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REVIEW PAPER

Hormonal regulation of reproductive growth under normal and heat-stress conditions in legume and other model crop species

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Abstract

Legume crops are grown throughout the world and provide an excellent food source of digestible protein and starch, as well as dietary fibre, vitamins, minerals, and flavonoids. Fruit and seeds from legumes are also an important source of vegetables for a well-balanced diet. A trend in elevated temperature as a result of climate change increases the risk of a heat stress-induced reduction in legume crop yield. High temperatures during the crop reproductive development phase are particularly detrimental to fruit/seed production because the growth and development of the reproductive tissues are sensitive to small changes in temperature. Hormones are signalling molecules that play important roles in a plant's ability to integrate different environmental inputs and modify their developmental processes to optimize growth, survival, and reproduction. This review focuses on the hormonal regulation of reproductive development and heat stress-induced alteration of this regulation during (i) pollination, (ii) early fruit set, and (iii) seed development that affects fruit/seed yield in legume and other model crops. Further understanding of hormone-regulated reproductive growth under non-stress and heat-stress conditions can aid in trait selection and the development of gene modification strategies and cultural practices to improve heat tolerance in legume crops contributing to improved food security.

Key words: Abiotic stress, abscisic acid, auxins, cytokinins, ethylene, fruit and seed development, gibberellins, heat stress, jasmonic acid, legumes.

Introduction

Grain legumes are globally important food crops that can provide substantial nutritional and health benefits to the human diet, and they can be grown sustainably because they have the ability to develop root nodules and to fix nitrogen in symbiosis with compatible rhizobia (Graham and Vance, 2003; Foyer *et al.*, 2016). Vegetables from the legume family [for example, young pea fruits and seeds (*Pisum sativum* L.), young common bean fruits (*Phaseolus vulgaris* L.), and immature soybean seeds (*Glycine max* L.)] are also eaten as part of a well-balanced diet. In many areas of the world the trend in rising ambient temperature has focused attention on the adverse effects of heat stress on crop yield (Lobell and Field, 2007;

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Wahid *et al.* 2007; Hedhly *et al.*, 2009). In food crops including legumes, heat-stress conditions occurring during reproductive development can have marked negative effects on fruit/seed yield (Driedonks *et al.*, 2016). In soybean, abiotic stress (including heat stress) occurring at the flowering and early fruit development stage decreased seed yield up to 40% (Muchow and Sinclair, 1986). The heat-stress effect on fruit/seed yield strongly depends on the magnitude and the duration of the heat stress received. For example, severe heat stress interrupted pea fruit development regardless of the age or position of the fruit on the plant, resulting in fruit abortion (Guilioni *et al.*, 1997; Guilioni *et al.* 2003), whereas moderate heat stress mainly affected the development of reproductive organs in the apical phytomers (Guilioni *et al.*, 1997).

Heat stress negatively affects the developmental processes required for pollination (Gross and Kigel, 1994; Sage *et al.*, 2015). Fruit abscission and seed abortion can occur following ovule fertilization and initial seed development under heat-stress conditions (Jeuffroy *et al.*, 1990). In addition, heat stress during seed development up to harvest maturity can lead to reduced seed size and quality (Prasad *et al.*, 2002; Egli *et al.*, 2005; Tacarindua *et al.*, 2012, 2013). Wang *et al.* (2006) found that heat stress applied during mid-reproductive growth (seed filling stage) of chickpea (*Cicer arietinum* L.) had a larger effect on the number of seeds per plant and seed size than when applied during early flowering.

Plants respond to stressful environment conditions at the transcriptional, hormonal, biochemical, physiological, and morphological levels (Ahuja *et al.*, 2010; Bita and Gerats, 2013; Bokszczanin *et al.*, 2013). Plants have the ability to monitor and adapt to adverse environmental conditions; however, the degree of adaptability or tolerance to specific stresses varies among species and genotypes. Plant hormones and their signalling pathways integrate different environmental inputs and modify the plant's developmental processes to optimize growth, survival, and reproduction. This review will focus on hormonal regulation of reproductive development during stages that are particularity sensitive to abiotic/heat-stress events, including pollination, early fruit set, and seed development. The physiological effects of heat stress (and in some cases other abiotic stresses) on reproductive development will be related to stress-induced changes in hormonal pathways in legume and other model crops to gain a better understanding of hormone-regulated reproductive growth under heat-stress conditions. This knowledge, in turn, can be used to aid in trait selection and the development of gene modification strategies and cultural practices to improve heat tolerance in legume crops.

Physiological effects of heat stress on pollination events

The developmental processes required for pollination to lead to successful fertilization of the ovules are negatively affected by heat stress (Sage *et al.*, 2015). Pollen development is highly sensitive to elevated temperatures and a few degrees rise in temperature can negatively impact development (Hedhly, 2011; Paupière *et al.*, 2014). Under heat-stress conditions, plants, including legumes, have a tendency to produce abnormal pollen grains and/or to exhibit reduced anther dehiscence, pollen production, pollen viability, pollen germination, pollen tube growth, and stigma receptivity [common bean, Gross and Kigel, 1994; Porch and Jahn, 2001; Suzuki *et al.*, 2001*a*,*b*; Prasad *et al.*, 2002; soybean, Koti *et al.*, 2005; Salem *et al.*, 2007; pea, Jiang *et al.*, 2015; faba bean (*Vicia faba* L.), Bishop *et al.*, 2016; chickpea, Devasirvatham *et al.*, 2012], substantially contributing to poor seed set and yield.

During sporogenesis, the meiotic phase of pollen development in which the pollen mother cell undergoes meiosis did not appear to be thermo-sensitive in the common bean (Gross and Kigel, 1994; Porch and Jahn, 2001). However, the stage just after meiosis, the formation of a tetrad of four haploid microspores, was affected by heat stress, resulting in abnormal microspore production in heat-sensitive lines [common bean, Gross and Kigel, 1994; Porch and Jahn, 2001; cowpea (*Vigna unguiculata*), Ahmed and Hall, 1993]. In bean and cowpea, heat stress at sporogenesis also inhibited anther dehiscence, likely due to the interlocular septa between the pollen sacs failing to break down and to changes to the endothecial anther wall layer (Ahmed and Hall, 1993; Gross and Kigel, 1994; Porch and Jahn, 2001). Heat-stress conditions also resulted in the premature degeneration of the tapetum layer in anthers of the common bean, which was associated with pollen abnormalities and male sterility (Suzuki *et al.*, 2001*a*); the tapetum is the innermost layer of the anther locule that nourishes the haploid microspores released from tetrads after meiosis at later stages of pollen development. Additionally, the number of pollen grains adhering to the stigma was dramatically reduced by heat stress, which may be the result of a heat stress-induced decrease in stigmatic fluid secretion and/or changes to the pollen exine (Gross and Kigel, 1994; Porch and Jahn, 2001).

Hormonal regulation of stamen and pollen development

Auxins

Auxins are involved in the regulation of reproductive growth and development. The ubiquitous naturally occurring auxin found in plants is indole-3-acetic acid (IAA). In addition to IAA, some legume species, particularly in the Vicieae tribe of the Fabaceae family [e.g. pea, grass pea (*Lathyrus sativus* L.), lentil (*Lens culinaris* L.), and faba bean], also contain the naturally occurring chlorinated form of auxin, 4-chloroindole-3-acetic acid (4-Cl-IAA), which is biologically more active than IAA in auxin bioassays (Reinecke *et al.*, 1995; Reinecke, 1999). 4-Cl-IAA has not been detected in *Arabidopsis thaliana* or other legumes such as soybean, chickpea, and common bean (Reinecke, 1999; Lam *et al.*, 2015). 4-Cl-IAA has been proposed to have a role in pea fruit development (see 'Hormonal regulation of fruit set').

A relatively large body of work in Arabidopsis and other species suggests that auxins are required for normal stamen and pollen development. In the predominant tryptophan-dependent auxin biosynthetic pathway, tryptophan is converted to indole-3-pyruvate (IPA) by tryptophan aminotransferase (TAA). Subsequently, IPA is converted

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to IAA by the YUCCA family of flavin monooxygenases (Arabidopsis, Zhao, 2012; pea, Tivendale *et al.*, 2010, 2012). Loss-of-function auxin biosynthesis *yucca* mutants (the double mutants *yucca1yucca4* and *yucca2yucca6*, and all of the triple and quadruple mutants of the four *YUCCA* genes) in Arabidopsis exhibited severe defects in floral organ development and either had highly reduced or no pollen production (Cheng *et al.*, 2006). Pollen and stamen filament development abnormalities were also reported in mutants of the PIN-FORMED family proteins that mediate auxin transport (efflux; *pin8*; Ding *et al.*, 2012), and the P-glycoprotein (ABCB/PGP) auxin transport family that belongs to the ATP Binding Cassette subfamily B (Cecchetti *et al.*, 2008, 2015). In Arabidopsis auxin receptor transport inhibitor response 1 (*tir1*) auxin signaling F-box (*afb*) triple and quadruple mutants, anther dehiscence and pollen maturation occurred precociously, resulting in the release of mature pollen grains before the completion of filament elongation (Cecchetti *et al.*, 2008). In pea, plants transformed to express the β-glucuronidase (GUS) reporter gene driven by the DR5 promoter (a highly active synthetic auxin-response element), GUS expression was uniform in the pollen grains, and it was associated with the initiation of stamens within the floral bud. GUS staining was also intense at the distal region of the filaments and at their fused base during stamen development and maturation (DeMason and Polowick, 2009). These GUS expression patterns suggest that auxin is also needed for normal filament and pollen development in pea.

As an early response to heat-stress exposure, the endogenous level of auxin was reduced in the developing anthers of barley (*Horedum vulgare* L.) and Arabidopsis (Higashitani, 2013; Sakata and Higashitani, 2008; Sakata *et al.*, 2010). The expression of YUCCA auxin biosynthesis genes (*YUCCA2* and *YUCCA6*) was also repressed in Arabidopsis and barley stamens following heat stress (Sakata *et al.*, 2010). Immunohistochemical studies using anti-IAA antibodies suggested that the endogenous level of auxin was reduced in anther parietal and epidermal cells as well as in pollen mother and tapetal cells in response to an increase in temperature (Sakata *et al.*, 2010). GUS expression in DR5-GUS recombinant lines was also diminished in the developing anthers of Arabidopsis when exposed to heat stress at 31°C or 33°C for 1, 3, or 7 days (Sakata *et al.*, 2010). Furthermore, two applications of auxin (IAA, 1-napthaleneacetic acid or 2,4-dichlorophenoxyacetic acid) restored anther development in heat-treated barley (Sakata *et al.*, 2010). These data collectively suggest that exposure to high temperatures represses auxin biosynthesis and signalling in developing anthers, resulting in pollen developmental abnormalities in these species. Given the critical role auxins play in the production of normal pollen grains, the application of auxins to plants may be a useful tool to promote the fertility and maintenance of crop yields. Further to this point, we found that a single application of 4-Cl-IAA or the auxin analogue 4-methylindole-3-acetic acid at or just prior to initial flowering partially ameliorated the negative effects of moderate heat stress (35°C for 6 h per day for 4 days) on seed yield in field pea under controlled environmental conditions (Abeysingha, 2015). Enhancing mechanisms that maintain auxin function during moderate heat stress in reproductive tissues may also be useful to maintain fertility. Recently, Wang *et al.* (2016) reported that heat-shock protein 90 (HSP90) is required for maintaining the TRANSPORT INHIBITOR RESPONSE1 (TIR1) auxin receptor levels during elevated temperatures in Arabidopsis seedlings, leading the authors to postulate that as the temperature rises, increased HSP90 stabilizes TIR1 to promote auxin signalling.

Gibberellins

Arabidopsis gibberellin (GA)-deficient lines containing mutations in GA biosynthesis genes at early or later steps in the GA biosynthesis pathway (*ga1-3*, mutation in the gene that encodes *ent*-copalyl diphosphate synthase; *kao1 kao2* double mutants, mutations in genes that encode ent-kaurenoic acid oxidases; *ga20ox1 ga20ox2 ga20ox3-1* triple mutants, mutation in genes that encode GA 20-oxidases) show abnormalities in stamen development such as negative effects on filament elongation and/or arrested anther development (including the tapetum prior to or following pollen mitosis) that prevent the formation of mature pollen (Cheng *et al.*, 2004; Yu *et al.*, 2004; Plackett *et al.*, 2012; Regnault *et al.*, 2014). Normal anther development in the GA biosynthesis mutants could be rescued by exogenous GA treatment, confirming that GA plays an essential role in stamen and pollen development (Plackett *et al.*, 2012).

Mutations in genes involved in the GA signalling pathway, including the GA receptor (GIBBERELLIN INSENSITIVE DWARF1, GID1) triple mutant (*gid1a gid1b gid1c*), also displayed defects in stamen development due to the accumulation of DELLA proteins (nuclear-localized proteins that function as transcriptional regulators; Griffiths *et al.*, 2006; Achard and Genschik, 2009). GA de-represses its signalling pathway by GID1-induced degradation of DELLA proteins via an ubiquitin–proteasome pathway (Sun, 2011). Of the five DELLA proteins in Arabidopsis, REPRESSOR OF GA1-3 (RGA), RGA-LIKE1 (RGL1), and RGL2 are known to participate in modulating stamen development (Cheng *et al.*, 2004; Tyler *et al.*, 2004). DELLA activity in Arabidopsis stamens can inhibit development, but it is also necessary for successful pollen production because *della* mutants are male sterile (Plackett *et al.*, 2014). Cheng *et al.* (2009) also reported that GA represses DELLAs and activates the expression of the jasmonic acid (JA) biosynthesis genes *DAD1* (DEFECTIVE IN ANTHER DEHISCENCE 1, belonging to the phospholipase A_1 family) and *LOX1* (lipoxygenase) to control expression of the transcription factors MYB21 (myeloblastosis), MYB24, and MYB57, which are responsible for normal stamen development. Furthermore, wheat (*Triticum aestivum*) microRNA *TamiR159* directs cleavage of *TaGAMYB1* and *TaGAMYB2* (encoding for GAMYBs, which are MYB transcription factors downstream of DELLAs in the GA signalling pathway), and its overexpression in rice (*Oryza sativa* L. *japonica*) resulted in delayed heading time, male sterility, and increased sensitivity to heat stress (Wang *et al.*, 2012).

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Jasmonic acid

Plants with mutations in genes involved in JA biosynthesis (*dad1* single and *lox3 lox4* double mutants), perception (coronatine insensitive1, *coi1* mutant), or signalling (jasmonate ZIM-domain (JAZ) mutants or plants overexpressing JAZ1ΔJas and JAZ10.4 that lack the full Jas domain) fail to produce stamens with elongated filaments, are defective in anther dehiscence, and produce non-viable pollen (Ishiguro *et al.*, 2001; Thines *et al.*, 2007; Browse, 2009; Chung and Howe, 2009; Caldelari *et al.*, 2011). Stamen development can be restored only in JA biosynthesis mutants by exogenous JA, highlighting that JA signalling is required for stamen development and fertility. Upon JA perception by the COI1 receptor, JAZ repressors are degraded and the transcription of genes downstream of the JA signalling transcription factors MYB21 and MYB24 are activated to regulate stamen development (Mandaokar *et al.*, 2006). The ectopic expression of JAZ1ΔJas and JAZ10.4 (JAZ genes that lack the full Jas domain, making them resistant to degradation) inhibits downstream transcriptional activity, resulting in male sterility. However, some mutants of JA signalling, such as jasmonate insensitive 3 (*jai3-1*; expresses truncated JAZ3 without the Jas domain) and JAZ10.3 (which has lost a portion of the JAZ domain), have a reduced capacity to interact with COI, are resistant to JA-mediated protein degradation, and are still male fertile, suggesting that a small amount of JA is needed for stamen development (Chini *et al.*, 2007; Yan *et al.*, 2007).

In pea, a heat stress-induced (36°C) decrease in seed number per pod was associated with reduced *in vitro* pollen germination and pollen tube growth, with pollen germination being less affected in one of the two cultivars tested (Jiang *et al.*, 2015). The authors suggest that the pollen surface lipid acyl chain change associated with heat treatment in the more heat-sensitive line (CDC Golden; with respect to pollen germination) could result in a lower percentage of pollen germination compared to the more heat-tolerant line (CDC Sage). Lipids accumulate near pore apertures in pollen during pollen germination, helping to maintain the membrane stability and pollen hydration needed to direct pollen tube growth into the stigma (Wolters-Arts *et al.*, 1998). Transgenic lines altered in JA-mediated oxylipin signalling may serve as a tool to study a potential link between heat stress-induced changes in pollen surface lipids and hormone-regulated lipid signalling and phosphoinositides in the pollen membrane during pollen germination and tube growth (Heilmann and Ischebeck, 2016; Hou *et al.*, 2016).

Ethylene

Larkindale *et al.* (2005) showed that seedlings of the Arabidopsis ethylene signalling mutants ethylene insensitive 2 (*ein2*) and ethylene response 1 (*etr1*) are defective in basal thermo-tolerance. However, the involvement of ethylene in pollen development is suggested by results showing a reduction in pollen germination under optimal growing conditions following pre-treatment of tomato plants (*Solanum lycopersicum*) with the ethylene biosynthesis inhibitor aminoethoxyvinylglycine (AVG; Firon *et al.*, 2012). In tomato *Never ripe* (*Nr*) mutants (defective in an ethylene response sensor-like ethylene receptor), heat stress has a greater adverse effect on pollen production and viability than it does in the wild type (Firon *et al.*, 2012). Pollen viability and germination under heat stress was increased by pre-treatment of tomato plants with an ethylene-releasing agent, ethephon, whereas it was decreased by pre-treatment with the ethylene biosynthesis inhibitor AVG (Firon *et al.*, 2012). Rieu *et al.* (2003) found that ethylene-treated tobacco flowers (*Nicotiana tabacum* L.) exhibited accelerated anther dehiscence, whereas treatment with the ethylene response inhibitor 1-methylcyclopropene delayed anther dehiscence. It is possible that heat stress affects ethylene biosynthesis/signalling pathways in the developing anther, which leads to reduced anther dehiscence. As discussed above, heat stress during sporogenesis results in anther indehiscence in a number of species, including common bean (Porch and Jahn, 2001).

Furthermore, microarray data analysis [using 26 hormone responsive *cis*-element motifs previously reported in the PLACE database (Plant *cis*-acting regulatory DNA elements)] suggests that a complex network of hormone-mediated processes are involved in anther dehiscence and pollen germination in rice. Analysis of the database revealed 291 highly expressed anther-specific genes with 4-fold or higher changes, with 251 of these anther-specific genes having *cis*-elements responsive to one or more hormones including abscisic acid (ABA; 107 genes), auxin (138 genes), GA (141 genes), and JA (192 genes) (Ling *et al.*, 2015). Overall, these studies show that normal stamen development is dependent on hormonal signalling, and heat stress likely alters these hormonal pathways and their interactions, disrupting normal developmental processes. Although our understanding of hormonal regulation of stamen development is derived from a limited number of species, the models developed from these species can be further tested in legume crops species to extend our knowledge of hormonal regulation of stamen development under non-stress and heat-stress conditions.

Physiological effects of heat stress on fruit set

Fruit abscission and seed abortion can occur following ovule fertilization under heat-stress conditions in legumes (Araújo *et al.*, 2015). In a fully open-air field experiment conducted by Siebers *et al.* (2015), heat treatments (temperatures elevated 6°C above ambient for 3 days) were imposed on soybean plots at different stages of reproductive development using infrared heating technology. The authors found that the end-of-season seed yield was reduced by approximately 10% only when heat treatments were applied during the early pod developmental stages (R3–4 stages;). These authors concluded that high-temperature-tolerant pod set and development in soybean should be considered a target for introgression to improve seed yield after high temperature events.

Hormonal regulation of fruit set

Auxin and ethylene

The abscission of reproductive organs, an important effect of heat stress, involves auxin and ethylene (Brown, 1997). Auxin inhibited ethylene-facilitated pedicel abscission

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(the pedicel attaches the fruit to the plant) in soybean under non-stress conditions (Oberholster *et al.*, 1991). Pedicel abscission was more pronounced under drought-stress conditions than under non-stress conditions, and IAA treatment was very effective in reducing pedicel abscission under the stress conditions (Oberholster *et al.* 1991). In common bean, Ofir *et al.*, (1993) found a strong correlation between heat stress-induced decreases in pod and seed numbers and the amount of IAA exported from flowers. Cultivars with a higher resistance to pod loss with heat stress had a smaller reduction in exported IAA than the more heat-sensitive cultivars. The authors suggest that the association between the two effects is due to heat stress-induced inhibition of IAA transport, resulting in abscission of the pods from the plant. It is possible that heat stress reduces the auxin flux through the pedicel, allowing ethylene-facilitated pedicel abscission and fruit loss to occur.

Auxins and gibberellins

The function of the ovary is to provide an ideal environment for seed growth. After fertilization, normal ovary (pericarp) growth and fruit set requires the presence of developing seeds (pea, Eeuwens and Schwabe 1975; Ozga *et al.*, 1992). Developing pea seeds and pericarps contain GAs (Garcıá -Martínez et al., 1991; Rodrigo *et al.*, 1997) and auxins (4-Cl-IAA and IAA; Marumo *et al.*, 1968; Magnus *et al.*, 1997). Data from a number of studies support the hypothesis that auxin (4-Cl-IAA) produced in the seeds is transported to the pericarp tissue, where it differentially regulates the expression of pericarp GA biosynthesis and catabolism genes to modulate the level of bioactive GA_1 required for initial fruit set and growth in pea (Ozga *et al.*, 2002, 2003, and 2009). Heat stress-induced seed abortion would likely affect the level of seed-derived auxins and other seed signalling molecules transported to the pericarp, potentially having a negative effect on pericarp growth and facilitating pedicel abscission (See 'Auxin and ethylene').

Physiological effect of heat stress on seed development and maturation

Cell division within the embryo, followed by normal cell expansion, and seed filling and maturation during seed development determine the final size of individual seeds of pea and soybean (Munier-Jolain and Ney, 1998). Exposure to high day-time temperatures (33–35°C) during seed filling reduced soybean seed yield by 23–29% compared to controls grown at optimal temperatures (27–29°C; Dornbos Jr and Mullen, 1991). In chickpea, Wang *et al.* (2006) reported more severe losses in seed yield when plants experienced high temperature stress (35/16°C, day/night for 10 days) during pod development (59% for Myles and 53% for Xena cultivars) than during the early flowering stage (39% for Myles and 42% for Xena cultivars). Tacarindua *et al.* (2012) used a temperature gradient chamber to examine the response of soybean seed growth to increased temperature in a controlled environment that mimicked field conditions. The number of days to the beginning of seed fill and maturity were greater and the final single-seed weight was reduced by increased temperatures. Elevated temperature (3°C above ambient for the entire plant growth period) had no significant effect on cotyledonary cell volume, but there were fewer cells per cotyledon than in ambient-grown plants, indicating that the high temperature-induced decrease in seed size of soybean was associated with a reduced cotyledon cell number leading to decreased single-seed growth rate (Tacarindua *et al.*, 2012).

A decline in maize (*Zea mays*) kernel weight was associated with reduced starch biosynthesis enzyme activities (ADP-glucose pyrophosphorylase and soluble starch synthase) in the endosperm during grain filling when the temperature was increased above 22°C (up to 35°C) under *in vitro* conditions (Singletary *et al.*, 1994). Cheikh and Jones (1995) used ^{14}C-sucrose to establish that the impaired maize kernel growth when grown *in vitro* at 35°C for 8 days resulted from diminished invertase activity associated with reduced carbon degradation (from sucrose to hexose) and partitioning (to starch synthesis) within the endosperm, rather than being associated with limited carbon supply to the kernel. The legume embryo, a strong terminal sink for sucrose, is not vascularly connected to the maternal seed coat tissue (pea, Hardham, 1976). The seed coat sieve elements unload sucrose and other nutrients into the apoplastic space between the seed coat and the developing embryo (Thorne, 1985). A model has been proposed for invertase-mediated unloading of sucrose for the legume embryo during early seed development (faba bean, Weber *et al.*, 1996). As observed for maize, heat stress-induced perturbation of seed invertase activity could also markedly affect nutrient partitioning and seed growth in legume seeds.

High temperatures during seed fill and maturation can increase the proportion of seeds that are shrivelled and abnormal at physiological maturity, and result in seeds that exhibit reduced germination and seedling vigour (soybean, Spears *et al.*, 1997; Egli *et al.*, 2005). Additionally, high temperatures during this period can also lead to the retention of chlorophyll in mature seeds, which can reduce seed oil and meal quality in legume oil seed crops such as soybean (Teixeira *et al.*, 2016).

Hormonal regulation of seed development and maturation

Cytokinins

A correlation exists between the grain filling pattern and cytokinin (CK) accumulation in rice, suggesting CK plays a stimulatory role during grain filling (Yang *et al.*, 2000). The reduction in kernel weight and kernel number in heat-treated (35/25°C day/night for 7 days after anthesis) wheat spikes have been attributed to a 50–80% reduction in kernel CK levels (Banowetz *et al.*, 1999*a*, *b*). CK (6-benzylaminopurine) treatment mitigated the inhibitory effect of heat stress on grain fill rate, endosperm division rate, endosperm cell number, and 1000 grain weight in winter wheat cultivars (Yang *et al.*, 2016). CKs likely also play an important role in legume seed development (Emery *et al.*, 2000; Jameson and Song, 2016) and heat stress may similarly reduce seed CK levels leading to reduced seed cell number and seed growth rate.

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Gibberellins

GAs serve a vital role in coordinating growth and development in seed development. In pea, the GA biosynthesis mutant *lh-2* (mutation in the KO gene that encodes *ent*-kaurene oxidase; Davidson *et al.*, 2004) has very low GA levels in developing seeds, increased seed abortion, and markedly smaller seeds at maturity than wild-type plants (Swain *et al.*, 1993). Nadeau *et al.* (2011) correlated GA gene expression and GA levels with seed morphology and photoassimilate acquisition and storage during the mid-stages of pea seed development. They found that pea seed coat growth correlated with both transcript abundance of GA biosynthesis genes and the concentration of the growth effector GA GA_1, suggesting that GA_1 is involved in determining the rate of seed coat growth and sink strength. *PsGA20ox* transcript abundance and GA_{20} concentration in the endosperm increased markedly as the endosperm reached its maximum volume (12 days after anthesis, DAA), providing GA_{20} as the substrate for the GA 3-oxidases present in both the embryo and seed coat. Furthermore, *PsGA3ox* transcript profiles and trends in GA_1 levels in embryos 10–16 DAA and also in embryo axes at 18 DAA suggested localized GA_1-induced growth in these tissues.

The GA-deficient *lh-2* mutant also showed severely reduced cell expansion of the seed coat and photoassimilate partitioning within the seed, producing a small seed size at maturity, whereas seeds of a pea transgenic GA_1-overexpresser line exhibited enhanced cell expansion and photoassimilate partitioning into the seeds that was associated with increased seed size (Reinecke *et al.*, 2013;Waduthanthri, 2016). These data indicate that GA biosynthesis and catabolism are tightly regulated to bring about the unique developmental events that occur during seed growth, development, and maturation. However, the effect of heat stress on GA-regulated legume fruit and seed developmental processes has not been explored.

As growth regulators, GAs function mainly to promote growth in almost all plant organs by promoting cell elongation and, occasionally, cell division (Hedden and Thomas, 2012). Hence, an important mechanism by which plants respond to various environmental stresses is to reduce the bioactive GA level to reduce growth during stress (Achard *et al.*, 2008; Hedden and Thomas, 2012). Reducing bioactive GA levels allows DELLA proteins to accumulate, which promote stress tolerance by suppressing growth (Hedden and Thomas, 2012). GAs also play a role in the thermoperiodic response (plant response to rhythmic fluctuations in temperature) in pea (Stavang *et al.*, 2005). While day/night temperature regimes of 21°C/13°C or 17°C/17°C are optimal for growth, a day/night temperature regime of 13°C/21°C reduces pea stem elongation. This last temperature regime, while having little or no effect on the GA biosynthesis genes *PsGA20ox1* or *PsGA3ox1*, up-regulates the GA deactivation gene *PsGA2ox2* with a concomitant decrease in GA_1 levels, suggesting that GA deactivation is a prime thermoperiodic response leading to reduced stem elongation (Stavang *et al.*, 2005). If heat stress modulates GA biosynthesis and catabolism in developing seeds in a similar manner to that observed in vegetative tissues, heat stress likely reduces GA-associated seed growth and development processes.

Ethylene

Modulation of ethylene production is also an important mechanism by which reduced growth rate could be achieved as an immediate plant response to abiotic stresses. In general, abiotic stresses such as heat stress, salinity, and water deficit enhance ethylene levels, which aids in reducing growth; however, ethylene can also cause senescence and abscission of various plant organs (Jones and El-Abd, 1989; Kalantari *et al.*, 2000; Kukreja *et al.*, 2005; Hays *et al.*, 2007; Jackson, 2008; Abeles *et al.*, 2012). Ethylene may also play a role in protecting plants against heat stress-induced oxidative damage, possibly by acting as a signal to activate oxidative defences. The Arabidopsis ethylene-insensitive mutants *etr1* and *ein2* are more susceptible to heat stress due to increased oxidative stress as indicated by increased thiobarbituric acid reactive substances (TBARS; by-products of lipid peroxidation; Larkindale *et al.*, 2005). Pre-treating Arabidopsis plants with 1-aminocyclopropane-1-carboxylic acid (the immediate precursor of ethylene) before heat-stress exposure (40°C) reduces levels of TBARS, thereby increasing survival rate (Larkindale and Knight, 2002). Stress ethylene can also reduce photosynthesis and grain filling rates, and can cause embryo abortion in wheat (Rajala and Peltonen-Sainio, 2001; Hays *et al.*, 2007). In a heat-susceptible wheat cultivar, Karl 92, ethylene regulates heat stress-induced kernel abortion and kernel weight reduction. Heat stress (38°C) during early kernel development substantially increased the ethylene level in developing kernels, embryos, and flag leaves of Karl 92, while having no effect on ethylene production in the heat-tolerant cultivar Halberd. The application of 1-methylcyclopropene, an inhibitor of ethylene perception, prior to exposure to heat stress suppressed heat stress-induced kernel abortion and reduction in kernel weight (Hays *et al.*, 2007). The effect of heat stress on ethylene-related growth processes during legume seed development remains to be explored.

Abscisic acid

In seeds, ABA is involved in the regulation of maturation, desiccation tolerance, and dormancy (Finkelstein *et al.*, 2002). There are two peaks of ABA accumulation during seed development in many species (Finkelstein *et al.*, 2002). Wang *et al.* (1987) reported that developing pea seeds exhibit a biphasic distribution of ABA: they found that the first ABA maximum coincided with the point of maximum endosperm volume and a slowing in the growth of the testa, and that 90% of the ABA in the whole seed at this stage was in the testa (seed coat). During the second maximum (which occurred later in development, during seed maturation), 90% of the total ABA was in the embryo (Wang *et al.*, 1987). The initial, mainly maternally derived (from testa tissues) peak of ABA is associated with the promotion of seed storage reserves and the inhibition of vivipary (Finkelstein *et al.*, 2002). The second, embryo-derived ABA maximum during seed development is associated with the promotion of desiccation tolerance, dormancy, and the inhibition of germination (Finkelstein *et al.*, 2002).

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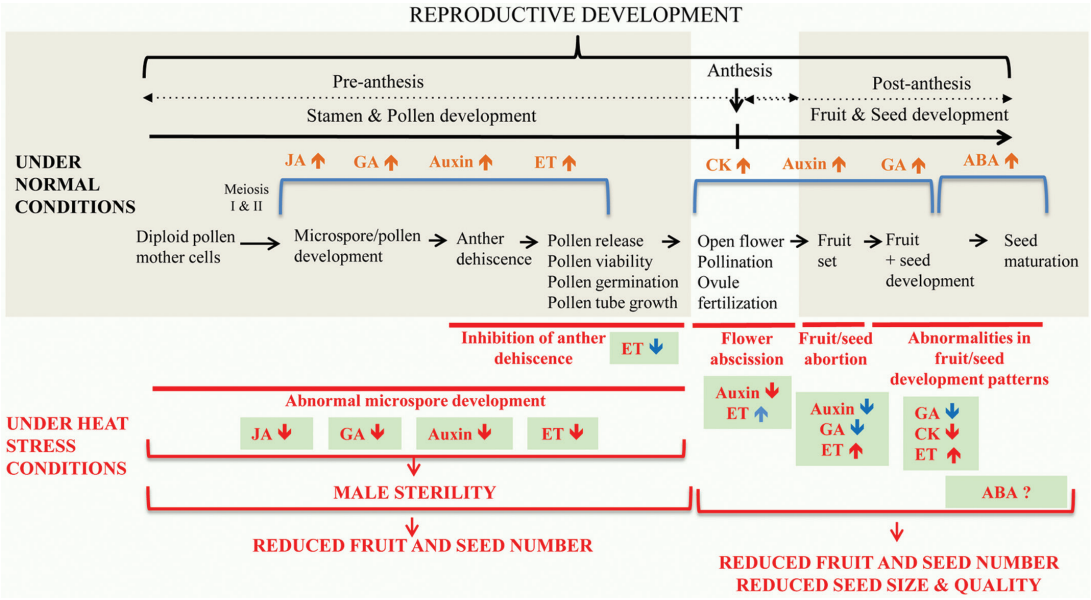


Fig. 1. Overview of hormone-regulated reproductive growth in plants under normal temperature or heat-stress conditions. Arrows indicate up-regulation (↑) and down-regulation (↓) of different hormone classes (hormone concentration and/or signalling) involved in reproductive growth of a plant under both normal and heat-stressed conditions, with blue-coloured arrows indicating postulated regulation. ABA, abscisic acid; ET, ethylene; GA, gibberellin; JA, jasmonic acid; CK, cytokinin.

Radchuk *et al.* (2010) studied the effect of reduced ABA levels on seed development during the transition of embryos from pre-storage to the maturation phase in pea seeds expressing a single-chain anti-ABA antibody (anti-ABA pea seeds). ABA deficiency in the anti-ABA pea seeds during the first ABA maximum led to transcriptional repression of carbohydrate oxidation, sucrose mobilization, glycolysis, and the tricarboxylic acid cycle/Krebs cycle metabolic pathways in the embryos. The expression of genes related to starch, amino acid, and storage protein biosynthesis was also reduced, indicative of decreased metabolic fluxes in the anti-ABA embryos during this transition phase. At maturity, the anti-ABA seeds were smaller, contained fewer globulin storage proteins, and showed lower dry matter accumulation compared with the wild type (Radchuk *et al.*, 2010).

In soybean, a set of proteins that accumulate late in embryogenesis (late-embryogenesis-abundant, or LEA, proteins) have been associated with desiccation tolerance in naturally maturing seed and the tissues of germinating seedlings (Blackman *et al.*, 1991). The levels of these maturation proteins were modulated by ABA (increases abundance) or osmotic stress during imbibition as well as by premature drying during seed development. Currently, little is known about the effects of heat stress on ABA levels during seed development and maturation in legume or other plant species. Given the important roles that ABA plays during seed development, and that ABA levels are modulated in plant tissues by environmental cues, research in this area would be timely.

As mentioned above, high temperature and drought stress can lead to the retention of chlorophyll in mature soybean seeds, which is associated with lower oil and seed quality (Teixeira *et al.*, 2016). Delmas *et al.* (2013) found that the ABA-dependent transcription factor ABSCISIC ACID INSENSITIVE 3 (ABI3), a B3 domain transcription factor that has a highly conserved and essential role in seed maturation, directs embryo degreening by regulating Mendel's stay-green genes (SGR; I locus). Targeting modifications in ABA or ABA signalling pathways (via ABI3) during seed degreening may aid in the development of soybean genotypes that are resistant to environmentally induced green-seed. Consistently, Teixeira *et al.* (2016) found that a soybean cultivar that exhibited reduced green-seed phenotype when grown under abiotic stress conditions had higher transcript abundance of *SGR1* and *SGR2* in the developing seeds than a more susceptible cultivar.

Conclusion

As the human population increases, it is important for our food security that we devise and implement strategies to lessen the impact of abiotic stresses on yield and quality of legume crops. It is apparent that hormones play critical roles in a plant's ability to integrate different environmental inputs and modify their developmental processes to optimize reproductive development (Fig. 1). There are three general phases of reproductive development in legume and other model crop species that are sensitive to abiotic stress, including heat stress: pollination, early fruit set, and seed development. Further knowledge of the hormone-regulation of these developmental processes and the extent they are modified by high temperatures will enable us to target traits and develop strategies to modify genes and cultural practices for the improvement of heat tolerance in legume food crops.

Author contributions

JAO conceived the review; compiled a review of the literature in specific areas covered in the review; and complied, drafted, and edited the final manuscript. HK, RPS, and DMR compiled a review of the literature in specific areas

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covered in the review, provided an initial draft covering these sections, and provided comments on the compiled manuscript. HK and DMR edited the final manuscript, and HK provided the initial figure draft.

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