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Temperature regulation of plant phenological development

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ABSTRACT

Gradual and abrupt changes in temperature under current and future climates pose a serious threat to ecological diversity and in sustaining global food security. Plants possess a robust network of thermal sensors to program their metabolic and hormonal framework, providing acclimation to short-term abrupt fluctuations or adaptation to gradual temperature change. Several cellular thermosensors are reported in plants and understanding their mode of operation in a potentially coordinated framework continues to be a persistent challenge. Despite growing insight into the molecular control of thermal perception, physiological significance of plant thermal responses under a complex interaction with other environmental cues is largely unaddressed. Plant thermal perception and signaling could be similar across growth habits such as herbaceous to perennial woody species while developmental transitions such as vegetative to reproductive stage, influenced by their immediate microclimate, are generally altered across growth habits. The overall aim is to connect the knowledge gained with thermal perception and the signaling that drives plant responses, with major focus on the latter.

1. Introduction

Plants are adapted to wide temperature regimes between cold and hot environments. Besides affecting all living processes, temperatures within and beyond the physiological optimum can have a contrasting impact on plant responses and developmental decisions. 'Physiologically optimal' is defined as the temperature range in which the plant's growth and developmental events, such as germination, flowering and seed set, are not negatively affected. Temperatures on either side of the 'physiological optimum' range extending to points beyond (heat stress) or below (cold stress) at which plant fitness and survival are significantly compromised are defined as 'critical thresholds' or 'temperature extremes'. Both 'physiological optimum' and 'critical threshold' can be plant or species specific within a defined environment. Historical records show a decadal global mean temperature increase leading to advancement in flowering time in different plant species, thus having serious implications for biodiversity and ecosystem services (Amano et al., 2010; Hulme, 2011). Further, incidences of temperature extremes during the past three decades have resulted in major socioeconomic losses (Mittler, 2006; Lobell et al., 2011, 2012; Bita and Gerats, 2013; Lyman et al., 2013). Global climate models predicting increased frequency and magnitude of temperature extremes (IPCC, 2013) show a serious threat to vulnerable ecosystems, such as agriculture, and pose a challenge to future global food security.

Plants can precisely sense the absolute and gradual change in diurnal and seasonal temperature with a wide array of thermosensors (cellular components that can perceive temperature change and relay a signal to downstream components) and alter thermal responsiveness in close association of phenological stage, tissue type, and metabolic composition. Moreover, plant thermal responses during developmental transitions (such as germination, flowering, dormancy) may differ with plant growth habit (herbaceous to perennial woody) and habitats (temperate to tropical). On the other hand, environmental factors such as relative humidity and light have considerable influence on the plant's response to temperature change. This update will briefly highlight the key research progress on plant thermal sensing in an attempt to connect the cellular perceptions to whole plant thermo-responsiveness regulated by hormones and metabolites. Moreover, in consideration of the natural environment in which plants survive, temperature, light, and humidity interactions that regulate plants' thermal responses are discussed.

2. Plant thermal sensing

Unlike other abiotic or biotic stresses, temperature change is perceived concurrently across all cellular components. A number of thermosensors proposed in plants have been recently reviewed (McClung and Davis, 2010; Ruelland and Zachowski, 2010; Knight and Knight 2012; Mittler et al., 2012; Qu et al., 2013), defining their

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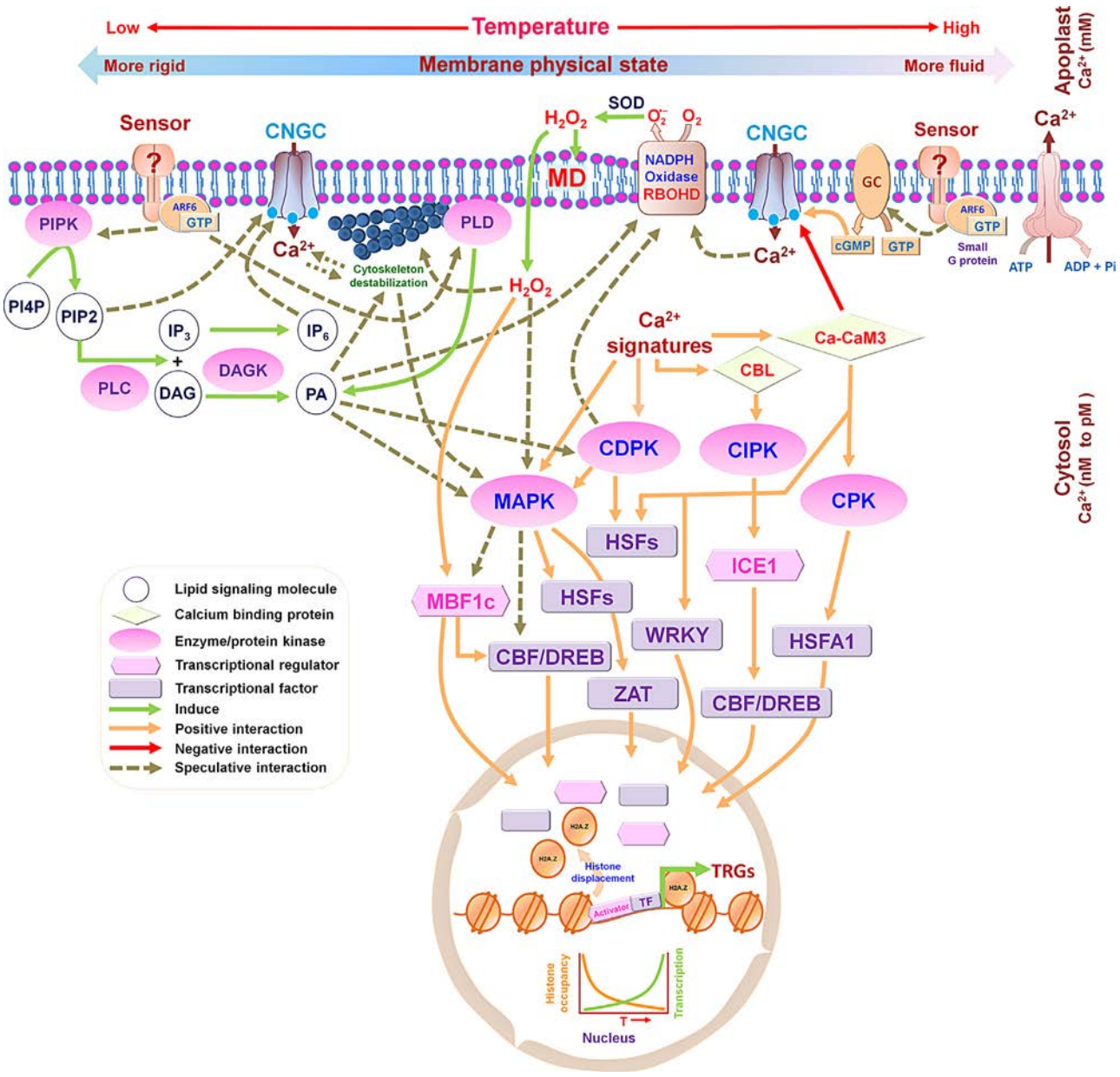

Fig. 1. Schematic model for temperature sensing and downstream signaling in plants.
Temperature-driven change in the membrane physical state (rigidification (cold) or fluidization (heat)) provides a mechanical or electrical signal to activate membrane localized calcium channel(s) to produce a transient influx of Ca^{2+} into the cytosol. Lipid synthesizing enzymes (PIPK, PLD, PLC) could be activated either through G-protein mediated signaling or directly by sensing membrane alterations to produce lipid signaling molecules (PIP2, IP6, PA). Accumulation of lipid molecules may induce Ca^{2+} influx and RBOHD-mediated ROS production. Conversely, cytoskeleton destabilization occurs with change in membrane fluidity, initial Ca^{2+} influx and accumulation of lipid molecule PA. In the nucleus, mild increase in temperature reduces the occupancy of H2A.Z in DNA and thus facilitates the binding of activator/suppressor proteins to regulate TRGs expression. Calcium oscillations in the cytosol are recognized/decoded by specific calmodulins (CaM3), calcium binding proteins (CBL) and several protein kinases (CDPK). CaM3,CBL and CDPK further activates CPK, CIPK and several MAP Kinases cascade and/or some transcription regulators (MBF1c, ICE1), and transcription factors such as WRKY, HSFs (HSFA1) and CBF/DREB. H_2O_2 signatures can alter cellular redox state and activate some transcriptional regulator (MBF1c) or MAP Kinases following activation of some transcription factors such as WRKY, ZAT and CBF/DREB.
Abbreviations: ARF6, ADP-ribosylation factor 6; CaM, calmodulin; CBF/DREB, C-repeat/dehydration response element binding factor; CBL, calcineurin B-like proteins; CDPK, calcium dependent protein kinase; cGMP, cyclic guanosine monophosphate; CIPK, CBL interacting protein kinases; CNGC, cyclic nucleotide gated channel; CPK, calcium/calmodulin-protein kinase; DAG, diacylglycerol; DAGK, diacylglycerol kinase; GC, guanylyl cyclase; GTP, guanosine-5′-triphosphate; H2A.Z, histone 2A.Z protein; HSFA1, heat shock factor A1; HSFs, heat shock factors; ICE1, inducer of CBF expression; IP3, inositol 1,4,5-trisphosphate; IP_6, phytic acid; MAPK, mitogen activated protein kinases; MBF1c, multiprotein bridging factor 1, a transcriptional co-activator; MD, membrane depolarization; PA, phosphatidic acid; PI4P, phosphatidylinositol phosphate; PIP_2, phosphatidylinositol-4,5-bisphosphate; PIPK, Phosphatidylinositol-4-phosphate 5-kinase; PLC, phospholipase C; PLD, phospholipase D; RBOHD, respiratory burst oxidase homolog D (NADPH oxidase); SOD, superoxide dismutase; TF, transcription factor; TRGs, temperature-regulated genes; WRKY, transcription factor with WRKY domain; ZAT, zinc transporter transcription factor.

role in thermal perception and signaling (Fig.1). Thermodynamically driven real-time alterations in the plasma membrane physical state are suggested as the most upstream primary sensor in the cellular thermal signaling pathway (Horváth et al., 1998, 2012; Saidi et al., 2010). Calcium channels in the plasma membrane are responsive to temperature changes (Fig. 1) and a transient extra cellular Ca^{2+} influx is triggered into the cytosol within milliseconds of cold- or heat-shock treatment (Penfield, 2008; Ruelland et al., 2009; Saidi et al., 2009). Cyclic nucleotide gated ion channels (CNGCs) are nonselective Ca^{2+} permeable cation transport

channels placed at the upstream of thermosensing pathway in *Arabidopsis* and *Physcomitrella patens* moss (Finka et al., 2012; Gao et al., 2012; Tunc-Ozdemir et al., 2013). Cytosolic heterotrimeric G-protein (ARF6 homolog in *Arabidopsis*, ARFB1a) mediated activation of transmembrane guanylyl cyclase (e.g., AtPepR1 in *Arabidopsis*) that produces cGMP to activate CNGCs is one proposed mechanism (Finka et al., 2012; Tunc-Ozdemir et al., 2013) but, the role of G-protein in temperature perception is still not clear in plants (Horváth et al., 2012). Only recently, Finka and Goloubinoff (2014) provided evidences that CNGCs in transgenic moss (*P. patens*) lines have the ability to sense fluidity changes in the plasma membrane under mild abrupt temperature upshift (from 25 up to 34 °C) and by application of artificial membrane fluidizer benzyl alcohol resulted in transient entry of apoplastic Ca^{2+} in to cytosol. The authors suggested that both the lipid composition of the plasma membrane and the embedded CNGC proteins (CNGCb and CNGCd) act as two cooperating moieties of an effective thermocouple. This interesting finding supports the plasma membrane as the most upstream thermosensor to date and the signal relayed to calcium channels (CNGCs) connect downstream components of thermal sensing pathways. Following a transient Ca^{2+} influx under cold temperature (Ruelland et al., 2002) or small G-proteins under high temperature (Horváth et al., 2012), phospholipid signaling is initiated by activating lipid signaling enzymes such as phosphatidylinositol-4-phosphate 5-kinase (PIPK) phospholipase D (PLD), and phospholipase C (PLC). Consequently, rapid accumulation of lipid-signaling molecules such as phosphatidylinositol (4,5)-bisphosphate (PIP2), phosphatidic acid (PA), and phytic acid (IP6) converge with Ca^{2+} and reactive oxygen species (ROS) mediated pathways during onset of thermal signaling (Fig. 1; for details see Ruelland et al., 2002; Mishkind et al., 2009; Horváth et al., 2012). Recently, a specific histone variant (H2A.Z)-chromatin interaction has been reported to sense mild temperature changes in the nucleus (temperature discrimination – as low as 1 °C) that regulates growth and reproductive physiology in *Arabidopsis* (Kumar and Wigge, 2010; Kumar et al., 2012). A possible post-translational modification such as histone acetylation is hypothesized to be directly thermo-responsive for changing H2A.Z occupancy in the chromatin (Kumar and Wigge, 2010). It could be intriguing to see how signaling of histone modification in the nucleus interacts with Ca^{2+} mediated thermo sensory pathway under a similar thermal cue. Also, the possibility of concurrent perception of temperature signal by plasma membrane protein or lipid-signaling protein similar to H2A.Z in the nucleus remains open, making thermal signaling a dynamic phenomenon and not merely a top-down process.

While thermal perception and signaling at the cellular level may involve similar components across plants, plant thermo-responsiveness may alter with phenological and developmental stages, tissue type and composition, influenced by other environmental factors such as humidity and light (photoperiod). Thus, there is a strong need to understand the physiological significance of plant thermal signaling and its link with plant thermal responses driven by hormonal and metabolic interplay at different developmental stages.

3. Plant thermal responses

Temperature cues perceived by thermosensors across the cell modulates developmental programming across complete plant life cycle with the help of a complex network of hormones and metabolites. Growth and developmental responses of plants are strongly influenced by temperature and its interaction with other factors such as relative humidity (RH) and light under natural environments. For example, the threshold temperature inducing floret sterility in rice is documented to be 35 °C (Jagadish et al., 2008), while rice paddies can sustain temperatures up to or above 40 °C when accompanied by adequate water supply and low RH, which allows the plant canopy microclimate to drop well below the critical threshold (~33 °C) by employing transpiration cooling effectively (Weerakoon et al., 2008). Likewise, plant development processes are determined by temperature and photoperiod interaction (Craufurd and Wheeler, 2009).

3.1. Germination

Soil temperature and moisture can alter the depth of seed dormancy, dictate the end of dormancy, and start of germination. A transition from belowground germination to aboveground emergence is critical for plant survival and depends mainly on soil temperature and moisture content (Footitt et al., 2011). Seed germination is controlled by a concerted action of and interaction between two diverse phytohormones, gibberellic acid (GA) and abscisic acid (ABA), as influenced by diverse endogenous and external cues (Fig. 2). Cold temperature (stratification) and light signals converge to promote the GA biosynthesis by upregulating the GA biosynthesis gene gibberellin 3-beta-dioxygenase 1 (*GA3ox1*; number in the enzyme nomenclature here and afterwards refers to carbon position and not the number of the GA) and down-regulating gibberellin 2-oxidases (*GA2ox*; inactivation of bioactive GAs) in *Arabidopsis* seeds to facilitate germination (Yamauchi et al., 2004). Both stratification and light regulate seed germination by repressing expression of basic helix-loop-helix (bHLH) transcription factor SPATULA (SPT) under low temperatures and a light-sensitive member of the bHLH PHYTOCHROME INTERACTING FACTOR 3-LIKE5 (PIL 5). SPT and PIL5 act as repressors of the GA biosynthesis gene *GA3ox*. However, suppression of SPT under low temperature and light dependent degradation of PIL5 protein allows GA accumulation required for seed germination (Penfield et al., 2005; Oh et al., 2006, 2009). Studies on *Arabidopsis* ABA-deficient (aba2-2) and GA loss-of-function (*spy*, *rgl2*) mutants revealed that temperature beyond physiological optimum (heat stress) inhibits seed germination (thermo-inhibition) by inducing ABA biosynthesis genes (*ABA1* and *NCED9*, and *NCED4*). These, subsequently, repress bioactive GA levels by inhibiting GA biosynthesis genes (*Ga3ox*, *GA20ox*) thus, signaling required for germination (Toh et al., 2008). Conversely, under optimum temperature and moisture, signaling molecules such as hydrogen peroxide (H_2O_2) in coordination with nitric oxide (NO) induces ABA catabolism genes (*ABA 8′-hydroxylase*; *CYP707As*) and GA biosynthesis genes to favor germination (Yamauchi et al., 2004; Liu et al., 2010).

3.2. Growth

Successful germination combined with seedling vigor are prerequisites for normal growth of plants. Temperature regulation on early growth phase is mediated by key phytohormones such as auxin and GA (Fig. 2). A rapid increase in auxin under mild to high temperature is associated with hypocotyl elongation in *Arabidopsis* (Gray et al., 1998; Stavang et al., 2009; Franklin et al., 2011). Temperature rise enhances the bHLH transcription factor PHYTOCHROME-INTERACTING FACTOR 4 (PIF4) levels. Binding of PIF4 to the promoter of auxin biosynthesis genes such as *YUCCA* (*YUC8*) and tryptophan aminotransferase-encoding gene (*TAA1*/*TAR*) enhance tissue auxin level (Sun et al., 2012) that regulates small auxin up-RNA (*SAUR*) genes responsible for hypocotyl elongation when grown under light conditions (Franklin et al., 2011). Likewise, two major biosynthesis genes of GA (*AtGA20ox1*, *AtGA3ox1*) are known to rapidly accumulate under temperature rise in *Arabidopsis* (Stavang et al., 2009). GA-mediated proteasomal degradation of DELLA proteins (negative regulators of gibberellic acid

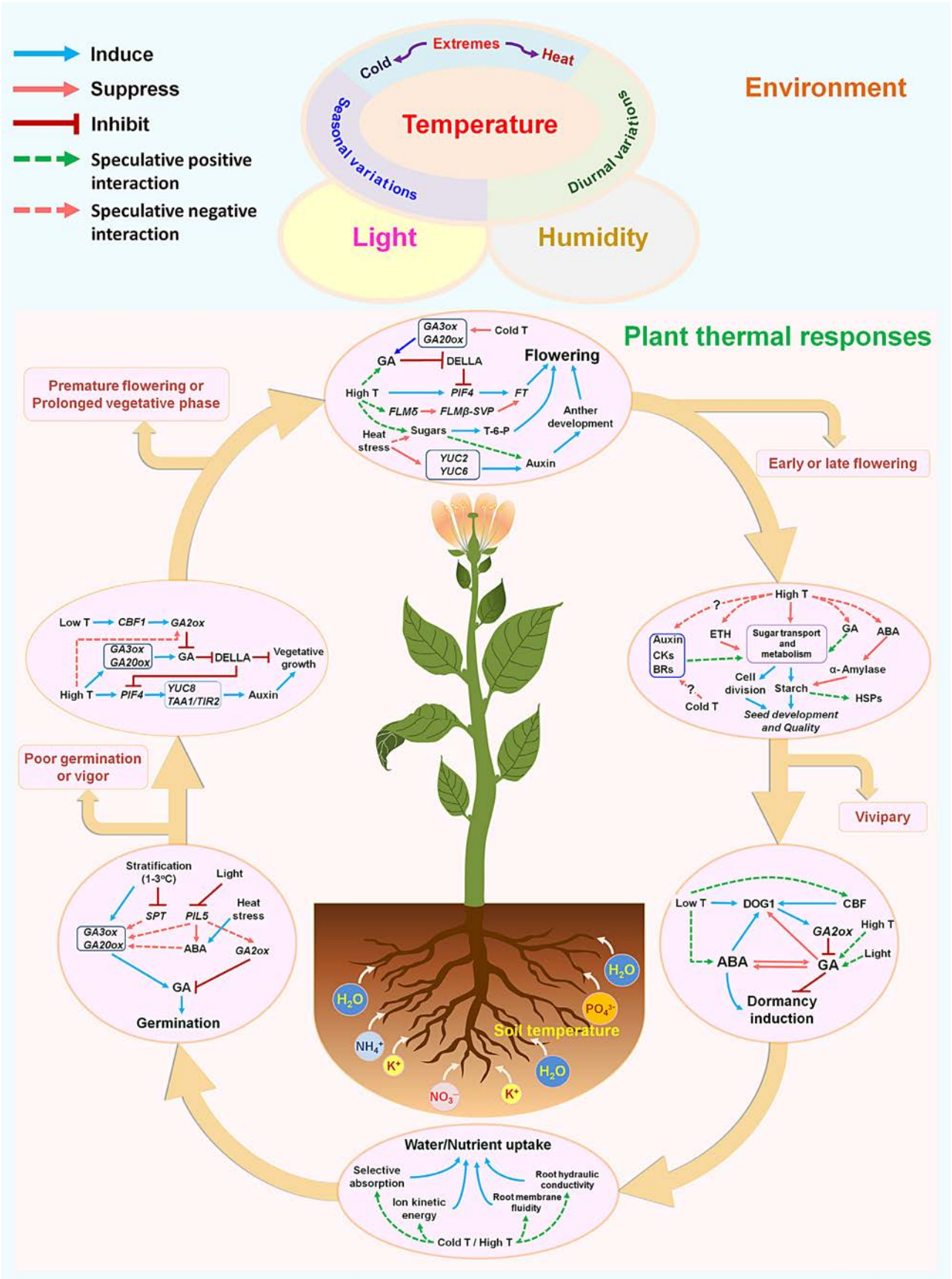

Fig. 2. Plant responses to temperature cues: phenological development, transition, and retraction.
Abbreviations: ABA, abscisic acid; BRs, brassinosteroids; CBF, C-repeat binding factor; CKs, cytokinins; DELLA, a negative regulator of GA response; DOG1, delay of germination 1; ETH, ethylene; FLM, FLOWERING LOCUS M; FT, Flowering Locus T; GA, gibberellic acid; *GA2ox*, GA 2-oxidase gene encode a GA degrading enzyme; *GA3ox*, GA3-oxidase, GA

response having an N-terminal DELLA domain required for GA regulation) releases the constraint on PIF4 (de Lucas et al., 2008; Feng et al., 2008). Thus, enhancing its binding to the promoters of PIF4-induced genes and stimulating growth under higher temperatures (Stavang et al., 2009). Moreover, suppression of gene (*AtGA2ox1*) under higher temperature increases bioactive GA levels that strongly suppress the DELLA proteinrepressor-of-GA1-3 (RGA) in the elongating hypocotyl (Stavang et al., 2009). In contrast, cold temperature induces the C-repeat/drought-responsive element binding factor (*CBF1*/*DREB1b*; transcription factor activated by cold stress and has a conserved 'CCGAC' core sequence, which is found in the promoter region of many cold-regulated (COR) genes) that allows RGA accumulation by stimulating GA inactivating gene (*GA2ox*). High GA-2-oxidase activity, thus, reduces GA content and restrains growth rate in the vegetative tissues (Achard et al., 2008; Achard and Genschik, 2009). On the other hand, effect of chilling temperature (5 °C) on wild type (Col-0), transgenic (*NahG*; transformed with the bacterial salicylic acid hydroxylase gene) and different salicylic acid mutants (*npr1*, *eds5*, *cpr1*) of *Arabidopsis* revealed that cold induced accumulation of salicylic acid contribute to growth inhibition at low temperatures (Scott et al., 2004). However, mechanism of salicylic acid action under cold stress and its interaction with other growth hormones such as GA during vegetative growth need further research.

3.3. Florogenesis

Plants respond to external (temperature, photoperiod; Craufurd and Wheeler, 2009) and internal (phytohormones, sugars; Bernier et al., 1993) factors for successful transition from vegetative to reproductive phase. The role of sugars, such as trehalose-6-phosphate, has recently been suggested to function as a proxy for carbohydrate status in the plant, required for timely initiation of flowering (Wahl et al., 2013). Likewise, the role of GA in flowering initiation (Moon et al., 2003; Porri et al., 2012) and auxin in male reproductive development (Sakata et al., 2010; Ding et al., 2012) are reported in coordination with external factors such as temperature and photoperiod. Temperature-induced flowering is dependent on the PIF4-mediated regulation of the floral pathway integrator gene *FLOWERING LOCUS T (FT)* expression independent of photoperiod pathway (Kumar et al., 2012). Warmer temperature allows release of H2A.Z-nucleosomes, increasing the accessibility of PIF4 binding site to FT promoter. DELLA protein- mediated-repression of PIF4 activity under cooler temperature results in delayed flowering which could be overcome by the phytohormone GA-mediated-degradation of DELLA proteins. DELLA proteins are suggested as key regulators by which GA influences PIF4 that regulate FT expression in a temperature-dependent process revealing a possible mechanism where GA and temperature converge to induce flowering (Kumar et al., 2012). Besides PIF4 pathways, small noncoding RNAs (miR172) regulated by a floral repressor SHORT VEGETATIVE PHASE (SVP), are involved in flowering time regulation in response to ambient temperature changes (see details Lee et al., 2010; Yamaguchi and Abe, 2012). Recently, two FLOWERING LOCUS M (FLM) protein splice variants, FLM-β; and FLM-δ, are reported to compete for interaction with the floral repressor SVP to regulate flowering in a temperature-dependent manner. SVP–FLM-β; complex formed predominantly at cool temperature (16 °C) restrains flowering while at a higher temperature (23 °C) competing SVP–FLM-δ complex acts as a dominant-negative activator of flowering (Pose et al., 2013). In contrast to temperature regulation for flowering induction, heat or cold stress during the reproductive stage could have serious negative impacts leading to abnormal gamete formation, tapetal dysfunction in anthers, reduced pollen viability, male and female reproductive organ developmental asynchrony, altered pollen tube growth and fertilization signaling, lower seed-set, and, in severe cases, a lack of seed formation (Jagadish et al., 2010; Thakur et al., 2010; Hedhly, 2011). Male reproductive microspores are strong photo-assimilate sink, with both short- and long-term heat stress during microspore meiosis resulting in irreversibly reduced cell wall invertase that alters carbohydrate metabolism, thereby inducing starch deficiency and pollen abortion in sorghum (Jain et al., 2010). At the cellular level, heat stress suppresses expression of auxin biosynthesis *YUCCA* (*YUCCA2*, *YUCCA6*) genes, leading to decreased auxin, specifically in the developing anthers, a main cause of male sterility in barley and *Arabidopsis* (Sakata et al., 2010). In contrast, moderate cool temperature (19 °C) in rice suppresses GA biosynthesis genes *GA20ox3* and *GA3ox1*, resulting in reduced levels of endogenous bioactive GAs (GA4, GA7) in the developing anthers causing male sterility (Sakata et al., 2014). Moreover, cold stress inhibits inflorescence gravitropism in *Arabidopsis* by inhibiting intracellular auxin cycling, thus affecting the functionality of auxin transport PIN genes (PIN3) and diminishing root–shoot auxin gradient (Wyatt et al., 2002).

3.4. Seed development

Following successful fertilization, a balanced source-sink facilitates the supply of adequate photoassimilates for normal seed-set. Indeed, sugars play a critical role during seed development, with adequate glucose repressing programmed cell death (PCD) and promoting cell division (Ruan et al., 2012). Temperatures beyond physiological optima could impede the grain filling or seed formation. For instance, cold stress decreases both the rate and duration of grain filling and seed-set in chickpea (Kaur et al., 2008; Thakur et al., 2010), while heat stress enhances the rate and reduces the duration significantly in wheat and *Brachypodium* (Lobell et al., 2012; Boden et al., 2013). Both stresses result in the inefficient use of available assimilates. High temperature reduces starch accumulation in developing seeds by limiting sucrose transport (Phan et al., 2013) and starch metabolism (Yamakawa et al., 2007; Yamakawa and Hakata, 2010; Phan et al., 2013) by suppressing genes involved in sucrose synthesis (*SuSy2*), sucrose transport (*SUT1*), sucrose breakdown (invertase, *INV3*), and starch synthesis (ADP-glucose pyrophosphorylase, *AGPS2b*; granule-bound starch synthase, GBSSI; branching enzyme, BEIIb) in developing seeds. Conversely, high temperature/heat stress induces genes for α-amylase (*Amy1A*, *Amy1C*, *Amy3A*, *Amy3D*, *Amy3E*), which breakdown starch in endosperm (Yamakawa et al., 2007; Hakata et al., 2012). Thus, starch breakdown, apparently required to aid HSPs synthesis during stress, could be a key factor in deteriorating grain quality under high temperature in major cereals such as rice, wheat, and maize (Yamakawa et al., 2007; Hurkman and Wood, 2011; Hakata et al., 2012; Phan et al., 2013). Plant hormones such as ABA, ethylene, GA, auxin, cytokinin, and brassinosteroids direct seed initiation and development. A synergistic action of auxin and GA in seed development initiation, role of cytokinin in cell division and differentiation in the endosperm during early seed development, brassinosteroids in cell elongation and a regulatory action of

biosynthesis enzyme; *GA20ox*, GA20-oxidase, GA biosynthesis enzyme; High T, high temperature; HSPs, heat shock proteins; Low T, low temperature; PIF4, basic helix-loop-helix PHYTOCHROME INTERACTING FACTOR 4; PIL5, basic helix-loop-helix PHYTOCHROME INTERACTING FACTOR 3-LIKE5; SPT, SPATULA, a basic helix-loop-helix transcription factor; SVP, SHORT VEGETATIVE PHASE, a floral repressor; *TAA1*/*TIR2*, TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS1/TRYPTOPHAN AMINOTRANSFERASE RELATED auxin biosynthesis pathway *genes*; T6P, trehalose-6-phosphate; *YUC2,6,8*, members of auxin biosynthesis *YUCCA* genes.

ethylene and ABA on sugar metabolism and seed maturation are evident (for details see: Sun et al., 2010; Zhu et al., 2011; Ruan et al., 2012; Liu et al., 2013; Sreenivasulu and Wobus, 2013). However, how these hormones respond with temperature cues is still a challenging aspect of research. For instance, high temperature reduces ABA and GA (GA_7, GA_{19}) accumulation in developing seeds of rice (Hakata et al., 2012), while cold shock reduced ABA with a concomitant increase in GA (GA_{19}) (Kondhare et al., 2014), resulting in higher α-amylase activity and starch breakdown in both cases. On the other hand, heat stress-induced ethylene (counteracting hormone to ABA) in developing seeds is suggested as a timing signal to arrest development and induce early seed maturity in wheat (Hays et al., 2007). Thus, tissue-specific regulation of these hormones—particularly under temperature within and beyond physiological optima—is yet to be elucidated.

3.5. Dormancy

Two antagonistic hormones, abscisic acid (ABA) and gibberellins (GAs), essentially control the equilibrium among induction, maintenance, and end-of-seed dormancy, i.e., germination. Temperature can modulate seed dormancy by regulating ABA and GA levels in the seed. Low temperature during seed maturation enhances C-repeat binding factor (CBF) and *DELAY OF GERMINATION1* (*DOG1*) gene expression required for inducing dormancy. Both CBF and DOG1 promote *GA2ox6* expression resulting in GA catabolism and enhancing ABA synthesis genes (*NCED*) to ensure high ABA levels (and dormancy) in the maturing seeds (Kendall et al., 2011). During dry storage, levels of ABA slowly reduce opening the option of germination to sense environmental cues under favorable conditions where heat or cold shock accompanied with light can promote GA synthesis in seeds to break dormancy for inducing successful germination (Finch-Savage and Leubner-Metzger, 2006).

3.6. Plant nutrient continuum

Similar to aboveground responses to ambient air temperature, light, and humidity, plant root growth morphology, nutrient extraction, and microbial interactions are determined by soil temperature and moisture content (Bassirirad, 2000). A change in soil temperature can alter root plasma membrane fluidity and kinetic energy of free inorganic ions determining nutrient availability and differential nutrient uptake by roots (Bassirirad, 2000). Evidences suggest that increasing temperature along with CO_2 can increase root colonization of AFM (arbuscular mycorrhiza) that benefits plants with enhanced nutrient uptake and a suite of physiological processes (Büscher et al., 2012). Conversely, *Arabidopsis* plants exposed to low temperature (10 °C) showed reduced root hydraulic conductivity than when exposed to 25 °C, reducing both root and shoot growth. This effect was overcome in the transgenic plants over expressing plasma membrane intrinsic protein 1;4 (PIP1;4) and PIP2;5 involved in aquaporin phosphorylation/dephosphorylation processes (Lee et al., 2012). This study highlights belowground root (soil) temperature effect on key physiological processes such as water transport affecting growth and development.

4. Future outlook and concluding remarks

The concurrent perception of temperature change with an array of thermosensors and differential responses during plant growth and developmental stages make temperature-induced signaling dynamically complex. Plants exhibiting large but opposing sensitivities to day and night temperature have been highlighted (Lobell and Ortiz-Monasterio, 2007; Welch et al., 2010). For instance, high night temperature-induced decline in overall biomass, nitrogen, and nonstructural carbohydrate partitioning reduced rice yield and grain quality (Shi et al., 2013), compared with increased spikelet sterility induced by high day temperature (Jagadish et al., 2010). Further, the contribution of the amplitude of daily variation of 15 °C (32.5/17.5 °C) can increase carbon-use efficiency in mature leaves and roots of orange trees, leading to increased leaf area index and photosynthetic rates compared with 0 °C (25/25 °C) daily variation (Bueno et al., 2012). On the other hand, temperature at the plant canopy or flower bud can be considerably different from the air temperature and is strongly dependent on the microclimate surrounding these critical plant organs, influencing flowering time and subsequent reproductive processes (Julia and Dingkuhn, 2013). Hence, investigating the cellular thermosensory network that interacts with the external (environmental signals such as relative humidity and light, differential day and night temperature, and variation with temperature amplitude) and internal (tissue metabolic composition, phenological stage) could provide novel opportunities to upscale cellular sensing translating into plant response (Fig. 3). Differential regulation of plant response with phytohormone signaling and metabolic programming varying with phenological stages continues to be a challenging area of research. However, emerging hormonal profiling technology shows promise for a holistic understanding of temperature-induced interactions and proportional changes among hormones and between hormones and metabolites (Pan et al., 2010). Hence, a better understanding of plant thermo-responsiveness under a multidimensional environment can lead to developing plants with enhanced resilience to temperature extremes to sustain global food security and biodiversity.

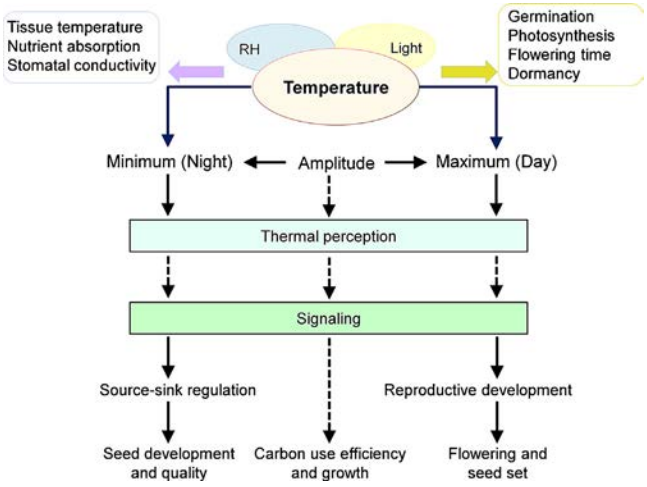

Fig. 3. Overview of temperature and associated physical factors (relative humidity (RH), light) affecting key physiological processes in plants. Figure shows differential plant responses with absolute values and amplitude of diurnal temperature variation. Broken arrows indicate unknown/insufficient information on the mechanism regulating respective physiological response.

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