

# Temperature sensitivity of food legumes: a physiological insight

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Received: 29 January 2016/Revised: 8 January 2017/Accepted: 20 January 2017/Published online: 6 February 2017  
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**Abstract** Of the various environmental stresses that a plant can experience, temperature has the widest and most far-reaching effects on legumes. Temperature extremes, both high (heat stress) and low (cold stress), are injurious to plants at all stages of development, resulting in severe loss of productivity. In response to unfavorable temperatures, plant biomolecules such as stress proteins, enzymatic and non-enzymatic antioxidants, organic osmolytes and phytohormones come into play, usually, as a part of the plant defense mechanisms. The accumulation of these molecules, which may be useful as metabolic indicators of stress tolerance, depend on the plant species exposed to the temperature stress, its intensity and duration. Some of these molecules such as osmolytes, non-enzymatic antioxidants and phytohormones may be supplied exogenously to improve temperature stress tolerance. Legumes show varying degrees of sensitivity to high and low-temperature stresses, which reduces their potential performance at various developmental stages. To address the ever-fluctuating temperature extremes that various legumes are being constantly exposed, efforts are being made to develop

tolerant plant varieties via conventional breeding methods as well as more recent molecular breeding techniques. In this review, we describe the progress made towards the adverse effects of abnormal temperatures on various growth stages in legumes and propose appropriate strategies to resolve these effects.

**Keywords** Food legumes · Molecular approach · Osmolytes · Physiological effects · Phytohormones · Temperature stress

## Abbreviations

ABA	Abscisic acid
APO	Ascorbate peroxidase
AsA	Ascorbate
ASA	Acetyl salicylic acid
BAC	Bacterial artificial chromosome
BR	Brassinosteroid
cADPR	Cyclic ADP-ribose
CAT	Catalase
CIAT	International Center for Tropical Agriculture
<i>cos</i>	Cold suppressed gene
CSP	Cold-shock proteins
FAOSTAT	Food and Agriculture Organization Statistics
GB	Glycine betaine
GR	Glutathione reductase
GroEL	A molecular chaperone
GSH	Glutathione
HSP	Heat-shock proteins
ICARDA	International Center for Agricultural Research in the Dry Areas
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
IP <sub>3</sub>	Inositol triphosphate
NO	Nitric oxide

Communicated by A. K. Kononowicz.

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OEC	Oxygen evolving complex
O–J–I–P	Transient fluorescence induction transient defined by the names of its intermediate steps
PAs	Polyamines
POX	Peroxidase
RCA	Ribulose activase
ROS	Reactive oxygen species
SA	Salicylic acid
SNP	Sodium nitroprusside
SOD	Superoxide dismutase

## Introduction

Temperature is one of the most important factors determining where crops are grown and, depending on their temperature sensitivities, affecting crop phenology and yield (Repo et al. 2008). Crops are exposed to a wide range of temperature fluctuations under natural growth conditions. Temperature instabilities may be experienced by crops at micro or macro-environment levels, but both can have serious implications on normal growth and production. Climatic hazards are likely to increase in the near future and plants will face lethal temperature leading to a pragmatic shift in temperature zones, differential rainfall patterns and agricultural production belts. Considering this, several studies have evaluated different legume species for their responses to temperature stress, e.g., broad bean (*Vicia faba*; Hamada 2001), soybean (*Glycine max*; Board and Kahlon 2011), chickpea (*Cicer arietinum*; Kaushal et al. 2013).

Several abiotic and biotic factors limit the production potential of legumes (Dita et al. 2006) with temperature stress as one of the most important (Kumar et al. 2010; Gaur et al. 2015). Global climate change is resulting in extreme temperature (high or low) situations in different

regions of the world (Porter and Semenov 2005), which affects the performance of winter as well as summer-season legumes (Stoddard et al. 2006; Board and Kahlon 2011). It is important to understand the responses of various legumes to high or low temperatures in order to address their stress tolerance to ensure global food availability, both now and in the future. Various cool-season legumes [chickpea, lentil (*Lens culinaris*), pea (*Pisum sativum*), broad bean] are susceptible to rising temperatures, as indicated by experiments in the field and in the controlled environment (Stoddard et al. 2006). Each legume species has its own range of maximum and minimum temperatures, threshold temperature (Table 1), and extreme variations in temperature will have serious repercussions on every stage of plant development (Zinn et al. 2010), resulting in severe loss of productivity.

Globally, legume production ranks third preceded by cereals and oilseeds (Popelka et al. 2004), contributing up to ~27% of total crop production (Graham and Vance 2003). The principal grain legumes in order of their respective global consumption are common bean, pea, chickpea, pigeon pea (*Cajanus cajan*), cowpea (*Vigna unguiculata*) and lentil (Reddy et al. 2012). Legumes, especially grain legumes, account for about 33% of dietary protein requirements, serve as an animal feed and fodder, and are source of income for small farmers, especially in developing and under-developing countries (Vance et al. 2000; Popelka et al. 2004). These are ecologically desirable but despite these facts, pulses are regarded as secondary crops worldwide, with the global area under cereal cultivation about ten times higher than that of pulses (Cernay et al. 2016).

The human population will grow to around 9 billion by 2050 and the demand for world food production is expected to rise by 70%. It will be challenging for agricultural experts to meet the food demand of the growing

**Table 1** Threshold temperature range of some legumes

Legumes	Threshold temperature range (°C)	References
Pea ( <i>Pisum sativum</i> )	15–20	Mahoney (1991)
	20–21	Fletcher et al. (1966)
Lentil ( <i>Lens culinaris</i> )	15–25	Barghi et al. (2012)
		Roy et al. (2012)
Chickpea ( <i>Cicer arietinum</i> )	15–30	Singh and Dhaliwal (1972)
		Wang et al. (2006)
Cowpea ( <i>Vigna unguiculata</i> )	18–28	Craufurd et al. (1997)
Pigeon pea ( <i>Cajanus cajan</i> )	18–29	Duke (1981)
Common bean ( <i>Phaseolus vulgaris</i> )	20–24	Kigel et al. (1991)
		Konsens et al. (1991)
Soybean ( <i>Glycine max</i> )	26–36	Boote et al. (2005)
Mung bean ( <i>Vigna radiata</i> )	28–30	Poehlman (1991)
Groundnut ( <i>Arachis hypogaea</i> )	30–35	Talwar et al. (1999)
		Prasad et al. (2000)

population, e.g., global legume demand has increased from 26–27 million tons in 1975–76 to 43–44 million tons in 2007 (FAOSTAT; Fig. 1) while production has not increased accordingly (Fig. 2).

Owing that, this review provides information on the responses of various important legumes to low and high-temperature regimes at different organizational levels and proposes suitable measures to manage such temperature stresses.

The harmful effects of temperature stress are summarized below in the context of legumes.

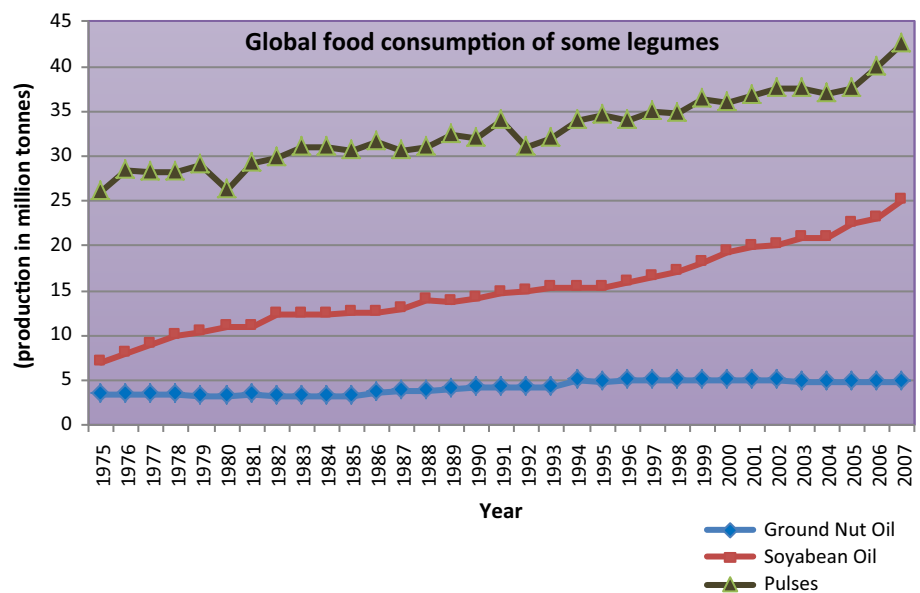
## Vegetative phase

Stressful temperatures affect the plants at all stages of development. Unfavorable temperatures can directly influence seed germination and emergence, early survival and growth of

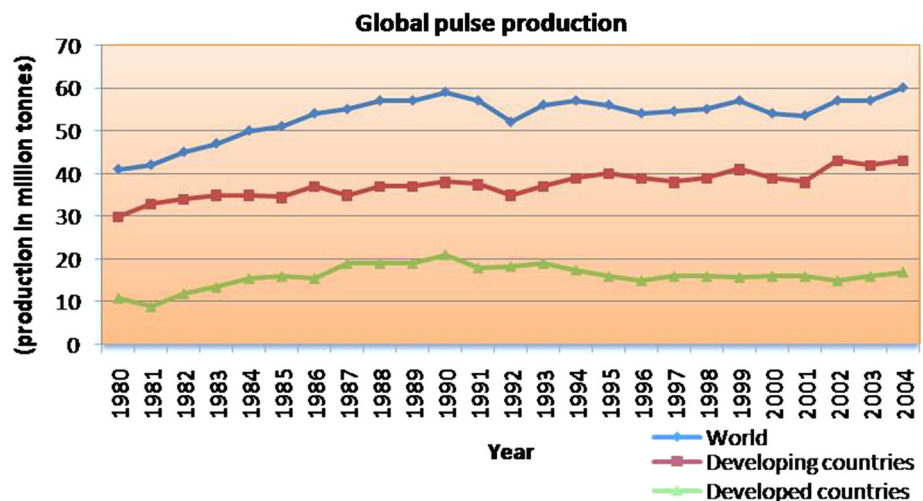
seedlings, e.g., in chickpea, chilling stress during germination not only enhanced the susceptibility to soil-borne diseases, but also led to poor crop establishment and even seedling death (Croser et al. 2003). Likewise, low temperature (1 °C for 4, 6 and 8 h) exposures led to early vegetative phase damage in soybean (1 °C; Posmyk et al. 2005), pea (3 °C for variable durations for different experiments; Badaruddin and Meyer 2001), broad bean (5 °C for 24 h; Hamada 2001), chickpea [(less than 10 °C from the onset of podding till maturity) Kaur et al. (2008); (−10 °C for 15 and 30 min) Heidarvand et al. 2011], and complete seedling death under extreme cold (Badaruddin and Meyer 2001).

High temperatures also potentially harm seed vigor, seed germination, seedling emergence and survival (Wahid et al. 2007) as observed in various legumes, e.g., alfalfa (*Medicago sativa*; Mingpeng et al. 2010), mungbean (Kumar et al. 2011a), and chickpea (Kaushal et al. 2011;

**Fig. 1** Global food consumption of some important legumes from 1975 to 2007. Pulses and soybean oil demand increased while that of groundnut oil hardly changed  
Source: FAOSTAT; <http://faostat3.fao.org>



**Fig. 2** Global pulse production from 1980 to 2004 Source: FAOSTAT; <http://faostat3.fao.org>



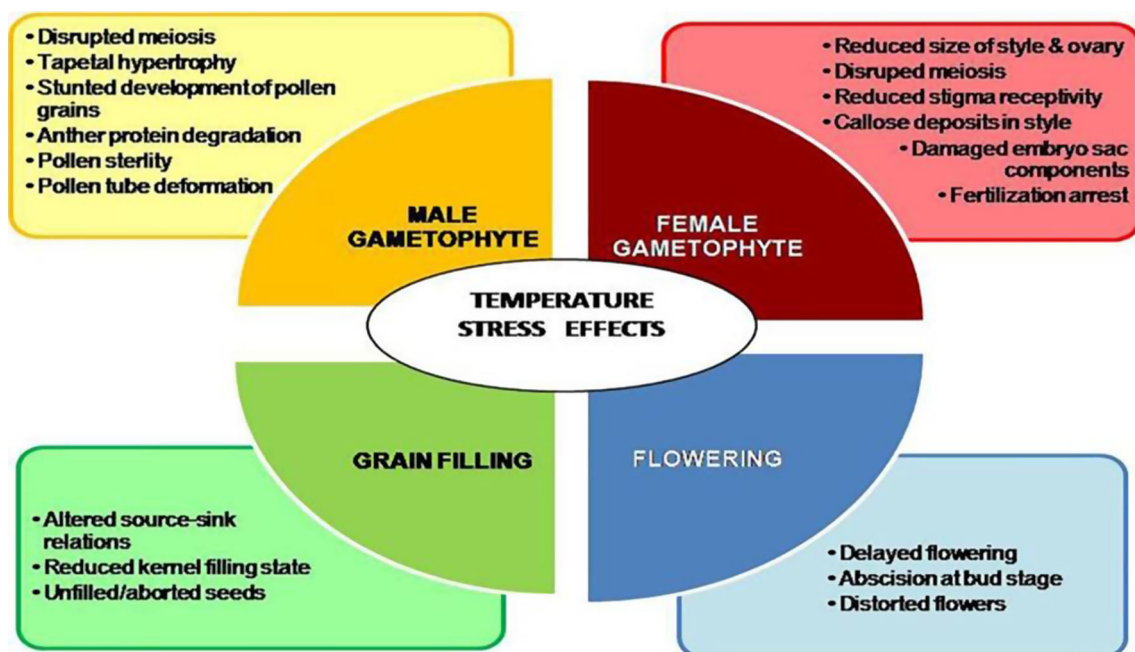
Piramila et al. 2012). Heat tolerance in three prominent legumes—bean, pea and soybean was investigated under different (D/N) temperature regimes—control (20 °C/10 °C), moderate high stress (MHT; 25 °C/25 °C) and severe heat stress (SHT; 30 °C/30 °C). As anticipated, the maximum heat stress injury was observed under SHT, with regard to reduced seedling length and increased dead seed percentage (Nemeskèri 2004). Growth of pea seedlings decreased, when subjected to heat shock (45, 50 °C), but surprisingly, the effects of heat injury were circumvented by pre-exposing the heat-stressed seedlings to chilling temperatures (Shereena and Salim 2006). Likewise, severe damage to mungbean seedlings was noticed in terms of mean seedling germination, growth and heat tolerance index upon exposure to 50 °C for 2 h in mungbean (Mansoor and Naqvi 2011) and 35–50 °C for 4 h in lentil (Chakraborty and Pradhan 2011). High temperatures similarly affected alfalfa plants resulting in stunted growth, increased susceptibility to diseases and even plant death in extreme cases (Mingpeng et al. 2010). Heat tolerance evaluation of some important food legumes, exposed to heat stress, revealed the following order: groundnut (most tolerant) > soya bean > pigeon pea > chickpea (least tolerant) on the basis of membrane stability and photosystem (PSII) function (Srinivasan et al. 1996). Such a comparative evaluation of all legumes under a similar set of experimental conditions would provide greater insight towards their relative sensitivities to low and high temperatures and such similar studies are in need for other legumes as well under varied temperature regimes.

## Reproductive development

Among all stages in a plant life cycle, reproductive phase is the most temperature vulnerable to many external constraints (Hedhly et al. 2008; Thakur et al. 2010). Unfavorable temperatures at this stage impair flower set and flower retention, gametophyte development, followed by ovule abortion, reduced fruit set and impaired grain filling (Fig. 3), eventually leading to the yield losses (Table 2).

Cool-season legumes, i.e., chickpea, lentil, pea and bean are sensitive to low temperature, especially during pod formation and seed filling (Maqbool et al. 2010). Low temperatures impair carbohydrate metabolism leading to energy-deprivation of various reproductive tissues such as tapetum, style and endosperm resulting in gametophyte sterility (Nayyar et al. 2005b; Oliver et al. 2005). Failed chickpea fertilization has been attributed to reduced pollen tube growth in the style thus leading to no pod set in cold-stressed plants (Clarke and Siddique 2004). Such observations were further extended by fluorescence studies which identified the loss in pollen load, reduced pollen germination on the stigmatic surface and reduced pollen tube growth under very low temperatures, thus leading to the fertilization failure (Kumar et al. 2010).

Low-temperature damage to phenology and grain filling has been well documented in various legumes (Table 2). Grain filling depends on the source–sink relationship, which declines under low temperature due to a reduction in the duration and rate of grain filling, and inhibition of accumulation of storage proteins, minerals and amino



**Fig. 3** Various effects of temperature stress on reproductive development stages in legumes

acids, as reported in chilling-stressed chickpea plants (Nayyar et al. 2007). In soybean, exposure to cold stress at flowering and podding stages reduced the yield drastically as compared to the same exposure at maturity (Board and Kahlon 2011) and the damage was more pronounced in cold-sensitive varieties (Kurosaki and Yumoto 2003).

Severe chilling injury was also observed in pea accessions from 34 countries at flowering and podding (Shafiq et al. 2012). The low-temperature damage in pea resulted in the appearance of aborted buds, flowers and fruit pods and smaller seeds. Such observations could be used to screen for cold-resistant and cold-tolerant accessions of various legumes and to develop new cold-tolerant varieties.

A rise of even 1–2 °C above the threshold temperature critically impairs the yield and related attributes of leguminous crops (Barghi et al. 2012; Kumar et al. 2013) as reported in snap bean (Omae et al. 2007; Kumar et al. 2008a), soybean (Board and Kahlon 2011; Djanaguiraman et al. 2011), and chickpea (Kumar et al. 2013). In chickpea, the yield loss has been proposed to be due to the heat stress which induced multiple structural and functional abnormalities such as callose deposition in both pollen as well as stigma, the former has been reported to be clearly more sensitive (Devasirvatham et al. 2013). Likewise, in green/snap bean, heat-tolerant genotype had higher pollen viability than sensitive one producing abnormal pods and abscised flowers at high temperatures (Suzuki et al. 2001, 2003) which was attributed to the greater loss of relative tissue water content (RWC) and leaf water potential (LWP; Omae et al. 2005; Tsukaguchi and Egawa 2006). Ultrastructural studies revealed that pollen sterility was due to degenerated tapetum owing to heat stress (Suzuki et al. 2001). In lentil, 15 °C was the most favorable temperature for pollen germination and pollen tube growth, with higher temperatures adversely affecting pollen tube growth (Barghi et al. 2013).

Not only cool-season legumes are susceptible to high temperatures; some warm-season legumes such as cowpea have experienced a reduction in pod set in response to the moderately to high night temperatures (Thiaw and Hall 2004). The relationship between yield loss and heat stress was so strong that yield and related attributes were advocated in the screening of heat-tolerant and heat-sensitive chickpea genotypes by exposing a reference collection of chickpea germplasm to supra-optimum temperatures at their reproductive phase (Krishnamurthy et al. 2011). Thus, various legumes are sensitive to both low and high-temperature stress from the vegetative to reproductive stage, resulting both in metabolic, reproductive and yield losses (Table 3).

Further studies are needed to dissect the sensitivity of various reproductive stages to the contrasting temperatures. In addition, molecular mechanisms of pollen development under cold or high-temperature stresses including genes responding to temperature stress need to be further

elucidated. Identifying mechanisms associated with reproductive temperature tolerance at different organizational levels in various legumes will be achieved more easily if contrasting genotypes with a relevant phenology are used.

## Cell membranes

Under low temperatures, membranes get more static thereby reducing fluidity and as a result, the membrane is more rigid and may lose its function (Jewell et al. 2010). The phase transitions in mungbean cell membranes were acknowledged as a pioneering study on legumes (Raison and Orr 1986). Five-day-old seedlings subjected to low temperature (4 °C) had an irreversible chilling injury inferred from increased electrolyte leakage (Chang et al. 2001). The solute leakage apparently resulted from disruption of the plasma membrane and tonoplast and the results were in agreement with similar studies in broad bean (Hamada 2001), chickpea (Croser et al. 2003; Nayyar et al. 2005a), and mungbean (Saleh 2007).

Membranes are also the primary sites of injury under heat stress (Wise et al. 2004) since high temperature affects membrane structure and function by increasing membrane fluidity (Wahid et al. 2007), and also activates the lipid-based signaling pathways (Horváth et al. 2012). Cellular membranes are susceptible to heat injury due to structural modification of component proteins leading to increased membrane permeability and hence increased electrolyte leakage which serves as an indicator of membrane damage and has been used to evaluate the thermostability of cell membranes also under heat stress.

The effects of high temperature on cell membranes have been studied in mungbean (Collins et al. 1995) and chickpea (Kumar et al. 2013). Higher membrane damage was observed in sensitive chickpea genotypes at 40/30 °C (D/N), which was further aggravated at 45/35 °C (D/N; Kumar et al. 2013). The extent of membrane injury can be thus used as a criterion for evaluating relative heat sensitivity of different genotypes, as studied in chickpea (Ibrahim 1994) and cowpea (Ismail and Hall 1999). Likewise, Srinivasan et al. (1996) tested cell membrane thermostability and correlated it with heat sensitivity in various legumes in the following order: groundnut (most tolerant) > soybean > pigeon pea > chickpea (most sensitive). Similar studies on cool-season legumes (chickpea, faba bean and lentil) revealed membrane thermostability to be closely related to plant heat tolerance (Ibrahim 2011). Recently, the heat tolerance studies on nine lentil genotypes, subjected to different temperatures ranging from 15 to 45 °C with 10 °C interval, proposed 15 °C to be the most favorable temperature as subsequent higher temperatures increased the electrolyte leakage due to heat stress-



**Table 2** Temperature-sensitive reproductive developmental stages in various legumes

Developmental stage	Effects	Cold stress (references)	Heat stress (references)
Pre-fertilization	Impaired microsporogenesis and megasporogenesis	<i>Cicer arietinum</i> (Kumar et al. 2010)	<i>Phaseolus vulgaris</i> (Porch and Jahn 2001; Suzuki et al. 2001)
		<i>Glycine max</i> (Ohnishi et al. 2010)	
	Loss of pollen viability	<i>Cicer arietinum</i> (Kumar et al. 2010)	<i>Cicer arietinum</i> (Kumar et al. 2013)
	Loss of pollen germination	<i>Cicer arietinum</i> (Srinivasan et al. 1999)	<i>Phaseolus vulgaris</i> (Porch and Jahn 2001)
		<i>Glycine max</i> (Koti et al. 2004; Salem et al. 2007)	<i>Arachis hypogaea</i> (Kakani et al. 2005)
			<i>Cicer arietinum</i> (Kumar et al. 2013)
	Pollen tube growth inhibition	<i>Cicer arietinum</i> (Clarke and Siddique 2004; Kumar et al. 2010)	<i>Arachis hypogaea</i> (Kakani et al. 2005)
		<i>Glycine max</i> (Koti et al. 2004; Salem et al. 2007)	<i>Cicer arietinum</i> (Kumar et al. 2013)
			<i>Lens</i> spp. (Barghi et al. 2013)
	Loss of stigma receptivity	<i>Cicer arietinum</i> (Nayyar et al. 2005b; Kumar et al. 2010)	<i>Cicer arietinum</i> (Kumar et al. 2013)
Loss of ovule viability	<i>Cicer arietinum</i> (Srinivasan et al. 1999; Nayyar et al. 2005b)	<i>Cicer arietinum</i> (Jakobsen and Martens 1994)	
Abscised flowers		<i>Phaseolus vulgaris</i> : (Gross and Kigel 1994)	
		<i>Glycine max</i> (Board and Kahlon 2011)	
Fertilization	Fertilization arrest	<i>Cicer arietinum</i> (Clarke and Siddique 2004)	<i>Cicer arietinum</i> (Kumar et al. 2013)
Post-fertilization	Reduced embryogenesis	<i>Glycine max</i> (Ohnishi et al. 2010)	
		<i>Cicer arietinum</i> (Srinivasan et al. 1999; Nayyar et al. 2005b)	<i>Cicer arietinum</i> (Kumar et al. 2013)
	Decreased ovule number and increased ovule abortion	<i>Cicer arietinum</i> (Srinivasan et al. 1999)	<i>Cicer arietinum</i> (Kumar et al. 2013)
	Abnormal pod formation and seed filling	<i>Glycine max</i> (Kurosaki and Yumoto 2003; Funatsuki et al. 2004)	<i>Phaseolus vulgaris</i> (Djanaguiraman et al. 2013)
	Poor seed quality	<i>Cicer arietinum</i> (Nayyar et al. 2005c; Kumar et al. 2010)	<i>Glycine max</i> (Board and Kahlon 2011)
	<i>Pisum sativum</i> (Shafiq et al. 2012)	<i>Cicer arietinum</i> (Kumar et al. 2013)	

The effects are indicated along with respective references

inflicted membrane damage (Barghi et al. 2013). Heat-induced membrane damage has also been reported in broad bean (Mansoor and Naqvi 2013), chickpea (Kumar et al. 2013) and soybean (Djanaguiraman et al. 2011).

On the whole, membrane damage can conveniently be considered a reliable indicator of stress tolerance in legumes and can be effectively employed to screen these crops for cold or heat tolerance.

## Metabolic effects

### Photosynthesis and respiration

The rate of photosynthesis varies in different plant species and is temperature dependent (Hikosaka et al. 2006). Low temperatures and high light intensity bring about photo-

oxidation of the photosynthetic machinery in chickpea (Nayyar et al. 2005a, b, c, d) which impairs electron transport, deactivates rubisco and closes stomata resulting in reduced CO<sub>2</sub> assimilation (Allen and Ort 2001). Low temperature affects the activity of enzyme ribulose activase (RCA), changes the availability of large and small subunits of rubisco, disrupts PSII oxygen-evolving complex (OEC) and damages the structure and functioning of D1 and D2 polypeptides of PSII (Aro et al. 1990). While studying temperature sensitivity in two pea cultivars, Georgieva and Lichtenthaler (2006) found that chlorophyll fluorescence and the chl/car ratio decreased while the chl a/b ratio increased under cold stress. Photosynthesis declined in soybean by more than 50% when subjected to only one night of chilling treatment (Van Heerden and Krüger 2000; Van Heerden et al. 2003). Chilling inhibited photosynthesis, which was further confirmed in soybean (Board and

**Table 3** The proposed stressful temperature ranges for various legumes and their effects

Plant	Stressful temperature	Stage	Effects	References
<i>Glycine max</i>	42–43 °C	Vegetative stage	Damaged PSII	Ferris et al. (1998)
	Above 35 °C	Reproductive stage	Abscised flowers	Koti et al. (2004)
				Reduced yield
<i>Cicer arietinum</i>	Below 15 °C	Reproductive stage	Abscised flowers	Srinivasan et al. (1999)
		Grain filling	Reduced pod set	Clarke and Siddique (2004); Nayyar et al. (2005c)
			Reduced yield	
	35/16 °C	Flower and pod formation	Reduced yield	Wang et al. (2006)
	45/35 °C	Reproductive stage	Damaged PSII	Kumar et al. (2013)
	Above 32/20 °C		Reduced rubisco activity and sucrose content	Kaushal et al. (2013)
<i>Vicia faba</i>	5 °C for 1 day	Vegetative stage	Impaired growth, decreased photosynthesis	Hamada (2001)
	42 °C for 1 day	Vegetative stage	Impaired growth, decreased photosynthesis	Hamada (2001)
<i>Phaseolus vulgaris</i>	10 °C	Vegetative stage	Damaged PS II	Tsonev et al. (2003)
<i>Cajanus cajan</i>	Below 10 °C	Seed germination till early growth	High mortality	Sandhu et al. (2007)
<i>Pisum sativum</i>	−4.8 °C for 4 h	Reproductive stage	Abscised flowers	Shafiq et al. (2012)
		Grain filling	Reduced pod set	
			Reduced yield	
<i>Lupinus angustifolius</i>	Above 27 °C	Reproductive stage	Floret sterility	Redden et al. (2013)
			Reduced yield	

Kahlon 2011), common bean (Tsonev et al. 2003), and broad bean (*Vicia faba*; Hamada 2001). The OJIP test (fluorescence induction transient defined by the names of its intermediate steps) measures rapid fluorescence transients (Strasser and Strasser 1995) and hence gives a clear idea about the efficiency of photosynthetic machinery, especially PSII function. The OJIP test thus can indicate stress in plants before appearance of symptoms on the leaves (Christen et al. 2007). When conducted on beans, this test revealed that cold-induced photosynthetic machinery damage was due to impeded chlorophyll a fluorescence (Goltsev et al. 2010).

An initial increase in temperature may increase photosynthetic activity, but prolonged exposure above the normal growth temperature range inhibits photosynthesis (Schuster and Monson 1990). Supra-optimal temperature deteriorates photosynthetic pigments and carboxylation function (Kumar et al. 2013) and damage photosynthetic machinery especially the thylakoid lamellae (Hamada 2001; Tambussi et al. 2004). Chlorophyll fluorescence parameters also decreased remarkably in heat-sensitive common bean genotypes over tolerant one (Petkova et al. 2007). Even short exposure to temperatures above 40 °C disrupted the normal functioning of PSII and impaired the structure and functioning of related proteins and enzymes

in soybean (Board and Kahlon 2011) and bird's foot trefoil (*Lotus japonicus*; Sainz et al. 2010). The studies carried out by Kumar et al. (2013) on the response of chickpea genotypes to heat stress also corroborated the heat sensitivity of photosynthetic machinery, which correlated with a severe reduction in growth and yield (Kaushal et al. 2013). However, some reports state that under moderately high temperature (35 °C), the functional potential of the photosynthetic apparatus was preserved, e.g., in pea (Haldimann and Feller 2005).

Thus, the performance of plants under temperature stress is directly related to their photosynthetic efficiency, and research aimed at elucidating detailed mechanisms underlying the response of photosynthetic machinery to temperature stress in terms of photosynthetic rate and chlorophyll fluorescence will provide a better understanding of the correlation between the two, and hence, may be used in screening large numbers of genotypes for temperature tolerance in food legumes.

Respiration in plants is a temperature-sensitive process and an initial increase in response to chilling has been reported (Kaur et al. 2008). A 68% decrease in cellular respiration was reported in chickpea (Nayyar et al. 2005c) at very low temperatures (5 °C/13 °C), possibly due to changes in mitochondrial structure, less kinetic energy and

impaired structure and function of some important house-keeping proteins and enzymes related to cytochrome activity, ubiquinone synthesis and phosphorylation reactions related to ATP-dependent metabolism (Munro et al. 2004). In some cases, respiration rates continue to be elevated even when cold exposure ends; this has been attributed to irreversible changes in metabolic machinery and generation of some high-energy intermediates (Yadegari et al. 2008). Under low temperature, the conventional cytochrome pathway of electron transport is inhibited such that, to improve the respiration rate, plants shift to alternative respiration pathways, i.e., AOX (alternative oxidase) and PUMP [(plant uncoupling mitochondrial protein) Vanlerberghe 2013; Chocobar-Ponce et al. 2014]. The involvement of alternative pathways is evident from the increased levels of AOX protein and cyanide-resistant respiration in the mitochondria (Vanlerberghe 2013), as observed in fully grown leaves of cold-stressed mungbean and pea (Gonzalez-Meler et al. 1999); however, the specific AOX gene isoforms preferentially expressed in legumes need to be tested yet. The findings were further corroborated in common bean seeds subjected to different cold treatments. The seeds at normal temperature respired normally for 1 week. However, at  $-19\text{ }^{\circ}\text{C}$  seeds respired for only 1 day and at  $3\text{ }^{\circ}\text{C}$  seeds respired for 5 days where the rate of respiration was even higher than at normal temperature. This adaptive behavior was attributed to the involvement of AOX and PUMP pathways (Srivastava et al. 2016). Some studies have suggested a possible cross-talk between alternative pathways and other stress mitigating mechanisms such as SA (salicylic acid)-mediated stress response in providing low temperature resistance (Lei et al. 2010).

Respiratory pathway has been found to be more heat sensitive than photosynthetic pathway. Respiration is directly related to minimum air temperature and high temperatures result in increased respiration and hamper biomass and yield (Hatfield et al. 2011). High night temperature-induced yield loss in soybean was also credited to increased respiration and decreased photosynthesis (Djanaguiraman et al. 2013). In response to an initial increase in temperature, rate of respiration increases exponentially but later plunges significantly (Hasanuzzaman et al. 2013). Decreased respiration under high temperature has been reported in chickpea (Kumar et al. 2013) and was most likely due to impaired structure and function of mitochondrial enzymes associated with electron transport chain as reported in some non-leguminous crops such as rice (*Oryza sativa*; Mohammed and Tarpley 2009), tomato (Sato et al. 2003) and turf grasses (*Festuca arundinacea* L., *Poa pratensis* L.; Jiang and Huang 2001).

Very sparse information is available in literature on the effects of heat stress on respiration-related biochemical

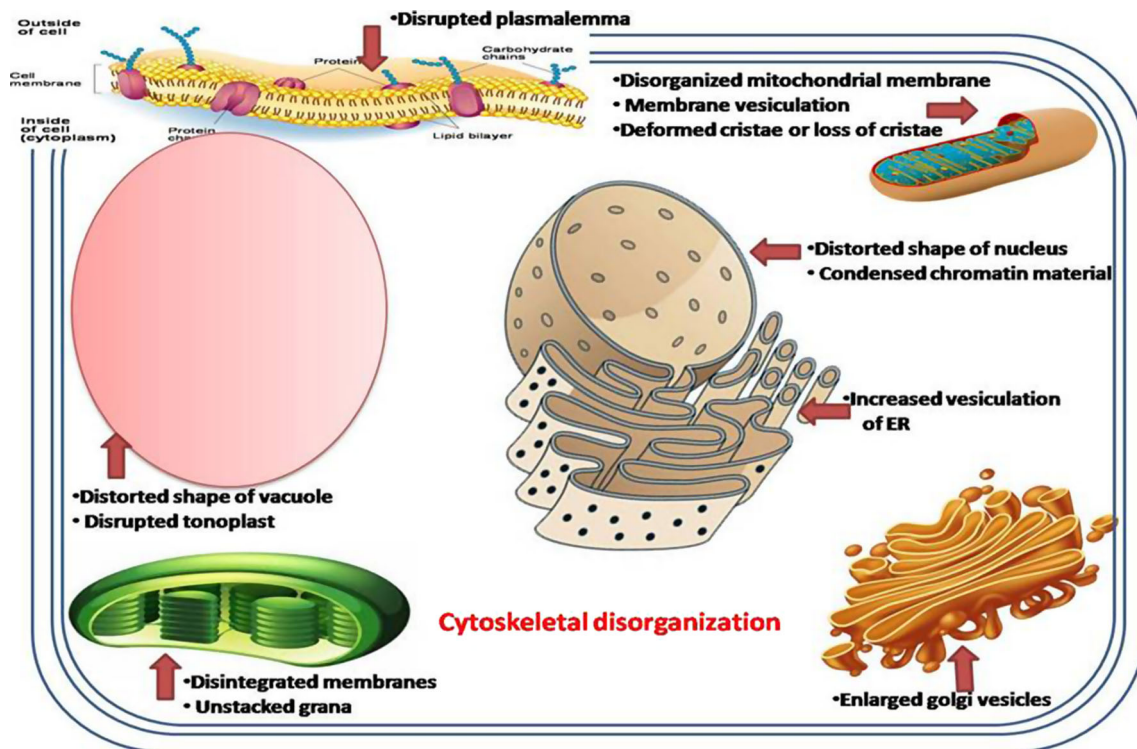
pathways. Evaluation of expression of some key enzymes/genes related to photosynthesis and respiration functions, simultaneously, in contrasting genotypes of various legumes growing under temperature extremes would reveal some useful insight on mechanisms associated with yield losses. Especially, profiling of endogenous levels of ATP, NADPH/NADH pool would be useful to assess the redox potential and energy status of the tissue under different temperature regimes.

### Effects at ultrastructural levels

Damage to cellular components at ultrastructural levels, in response to temperature stress, has been well researched (Fig. 4). The extent of damage depends on the relative sensitivity of the various organelles and the severity and damage of the temperature stress (Lee et al. 2002). On the basis of chilling experiments conducted by Wilson (1987) on pea and bean, various organelles can be arranged in decreasing order of chilling sensitivity: plastids > mitochondria > peroxisome > nuclear envelope > tonoplast > plasmalemma. Chilling-stressed ( $28\text{ }^{\circ}\text{C}$  dark grown) plants showed irreversible etiolation indicating damage to chloroplasts at the ultrastructural level and suppression of 12 chloroplast-related *cos* (cold-suppressed) genes (Yang et al. 2005).

Chilling-induced structural aberrations were noticed in mungbean (Ma et al. 1990) were manifested in the form of fewer and smaller starch granules and vesiculation of the inner chloroplastic membrane leading to the formation of peripheral reticulum. If unfavorable low temperatures continued further, the chloroplasts deteriorated by developing lipid granules, reducing or eliminating starch granules, unstacking grana, disintegrating membranes and even intermixing of chloroplastic and cytoplasmic content as observed in cultured mungbean cells (Ishikawa 1996). Likewise, chilling-inflicted ultrastructural damage in mitochondria was reported as swelling and vacuolation, membrane vesiculation, enlarged and deformed cristae or loss of cristae, membrane disruption or even complete loss of its contents thereby becoming transparent and resulting in intermixing of mitochondrial and cytoplasmic content (Kratsch and Wise 2000; Lee et al. 2002); however, further details about organelle behavior during recovery phase are not available for legumes. In cultured mungbean cells subjected to chilling, nuclei shape was distorted, the nuclear envelope was expanded, and chromatin material condensed. Moreover, fibrillar and dense material massively accumulated in the nucleoplasm and cytoplasm (Ishikawa 1996). Detailed studies reveal the cytoplasm and organelle content intermixing to be due to disorganization of cytoskeleton resulting in cell plasmolysis followed by





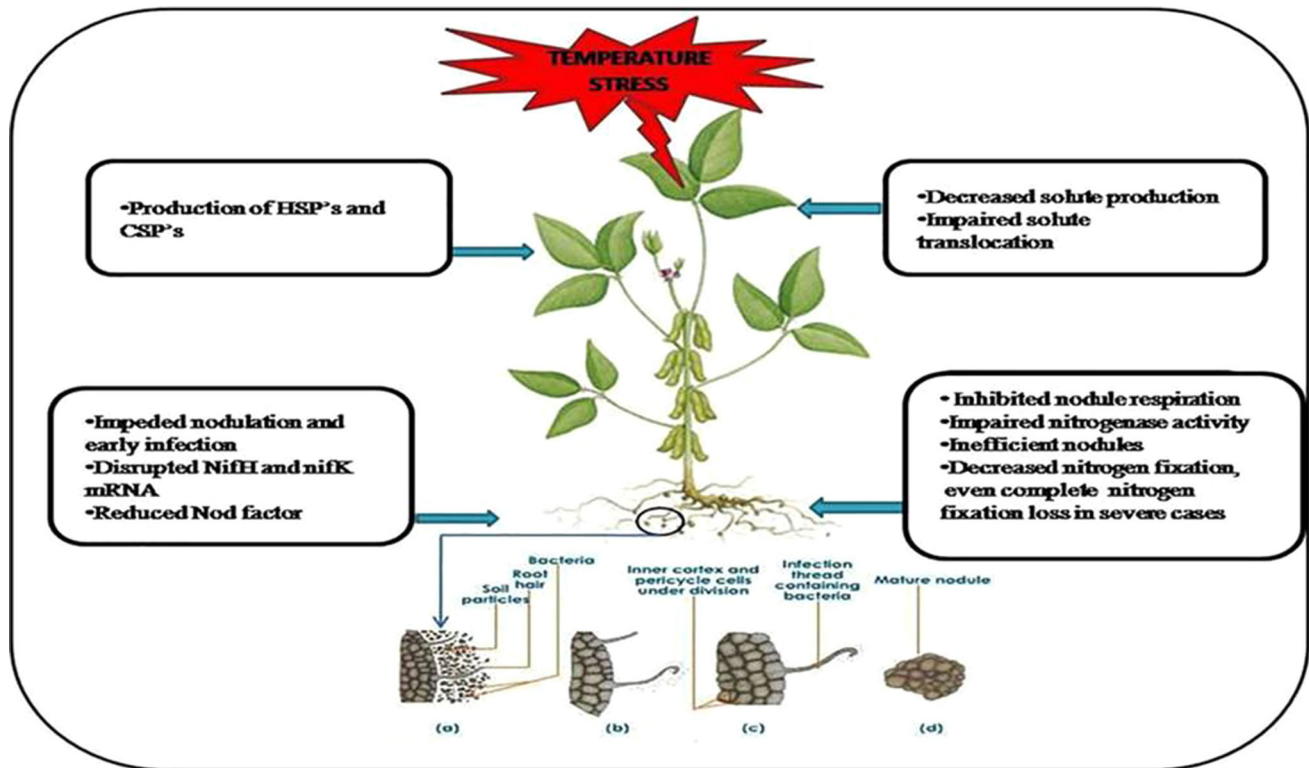
**Fig. 4** Effects of temperature stress on various organelles of a plant cell

vacuolation of cytoplasm and cellular organelles. Cellular content-laden vesicles then fuse with these vacuoles. Simultaneously, organelles are digested and aggregate into a single large vacuole and undergo phagocytosis, remarkably similar to programmed cell-death events. The stress recovery of different organelles is, however, species-dependent thereby making it almost impossible in case of extremely sensitive plants (Kratsch and Wise 2000). Other deformities included cells losing their shape and swelling, disrupted plasmalemma, disorganized tonoplast, enlarged Golgi vesicles, and increased vesiculation of ER. Chilling-induced aberrations in the cell wall and plasma membrane have been reported in mungbean (Yamada et al. 2002).

On the other hand, reports of ultrastructural damage under high temperature are not available for legumes; however, serious ultrastructural damage in non-leguminous crops has been well reported, e.g., damaged chloroplasts in turfgrass (Xu et al. 2006) and damaged mesophyll tissue, disorganized cristae and emptied mitochondria in grapes (*Vitis vinifera*; Zhang et al. 2005) and maize (*Zea mays*; Karim et al. 1997). Exploring the effects of heat stress on ultrastructure in legumes to determine the extent of damage at the organelle level would be useful to link mechanisms associated with heat tolerance. Observations on genotypes differing in cold or heat sensitivity would reveal finer cellular adaptations, which might be useful for further investigation of the tolerance-associated mechanisms.

### Symbiotic nitrogen fixation

Legumes contribute to about 40% of the biologically fixed nitrogen and hence increase soil fertility and decrease reliance on nitrogen fertilizers thereby, minimizing environmental and socio-economic hazards due to the indiscriminate use of fertilizers (Yadav 2008). However, the nitrogen-fixing ability of various bacterial strains is susceptible to numerous adverse conditions (Alexandre and Oliveira 2013; Niste et al. 2013) especially temperature (Fig. 5). Sub-optimal temperatures prolong root infection and impede nodule development and nitrogenase activity (Drouin et al. 2000). Under low temperatures, the production and secretion of Nod factors by *Rhizobium leguminosarum* bv. *trifolii* decreased thus retarding growth in alfalfa (Rice and Olsen 1988) and soybean (Lynch and Smith 1993). The threshold temperature for marked nodulation interruption is legume specific, e.g., common bean and soybean have a similar threshold whereas lentil is comparatively cold tolerant in such a way that only temperatures below 10 °C substantially diminish nodulation (Lira et al. 2005). The earliest account of heat shock proteins (HSPs) and cold-shock proteins (CSPs) induction in rhizobial strains, similar to other bacteria, was reported in heat as well as cold-treated temperate and arctic rhizobial strains (Cloutier et al. 1992). The findings were further confirmed in *Sinorhizobium meliloti* where a *cspA* cold-



**Fig. 5** Effect of temperature on symbiotic nitrogen fixation. Unfavorable temperatures impair nodulation and nitrogen fixation resulting in low solute production, transportation and synthesis of various heat and cold-shock proteins

shock operon similar to *E. coli cspA* was found (O'Connell and Thomashow 2000) followed by similar studies in *R. leguminosarum* bv. *viciae* (microsymbiont of *Lotus japonicus*, capable of growing at 5 °C; Drouin et al. 2000) and *Rhizobium* DDSS69 strain (symbiont of *Sesbania cannabina*; Sardesai and Babu 2001). The CSPs generated by cold-tolerant rhizobia bind to nucleic acids and maintain gene expression at low temperatures.

The temperature sensitivity of rhizobia, in turn, directly affects the nitrogen fixation in legumes, e.g., two soybean genotypes, differing in chilling sensitivity, under cold stress showed impaired nodule respiration, nitrogenase activity and *NifH* and *nifK* mRNA. After cold recovery, the cold-tolerant genotypes kept nodule respiration unlike the sensitive genotype, thereby fixing limited nitrogen and reducing nitrogen availability to the plant (Van Heerden et al. 2008).

While temperatures below 10 °C result in poor nodulation as well as rhizobial growth, some strains of *Rhizobium* and *Bradyrhizobium*, particularly from arctic and sub-arctic regions, are adapted to temperatures as low as 4 °C (Van Heerden et al. 2004). These well-adapted rhizobia are markedly competitive and could be used to improve symbiotic nitrogen fixation and hence the legume yield grown under cold conditions (Prévost et al. 1999), e.g., inoculation of soybean with *Bradyrhizobium japonicum* isolated from cold soils in Japan (Lynch and Smith 1993) and

temperate legume sanfoin (*Onobrychis viciifolia*) with rhizobial strains indigenous to Canadian high arctic (Prévost et al. 1999) effectively ameliorated dry matter, yield and nitrogen-fixing efficiency under low temperatures.

Compared to studies on cold stress, the impact of heat stress on rhizobia has been thoroughly studied (Lira et al. 2005). Although high-temperature stressed common bean plants (35 or 38 °C; 8 h/day) formed nodules, they were inefficient in nitrogen fixation and the control plants (grown at 28 °C) when exposed to even higher temperatures (40 °C; 8 h/day) at the flowering stage, displayed a substantial reduction in nitrogenase activity and hence nitrogen-fixation (Hungria et al. 1993). In a parallel study, no nodules were formed in peanut at 40 °C and soybean at 37 °C (Hungria and Vargas 2000), and it was further established that heat tolerance of *Bradyrhizobium* directly affects the symbiotic efficiency between the bacterium and host soybean at all stages of legume–rhizobium symbiosis (Yadav and Nehra 2013). Further, the correlation between thermo-tolerance and nitrogen-fixation efficiency of rhizobial strains has been demonstrated in some studies worldwide, e.g., *Bradyrhizobium* and *Rhizobium* strains capable of surviving at high temperatures showed efficient nitrogen-fixation also under heat stress (Kishinevsky et al. 1992; Nehra et al. 2007). Tolerant strains of *Mesorhizobium*, when exposed to heat shock, had increased *GroEL* (*HSP60*) gene expression

compared to susceptible strains (Alexandre and Oliveira 2011; Laranjo and Oliveira 2011). The GroEL (HSP60) is an HSP that acts as a chaperone and also regulates *nif* gene (Ribbe and Burgess 2001; Horwich and Fenton 2009). The proteome profiling of *Rhizobium tropici* strain PRF81 grown at 28 and 35 °C revealed up-regulation of about 59 different proteins under heat stress including HSPs such as DnaK and GroEL, along with various anti-oxidative proteins indicating some cross-talk between heat and oxidative stresses (Gomes et al. 2012). On the other hand, some additional studies have contradicted the positive correlation between temperature tolerance and symbiotic nitrogen fixation where either no correlation was observed, as reported in *Acacia nilotica* (Rustogi et al. 1996), *Bradyrhizobium* and *Rhizobium* (Gopalakrishnan and Dudeja 1999) or a negative correlation was reported, as observed in lentil (Moawad and Beck 1991).

On the whole, studies have strongly suggested temperature-tolerant nitrogen-fixing rhizobial strains as an efficient intervention in mitigation of temperature stress in legumes either directly (by inoculation) or indirectly (by providing genes) for raising temperature stress-tolerant transgenic plants.

### Temperature-induced oxidative stress

Abiotic stresses alter normal metabolic functioning of plants, which have developed some mechanisms to adjust to stress conditions including enhancing anti-oxidative machinery, recently reviewed by us in temperature-stressed crops (Awasthi et al. 2015). Reactive oxygen species (ROS) are normally produced as byproducts of various cellular oxidation processes (Perl-Treves and Perl 2002) and act as useful secondary messengers (Gechev et al. 2006; Yan et al. 2006); however, there is a delicate balance between ROS generation and its scavenging and over-production can be harmful (Esfandiari et al. 2007).

Each plant has its own anti-oxidative system where ROS-scavenging enzymes such as SOD (superoxide dismutase), CAT (catalase), APO (ascorbate peroxidase), POX (peroxidase) and GR (glutathione reductase) come into play along with non-enzymatic antioxidants such as glutathione (GSH), ascorbate (AsA) and carotenoids (Hasanuzzaman et al. 2013). ROS quenching by anti-oxidative machinery is linked to stress tolerance, e.g., higher cold tolerance was observed in plants with enhanced activities of anti-oxidative enzymes in chickpea (Kumar et al. 2011b) and alfalfa (Wang et al. 2009). Soybean seedlings exposed to very low temperature (1 °C) increased activities of anti-oxidative enzymes (Posmyk et al. 2005). Similarly, Kaur et al. (2008) reported increased activity of anti-oxidative enzymes in chickpea pod walls to protect pods and developing seeds from

chilling injury. The chilling experiments carried out by Wang et al. (2009) on alfalfa genotypes with diverse chilling sensitivities showed that the chilling-tolerant genotypes had higher anti-oxidative activity than the chilling-sensitive genotypes. Likewise, Turan and Ekmekçi (2011) exposed chickpea cultivars to low temperatures (2 and 4 °C) and reported enhanced activities of PSII and anti-oxidative enzymes in acclimated plants.

ROS generation has been also reported under heat stress (Potters et al. 2007) and is an indicator of cellular damage due to lipid peroxidation and altered membrane permeability. Under high temperatures, a plant's anti-oxidative system gears up for easing heat-induced oxidative stress as observed in selected fabaceous plants such as chickpea (Kumar et al. 2013), soybean (Djanaguiraman et al. 2011), mungbean (Mansoor and Naqvi 2013) and lentil (Chakraborty and Pradhan 2011). Chickpea plants exposed to 45/40 °C (D/N) showed varied expression of enzymatic (SOD, CAT, APX, GR) and non-enzymatic antioxidants (AsA, GSH) (Kaushal et al. 2011). Lipid peroxidation and H<sub>2</sub>O<sub>2</sub> levels were higher at higher temperature, i.e., at 40/30 °C (D/N), which further increased when the temperature reached 45/35 °C (D/N). Simultaneously, the expression of enzymatic and non-enzymatic antioxidants also increased at 40/30 °C but decreased with any further increase in temperature. Similar observations were recorded by Chakraborty and Pradhan (2011) in their heat treatment experiments on lentil, where tolerant varieties had higher anti-oxidative properties than sensitive ones when exposed to high temperatures (35–45 °C; D/N). Mungbean exposed to high temperatures (50 °C for 2 h) also expressed enhanced levels of anti-oxidative enzymes such as CAT, POD, SOD and APO in thermo-tolerant genotypes (Mansoor and Naqvi 2013). Ascorbic acid (Kumar et al. 2011a) and glutathione (Nahar et al. 2015) applications to heat-stressed mungbean decreased the oxidative damage by improving the endogenous levels of ascorbic acid, glutathione, proline and activating the enzymes of glyoxalase system.

Considering the vital role of various antioxidants in stress tolerance, further studies should focus on the use of these molecules on a wider plant range experiencing multiple stresses so as to validate their protective roles and to get an insight into the key strategies exercised by the plants in response to various stresses under field conditions.

### Osmolytes and phytohormones under temperature stress

Of all the molecules in cells affected by temperature stress, osmolytes and phytohormones have drawn the most attention. Endogenous levels of these molecules change to

varying degrees in response to stress possibly as a protection mechanism against the adverse conditions. Moreover, their exogenous application has been beneficial in ameliorating plant performance under stressful conditions. Previously, we have reported the detailed roles of various cryoprotectants involving osmolytes and phytohormones (Bhandari and Nayyar 2014); here we limit ourselves only to the discussion of their involvement in response to temperature stress and their potential application in improving stress tolerance.

The endogenous levels of proline were up-regulated in various cold-stressed legumes, e.g., soybean (Yadegari et al. 2008), chickpea (Kumar et al. 2010) and *Medicago* spp. (Zhang et al. 2011) and the increase was positively correlated to cold tolerance. In mungbean, an exogenous supply of proline during seed priming alleviated chilling injury (Posmyk and Janas 2007). Likewise, under heat stress also the endogenous levels of proline increased and particularly higher levels were observed in heat-tolerant genotypes (Kumar et al. 2013) suggesting a vital role for proline in heat tolerance. However, under extreme heat stress, proline levels in cowpea were reduced resulting in impaired pollen development (Tang et al. 2008). Thus, exogenous application of proline proved helpful in mitigating heat stress in chickpea by maintaining the efficiency of anti-oxidative machinery and carbon assimilation enzymes even under elevated temperatures (Kaushal et al. 2011). Moreover, transgenic soybean plants overproducing proline exhibited heat tolerance (de Ronde et al. 2004) thereby confirming its protective role.

Under cold stress, glycine betaine (GB) content decreased markedly in cold-stressed chickpea, which was related to reproductive failures (Nayyar et al. 2005d). Hence, the exogenous application of GB not only improved the reproductive biology attributes, but also increased plant biomass and yield. Similar cryoprotective effects of exogenously applied GB were reported in *Medicago* (Zhao et al. 1992) as well. The role of glycine betaine in the alleviation of heat stress injury for legumes needs to be explored though similar investigations in other crops such as wheat (Wang et al. 2010) and barley (Li et al. 2014) have already been reported.

Another protective biomolecule, salicylic acid (SA) has also been reported to impart temperature stress tolerance. Bean plants initially subjected to chilling (0 °C for 2 days) followed by heat stress (54 °C for 3 h) treated with SA or acetylsalicylic acid (ASA) showed 100% survival compared with untreated plants due to improved anti-oxidative machinery (Senaratna et al. 2000). Similar findings were reported for pea (Srivastava and Dwivedi 1998) and suggested by Chen et al. (1997) in rice. Results were further validated in heat-stress experiments in chickpea (Chakraborty and Tongden 2005). Additionally, SA also helps to

initiate and maintain legume–rhizobia symbiosis particularly during the initial stages of the plant–rhizobium interaction (Mabood and Smith 2007). The endogenous levels of SA are thus positively co-related with temperature tolerance and further studies on legumes in this regard will provide better insight about its role under adverse temperatures.

The role of an extra class of biomolecules, polyamines (PAs) has also been proposed. Cryoprotective role of PAs under low temperature stress has been reported in many studies (Groppa and Benavides 2008; Alcázar et al. 2010). Similar to other osmolytes, chilling-tolerant plants had higher PA levels than relatively sensitive *Phaseolus* spp. (Guye et al. 1986) and chickpea plants (Nayyar and Chander 2004; Nayyar 2005). Exogenous PA treatment hence alleviated cold-induced oxidative stress in chickpea by increasing endogenous levels of putrescine along with various enzymatic and non-enzymatic antioxidants (Nayyar and Chander 2004). Supplementation with exogenous PAs helped to maintain yield and other yield-related attributes in winter-sown chickpea under cold-stressed conditions (Nayyar 2005). Exogenous polyamines (putrescine, spermidine and spermine) supplementation augmented seedling growth by maintaining membrane stability in heat-stressed soybean (Nahar et al. 2015) by reducing oxidative damage in heat-stressed pea (Todorova et al. 2016).

Besides, other molecules such as nitric oxide (NO), abscisic acid (ABA) and brassinosteroids (BRs) may also serve as potential cryo- and thermoprotectants. Endogenous levels of NO were elevated in response to low temperatures in bird's foot trefoil (Shimoda et al. 2005) and pea (Corpas et al. 2008) and to short-term heat stress in alfalfa (Leshem 2001), thus suggesting its possible involvement in temperature stress responses. The involvement of NO in ABA-induced improvement in anti-oxidative defenses in chilling-stressed Brazilian lucerne (*Stylosanthes guianensis*) has also been reported (Zhou et al. 2005). Application of exogenous NO in the form of SNP (sodium nitroprusside as NO donor) during heat shock in mungbean maintained photosynthetic machinery stability, membrane integrity and improved the anti-oxidative defense (Yang et al. 2006). It also improved the chlorophyll concentration in pea (Leshem et al. 1997) and ameliorated heat shock damage in mungbean leaves (Yang et al. 2006). NO may interact with plant hormones to influence the stress response.

Extensive studies on ABA mutants of alfalfa confirmed the role of ABA in chilling tolerance (Mohapatra et al. 1988). Exogenous application of ABA is effective for cold stress mitigation when applied alone (Bakht et al. 2006) or in combination with other compounds such as SA (Szalai et al. 2011), as seen in chickpea (Nayyar et al. 2005a; Kumar et al. 2008b). Exogenous supplementation with



ABA not only mitigated stress injuries in chickpea by improving pollen viability and germination, but also improved yield and oxidative stress defense mechanisms (Kumar et al. 2008b). Under heat stress, endogenous ABA levels have reportedly increased suggesting its involvement in thermo-tolerance (Robertson et al. 1994; Teplova et al. 2000), which was further confirmed in chickpea by Kumar et al. (2012).

Brassinosteroids (BRs), naturally occurring steroid hormones, have also been implicated in temperature stress tolerance. The growth of chilling-stressed mungbean epicotyls improved with the application of exogenous 24-BR (Huang et al. 2006), which was in compliance with earlier studies on groundnut (Vardhini and Rao 1998). The beneficial effects of BRs have been reported under both cold stress and heat stress in mungbean (El-Bassiony et al. 2012). Also, application of BRs improved growth and biomass in these crops under temperature stress, thereby substantiating the similar reports by Upreti and Murti (2004) in water-stressed French bean.

Scarce data are available on the role and involvement of various thermoprotectants in temperature-stressed legumes. In view of their diverse and multiple roles in stress response, it would be vital to examine their endogenous levels in contrasting genotypes and to establish correlations with level of tolerance. Further, it would be worthwhile to investigate all these molecules at the same time in temperature-stressed legumes to examine their integrative role. The exogenous application of these molecules to temperature-stressed legumes needs to be extended to several species to authenticate their role in stress tolerance.

## Screening and breeding for temperature tolerance

In order to cope up with the ever-fluctuating temperature extremes (to which various legumes are exposed), efforts are being made to develop more tolerant plant varieties. Selection of temperature-tolerant lines has been done using various methods. Classically, two criteria have been followed to evaluate the tolerance of generated lines: survival percentage and empirical scoring. Yield-related attributes such as the number of filled pods, number of seeds and harvest index can also be used to select better plants (Canci and Toker 2009; Gaur et al. 2015). Additionally, pollen-based screening marker-assisted selections along with gametophytic selection and precise phenotyping can be employed for better temperature stress tolerance evaluation (Clarke et al. 2004; Gaur et al. 2015).

Using wild relatives of various cool-season legumes in breeding experiments is one strategy to address cold tolerance (Muehlbauer et al. 1994). Wild species have been collected from their supposed centers of origin (Van der Maesen and Pundir 1984; Muehlbauer et al. 1990) to serve as a potential genetic source of tolerance genes to various abiotic and biotic stresses. However, some classical plant breeders emphasize the need to first use the genomes of already-cultivated crops (Hawtin et al. 1988). Nevertheless, full use of wild germplasm has been limited due to the crossability barrier, the basis of which Harlan and de Wet (1971) divided various wild species into primary, secondary and tertiary gene pools (Table 4). The primary gene pool consists of species which can freely interbreed and produce fertile progenies while interbreeding is limited in

**Table 4** Primary, secondary and tertiary gene pool of some important food legumes (Muehlbauer et al. 1994)

Legume crop	Gene pools		
	Primary	Secondary	Tertiary
Chickpea	<i>Cicer arietinum</i> <i>Cicer reticulatum</i> <i>Cicer echinospermum</i>	–	<i>C. bijugum</i> <i>C. pinnatifidum</i> <i>C. judaicum</i> <i>C. chorassanicum</i> <i>C. montbretti</i>
Lentil	<i>Lens culinaris</i> ssp. <i>culinaris</i> <i>Lens culinaris</i> ssp. <i>orientalis</i> <i>Lens culinaris</i> ssp. <i>odemensis</i>	<i>Lens nigricans</i> ssp. <i>nigricans</i> <i>Lens nigricans</i> ssp. <i>ervoides</i>	–
Pea	<i>Pisum sativum</i> ssp. <i>sativum</i> <i>Pisum sativum</i> ssp. <i>elatius</i> <i>Pisum sativum</i> ssp. <i>humile</i>	<i>Pisum fulvum</i>	–
Faba bean	<i>Vicia faba</i>	–	<i>V. narbonensis</i> <i>V. hyaeniscyamus</i> <i>V. galilaea</i> <i>V. johannis</i> <i>V. bithynica</i>



**Table 5** The genetic sources (cultivars/accessions/elite lines/germplasm accessions) identified for cold and heat tolerance in various legumes

Crop	Cold tolerant	References	Heat tolerant	References
Chickpea	Hybrids of <i>C. bijugum</i>	Verma et al. (1990)	FLIP 87-59C	Singh et al. (1996)
	<i>C. judaicum</i>	Singh et al. (1995)	FLIP 92-154C	Toker and Cagirgan (1998)
	<i>C. pinnatifidum</i>		ICCV 92944, ICCV 93952	Gaur et al. (2015)
	<i>C. reticulatum</i>		ICCV 96970, ICCV 94954	
	<i>C. echinospermum</i>	Malhotra (1998)	ICCV 07102, ICCV 07110	
	ILC 8262, ILC 8617,		ICCV 07109, ICCV 07118	
	FLIP 87-82C		ICCV 07117, ICCV 07105	
	SP1.563, Gully, 940–26	O'Toole et al. (2001)	ICCV 07108, ICCV95332	
			FLIP 87-59C	
			Salawa, Burguieg	
			S051708, S00998	
			S03308, S03525	
			S051702, S051412	
			S03302, S02266	
			S051685, S051703	
Faba beans	Côte d'Or, BPL 4628	Duc and Petitjean (1995)	Shendi	Gaur et al. (2015)
	ILB 12, ILB 14	Olszewski (1996)	Marawa	
	ILB318, ILB 3187			
	ILB 2999			
Lentil	LC9978057, LC9977006	Hamdi et al. (1996)	ILL2181, ILL 82	Gaur et al. (2015)
	LC9977116, LC9978013		ILL 5151, ILL5416	
	ILL759, ILL1878,ILL4400		ILL 4587, ILL 956	
	ILL7155, ILL8146,ILL8611		ILL 598,	
	ILL9832, Kafcas, Cifei, Ubek		FLIP 2009-55L	
	Balochistan local, ILL5865	Ali et al. (1999)	ILL 2507, ILL 4248	Gaur et al. (2015)
	WA8649041	Kahraman et al. (2004)		
	WA8649090			
ILL1878	Sarker et al. (2002)			
ILL662, ILL857,				
ILL975, ILL1878				
Pea	EFB33, Unrra	Urbatzka et al. (2005)	Arka Ajit	Upreti et al. (2000)
	Württembergische		Acc. 623, 765	Srikanthbabu et al. (2002)

the secondary gene pool and hybrids are less fertile. In tertiary gene pool, intercrossing is not feasible and, if carried out, the progeny is sterile.

Following is an account of the potential genetic sources (Table 5) identified worldwide for cold and heat tolerance for various legumes.

**Chickpea** It is one of the most important cool-season legumes and is temperature sensitive. Wild chickpea germplasm, when screened, exhibited cold tolerance and thus can be used in breeding experiments. The cold tolerance trait was found to be affected by additive and non-additive gene actions along with other genic interactions (Singh et al. 1994). Many studies have been conducted to screen for heat-tolerant chickpea genotypes using parameters such as pollen viability, stigma receptivity and yield.

ICRISAT (International Crops Research Institute for the Semi-arid Tropics) and ICARDA (International Center for Agricultural Research in the Dry Areas) have identified several heat-tolerant genotypes (Table 5) for both desi and kabuli chickpea. Of these, ICCV92944 (desi chickpea) has been released in developing countries such as India, Myanmar and Kenya with supra-optimum temperature exposures and is being quickly adopted by farmers (Gaur et al. 2015).

**Common bean** It is among the heat-sensitive legumes with yield severely affected by high temperatures. Tepary bean (*Phaseolus acutifolius*) is inherently heat tolerant and thus has been exploited in various breeding experiments at CIAT (International Center for Tropical Agriculture). The derived interspecific lines have recorded higher yields even

under high-temperature conditions when compared with common bean (Gaur et al. 2015).

**Faba bean** This legume is sensitive to water, cold and heat stress. Studies evaluating winter hardiness and frost tolerance in faba bean genotypes have indicated that traits such as changes in fatty acid composition, ion leakage and free proline content are strongly correlated with frost tolerance (Arbaoui et al. 2008; Link et al. 2010), and hence, may be used for screening tolerant lines. Two heat-tolerant varieties of faba bean (Shendi and Marawi) have been released in Sudan (Table 5; Gaur et al. 2015).

**Lentil** *Lens culinaris* ssp. *orientalis* is considered the best source for winter hardiness (Hamdi et al. 1996), and the progenies thus generated have been listed among the elite lines in Lentil International Trials (Erskine et al. 1994). Numerous late-sowing experiments have reported heat sensitivity in lentil and a few heat-tolerant genotypes have been identified (Gaur et al. 2015).

### Molecular approaches and efforts in developing transgenics

Conventional plant breeding methods often transfer undesirable donor DNA fragments which may be harmful and should be removed (Vogan and Higgs 2011). Thus, a system based on foreground and background selection involving molecular markers and linkage maps was devised to minimize transfer of undesirable genes. Genetic linkage maps have been developed for various cool-season legumes such as pea (Weeden and Wolko 1990; Ellis et al. 1992), lentil (Weeden et al. 1992; Simon et al. 1993) and chickpea (Simon and Muehlbauer 1991, Flandez-Galvez et al. 2003).

With the revolutionary progress made in technologies such as gene isolation, promoter identification, gene transfer to monocots or dicots, and tissue-specific gene expression, transgenic approaches have surpassed classical

and neo-classical plant breeding techniques. From the construction of BAC (bacterial artificial chromosome) libraries (in chickpea the first one, Rajesh et al. 2004) for map-based isolation of genes to the sequencing of entire genomes of several pulses, e.g., pigeon pea (Singh et al. 2012; Varshney et al. 2011), chickpea (Varshney et al. 2013), soybean (Schmutz et al. 2010), bird's foot trefoil (Sato et al. 2008) and barrel medic or clover (Young et al. 2011), gene identification and isolation is now faster and easier. Advances in molecular biology have brought functional genomics within the reach of common labs, enabling elucidation of gene function using a process called reverse genetics.

Transgenics using genes from several sources have been reported for some pulses (Table 6) such as *Medicago* spp. and chickpea, and have outperformed wild types under stressful temperatures, e.g., transgenic chickpea possessing choline oxygenase gene from *Arthrobacter globiformis* accumulated higher levels of glycine betaine thereby, tolerating low temperature stress (Pardha Saradhi and Sharmila 2003).

The complexity of tolerance mechanisms to low and high temperatures, which involves several genes and many regulatory pathways, is a major bottleneck in the selection of one or a few genes that provide high levels of tolerance to abiotic stresses in transgenic plants. Another challenge is an incomplete understanding of mechanisms in temperature stress tolerance. Further studies to identify the genes related to cold or heat tolerance in food legumes are needed to assist in the development of temperature-tolerant transgenics.

Our findings on genes controlling pollen function in chickpea have revealed that stable sucrose metabolism in anthers is vital which affects pollen development during cold stress. Investigations on the regulation of expression of differentially expressed genes in anthers of cold-tolerant genotypes under cold stress indicated that the main categories of genes governing cold tolerance in anthers were

**Table 6** List of some temperature stress-tolerant transgenic legumes

Transgenic plant	Source	Gene transferred	Stress mitigated	References
<i>Medicago sativa</i>	<i>Nicotiana plumbaginifolia</i>	Mn-SOD cDNA Fe-SOD cDNA	Freezing tolerance Enhanced ROS dismutation	McKersie et al. (1993, 2000)
<i>Cicer arietinum</i>	<i>Arthrobacter globiformis</i>	cod A (choline oxygenase)	Frost resistance	Pardha Saradhi and Sharmila (2003)
<i>Medicago sativa</i>	<i>Saccharomyces cerevisiae</i>	ScTPS1-ScTPS2	Freezing, heat tolerance	Suárez et al. (2009)
<i>Medicago truncatula</i>	<i>Medicago truncatula</i>	DREB1C	Freezing tolerance	Chen et al. (2010)
<i>Medicago falcata</i>	<i>Medicago falcata</i>	MfGolS1	Raffinose accumulation Cold tolerance	Zhuo et al. (2013)

carbohydrate/triacylglycerol metabolism, signal transduction, pollen development and transport (Sharma and Nayyar 2014). Most of the genes in these categories were up-regulated. Regulation of gene expression suggests that chickpea anthers use a dual cold tolerance mechanism wherein anthers sustain development under cold by enhancing triacylglycerol and carbohydrate metabolism while pollen grains maintain normal development by regulating pollen development genes (Sharma and Nayyar 2014).

### Final remarks and conclusions

Food legumes are sensitive to both high and low-temperature conditions at all phases of development in general, and reproductive phase in particular. The plants are affected at various physiological, metabolic and ultra-structural levels and hence ultimately experiencing a huge yield losses. These crops, in response, evoke numerous defense mechanisms, such as the accumulation of various osmolytes, but their concentrations usually remain low for a high degree of temperature tolerance. Under such circumstances, cell protection occurs by exogenous supplementation of the osmolytes or by raising temperature-resistant lines via various plant breeding and genetic transformation techniques. There are many instances when transgenics did not meet the expected results while tested under field conditions. Attention, therefore, must be focused on elaborate studies of the wild germplasm of the target crops and their ecological adaptations to gain insights into their performance and stability under field conditions. Similarly, efforts should be made to understand the mechanisms and possibly the master genes by which some accessions of wild species provide higher levels of tolerance to temperature extremes. More consistent and comprehensible lab selection processes involving testing under more pragmatic controlled conditions are also essential. This will not only assist in the formation of a sound basis for protecting leguminous crops from the evident temperature hazards, also ensure their availability of improved quality seed in the future.

**Author contribution statement** HN and KB developed the concept of this article and compiled the information. KDS contributed towards section on molecular approaches and transgenics. KHMS, SKA, PG, RMN and BHR contributed to various sections in functional physiology, thermoprotectants and breeding.

**Acknowledgements** The authors thank DST (Department of Science and Technology), UGC (University Grants Commission), DBT (Department of Biotechnology), New Delhi, ICARDA, Morocco,

ICRISAT, India, and World Vegetable Center, Hyderabad, India, for the financial support for working on food legumes.

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