.3 | Genes for heat sock proteins

During heat stress, plants generate such type of proteins that stop denaturation and aggregation of functional proteins leading to a proper functioning of various bio-membranes and physiological process such as photosynthesis, assimilate partitioning, water, and nutrient use efficiency in heat tolerant plants (Fragkostefanakis et al., 2016; Ohama et al., 2016). These proteins that act as molecular chaperones are known as heat shock proteins (HSPs), and these are to be 10 to 200 kDa (Schöffl, Prändl, & Reindl, 1999). Therefore, use of the genes encoding synthesis of these HS proteins in breeding programs for developing heat tolerant cultivars can be an important adaptive strategy for tackling the problem of heat stress (Feder & Hofmann, 1999). Therefore, the role of these proteins in the heat stress tolerance has been studied in several legume crops. In soybean, HSPs provided the heat tolerance at seedling stage (Das et al., 2016) and an HSP gene family has been involved to control drought and heat stress at seedling stage (Zhang et al., 2015). In another study, functional markers developed from genes encoding HSP90 of Medicago, HSP70 of Glycine, HSP 17 and HSP 18 of Pism proteins could not differentiate the heat sensitive and tolerant genotypes of lentil (Kumar, Gupta, et al., 2018). Therefore, more efforts are required to identify the genes for those HSPs that impart heat tolerance in lentil.

3.4 | Network of metabolic pathways responsible for heat tolerance

Heat stress tolerance as a complex trait has a network of different metabolic pathways in crops plants (Bita & Gerats, 2013). Recent reviews have discussed role of different metabolites in controlling heat stress tolerance in food legume crops (Liu et al., 2019; Sita, Sehgal, Kumar, et al., 2017). In kidney bean, a more accumulation of soluble leaf carbohydrates and higher activity of adenosine-5′-diphosphoglucose pyrophosphorylase have been observed under high temperature (Prasad, Boote, Jcv, & Lhjr, 2004). In bermudagrass, upregulation of some important metabolic pathways, including photosynthesis, respiration, amino acid, and GABA shunt led to the synthesis of proteins and metabolites responsible to tolerate heat stress under elevated CO2 (Yu, Li, Fan, Yang, & Huang, 2017). Several metabolic pathways, including altered energy pathways, lipid super pathway, and increased production of branched-chain amino acids, raffinose family oligosaccharides (RFOs), lipolysis products, and tocopherols help plants to tolerate heat stress (Serrano, Ling, Bahieldin, & Mahfouz, 2019). A crosstalk between carbohydrate and tyrosine metabolism produces metabolites like salidroside that helps plants to recover under heat stress. These metabolic pathways can be considered in plant breeding to maximize crop yields under adverse conditions (Serrano et al., 2019). Further, in cool-season creeping bentgrass, an increased level of the γ-amino butyric acid (GABA), a nonprotein amino acid, helps to improve heat tolerance because it regulated major metabolic pathways responsible for accumulation of amino acids, organic acids, sugars, and sugar alcohols under heat stress conditions (Li, Yu, Peng, & Huang, 2016). Thus, a regulatory network of genes controlling different metabolic pathways works under heat stress conditions in crop plants. However, little is known about the role of different metabolites or metabolic pathways for controlling heat stress tolerance in lentil, and only few transcriptome studies identified the candidate genes that encode synthesis of secondary and primary metabolites that were involved in heat tolerance in lentil (Singh et al., 2019). However, metabolomics study can directly exhibit the metabolite changes induced by stress as compared with transcriptomics. Therefore, there is a need to apply metabolomics for exploring the metabolites involved in heat-stress regulation in lentil like other crop plants (De Leonardis et al., 2015; Obata et al., 2015). Further, a combination of transcriptomics with metabolomics can help to elucidate the gene-to-metabolite pathways as investigated in rice in the response to heat stress (Glaubitz et al., 2017).

4 | Future ways for tackling the problem of heat stress

Lentil crop is highly affected by heat stress at terminal stage and in coming years, this problem can be more serious due to global warming. Different ways for tackling the problem of heat stress in lentil has been presented in Figure 2 and discussed below.

- Morphological, physiological, and biochemical traits can be used for developing the heat tolerant cultivars (Kumar, Pratap, & Kumar, 2015). During the past years, in lentil, focus has been made to identify the donors for heat tolerance (Kumar et al., 2016; Singh et al., 2016). However, use of automated phenotyping platforms can accelerate the identification of new genetic resources with more precision and accuracy and their use in future. The significant progress has been made in other crops towards the development of such platforms that are equipped with sensor and image based
systems, leading to nondestructive phenotyping of the traits imparting heat tolerance (Kumar, Pratap, & Kumar, 2015). Also, several instruments have been developed for measuring physiological traits like stomatal mechanism and transpiration, osmotic adjustment, leaf water potential, and canopy temperature directly in the field (Basu et al., 2015). These advances are required to be used for heat tolerance studies in lentil and the reverse phenomics can be used to discover the mechanisms and gene(s) for the traits imparting heat tolerance in lentil (Kumar, Pratap, & Kumar, 2015).

- In lentil, limited studies have been conducted on mapping of genes controlling heat tolerance in lentil (Singh et al., 2017) that is needed for key physiological traits. As NGS-based transcriptome analysis and comparative genomics have opened the opportunity to identify the expressed sequence tags (ESTs), candidate genes, and metabolic pathways involving in the heat tolerance (Singh et al., 2017), more efforts are required to work in this direction. In wheat, new alleles belonging to \textit{Hsp26} gene family encoding chloroplast-localized small (s)HSPs have been identified through high throughput Targeting Induced Local Lesions in Genomes (TILLING) approach of reverse genetics. These alleles encode such HSPs that protect the photosynthetic machinery from high temperature stress (Comastri et al., 2018). Therefore, use of this reverse genetic approach can be focused by developing TILLING populations for identification of heat tolerant genes in lentil. Candidate genes or ESTs those are involved in heat tolerance can be used to develop functional markers for breeding (Kumar, Gupta, et al., 2018). In wheat, a set of Kompetitive Allele Specific PCR (KASP) markers has been developed from genes encoding chloroplast-localized sHSPs in order to identify the heat tolerant genes in breeding populations (Comastri et al., 2018).

- Genome editing is emerging area of genomics for developing the heat tolerant cultivars. The CRISPR/Cas9 based targeted gene editing has great potential to produce high-yielding crops under heat stress (Abdelrahman, Al-Sadi, Pour-Aboughadareh, Burritt, & Tran, 2018). In Arabidopsis \textit{thaliana}, this approach has been used to modify the abiotic stress response. It also helps to suppress or activate a target gene leading to identification of function of that gene (Osakabe et al., 2016). In cowpea, it has been used to know the function of genes related to nitrogen fixation (Ji et al., 2019). In lentil, candidate genes imparting tolerance to heat stress have been identified through transcriptome analysis (Singh et al., 2019). The role of these genes for heat tolerance can be studied using CRISPR/Cas9 based targeted gene editing. The mutant population generated after editing of a target gene can be screened for heat tolerance and identified mutants can used in breeding programs for strengthening food security in the future (Kumar, Choudhary, Gupta, & Kumar, 2019).

- The epigenetic breeding is one of the ways to tackle the problem of heat stress in crop plants (Kumar et al., 2019). Several studies have demonstrated that DNA methylation causing epigenetic variation in crop plants has its role in tolerance to heat stress. For example, in cotton, high temperature disrupted the genome methylation leading to pollen abnormalities, and heat tolerant lines showed an overall high level of genome-wide DNA methylation compared with sensitive lines (Ma et al., 2018). These DNA methylations have occurred in the genes involved in the starch, auxin, and sugar metabolic pathways that are crucial for proper pollen development (Min et al., 2014). Therefore, in future, it needed to handle the heat-methylome variation in breeding programs for developing the heat tolerant cultivars in lentil (Harkess, 2018; Kumar et al., 2019). The breeding strategies of using the epigenetic variation towards the development climate smart pulses have been elaborated in a recent review (Kumar et al., 2019).

- In crop plants, transcriptional, translational and post-translational mechanisms, and signaling pathways regulate heat tolerance response, and different omics approaches are now available to study the regulation of heat tolerance in crop plants. In lentil, use of these omics approaches is still limited and only few studies used the genomics and transcriptomic approaches for identification of genes responsible for heat tolerance. In crop plants, expressions of several genes are modified towards the tolerance against a particular stress after transcription through non-coding micro RNA (Chinnusamy, Zhu, Zhou, & Zhu, 2007). The role of these micro RNAs for controlling heat tolerance has been studied in different crops under micromics, and heat responsive miRNAs that up- or down-regulate genes responsible for heat tolerance have been
identified (Chinnusamy et al., 2007). Translation of the coding RNA into proteins that work as HSPs (discussed above in details) take part in several biochemical processes leading to the generation of metabolites (metabolome) under heat stress conditions. The role of different metabolites in heat stress tolerance can be studied in lentil as identified in other plant species (Caldana et al., 2011; De Block, Verdun, De Brouwer, & Cornelissen, 2005; Maruyama et al., 2009; Wienkoop et al., 2008). Thus, advances in different omics approaches can help to integrate the metabolites with transcriptionomes for elucidating gene-to-gene and metabolite-to-gene networks in lentil (Hirai et al., 2005). Therefore, a lot of efforts are still required by following different ways of tackling the heat stress problem in lentil.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Writing - original draft and review and editing: JK. Writing - review and editing: DSG. All authors read and approved the final manuscript.

FUNDING INFORMATION
Authors work on heat tolerance in lentil is supported by the project “National Innovations in Climate Resilient Agriculture (NICRA)” funded by ICAR (Indian Council of Agricultural Research), New Delhi.

DATA AVAILABILITY STATEMENT
Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID
Jitendra Kumar https://orcid.org/0000-0003-1144-1111

REFERENCES
Abdelrahman, M., Al-Sadi, A. M., Pour-Aboughadareh, A., Burritt, D. J., & Tran, L. P. (2018). Genome editing using CRISPR/Cas9–targeted mutagenesis: An opportunity for yield improvements of crop plants grown under environmental stresses. Plant Physiology and Biochemistry, 131, 31–36. https://doi.org/10.1016/j.plaphy.2018.03.012
Abdelrahman, M., Burritt, D. J., Gupta, A., Tsujimoto, H., & Tran, L. P. (2019). Heat stress effect on source-sink relationships and metabolome dynamics in wheat. Journal of Experimental Botany, 71, 543–554. https://doi.org/10.1093/jxb/erz296
Barakat, M. N., Al-Doss, A. A., Elshafei, A. A., & Moustafa, K. A. (2011). Identification of new microsatellite marker linked to the grain filling rate as indicator for heat tolerance genes in F2 wheat population. Australian Journal of Crop Science, 5, 104–110.
Barghi, S. S., Mostafalii, H., Peighami, F., & Zakaria, R. A. (2012). Path analysis of yield and its components in lentil under end season heat condition. International Journal of Agricultural Research Review, 2, 969–974.
Basu, P. S., Srivastava, M., Singh, P., Porwal, P., Kant, R., & Singh, J. (2015). High-precision phenotyping under controlled versus natural environments. In J. Kumar, A. Pratap, & S. Kumar (Eds.), Phenomics in crop plants: Trends, options and limitations (pp. 27–40). New Delhi, India: Springer, India.
Bhandari, K., Siddique, K. H., Turner, N. C., Kaur, J., Singh, S., Agrawal, S. K., & Nayar, H. (2016). Heat stress at reproductive stage disrupts leaf carbohydrate metabolism, impairs reproductive function, and severely reduces seed yield in lentil. Journal of Crop Improvement, 30, 118–151.
Bita, C. E., & Gerats, T. (2013). Plant tolerance to high temperature in a changing environment: Scientific fundamentals and production of heat stress-tolerant crops. Frontiers in Plant Science, 4, 273. https://doi.org/10.3389/fpls.2013.00273
Caldana, C., Degenkolbe, T., Cuadros-Inostroza, A., Klie, S., Sulpirce, R., Leisse, A., ..., Hannah, M. A. (2011). High-density kinetic analysis of the metabolomic and transcriptomic response of Arabidopsis to eight environmental conditions. Plant Journal, 67, 869–884.
Chakraborty, U., & Pradhan, D. (2011). High temperature-induced oxidative stress in Lens culinaris, role of antioxidants and amelioration of stress by chemical pre-treatments. Journal of Plant Interactions, 6(1), 43–52.
Chen, S., Guo, Y., Sirault, X., Stefanova, K., Saradadevi, R., Turner, N. C., ..., Cowling, W. A. (2019). Nondestructive phenomic tools for the prediction of heat and drought tolerance at anthesis in Brassica species. Plant Phenomics, 2019, 1–16. https://doi.org/10.34133/2019/3264872
Chinnusamy, V., Zhu, J., Zhou, T., & Zhu, J. K. (2007). Small RNAs: Big role in abiotic stress tolerance of plants. In M. A. Jenks, P. M. Hasegawa, & S. M. Jain (Eds.), Advances in molecular breeding toward drought and salt tolerant crops (pp. 223–260). Dordrecht, The Netherlands: Springer.
Comastri, A., Janni, M., Simmonds, J., Uauy, C., Pignone, D., Nguyen, H. T., & Mamirola, N. (2018). Heat in wheat: Exploit reverse genetic techniques to discover new alleles within the Triticum durum sHsp26 family. Frontiers in Plant Science, 9, 1337. https://doi.org/10.3389/fpls.2018.01337
Cossani, E., & Reynolds, M. P. (2012). Physiological traits for improving heat tolerance in wheat. Plant Physiology, 160(4), 1710–1718.
Das, D., Eldakak, M., Paudel, B., Kim, D. W., Hemmati, H., Basu, C., & Rohila, J. S. (2016). Leaf proteome analysis reveals prospective drought and heat stress response mechanisms in soybean. BioMed Research International, 8, 1–23.
De Block, M., Verdun, C., De Brouwer, D., & Cornelissen, M. (2005). Poly(ADP-ribose) polymerase in plants affects energy homeostasis, cell death and stress tolerance. Plant Journal, 41, 95–106.
De Leonidis, A. M., Fragasso, M., Beleggia, R., Ficco, D. B. M., De Vita, P., & Mastrangelo, A. M. (2015). Effects of heat stress on metabolite accumulation and composition, and nutritional properties of durum wheat grain. International Journal of Molecular Sciences, 16, 30382–30404.
Delahunty, A., Nuttall, J., Nicolas, M., Brand, J. (2015). Genotypic heat tolerance in lentil. In: Proceedings of the 17th ASA Conference 2015 September (pp. 20–24).
Delahunty, A., Nuttall, J., Nicolas, M., & Brand, J. (2018). Response of lentil to high temperature under variable water supply and carbon dioxide enrichment. Crop & Pasture Science, 69(11), 1103–1112.
Duan, S., Liu, B., Zhang, Y., Li, G., & Guo, X. (2019). Genome-wide identification and abiotic stress-responsive pattern of heat shock transcription factor family in Triticum aestivum L. BMC Genomics, 20(1), 257.
Economic Times. (2019). India set to launch drought resistant chickpea developed with genomic assisted breeding. Read more at: //economictimes.indiatimes.com/articleshow/71225122.cms?from=mdr&utm_source=contentofinterest &utm_medium=text&utm _campaign=cppst (September 20, 2019).
El Hassouni, K., Belkadi, B., Filali-Maltouf, A., Tidiane-Sall, A., Al-Abdallah, A., Nachit, M., & Bassi, F. M. (2019). Loci controlling adaptation to heat stress occurring at the reproductive stage in durum wheat. Agronomy, 9(8), 414.
Feder, M. E., & Hofmann, G. E. (1999). Heat-shock proteins, molecular chaperones, and the stress response: Evolutionary and ecological physiology. Annual Review of Physiology, 61(1), 243–282.

Fragkostefanakis, S., Meshiovich, A., Simm, S., Paupière, M. J., Hu, Y., Paul, P., ... Scharf, K. D. (2016). HsfA2 controls the activity of developmentally and stress-regulated heat stress protection mechanisms in tomato male reproductive tissues. Plant Physiology, 170, 2461–2477.

Gaur, P. M., Samineni, S., Krishnamurthy, L., Varshney, R. K., Kumar, S., Ghanem, M. E., ... Nayyar, H. (2015). High temperature tolerance in grain legumes. Legume Perspectives, 7, 23–24.

Glaubitz, U., Li, X., Schaedel, S., Erban, A., Sulpice, R., Kropka, J., ... Zuther, E. (2017). Integrated analysis of rice transcriptomic and metabolomic responses to elevated night temperatures identifies sensitivity- and tolerance-related profiles. Plant, Cell & Environment, 40, 121–137.

Gross, Y., & Kigel, J. (1994). Differential sensitivity to high temperature of stages in the reproductive development of common bean (Phaseolus vulgaris L.). Field Crops Research, 36, 201–212.

Gupta, D. S., Kumar, J., Gupta, S., Dubey, S., Gupta, P., Singh, N. P., & Sablok, G. (2016). Identification, development, and application of cross-species intron-spanning markers in lentil (Lens culinaris Medik.). The Crop Journal, 4(3), 299–305.

Hamwieh, A., Udupa, S. M., Sarkar, A., Jung, C., & Baum, M. (2009). Development of new microsatellite markers and their application in the analysis of genetic diversity in lentils. Breeding Science, 59, 77–86. https://doi.org/10.1270/jsbbs.59.77

Harkess, A. (2018). Handling the heat-methylome variation underlying heat tolerance in cotton. The Plant Cell, 30, 1947–1948. https://doi.org/10.1105/tpc.18.00698

Hirai, M. Y., Klein, M., Fujikawa, Y., Yano, M., Goodenowe, D. B., Yamazaki, Y., ... Salto, K. (2005). Elucidation of gene-to-gene and metabolite-to-gene networks in Arabidopsis by integration of metabolomics and transcriptomics. Journal of Biological Chemistry, 280, 25590–25595. https://doi.org/10.1074/jbc.M502332200

Ibrahim, H. M. (2011). Heat stress in food legumes: Evaluation of membrane thermostability methodology and use of infra-red thermometry. Euphytica, 180, 99–105.

Ji, J., Zhang, C., Sun, Z., Wang, L., Duanmu, D., & Fan, Q. (2019). Genome editing in cowpea Vignaunguiculata using CRISPR-Cas9. International Journal of Molecular Sciences, 20(10), 2471.

Jiang, Y., Lahilai, R., Karunakan, C., Kumar, S., Davis, A. R., & Buckert, R. A. (2015). Seed set, pollen morphology and pollen surface composition response to heat stress in field pea. Plant, Cell & Environment, 38, 2387–2397.

Kalender, R., Flavell, A. J., Ellis, T. H. N., Sjästè, T., Moisy, C., & Schulman, A. H. (2011). Analysis of plant diversity with retrotransposon-based molecular markers. Heredity, 106, 520–530. https://doi.org/10.1038/hdy.2010.93

Kaloki, P., Devasirvatham, V., & Tan, D. K. (2019). Chickpea abiotic stresses: Combating drought, heat and cold. In: Abiotic and biotic stress in plants. IntechOpen. doi: https://doi.org/10.5772/intechopen.83404

Kaur, R., Bains, T. S., Bindumadhava, H., & Nayyar, H. (2015). Responses of mungbean (Vignaradiata L) genotypes to heat stress: Effects on reproductive biology, leaf function and yield traits. Scientia Horticulturae, 197, 527–541.

Kaur, R., Sinha, K., & Bhunia, R. K. (2019). Can heat survive in heat? Assembling tools towards successful development of heat stress tolerance in Triticum aestivum L. Molecular Biology Reports, 46(2), 2577–2593.

Kaur, S., Cogan, N., Pembleton, L. W., Shinozuka, M., Savin, K. W., Materne, M., & Forster, J. W. (2011). Transcriptome sequencing of lentil based on second generation technology permits large-scale unigene assembly and SSR marker discovery. BMC Genomics, 12, 265. https://doi.org/10.1186/1471-2164-12-265

Kaur, S., Cogan, N. I., Stephens, A., Noy, D., Butsch, M., Forster, J., et al. (2014). EST-SNP discovery and dense genetic mapping in lentil (Lens culinaris Medik.) enable candidate gene selection for boron tolerance. Theoretical and Applied Genetics, 127, 703–713.

Kugbelenu, Y. O., Danso, E. O., Ofori, K., Andersen, M. N., Abney-Mickson, S., Sabi, E. B., ... Jørgensen, S. T. (2013). Screening tomato genotypes for adaptation to high temperature in West Africa. ActaAgriculturaeScandinavica, Section B-Soil & Plant Science, 63(6), 516–522.

Kumar, J., Basu, P. S., Gupta, S., Dubey, S., Gupta, D. S., & Singh, N. P. (2018). Physiological and molecular characterisation for high temperature stress in Lens culinaris. Functional Plant Biology, 45(4), 474–487.

Kumar, J., Choudhary, A. K., Gupta, D. S., & Kumar, S. (2019). Towards exploitation of adaptive traits for climate-resilient smart pulses. International Journal of Molecular Sciences, 20(12), 2971.

Kumar, J., Choudhary, A. K., Solanki, R. K., & Pratap, A. (2011). Towards marker-assisted selection in pulses: A review. Plant Breeding, 130(3), 297–313.

Kumar, J., Gupta, S., Gupta, D. S., & Singh, N. P. (2018). Identification of QTLs for agronomic traits using association mapping in lentil. Euphytica, 214(4), 75.

Kumar, J., Kant, R., Kumar, S., Basu, P. S., Sarker, A., & Singh, N. P. (2016). Heat tolerance in lentil under field conditions. Legume Genomics & Genetics, 7, 1–11.

Kumar, J., Pratap, A., & Kumar, S. (2015). Plant phenomics: An overview. In J. Kumar, Pratap, & S. Kumar (Eds.), Phenomics in crop plants: Trends, options and limitations (pp. 1–10). New Delhi, India: Springer.

Kumar, S., Rajendran, K., Kumar, J., Hamwieh, A., & Baum, M. (2015). Current knowledge in lentil genomics and its application for crop improvement. Frontiers in Plant Science, 6, 78. https://doi.org/10.3389/fpls.2015.00078

Li, Z., Yu, J., Peng, Y., & Huang, B. (2016). Metabolic pathways regulated by γ-aminobutyric acid (GABA) contributing to heat tolerance in creeping bentgrass (Agrostis stolonifera). Scientific Reports, 6, 30338.

Liu, Y., Li, J., Zhu, Y., Jones, A., Rose, R. J., & Song, Y. (2019). Heat stress in legume seed setting: Effects, causes, and future prospects. Frontiers in Plant Science, 10, 938. https://doi.org/10.3389/fpls.2019.00938

Ma, Y., Min, L., Wang, M., Wang, C., Zhao, Y., Li, Y., ... Zhang, X. (2018). Disrupted genome methylation in response to high temperature has distinct effects on microspore abortion and anther indhescence. Plant Cell, 30, 1387–1403. https://doi.org/10.1105/tpc.18.00074

Manavalan, L. P., Guttikonda, S. K., Tran, L. S., & Nguyen, H. T. (2009). Physiological and molecular approaches to improve drought resistance in soybean. Plant & Cell Physiology, 50, 1260–1276.

Mannur, D. M., Babbab, A., Thudi, M., Sabbavarapu, M. M., Roorkiwal, M., Sharanabasappa, B. Y., ... Varshney, R. K. (2019). SuperAnngeri 1 and improved JG 74: Two Fusarium wilt-resistant introgression lines developed using marker-assisted backcrossing approach in chickpea (Cicer arietinum L.). Molecular Breeding, 39(1), 2.

Maruyama, K., Takeda, M., Kidokoro, S., Yamada, K., Sakuma, Y., Urano, K., ... Yamaguchi-Shinozaki, K. (2009). Metabolic pathways involved in cold acclimation identified by integrated analysis of metabolites and transcripts regulated by DREB1A and DREB2A. Plant Physiology, 150, 1972–1980. https://doi.org/10.1104/pp.109.135327

Min, L., Li, Y., Hu, Q., Zhu, L., Gao, W., Wu, Y., ... Zhang, X. (2014). Sugar and auxin signaling pathways respond to high-temperature stress during anther development as revealed by transcript profiling analysis in cotton. Plant Physiology, 164, 1293–1308.

Obata, T., Witt, S., Liscic, J., Palacios-Rojas, N., Florez-Sarasa, I., Yousfi, S., ... Fernie, A. R. (2015). Metabolite profiles of maize leaves in drought, heat and combined stress field trials reveal the relationship between metabolism and grain yield. Plant Physiology, 169, 2665–2683.

Ohama, N., Kusakabe, K., Mizoi, J., Zhao, H., Kidokoro, S., Koizum, S., et al. (2016). The transcriptional cascade in the heat stress response of...
Abundant evidence suggests the importance of accurately quantifying abiotic stress responses and tolerance in rice. Current Opinion in Plant Biology, 130, 18–23.

Redden, R. J., Hatfield, P. V., Prasad, V., Ebert, A. W., Yadav, S. S., & O’Leary, G. J. (2014). Temperature, climate change, and global food security. In: K. A., Franklin & P. A., Wiggers (Eds.), Temperature and Plant Development. (pp. 181–202), John Wiley & Sons, Inc.

Reynolds, M., Manes, Y., Izanloo, A., & Langridge, P. (2009). Phenotyping approaches for physiological breeding and gene discovery in wheat. The Annals of Applied Biology, 155, 309–320.

Roy, S. J., Tucker, E. J., & Tester, M. (2011). Genetic analysis of abiotic stress tolerance in crops. Current Opinion in Plant Biology, 14, 232–239.

Sage, T. L., Bagha, S., Lundsgaard-Nielson, V., Branch, H. A., Sultmanis, S., & Sage, R. F. (2015). The effect of high temperature stress on male and female reproduction in plants. Field Crops Research, 182, 30–42.

Schöffl, F., Prändl, R., & Reindl, A. (1999). Molecular responses to heat stress. In K. Shinozaki, & K. Yamaguchi-Shinozaki (Eds.), Molecular responses to cold, drought, heat and salt stress in higher plants (pp. 81–98), Austin, Texas: R.G. Landes Co.

Sehgal, A., Sita, K., Bhandari, K., Kumar, S., Kumar, J., Vara Prasad, P.V., ... Nayyar, H. (2019). Influence of drought and heat stress, applied independently or in combination during seed development, on qualitative and quantitative aspects of seeds of lentil (Lens culinaris Medikus) genotypes, differing in drought sensitivity. Plant, cell & environment, 42 (1), 198–211.

Sehgal, A., Sita, K., Kumar, J., Kumar, S., Singh, S., Siddique, K.H., & Nayyar, H. (2017). Effects of drought, heat and their interaction on the growth, yield and photosynthetic function of lentil (Lens culinaris Medikus) genotypes varying in heat and drought sensitivity. Frontiers in plant science, 8, 1776.

Serrano, N., Ling, Y., Bahieldin, A., & Mahfouz, M. M. (2019). Thermopriming reprograms metabolic homeostasis to confer heat tolerance. Scientific Reports, 9(1), 181.

Singh, D., Singh, C. K., Singh, T., & Pal, M. (2017). Genetics and molecular mapping of heat tolerance for seedling survival and pod set in lentil. Crop Science, 57(6), 3059–3067.

Singh, D., Singh, C. K., Taunk, J., Jadon, V., Pal, M., & Gaikwad, K. (2019). Genome wide transcriptome analysis reveals vital role of heat responsive genes in regulatory mechanisms of lentil (Lens culinarisMedikus). Scientific Reports, 9(1), 1–9.

Singh, D., Singh, C. K., Tomar, R. S., Chaturvedi, A. K., Shah, D., Kumar, A., & Pal, M. (2016). Exploring genetic diversity for heat tolerance among lentil (Lens culinarisMedikus) genotypes of variant habitats by simple sequence repeat markers. Plant Breeding, 135(2), 215–223.

Sita, K., Sehgal, A., HanumantaraRao, B., Nair, R. M., Prasad, P. V. V., Kumar, S., ... Nayyar, H. (2017). Food legumes and rising temperatures: Effects, adaptive functional mechanisms specific to reproductive growth stage and strategies to improve heat tolerance. Frontiers in Plant Science, 8, 1658.

Sita, K., Sehgal, A., Kumar, J., Kumar, S., Singh, S., Siddique, K. H., & Nayyar, H. (2017). Identification of high-temperature tolerant lentil (Lens culinarisMedikus) genotypes through leaf and pollen traits. Frontiers in Plant Science, 8, 744.

Subbarao, G., Rao, J. Y. D. K., Kumar, J., Johansen, C., & Deb, U. (2001). Spatial distribution, and quantification of rice-fallow in South Asia-potential for legumes. International Crops Research Institute for the Semi-Arid Tropics. Spatial distribution and quantification of rice-fallow in South Asia-potential for legumes. (ICRISAT: Patancheru, India).

Talukder, S. K., Babar, M. A., Vijayalakshmi, K., Poland, J., Prasad, P. V. V., Bowden, R., & Fritz, A. (2014). Mapping QTLs with heat tolerance in wheat (Triticum aestivumL.). BMC Genetics, 15, 97–110. https://doi.org/10.1186/s12863-014-0097-4

Teale, W. D., Poponov, I. A., & Palme, K. (2006). Auxin in action: Signalling, transport and the control of plant growth and development. Nature Reviews Molecular Cell Biology, 7, 847–859.

Todaka, D., Nakashima, K., Shinozaki, K., & Yamaguchi-Shinozaki, K. (2012). Toward understanding transcriptional regulatory networks in abiotic stress responses and tolerance in rice. Rice, 5, 6.

Verma, P., Sharma, T. R., Srivastava, P. S., Abdin, M. Z., & Bhatia, S. (2014). Exploring genetic variability within lentil (Lens culinarisMedik) and across related legumes using a newly developed set of microsatellite markers. Molecular Biology Reports, 41, 5607–5625.

Wienkoop, S., Margenthal, K., Wolschin, F., Scholz, M., Selbig, J., & Weckwerth, W. (2008). Integration of metabolomic and proteomic phenotypes: Analysis of data covariance dissects starch and RFO metabolism from low and high temperature compensation response in Arabidopsis thaliana. Molecular and Cellular Proteomics, 7, 1725–1736.

Yu, J., Li, R., Fan, N., Yang, Z., & Huang, B. (2017). Metabolic pathways involved in carbon dioxide enhanced heat tolerance in Bermuda grass. Frontiers in Plant Science, 8, 1506.

Zhang, L., Zhao, H. K., Dong, Q. L., Zhang, Y. Y., Wang, Y. M., Li, H. Y., ... Dong, Y. S. (2015). Genome-wide analysis and expression profiling under heat and drought treatments of HSP70 gene family in soybean (Glycine maxL.). Frontiers in Plant Science, 6, 773.

How to cite this article: Kumar J, Sen Gupta D, Djalovic I. Breeding, genetics, and genomics for tolerance against terminal heat in lentil: Current status and future directions. Legume Science. 2020;2:e38. https://doi.org/10.1002/leg3.38