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Temperature regulation of plant hormone signaling during stress and development

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13 **Running Title:** Temperature regulation of plant hormone signaling

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15 **Highlight**

16 In this review, we present our current understanding of how temperature regulates plant

17 hormone pathways during immunity, stress tolerance and development – highlighting

18 key temperature-sensitive and temperature-activated molecular hubs.

19

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23

Abstract

Global climate change has broad-ranging impacts on the natural environment and human civilization. Increasing average temperatures along with more frequent heat waves collectively have negative effects on cultivated crops in agricultural sectors and wild species in natural ecosystems. These aberrantly hot temperatures, together with cold stress, represent major abiotic stresses to plants. Molecular and physiological responses to high and low temperatures are intricately linked to the regulation of important plant hormones. In this review, we shall highlight our current understanding of how changing temperatures regulate plant hormone pathways during immunity, stress responses and development. This article will present an overview of known temperature-sensitive or temperature-reinforced molecular hubs in hormone biosynthesis, homeostasis, signaling and downstream responses. These include recent advances on temperature regulation at the genomic, transcriptional, post-transcriptional and post-translational levels – directly linking some plant hormone pathways to known thermosensing mechanisms. Where applicable, diverse plant species and various temperature ranges will be presented, along with emerging principles and themes. It is anticipated that a grand unifying synthesis of current and future fundamental outlooks on how fluctuating temperatures regulate important plant hormone signaling pathways can be leveraged towards forward-thinking solutions to develop climate-smart crops amidst our dynamically changing world.

Abbreviations:

ABA, abscisic acid; ABF, ABRE BINDING FACTOR; ACO2; ACYL-COA OXIDASE 2; ACS, AMINOCYCLOPROPANE-1-CARBOXYLIC ACID SYNTHASE; AHK, ARABIDOPSIS HISTIDINE KINASE; AHP, ARABIDOPSIS HISTIDINE PHOSPHOTRANSFER PROTEIN; AMP, adenosine monophosphate; AOX, ALLENE OXIDE SYNTHASE; ARF, AUXIN RESPONSE FACTOR; ARR, ARABIDOPSIS RESPONSE REGULATOR; AUX, AUXIN-SENSITIVE; BES1, BRI1-EMS-SUPPRESSOR 1; bHLH, BASIC LOOP-HELIX-LOOP; BIN2, BRASSINOSTEROID INSENSITIVE 2; BR, brassinosteroid; BRI1, BRASSINOSTEROID INSENSITIVE 1; BZR1, BRASSINAZOLE-RESISTANT 1; CAMTA, CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR; CBF, C-REPEAT/DRE BINDING FACTOR; CK, cytokinin; CKX2, CYTOKININ OXIDASE 2; COI1, CORONATINE-INSENSITIVE 1; CTR, CONSTITUTIVE TRIPLE RESPONSE; D3, DWARF 3; D14, DWARF 14; D53, DWARF 53; DET2, DE-ETIOLATED 2; DOG1, DELAY OF GERMINATION 1; DWF4, DWARF 4; DWF7, DWARF 7; EDS1, ENHANCED DISEASE SUSCEPTIBILITY 1; EIN2, ETHYLENE-INSENSITIVE 2; EIN3, ETHYLENE-INSENSITIVE 3; ELF3, EARLY FLOWERING 3; ERF, ETHYLENE RESPONSE FACTOR; ET, ethylene; ETR, ETHYLENE RESPONSE; GA, gibberellin; GID1, GIBBERELLIN INSENSITIVE DWARF 1; HDA, HISTONE DEACETYLASE; HOS1, HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENE1; HSF, HEAT SHOCK FACTOR; HTS, high temperature susceptible; IAA, INDOLE-3-ACETIC ACID-INDUCIBLE; ICS1, ISOCHORISMATE SYNTHASE 1; JA, jasmonic acid; JAZ, JASMONATE ZIM-DOMAIN; MeJA; methyl jasmonate; MYB, MYB DOMAIN PROTEIN; NCED, 9-CIS-EPOXYCAROTENOID

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70   DIOXYGENASE; NPR1, NONEXPRESSER OF PR GENES 1; PAD4, PHYTOALEXIN-

71   DEFICIENT 4; phyB, Phytochrome B; PIF, PHYTOCHROME-INTERACTING FACTOR;

72   PILS6, PIN-LIKES 6; PIN, PIN-FORMED; PP2AC, PROTEIN PHOSPHATASE 2A

73   CATALYTIC SUBUNIT; PR1, PATHOGENESIS-RELATED 1; PYL, PYR1-LIKE; PYR,

74   PYRABACTIN RESISTANCE; ROT3, ROTUNDIFOLIA 3; RPS4, Resistance to

75   Pseudomonas syringae4; SA, salicylic acid; SL, strigolactone; SNC1, Suppressor of

76   npr1-1 constitutive1; SnRK; SNF1-RELATED KINASE; SNX1, SORTING NEXIN1;

77   STE1, STEROL1; TAA, TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS;

78   TCP, TEOSINTE BRANCHED 1, CYCLOIDEA, PCF; TGA, TGACG SEQUENCE-

79   SPECIFIC BINDING PROTEIN; TIR1, TRANSPORT INHIBITOR RESPONSE 1;

80   UGT76F1, UDP-GLYCOSYLTRANSFERASE 76F1; ZEP, ZEAXANTHIN EPOXIDASE

81

82

Introduction

Climate change presents an existential threat to present and succeeding generations, as global warming and extreme temperatures can drastically influence agricultural productivity (Zhao et al., 2017) and natural ecosystems (Lippman et al., 2019). Together with cold and freezing temperatures, these sub-optimal temperatures disturb the physiological balance of plants by modifying cellular and molecular activity (Velasquez et al., 2018; Lippman et al., 2019). Temperature is an important environmental parameter that affects morphology and physiology, as plants need to preserve an optimal environment or acclimate to stresses (Way and Yamori 2014; Ding et al., 2020). Thus, climatic/environmental aberrations typically lead to dramatically decreased plant performance, eventually causing death under extreme circumstances.

Plant physiological processes under optimal and sub-optimal conditions are majorly governed by hormones (Bürger and Chory, 2020). Hormones are protein-, lipid-, nucleotide- and/or specialized metabolite-derived molecules that mediate and/or directly activate diverse cellular pathways during defense and development (for reviews, see Berens et al., 2017; Robert-Seilaniantz et al., 2011; Blázquez et al., 2020; Bürger and Chory, 2020). Hormones display a tight relationship with temperature and other environmental factors. When plants are exposed to high or low temperatures, physiological mechanisms can be compromised, as these stresses can disrupt certain molecular components of hormone pathways and eventually affect global plant performance (Lippmann et al., 2019; Dai Vu et al., 2019; Ding et al., 2020; Kim et al., 2021).

105   A comprehensive and fundamental understanding of how these aberrant

106   temperatures regulate plant signaling mechanisms and physiological responses is

107   paramount. In this review, we focus specifically on how deviations (higher/lower) from

108   the optimal temperature influence plant hormone production and signaling pathways.

109   We first provide an overview of plant thermosensing mechanisms. The bulk of this

110   review then covers how changing temperature impacts the nine major classes of

111   hormones. At various levels of gene/protein regulation, we highlight temperature-

112   sensitive (downregulated/repressed) and temperature-reinforced molecular components

113   (upregulated/activated) of these pathways. Ultimately, this global regulatory landscape

114   contributes to temperature-regulated physiological responses, like

115   thermomorphogenesis, stress tolerance and immunity.

116

Plant thermosensing mechanisms

118   Thermosensing mechanisms in plants have recently been reviewed (see Quint et al.,

119   2016; Casal and Balasubramanian, 2019; Hayes et al., 2020). Here, we provide a brief

120   synopsis of recognized temperature perception mechanisms as a guide to currently

121   known connections (or lack thereof) to hormone pathways in subsequent sections.

122

123   ***Phytochrome B (phyB).*** The red/far-red light receptor phyB acts as a temperature

124   sensor by interconverting between active Pfr forms at ambient temperatures and

125   inactive Pr forms at elevated temperatures (Jung et al., 2016; Legris et al., 2016). PhyB

126   inactivation at high temperatures leads to derepression of the central transcription factor

127   PHYTOCHROME-INTERACTING FACTOR 4 or PIF4 (Casal and Balasubramanian,

128 2019), activating downstream genes important for temperature-responsive growth and

129 development (Quint et al., 2016; Casal and Balasubramanian, 2019). At low

130 temperatures, phyB is stabilized by preferred interaction of PIF3 (and other PIFs) with

131 the cold master regulators C-REPEAT/DRE BINDING FACTORs (CBFs), leading to

132 phyB-mediated stress tolerance (Jiang et al., 2020).

133

134 **Phototropins.** Another class of proposed thermosensors are phototropins, as

135 demonstrated experimentally in *Arabidopsis thaliana* and *Marchantia polymorpha*. Their

136 temperature sensing mechanism relies on the phototropin LOV domain and FMN

137 chromophore linkage due to its temperature-dependent degradation, leading to less

138 activity when temperatures increase (Hayes et al., 2020).

139

140 **EARLY FLOWERING 3 or ELF3.** Apart from receptor proteins, direct thermosensing is

141 accomplished through temperature-sensitive promoter binding of the transcriptionally

142 repressive Evening Complex (Ezer et al., 2017). Elevated temperature leads to inactive

143 biomolecular condensate formation of the Evening Complex component ELF3, which

144 relieves repression of the thermomorphogenic gene *PIF4* (Jung et al., 2020). ELF3 is

145 also functionally associated with phyB, as they interact directly during plant temperature

146 responses (Ezer et al., 2017).

147

148 **H2A.Z chromatin remodeling.** Another thermosensing mechanism associated directly

149 with DNA is eviction of histone variant H2A.Z-containing nucleosomes, promoting active

150 transcription of temperature-responsive *PIF4* and flowering genes (Kumar and Wigge,

151 2010). H2A.Z eviction seems to be facilitated by enhanced binding of HEAT SHOCK

152 FACTOR 1 or HSF1 at elevated temperature (Cortijo et al., 2017). Interestingly, HSF

153 translation itself is regulated by temperature, through an RNA hairpin loop

154 thermosensing mechanism (Chung et al., 2020).

155

156 Molecular mechanisms governing hormone pathways under

157 changing temperatures

158 There exists a global plant hormonal landscape of regulatory players and molecular

159 mechanisms in response to temperature changes. Because of extensive crosstalk

160 among hormone networks (Altmann et al. 2020), we provide a comprehensive coverage

161 of how these are targeted or enhanced by aberrant temperatures (see Tables 1-4). The

162 following sections highlight various temperature-vulnerable and temperature-enhanced

163 components of major hormone pathways, and how these lead to diverse temperature-

164 regulated physiological processes (see Figures 1-2). We present emerging trends and

165 cross-cutting themes in the temperature regulation of hormone biosynthesis,

166 homeostasis, receptors and signaling, while acknowledging critical knowledge gaps that

167 need to be addressed.

168

169 The impact of temperature on hormone biosynthesis

170

171 **Auxin.** Auxins are crucial to plant growth, and are found in high concentration in

172 embryos, apical meristems and developing leaves (Lavy and Estelle, 2016). In

173   *Arabidopsis*, the main auxin indole-3-acetic acid (IAA) is primarily synthesized from

174   tryptophan through a two-step reaction involving TRYPTOPHAN

175   AMINOTRANSFERASE OF ARABIDOPSIS/TAA and YUCCA (Korasick et al., 2013).

176   Arguably, auxin biology has contributed the most towards understanding of

177   thermoregulated hormone pathways. Numerous studies rely on temperature-sensitive

178   phenotypic outputs, like hypocotyl and stem elongation, which heavily depend on auxin

179   (Quint et al., 2016; Casal and Balasubramanian, 2019).

180   The impact of high temperature on auxin was demonstrated in a seminal study

181   by Gray et al. (1998) showing higher production in *Arabidopsis*, resulting in a hallmark

182   phenotype of thermomorphogenesis – increased hypocotyl elongation (Table 1).

183   Increased auxin production is due to promotion of auxin biosynthetic gene expression

184   (*TAA1*, *CYP79B2* and *YUCCA8*) by the master transcription factor PIF4 (Franklin et al.,

185   2011; Sun et al., 2012). In agreement, mutating the auxin-responsive *IAA3* (*shy2-2*

186   mutation) abolishes thermomorphogenic growth (Sun et al., 2012), while overexpressing

187   auxin-inducible *SAUR19* rescues the *pif4* mutant phenotype (Franklin et al., 2011).

188   Apart from *Arabidopsis*, high temperature increases indole-3-pyruvate (IPA) levels and

189   hypocotyl elongation in soybean, along with increased biosynthetic gene expression

190   (Bawa et al., 2020). Warm-induced auxin biosynthesis has also been observed in

191   lettuce (Hao et al., 2018) and apples (Song et al., 2020), where PIF4 directly activated

192   auxin biosynthetic gene *MdYUCCA8a*. Other biosynthetic genes were also induced, but

193   two genes were interestingly downregulated (*MdYUCCA2b* and *MdYUCCA6b*),

194   indicating that increased biosynthesis at warm temperatures may not be universal

195   (Song et al., 2020).

196   The PIF4-auxin module is driven by tissue specificity; thermomorphogenesis is

197   only observed with epidermal but not vasculature-specific *PIF4* expression (Kim et al.,

198   2020). High temperature promotes *PIF4* transcription and PIF4 promoter binding in the

199   epidermis, which is countered by overexpressing epidermis-specific *PhyB* (Kim et al.,

200   2020). PIF4 recruitment to promoters, like the biosynthetic gene *YUCCA8*, is promoted

201   at high temperatures through histone deacetylation by HISTONE DEACETYLASE 9

202   (HDA9) and eviction of the thermosensing histone variant H2A.Z (van der Woude et al.,

203   2019).

204   Although most studies have found increased auxin levels at moderately elevated

205   temperatures (27°C-29°C), higher temperatures (>31°C) can decrease levels in the

206   case of developing *Arabidopsis* and barley anthers, leading to male sterility and

207   decreased fitness (Sakata et al., 2010). Apart from reproductive tissues, heat shock

208   temperatures also reduce auxin levels in *Arabidopsis* roots (Prerostova et al., 2020).

209   Even in vitro, auxin-responsive gene expression in tobacco protoplasts is suppressed

210   (Dong et al., 2007). Heat stress (at 40°C) have opposite effects depending on genotype,

211   as auxin levels increased in wild-type Nipponbare rice pistils but decreased in high

212   temperature susceptible (HTS) mutants (Zhang et al., 2018). Late-stage cotton anthers

213   also have higher IAA levels during heat stress, but only in the tolerant strain (Min et al.,

214   2014; Ding et al., 2017). In contrast, cooler temperatures decrease auxin levels through

215   repression of biosynthetic genes, leading to reduced meristem size and quantity (Zhu et

216   al., 2015; Table 2).

217

218 **Brassinosteroid.** Auxins work coordinately with brassinosteroids (BRs) in regulating

219 phyB-PIF4-directed thermomorphogenesis (Oh et al., 2012; Ibañez et al., 2018). Plants

220 possess multiple biosynthetic pathways for BRs, which are derived from steroid

221 precursors (Kim and Russinova, 2020). BRs stimulate cell division and elongation, but

222 also regulate tissue differentiation and development (Belkhadir and Jaillais 2015;

223 Planas-Riverola et al., 2019).

224   *Arabidopsis* roots sense high temperature to induce auxin levels and transport to

225 shoots, resulting in local cell elongation mediated by BRs (Bellstaedt et al., 2019; Table

226 1). Propiconazole (PPZ) inhibition of BR biosynthesis reduces temperature-sensitivity of

227 hypocotyl elongation (Oh et al., 2012). In agreement, a genetic screen isolated

228 temperature-insensitive mutants in BR biosynthetic genes *DWARF7 (DWF7)/ STEROL*

229 *1 (STE1)/ BOULE 1 (BUL1)* and *ROTUNDIFOLIA 3 (ROT3/CYP90C)* (Ibañez et al.,

230 2018). The former catalyzes the delta-7-sterol-C-5 desaturation step, while the latter

231 converts typhasterol to castasterone (Ibañez et al., 2018). Amplified BR biosynthetic

232 gene expression seems to be promoted by the thermomorphogenic transcription factor

233 PIF4, by competing with homodimerization of the modulatory BR regulator BRI1-EMS-

234 SUPPRESSOR 1/ BES1 (Martínez et al., 2018). Expectedly, *bes1-D* mutants exhibit

235 temperature-insensitive growth (Martins et al., 2017). Colder temperatures (4°C) also

236 induce expression of biosynthetic genes *DWF4* and *DET2* (Kim et al., 2019; Table 2).

237

238 **Cytokinin.** Another hormone intricately linked with plant development is cytokinin (CK).

239 One of the most common CKs is zeatin, which is synthesized through the tRNA or AMP

240 pathways (Kieber and Schaller 2018). CKs are involved in cell division and leaf

241   expansion, working synergistically or antagonistically with auxin during meristem

242   formation and maintenance (Hwang et al., 2012; Wybouw and De Rybel 2019).

243   Although majorly known as development-related hormones, CKs also mediate stress

244   responses (Cortleven et al., 2019).

245   In contrast to auxin and BR, *Arabidopsis* CK levels are repressed at high

246   temperature (Todorova et al., 2005; Table 1). This reduction occurs in various plant

247   organs, including apices, leaves and roots (Prerostova et al., 2020). The temperature

248   impact is conserved in rice, where CK levels and biosynthetic activity

249   (isopentenyltransferase, LONELY GUY, cytochrome P450 monooxygenase) are

250   inhibited (Wu et al., 2017). This leads to heat injury and reduced spikelets per panicle,

251   which is rescued by exogenous CK treatment (Wu et al., 2017). In agreement, heat-

252   tolerant rice (SY63) has temperature-resilient CK phenotypes (Wu et al., 2017), and

253   heat-resilient passion fruit (*Passiflora edulis* Sims) possesses higher CKs at high

254   temperature (Sobol et al., 2014). Heat-reduced CK abundance has also been shown in

255   *Pinus radiata*, resulting in decreased somatic embryo maturation and germination rates

256   (Moncaleán et al., 2018). The opposite trend is observed during cold incubation, as

257   *Arabidopsis* plants accumulated more CKs (Todorova et al., 2005; Jeon et al., 2010;

258   Table 2).

259

260   **Strigolactone.** Like the previous three hormones, plant developmental processes are

261   also regulated by strigolactones (SLs). SLs are biosynthesized through a multi-step

262   pathway in plastids and subsequent conversions in the cytoplasm (Seto and

263   Yamaguchi, 2014). These hormones regulate germination, shoot branching, secondary

264   thickening of stems and root development, while also mediating interactions with

265   symbiotic and parasitic organisms (Waters et al., 2017; Bürger and Chory, 2020; Wani

266   et al., 2020).

267   The impact of warm temperature on SLs initially came from investigations on

268   seed thermoinhibition. SL biosynthetic mutants show increased sensitivity to seed

269   thermoinhibition (Table 1), which is alleviated by exogenous SL (Toh et al., 2012).

270   Although SL levels were not quantified, one can speculate that biosynthesis may be

271   altered since SLs are derived from carotenoid precursors, like the warm-induced

272   abscisic acid (ABA) (Toh et al., 2008; Huot et al., 2017); increased metabolic flux to

273   ABA may occur at the expense of SL biosynthesis. On the other hand, cold exposure

274   leads to induced acropetal gradient of *RwMAX1* (SL biosynthetic gene) expression in

275   rose internodes, facilitating burst in quiescent medial and proximal buds (Djennane et

276   al., 2014; Tables 2).

277

278   **Gibberellin.** Gibberellins (GAs) are the largest class of hormones, which are derived

279   from diterpenoids (Hedden and Thomas 2012). They promote cell division, growth and

280   elongation, but are also crucial for germination and breaking dormancy (Davière and

281   Achard 2013). During phyB-PIF4-regulated thermomorphogenesis, auxin and BR

282   functionally crosstalks with GAs (Li et al., 2016). GAs also coordinately functions with

283   SLs in modulating germination at high temperatures (Toh et al., 2012).

284   In *Arabidopsis*, increased petiole and hypocotyl growth at elevated temperature

285   are related to GA biosynthetic gene *GA20ox1* induction (Table 1) through enhanced

286   PIF4 binding to its promoter (Ferrero et al., 2019). This is facilitated by PIF4-interacting

287   transcription factors Class I TEOSINTE BRANCHED 1, CYCLOIDEA, PCF 14 and 15

288   (TCP14 and TCP15); expectedly, *tcp14 tcp15* mutants show reduced temperature-

289   sensitivity (Ferrero et al., 2019). In contrast to shoots at 28°C-29°C, GA levels and

290   biosynthetic gene expression (*GA20ox1, GA20ox2, GA20ox3, GA3ox1, GA3ox2*) are

291   suppressed in seeds at 32°C (Toh et al., 2008). This is rescued in *aba2-2* mutants,

292   suggesting ABA involvement in antagonizing seed GA biosynthesis during heat stress

293   (Toh et al., 2008). Apart from *Arabidopsis*, GA levels are influenced by temperature in

294   other species. Carrizo citrange seedlings exhibit temperature-responsive growth

295   associated with higher biosynthetic gene transcripts and bioactive GA accumulation

296   (Vidal et al., 2003). Similarly, soybean hypocotyl elongation at warm temperature

297   corresponds to increased GA levels and biosynthetic gene expression (Bawa et al.,

298   2020). GA levels and related gene expression also increase in wheat, in relation to

299   temperature-dependent seed dormancy (Tuan et al., 2020).

300   In contrast, cold reduces bioactive GAs in *Arabidopsis* leaves by promoting *GA*

301   *2-oxidase* expression (Achard et al., 2008; Table 2). The opposite trend is observed in

302   seeds as certain biosynthetic genes (e.g. *GA3ox1*) are upregulated, resulting in higher

303   bioactive GA levels (Yamauchi et al., 2004). This may be mediated by phyB

304   thermosensing since *GA3ox1* expression is enhanced by active phytochrome

305   (Yamauchi et al., 2004). The cold temperature effect on GAs may be species-specific.

306   Rice microsporogenesis and fertility are impacted by lower temperatures, due to lower

307   bioactive GA levels and biosynthetic gene (*GA20ox3* and *GA3ox1*) expression in

308   developing anthers (Sakata et al., 2014). Exogenous GA treatment reverses this male

309   sterility, while GA pathway mutants (e.g. *sd1, d35, slr1-d, gid1*) are cold-hypersensitive

310   (Sakata et al., 2014). Lower GA levels at cooler temperatures have also been observed

311   in wheat, leading to temperature-sensitive leaf elongation (Pinthus et al., 1989). Still,

312   year-round meta-analyses of deciduous trees showed correlation between low

313   temperatures and higher GA levels, which regulate timing of senescence (Zhang et al.,

314   2020). Finally, bioactive GAs increased in tomatoes leading to enhance locule number

315   (Li et al., 2019).

316

317   **Abscisic acid.** Derived from carotenoids in plastids, abscisic acid (ABA) is crucial for

318   seed/bud dormancy, cell division/elongation, and stomatal movements (Nambara and

319   Marion-Poll 2005; Cutler et al., 2010). As previously mentioned, ABA regulates

320   germination in conjunction with GA (Toh et al., 2008), but also plays central roles during

321   stress responses (Cutler et al., 2010).

322   Consistent with its role during stress, ABA levels increase at both moderately

323   elevated temperatures and heat shock. In *Arabidopsis* seeds, elevated ABA levels are

324   observed at 32°C (Table 1), along with upregulated ABA biosynthetic genes

325   *ZEAXANTHIN EPOXIDASE* (*ABA1/ZEP*) and *9-CIS-EPOXYCAROTENOID*

326   *DIOXYGENASE* (*NCED2/5/9*) (Toh et al., 2008). At 30°C, ABA biosynthesis and

327   *NCED3* gene expression are also upregulated after *Pseudomonas syringae* pv. *tomato*

328   (*Pst*) DC3000 infection (Huot et al., 2017). ABA also mediates loss of autoimmunity and

329   effector-triggered immunity (ETI) at high temperature, since ABA-deficiency restores

330   nuclear accumulation of intracellular immune receptors Suppressor of npr1-1

331   constitutive1 (SNC1) and Resistance to Pseudomonas syringae4 (RPS4) at warm

332   temperatures (Mang et al., 2012). Even more extreme temperatures (at 45°C) lead to

333 increased ABA levels in leaves and apices, although a decrease is observed in roots

334 (Prerostova et al., 2020). Likewise, red-skinned grape ABA production also increases at

335 35°C (Gao-Takai et al., 2019), with a similar trend in cucumber (Li et al., 2014).

336   On the other end of the temperature spectrum, ABA is also elevated. Zhang et al.

337 (2020) observed an association between increased ABA and cooler temperatures in

338 deciduous trees (Table 2), to directly trigger/promote senescence. Similarly, increased

339 ABA synthesis was shown in rice seeds leading to delayed germination (Wang et al.,

340 2018).

341

342 **Salicylic acid.** While ABA is predominantly involved in abiotic stresses, salicylic acid

343 (SA) majorly regulates biotic stress responses (Klessig et al., 2018; Zhang and Li, 2019;

344 van Butselaar and Van den Ackerveken, 2020; Ding and Ding, 2020). The plant immune

345 system (Zhou and Zhang, 2020; Kim and Castroverde, 2020) induces SA biosynthesis

346 primarily through the isochorismate pathway, but SA can be produced via phenylalanine

347 ammonia lyase (Zhang and Li, 2019). SA triggers production of pathogenesis-related

348 proteins and volatile signals that promote resistance (Klessig et al., 2018).

349   Pathogen-induced SA biosynthesis is suppressed at elevated temperature, as

350 demonstrated in tobacco mosaic virus-infected tobacco (Malamy et al., 1992) and *Pst*

351 DC3000-infected *Arabidopsis* (Huot et al., 2017) (Table 1). High temperature

352 suppression of SA seemingly depends on reduced biosynthetic gene

353 *ISOCHORISMATE SYNTHASE 1* (*ICS1*) expression, as temperature-sensitive

354 susceptibility is abolished in *ics1* mutants (Huot et al., 2017). In agreement, deleting SA

355 accumulation genes *ENHANCED DISEASE SUSCEPTIBILITY 1* (*EDS1*) and

356 *PHYTOALEXIN-DEFICIENT 4* (*PAD4*) leads to equal susceptibility at ambient (22°C)

357 and elevated (28°C) temperatures (Wang et al., 2009). In addition to pathogen-induced

358 SA, constitutively high basal SA in autoimmune mutants are also downregulated at

359 28°C (Mang et al., 2012).

360   Cold conditions (4°C) induce SA accumulation and biosynthetic gene expression

361 (*ICS1, CBP60g* and *SARD1*), which are derepressed by loss of CALMODULIN-

362 BINDING TRANSCRIPTION ACTIVATOR (CAMTA) repressor activity (Kim et al., 2013;

363 Table 2). CAMTA repression depends on its N-terminal repression module (NRM)

364 independent of its calmodulin-binding domains (Kim et al., 2017). At cool temperatures

365 within normal growing range (16°C), SA levels are also higher and SA derepression

366 seemingly depends on ethylene (Li et al., 2020B) and/or the recently identified

367 bHLH059 thermoresponsive SA regulator (Bruessow et al., 2021). The involvement of

368 bHLH059 in modulating basal SA was discovered through a genome-wide association

369 study of natural *Arabidopsis* accessions (Bruessow et al., 2021).

370

371 **Jasmonic acid.** While SA regulates defenses against biotrophic/hemibiotrophic

372 pathogens and phloem-feeding insects, jasmonic acid (JA) activates immunity against

373 necrotrophs and chewing insects that cause significant mechanical damage (Zhang et

374 al., 2017; Howe et al., 2018). JA is derived from linolenic acid in plastids, and is the

375 major wounding-related hormone during biotic and abiotic stresses (Howe et al., 2018).

376 However, it also plays important functions in plant growth and development (Huang et

377 al., 2017).

17

378   In *Arabidopsis*, moderately elevated temperature at 29°C-30°C leads to higher

379   JA biosynthetic gene expression (Tables 1) after *Pst* DC3000 infection (Huot et al.,

380   2017) or wounding (Havko et al., 2020B). Higher heat shock temperatures (42°C-45°C)

381   also increase hormone levels (Prerostova et al., 2020). However, this trend is limited to

382   leaves as JA was unchanged in apices and strikingly decreased in roots (Prerostova et

383   al., 2020), pointing to tissue-specificity of the temperature effect or heat influence on JA

384   systemic transport. In agreement, mutations in JA biosynthetic genes compromise basal

385   thermotolerance, while exogenous methyl jasmonate (MeJA) treatment has a protective

386   effect (Clarke et al., 2009; Balfagón et al., 2019).

387   The trend is also species-specific as cotton plants exhibit reduced JA levels and

388   biosynthetic gene expression (*ACYL-COA OXIDASE 2* or *ACO2*) at high temperatures,

389   with night temperature being critical, leading to flower size and male fertility defects

390   (Khan et al., 2020). Exogenous MeJA rescued the pollen and anther phenotypes (Khan

391   et al., 2020). In tomato, JA supplementation also rescues heat-induced stigma exsertion

392   (Pan et al., 2019). After wounding, induction of both JA and JA-Ile in tomato leaves

393   increase at elevated temperature (Havko et al., 2020A).

394   Like warm temperatures, the effect of cooler temperatures on JA is species-

395   specific. For example, JA is reduced in maize (Pál et al., 2020) and deciduous trees

396   (Zhang et al., 2020; Table 2). The opposite trend is observed in tea plants (*Camellia*

397   *sinensis*) where wounding-induced JA is higher at 15°C vs. 25°C (Zhou et al., 2020).

398

399   **Ethylene.** Ethylene is a gaseous hormone derived from methionine through a multi-step

400   pathway involving SAM synthetase, ACC synthase and ACC oxidase (Dubois et al.,

401 2018). This hormone is involved in diverse processes, including abscission, senescence

402 and responses to environmental signals (Yang et al., 2015; Binder 2020). In terms of

403 pathogen defenses, ethylene typically functions synergistically with JA against

404 necrotrophs but antagonistically with SA against hemi/biotrophs (Bürger and Chory,

405 2020).

406 Studies have shown temperature-sensitivity or insensitivity of ethylene depending

407 on experimental conditions, species and tissues. At 45°C, ethylene levels were

408 unchanged in *Arabidopsis* apices and roots but were induced in leaves (Prerostova et

409 al., 2020; Table 1). At 27°C, Fei et al. (2017) observed a two-fold ethylene increase in

410 *Arabidopsis*. In tomato plants, mature pollen had elevated ethylene, along with

411 increased biosynthetic gene (*SlACS3/11*) expression (Jegadeesan et al., 2018).

412 Developmental stage-specificity also occurs in pea; heat induces ethylene in pre-

413 pollinated ovaries, but suppresses production in ovaries, stigma/style and petals after

414 fertilization (Savada et al., 2017).

415 In *Arabidopsis* wild-type and ethylene-overproducing plants, production and

416 biosynthetic gene expression decrease at cold temperatures (Shi et al., 2012; Table 3).

417 Ethylene seems to become limiting under colder day conditions, since production and

418 biosynthetic gene expression (*ACS2*) were altered, while exogenous treatment restored

419 ethylene-regulated responses (Bours et al., 2013). This negative regulation may be

420 linked to phyB-thermosensing, as phyB restricts ethylene biosynthesis (Bours et al.,

421 2013). In addition to transcription, post-translational regulation is also impacted, as

422 ethylene-dependent RCI1A can reduce hormone production by decreasing stability of

423 biosynthetic enzymes (Catalá et al., 2014).

424

The impact of temperature on hormone homeostasis and transport

Downstream of biosynthesis, hormone accumulation needs proper spatio-temporal maintenance, requiring mechanisms for metabolic homeostasis and transport. Although less characterized than biosynthesis, increasing evidence suggest that temperature also influences hormonal balance.

The first mechanism involves maintaining hormone levels through precursor modifications. In the auxin pathway, the thermomorphogenic regulator PIF4 not only enhances levels at high temperature by promoting biosynthesis, but it also negatively regulates precursor modifications. PIF4 directly represses transcription of *UGT76F1* encoding a UDP-glycosyltransferase that glucosylates the precursor indole-3-pyruvic acid (Chen et al., 2020).

The second mechanism involves temperature-regulated transport. At elevated temperature, roots counteract increased auxin intracellularly by promoting auxin efflux carrier PIN-FORMED2/PIN2 sorting to the plasma membrane from late endosomes via SORTING NEXIN1/SNX1 (Hanzawa et al., 2013). This enhances PIN2-dependent auxin efflux to shoots, increasing root elongation and gravitropism; mutating *SNX1* therefore abolishes warm-induced root phenotypes (Hanzawa et al., 2013). Another carrier PIN-LIKES 6 (PILS6), which negatively regulates nuclear auxin availability, is repressed by high temperature at the protein level, contributing to root phenotypes (Feraru et al., 2019). In contrast, cooler temperatures decrease auxin through repression of transport

446 genes (*PIN1/3/7*), leading to reduced meristem size/quantity (Zhu et al., 2015; Table 2).

447 This trend is reinforced by results showing reduced auxin and root growth via cold-

448 inhibited intracellular trafficking of auxin efflux carriers (Shibasaki et al., 2009). Apart

449 from auxin, temperature-regulated transport has been observed for GAs (Camut et al.,

450 2019) and CKs (Wu et al., 2017).

451

The impact of temperature on hormone receptors

453 To initiate appropriate signaling cascades, gene expression networks and physiological

454 responses, hormones need to bind their cognate receptors. The importance of hormone

455 perception is underscored by multi-level regulation by temperature (Tables 3-4).

456

457 **Protein stability.** Downstream of accumulation, warm temperatures increase auxin co-

458 receptor TIR1 levels due to stabilization by the molecular chaperone HSP90 (Wang et

459 al., 2016). Chemical inhibition of HSP90 abolishes TIR1 accumulation and

460 thermomorphogenic phenotypes (Wang et al., 2016). Similarly, JA responses are

461 enhanced at warm temperatures through increased HSP90-stabilization of JA receptor

462 COI1 (Havko et al., 2020A).

463

464 **Protein abundance.** Root-auxin to shoot-BR signaling during thermomorphogenic

465 hypocotyl elongation is reinforced systemically by BR-regulation of thermomorphogenic

466 root growth (Martins et al., 2017). High temperature negatively affects BR receptor BRI1

467 protein abundance to downregulate signaling, promoting primary root elongation but

468 decreasing meristem size/number (Martins et al., 2017). Remarkably, decreased BRI1

469   is reminiscent of heat-decreased abundance of FLS2 (another BAK1-interacting

470   receptor) involved in immunity (Janda et al., 2019).

471

472   **Protein localization.** Another target of temperature is receptor localization. SA-induced

473   nuclear localization of SA receptor NPR1 is intact at high temperature, as well as NPR1-

474   mediated disease protection (Huot et al., 2017). In agreement to the temperature

475   resilience of NPR1, SA-induced stomatal closure, which occurs via NPR1, is also intact

476   (Yan et al., 2019). However, colder temperatures enhance NPR1 nuclear accumulation

477   and greater interaction with HSF1A transcription factor (Olate et al., 2018).

478

479   **Transcript levels.** Temperature also impacts receptor gene transcription. Basal levels

480   of the SL receptor gene *DWARF 14* (*D14*) are higher during heat shock in tall fescue

481   plants, as well as *DWARF 3* (*D3*) encoding for the receptor-interacting F-box protein

482   (Hu et al., 2019). Because the SL receptor complex shares a similar F-box protein

483   module as auxin (Korasick et al., 2013; Lavy and Estelle 2016), SL signaling

484   potentiation by high temperature may also occur via HSP90-stabilization of client F-box

485   protein D3, as in the case of auxin and JA (Wang et al., 2016; Havko et al., 2020A).

486   Cold exposure may also increase SL-sensitivity since this induces *RwMAX2* (*D3*)

487   expression in roses (Djennane et al., 2014). Temperature-influenced receptor gene

488   expression is also observed with ethylene. High temperature enhances expression of

489   *Arabidopsis ETR1* (Fei et al., 2017) and tomato *SlETR3/SlCTR2* (Jegadeesan et al.,

490   2018). In grapefruit, ethylene receptor genes *ETR1/3* are induced by cold (Lado et al.,

491   2015).

492

The impact of temperature on hormone signaling and responses

Temperature regulation of biosynthesis, homeostasis and receptors eventually lead to temperature-repressed or temperature-activated signaling, gene responses and phenotypic outputs (Tables 3-4).

Auxin. In line with increased biosynthesis and TIR1 receptor stability at high temperatures, auxin-induced gene expression also increases in *Arabidopsis* resulting in hypocotyl elongation (Gray et al., 1998). Another route for high temperature-reinforcement is through the warm-induced monothiol glutaredoxin *AtGRXS17,* which potentiates auxin-responsiveness (Cheng et al., 2011). At low temperatures, temperature-sensitivity of auxin signaling appears to depend on CK since mutants in CK-response regulators *ARR1* and *ARR2* are less sensitive to cold-suppression of auxin-related phenotypes (Zhu et al., 2015). Nonetheless, cold-suppression of auxin may be species-dependent since auxin-sensitivity increases in tulip internodes (Rietveld et al., 2009).

Brassinosteroid. Downstream of BR biosynthesis and perception, BRASSINAZOLE RESISTANT 1 (BZR1) transcription factor interacts with PIF4 at high temperature to synergistically regulate common genes, including cell elongation regulators (Oh et al., 2012). Apart from PIF4 interaction, BZR1 accumulates in the nucleus at warm temperature to induce *PIF4* transcription (Ibañez et al., 2018); BZR1 nuclear accumulation/stabilization may be mediated by HSP90 interaction (Shigeta et al., 2015).

515   BZR1-regulated thermomorphogenesis requires localized thermosensing, as cotyledon

516   ablation reduces temperature-hypersensitivity of *bzr1-1D-OX* mutants (Bellstaedt et al.,

517   2019). Strikingly, PIF4 is a convergent hub for thermoregulated BR signaling; it is

518   phosphorylated and targeted for degradation by the BR signaling kinase

519   BRASSINOSTEROID-INSENSITIVE 2/BIN2 (Bernardo-García et al., 2014). Expectedly,

520   BR-mediated root inhibition is weaker at elevated temperature (Martins et al., 2017).

521   Cold regulation of BR signaling is exemplified during seed dormancy release.

522   BR-insensitive *bri1-5* mutants are less sensitive to cold-induced germination and does

523   not induce cold-responsive genes (Kim et al., 2019). Moreover, at lower temperatures,

524   BIN2 phosphorylates and targets *Arabidopsis* INDUCER OF CBF EXPRESSION1

525   (ICE1) for HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENE1 (HOS1)-

526   mediated degradation (Ye et al., 2019). BIN2 activity is repressed during early cold

527   incubation stages but is restored after ICE1-activated *CBF* expression; consistent with

528   this, *bin2-3 bil1 bil2* mutants have improved cold tolerance than wild-type plants (Ye et

529   al., 2019). Finally, BR signaling contributes to cold-regulated phenylpropanoid

530   metabolism since mutations in BR-responsive transcription factor BRASSINOSTEROID

531   ENHANCED EXPRESSION1 (BEE1) had altered anthocyanin regulatory genes

532   (Petridis et al., 2016).

533

534   **Cytokinin.** Majority of heat-induced gene expression is modulated by CK in

535   *Arabidopsis*, thus *ahk2 ahk3* signaling mutants and *CYTOKININ OXIDASE 2 (CKX2)*

536   over-expressing plants have decreased thermomorphogenesis (Cerný et al., 2014). As

537   demonstrated in pineapple, higher night temperature leads to increased CK-related

538   nitrate reductase activity (Freschi et al., 2009).

539   During cold incubation, *Arabidopsis* plants accumulate more CK-related

540   transcripts (Todorova et al., 2005; Jeon et al., 2010). As expected, *arr1-3 arr12-1* CK

541   signaling mutants exhibit less temperature-sensitive root growth and meristem cell

542   numbers (Zhu et al., 2015). Because lower temperatures had less impact on this

543   mutant's auxin and *PIN1/3* levels, this suggested that CK mediates low temperature-

544   suppression of auxin to inhibit root growth (Zhu et al., 2015). CK also modulates

545   freezing tolerance since *ahk2 ahk3*, *ahk3 ahk4* and *arr7* signaling mutants exhibit

546   increased tolerance (Jeon et al., 2010), while mutants in CYTOKININ RESPONSE

547   FACTOR 4 (CRF4) show greater sensitivity (Zwack et al., 2016). In agreement,

548   *CRF2/3/4* are induced by low temperatures (Zwack et al., 2016; Jeon et al., 2016).

549

550   **Strigolactone.** Changing temperatures leads to SL-dependent developmental and

551   morphological changes in pea and *Arabidopsis*, including altered shoot biomass, leaf

552   numbers and leaf area (Cooper et al., 2018).

553

554   **Gibberellin.** During thermomorphogenesis, there is direct physical interaction between

555   PIFs and GA regulatory repressor DELLAs (Li et al., 2016). GA signaling is also

556   impacted by cold, as exemplified by increased nuclear DELLA accumulation to restrain

557   *Arabidopsis* growth (Achard et al., 2008). Expectedly, GA pathway mutants (e.g. *sd1*,

558   *d35*, *slr1-d* and *gid1*) are cold-hypersensitive (Sakata et al., 2014). In terms of

559   temperature-regulated germination, a possible mechanism is through the dormancy

560　regulator *DELAY OF GERMINATION 1/DOG1* (Graeber et al., 2014). In contrast, low-

561　temperature (15°C) treatment leads to slower germination in rice, accompanied by GA

562　deactivation and reduced signaling (Wang et al., 2018).

563

564　**Abscisic acid.** In rice, ABA-induced gene expression is upregulated during heat stress

565　(Liu et al., 2019) and Xa7-activated immunity against *Xanthomonas oryzae* (Cohen et

566　al., 2017). Xa7-mediated resistance is atypical of other immune responses, since it is

567　enhanced rather than inhibited by warm temperatures (Cohen et al., 2017). Apart from

568　its role in immunity, heat tolerance is also improved with exogenous ABA by decreasing

569　pollen sterility and leaf rolling (Rezaul et al., 2019; Li et al., 2020). Strikingly, ABA-

570　associated gene expression decreases in wheat and *Vellozia* species in relation to high

571　temperature-dependent seed dormancy, indicating species- and/or tissue-specificity in

572　temperature regulation of ABA (Vieira et al., 2017; Tuan et al., 2020).

573　　　*Arabidopsis* ABA signaling may also be integrated with cold signaling via 2R3-

574　type MYB transcription factor MYB96 to promote freezing tolerance (Lee and Seo

575　2015). MYB96 activates *HEPTAHELICAL PROTEIN* genes encoding interacting

576　proteins of ICE and CAMTA3 – transcriptional activators of the cold-CBF pathway (Lee

577　and Seo 2015). The ABA requirement for cold/freezing tolerance also extends to

578　bryophytes, as demonstrated in *Physcomitrium patens* (Bhyan et al., 2012; Tan et al.,

579　2017). In contrast, ABA signaling is thought to be repressed by dormancy-regulating

580　DOG1 during cold-induced *Arabidopsis* germination (Dekkers et al., 2016).

581

582   **Salicylic acid.** Downstream of its accumulation, SA-responsive gene expression is

583   differentially affected by temperature, resulting in temperature-downregulated (e.g.

584   *PATHOGENESIS-RELATED 1/PR1, ICS1*) and temperature-resilient gene groups (e.g.

585   *NPR1*) (Huot et al., 2017). SA-induced *PR1* depends on phytochromes (Genoud et al.,

586   2002), so it is intriguing to speculate that temperature-downregulated SA genes are

587   linked to phyB-thermosensor inactivation at elevated temperature. However, constitutive

588   phyB activation does not rescue temperature-sensitive immune phenotypes (Huot et al.,

589   2017).

590   Similarly, basal expression of the SA marker gene *PR1* is lower in autoimmune

591   *snc1* mutants at 28°C (vs. 22°C) leading to abolished growth suppression (Zhu et al.,

592   2010). Temperature-sensitive autoimmunity is rescued in *snc1 pif4* (Gangappa et al.,

593   2017), *snc1 cop1* (Gangappa and Vinod Kumar 2018) and *snc1 det1* mutants

594   (Gangappa and Vinod Kumar 2018), suggesting involvement of phyB-PIF4

595   thermosensing in *Arabidopsis* autoimmunity. Similarly, *snc1 siz1* mutants partially

596   rescue temperature-sensitive growth, *PR1* gene expression and bacterial resistance,

597   implicating SUMOylation in thermoregulated autoimmunity (Hammoudi et al., 2018). SA

598   signaling downregulation also occurs even in resistance enhanced by high temperature.

599   Xa7-mediated rice immunity is more effective at warmer temperatures, but the SA-

600   responsive transcriptome is still downregulated (Cohen et al., 2017). At low

601   temperatures, increased SA-mediated immunity has been demonstrated in various plant

602   species (Koeda et al., 2011; Pál et al., 2020).

603

604   **Jasmonic acid.** In *Arabidopsis*, moderately elevated temperature (29°C-30°C) leads to

605   induced JA signaling. This abrogates typical thermomorphogenesis and leaf cooling,

606   although herbivory still increased because of greater insect metabolism (Havko et al.,

607   2020A/B). Higher temperatures (42°C-45°C) also result in increased JA-associated

608   gene expression (Balfagón et al., 2019). In agreement, mutations in JA signaling genes

609   compromise basal thermotolerance (Clarke et al., 2009). Heat shock also induces JA-

610   responsive gene expression in *Aquilaria sinensis*, resulting in higher accumulation of

611   sesquiterpenes (Xu et al., 2016). Expectedly, JA inhibition by nordihydroguaiaretic acid

612   decreases sesquiterpene abundance, while exogenous MeJA promotes sesquiterpene

613   production (Xu et al., 2016).

614   On the other hand, low temperatures promote interaction between the cold

615   regulator CsICE2 with JA signaling repressor CsJAZ2 in *Camellia*, derepressing

616   CsMYC2a to direct JA-associated gene expression (Zhou et al., 2020). This is further

617   supported in *Arabidopsis* at even colder temperatures, showing a positive role for JA

618   during freezing tolerance; cold induces JA and relieves JAZ repression of ICE1/2

619   transcription factors (Hu et al., 2013).

620

621   **Ethylene.** High temperatures influence components of ethylene signaling. At 27°C,

622   *EIN2* gene expression is downregulated in *Arabidopsis* (Fei et al., 2017). At 37°C, there

623   is enhanced interaction between ethylene response factors ERF95 and ERF97, allowing

624   them to regulate a common transcriptional regulon, including the heat shock factor

625   *HSFA2* gene (Huang et al., 2020). In agreement, higher-order *erf* mutants exhibit

626   reduced thermotolerance (Huang et al., 2020). ERF95 and ERF97 are directly regulated

627   by EIN3, which is stabilized by elevated temperature due to degradation of negative

628   regulators EBF1/2 via SIDR1 (Hao et al., 2021). However, the effect may depend on the

629   phenotypic output, as moderately elevated temperature (28°C) suppresses ethylene-

630   triggered developmental processes like exaggerated hook formation (Jin et al., 2018).

631   At low temperature, signaling downregulation may be necessary, as ethylene

632   negatively affects freezing tolerance (Shi et al., 2012). Transcription factor EIN3

633   represses cold-induced *CBF* gene expression, modulating tolerance to extremely low

634   temperatures (Shi et al., 2012). Remarkably, this negative impact is not universal.

635   Soybean has enhanced ethylene signaling at low temperatures, facilitating EIN3-

636   mediated repression of the cold-CBF pathway, possibly explaining cold susceptibility of

637   this species (Robison et al., 2019). Apple ethylene signaling is also enhanced by low

638   temperature (Wang et al., 2021).

639

640 Current outlook: Integrating how temperature regulates plant

641 hormone pathways

642   It is important and imperative to have a good theoretical framework of how changing

643   climatic factors, like temperature, influence plant physiological processes. Excellent

644   reviews have directly discussed the impacts of temperature on plant immunity and

645   disease susceptibility (Velasquez et al., 2018; Cheng et al., 2019; Cohen and Leach

646   2020; Desaint et al., 2020; Kim et al., 2021), plant growth and development (Quint et al.,

647   2016; Casal and Balasubramanian 2019; Lippmann et al., 2019; Dai Vu et al., 2019;

648   Ding et al., 2020), photosynthesis (Way and Yamori 2014) and plant stress responses

649   (Ding et al., 2020). Because hormones govern diverse physiological processes –

650   globally influencing signaling networks and gene regulatory landscapes – we highlighted

651   general themes and overarching principles (when applicable) in the regulation of

652   hormone pathways by both high and low temperatures (Figures 1-2).

653   Temperature affects various aspects of plant hormone pathways. There can be

654   positive, negative or even neutral influences on biosynthesis, modification, transport,

655   receptor and sensitivity, signaling components, transcription factors, expression profiles

656   and phenotypic output. These temperature perturbations include changing

657   genomic/chromatin organization, differential transcriptional regulation, post-

658   transcriptional changes, post-translational modifications, protein degradation, protein-

659   protein interactions and metabolite levels.

660   Depending on the hormone, some regulatory mechanisms could be linked to

661   known temperature-sensing mechanisms. For example, temperature-regulated auxin,

662   BR and GA biosynthesis have been linked to the known phyB-PIF temperature-sensing

663   pathway (Franklin et al., 2011; Sun et al., 2012; Ibañez et al., 2018; Martínez et al.,

664   2018; Ferrero et al., 2019), while the mechanistic bases of other temperature-regulated

665   hormones remain elusive. What is becoming clear is that temperature affects hormone

666   levels and biosynthetic gene expression, whether they are derived from amino acids

667   (auxin, SA, ethylene), lipids (BR, JA), nucleotides (CK) or specialized metabolites (SL,

668   GA, ABA). Plant hormone homeostasis and transport are also influenced by

669   temperature through precursor modifications, altered intracellular trafficking and

670   perturbed whole-plant transport. In terms of receptors, temperature intercepts transcript

671   levels, protein abundance, stability and/or localization. Finally, temperature-regulated

672   hormone signaling typically depends on transcriptional, post-transcriptional and post-

673   translational mechanisms, some of which have been directly connected to canonical

674   high temperature-phyB-PIF signaling (Jung et al., 2016; Legris et al., 2016) and/or low

675   temperature-ICE-CBF signaling (Jiang et al., 2020).

676   Remarkably, the temperature impact on biosynthesis, homeostasis, receptors

677   and signaling may be uncoupled. For example, during temperature-dependent growth,

678   auxin biosynthesis/homeostasis are mediated by phyB-PIF (Franklin et al., 2011; Sun et

679   al., 2012); however, receptor stability relies on HSP90 (Wang et al., 2016). During

680   temperature-dependent immunity, SA receptor NPR1 retains similar protein levels at

681   high temperature, even though a significant number of SA-responsive genes are

682   downregulated (Huot et al., 2017). It is possible that a convergent upstream regulator

683   then controls and integrates these pathways, but this remains to be elucidated.

684

685   # Future perspectives

686   Hormones are intricately linked to one another (Altmann et al., 2020), so we provided an

687   encyclopedic survey of recent temperature studies on hormone production and

688   signaling (Tables 1-4). Nevertheless, major knowledge gaps and challenges remain,

689   providing opportunities for strategically planned investigations in the future.

690   First, although some hormone pathways have now been directly linked to well-

691   characterized thermosensing mechanisms (Figure 1), like the auxin and BR pathways

692   with the phyB-PIF module (Franklin et al., 2011; Sun et al., 2012; Ibañez et al., 2018;

693   Martínez et al., 2018), the direct link of other thermoregulated hormone pathways to

694   temperature sensing remain unclear, like the SA and JA pathways (Huot et al., 2017;

695 Velasquez et al., 2018). Targeted genetic screens to isolate temperature-insensitive

696 mutants (Zhao et al., 2020) or genome-wide association studies of intra-species

697 diversity (Lu et al., 2021) can provide clues into novel plant temperature sensors that

698 connect to biosynthesis and signaling of all major plant hormones.

699   Second, our concept of high and/or low temperature ranges and their

700 downstream impacts on hormone pathways can be species-specific (Tables 1-4). One

701 temperature may be elevated for one species, while it could be ambient or even low for

702 another (e.g. 28°C for *Arabidopsis* vs. tomato or rice). Therefore, we need to expand

703 beyond our reliance on a limited number of model organisms and dominant

704 accessions/varieties. The availability of pan-genomes and kingdom-wide genome

705 sequences (Zhao et al., 2018; Liu et al., 2020), together with advances in genome

706 editing (Zhu et al., 2020), can be leveraged toward more mechanistic studies on a

707 diversity of plant species.

708   Third, overarching trends on the impact of a specific temperature on plant

709 hormone levels and downstream signaling may be challenging to postulate. These can

710 sometimes depend on the stage of development, tissue of interest, other confounding

711 environmental factors and even the phenotypic output being measured. Temperature

712 studies need to account for the diversity in thermoregulated phenotypes, from

713 developmental outputs to defense responses (Velasquez et al., 2018; Lippman et al.,

714 2019). In the future, comprehensive spatial coverage (in various organs) in hormone

715 quantification could be facilitated across virtually all plant species (Novák et al., 2017).

716 Furthermore, untargeted metabolomic profiling can include not just hormones but their

717 global metabolite landscape (Hirai and Shiraishi, 2018). Plant hormone signaling and

718   responses to changing temperatures can be integrated by coupling transcriptome

719   analyses, genome-wide transcription factor binding datasets (ChIP/DAP-Seq) and

720   proteomic technologies (O'Malley et al., 2016; One Thousand Plant Transcriptomes

721   Initiative, 2019; McWhite et al., 2020; Mergner et al., 2020). Remarkably, hormone

722   pathways (from biosynthesis to signaling) can even be illuminated by high-resolution

723   single-cell technologies, so as not to overlook cell-cell dynamics missed by whole-plant

724   analyses (McFaline-Figueroa et al., 2020). Altogether, these multi-omic approaches will

725   hopefully enable the elucidation of an extensive and sweeping regulome – "the whole

726   set of regulatory components in a cell, including regulatory elements, genes, mRNAs,

727   proteins and metabolites" (Townsley et al., 2020) – of various plant species in response

728   to high and/or low temperatures.

729

Conclusion

730

731   One of the grand challenges of the plant sciences is to successfully implement

732   resilience engineering technologies for cultivated crops and to effectively execute

733   climate mitigation strategies for wild plant species in natural ecosystems. Therefore, a

734   fundamental understanding of temperature-vulnerable and/or temperature-activated

735   components of plant hormone pathways offer a molecular roadmap to these ambitious

736   long-term goals. Because plant hormone crosstalk is central during the temperature-

737   regulation of development and defense, translational studies should take this systems-

738   wide plant hormonal landscape into account to fine-tune traits of interest without

739   adversely affecting "collateral" signaling networks. By carefully uncovering the molecular

740   mechanisms underpinning how changing temperatures regulate plant hormone

741 pathways, we can leverage these basic discoveries to hopefully design climate-smart

742 plants for future societies and environments.

743

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751

752 Authors' contributions:

753 C.D.M.C conceptualized the review. D.D. performed the initial literature search and

754 wrote initial section drafts. C.D.M.C. synthesized the literature sources and wrote the

755 final version of the paper.

756

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1 Tables

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3 **Table 1. Regulation of plant hormone biosynthesis and accumulation at high temperatures.**

Plant Hormone	Species	Temperature Comparison	Observation at High Temperature	Reference
Auxin	*Arabidopsis thaliana*	20°C vs. 29°C	Increased auxin levels leading to increased hypocotyl elongation	Gray et al., 1998
	A. thaliana	20°C vs. 31°C-33°C	Decreased auxin levels and biosynthetic gene expression in developing anthers	Sakata et al., 2010
	Barley	20°C vs. 31°C-33°C	Decreased auxin levels and biosynthetic gene expression in developing anthers	Sakata et al., 2010
	A. thaliana	20°C vs. 28°C	Increased auxin levels and biosynthetic gene expression due to PIF4 activation	Franklin et al., 2011
	Barley	20°C/15°C vs. 30°C/25°C	Decreased auxin levels leading to suppression of DNA proliferation	Oshino et al., 2011
	A. thaliana	22°C vs. 29°C	Increased auxin biosynthetic gene expression and hypocotyl elongation due to PIF4 activation	Sun et al., 2012
	A. thaliana	23°C vs. 29°C	Roots promote shootward auxin efflux by enhancing PIN2 sorting to the plasma membrane	Hanzawa et al., 2013
	Cotton	28°-35°C/20°-28°C day/night vs. 35°-39°C/29°-31°C day/night	Increased auxin levels in late-stage anthers	Min et al., 2014
	Lettuce	20°C vs. 30°C	Increased expression of genes involved in auxin biosynthesis and tryptophan metabolism	Hao et al., 2018
	A. thaliana	22°C vs. 28°C	Decreased auxin levels in response to ethylene	Jin et al., 2018
	Rice	30°C vs. 40°C	Increased auxin levels in wild-type but decreased levels in the mutant High temperature susceptible (HTS)	Zhang et al., 2018
	A. thaliana	22°C vs. 27°C	Increased auxin biosynthetic gene expression due to increased histone deacetylation by HDA9	van der Woude et al., 2019
	A. thaliana	20°C vs. 28°C	Increased mobile auxin from cotyledon to hypocotyl	Bellstaedt et al., 2019
	A. thaliana	21°C vs. 29°C	Increased nuclear availability of auxin due to decreased PILS6 protein levels	Feraru et al., 2019
	A. thaliana	22°C vs. 28°C	Increased auxin levels due to negative regulation of UGT76F1 by PIF4	Chen et al., 2020
	A. thaliana	20°C vs. 28°C	Increased auxin levels and hypocotyl elongation due to PIF4 in the epidermis but not vasculature	Kim et al., 2020
	Apple	23°C vs. 28°C and 33°C	Increased auxin biosynthetic gene expression	Song et al., 2020

	Soybean	25°C vs. 35°C	Increased auxin (IPA) levels and biosynthetic gene expression leading to increased hypocotyl elongation	Bawa et al., 2020
	A. thaliana	20°C vs. 45°C	Decreased auxin levels in roots but unchanged in apices and leaves	Prerostova et al., 2020
Brassinosteroid (BR)	*A. thaliana*	20°C vs. 28°C	BR biosynthesis is required for temperature-sensitive hypocotyl elongation	Oh et al., 2012
	A. thaliana	20°C vs. 28°C	BR biosynthetic genes DWF7/STE1/BUL1 and ROT3/CYP90C are required for temperature-sensitive hypocotyl elongation	Ibañez et al., 2018
	A. thaliana	22°C vs. 28°C	Increased BR biosynthetic gene expression due to PIF4 activation and decreased BES1 homodimerization	Martínez et al., 2018
Cytokinin (CK)	*A. thaliana*	26°C vs. 38°C	Decreased CK levels	Todorova et al., 2005
	Pineapple	28/15°C vs. 28/28°C	Increased CK levels and shoot NR activity	Freschi et al., 2009
	Passion fruit	22/16 °C vs. 34/28 °C	Increased CK levels	Sobol et al., 2014
	Rice	31.9/27.2 vs. 33.5/31.9°C, 36.1/26.7°C and 38.3/31.5°C	Decreased CK levels in panicles due to inhibition of CK biosynthetic enzymes, CK transportation rate	Wu et al., 2017
	Pinus radiata	23°C vs. 28°C	Decreased CK levels leading to lower somatic embryo numbers	Moncaleán et al., 2018
	A. thaliana	20°C vs. 45°C	Decreased CK levels in leaves, apices and roots	Prerostova et al., 2020
Strigolactone (SL)	*A. thaliana*	24°C vs. 32°C	SL biosynthesis is required for decreased sensitivity to seed thermoinhibition.	Toh et al., 2012
Gibberellin (GA)	Carrizo citrange	17/12 °C vs. 32/27 °C	Increased bioactive GA(1) and GA biosynthetic gene *CcGA20ox1* expression and in the shoot	Vidal et al., 2003
	A. thaliana	24°C vs. 32°C	Decreased bioactive GA levels through suppression of *GA 20-oxidase* and *GA 3-oxidase* gene expression	Toh et al., 2008
	A. thaliana	23°C vs. 29°C	Increased GA biosynthetic gene *GA20ox1* expression due to enhanced PIF4 and TCP14/15 binding	Ferrero et al., 2019
	A. thaliana	20°C vs. 28°C	Enhanced root-to-shoot translocation of GA12 (precursor of bioactive GAs)	Camut et al., 2019
	Soybean	25°C vs. 35°C	Increased GA(3) and GA(7) levels, along with increased GA biosynthetic gene expression leading to increased hypocotyl elongation	Bawa et al., 2020
	Wheat	13°C vs. 28°C	Increased bioactive GA levels and biosynthetic gene expression	Tuan et al., 2020
Abscisic acid (ABA)	Lettuce	20°C vs. 35°C	Increased ABA levels and biosynthetic gene expression	Argyris et al., 2008
	A. thaliana	24°C vs. 32°C	Increased ABA levels and biosynthetic gene expression in seeds	Toh et al., 2008
	A. thaliana	22°C vs. 28°C	ABA biosynthesis leads to loss of NLR accumulation in the nucleus	Mang et al., 2012
	Cucumber	25°C vs. 40°C	Increased ABA level and transport	Li et al., 2014
	A. thaliana	23°C vs. 30°C	Increased ABA levels and biosynthetic gene expression after *Pst* DC3000 infection	Huot et al., 2017
	Vellozia sp.	25°C vs. 30°C	Decreased ABA level during imbibition	Vieira et al., 2017
	Rice	30-34°C/24°C vs. 39-41°C/30°C	ABA biosynthesis is required to reduce pollen sterility during heat stress	Rezaul et al., 2019
	Grape	25°C vs. 35°C	Increased ABA levels	Gao-Takai et al., 2019
	Rice	28°C vs. 38°C	Increased ABA levels and biosynthetic gene expression	Liu et al., 2019

	A. thaliana	20°C vs. 45°C	Increased ABA levels in leaves and apices, but decreased in roots	Prerostova et al., 2020
	Wheat	13°C vs. 28°C	Decreased ABA levels and biosynthetic gene expression	Tuan et al., 2020
Salicylic acid (SA)	Tobacco	20°C vs. 45°C	Abolished SA levels in the ETI response to avirulent tobacco mosaic virus	Malamy et al., 1992
	A. thaliana	22°C vs. 28°C	SA biosynthetic genes *EDS1* and *PAD4* are required for immunity at high temperature	Wang et al., 2009
	A. thaliana	22°C vs. 28°C	Decreased basal SA levels and SA biosynthetic gene *ICS1* expression in wild-type and autoimmune mutants	Mang et al., 2012
	A. thaliana	23°C vs. 30°C	Decreased SA levels and *ICS1* expression in response to *Pst* DC3000 leading to increased disease susceptibility	Huot et al., 2017
Jasmonic acid (JA)	*A. thaliana*	22°C vs. 38°C	JA biosynthetic genes are required for basal thermotolerance of an autoimmune mutant	Clarke et al., 2009
	Aquilaria sinensis (heartwood tree)	25°C vs. 50°C	Increased JA levels leading to increased sesquiterpene accumulation	Xu et al., 2016
	A. thaliana	23°C vs. 30°C	Increased JA biosynthetic gene expression in response to *Pst* DC3000	Huot et al., 2017
	A. thaliana	23°C vs. 42°C	Increased JA and JA-Ile levels	Balfagón et al., 2019
	Tomato	25°C/20°C vs. 35°C/30°C	Decreased JA and JA-Ile levels in stamens, and decreased JA levels in pistils leading to stigma exsertion	Pan et al., 2019
	Tomato	28°C/18°C vs. 38°C/28°C	Increased JA and JA-Ile levels after wounding	Havko et al., 2020A
	A. thaliana	22°C vs. 29°C	Increased JA levels but decreased JA-Ile in response to wounding	Havko et al., 2020B
	A. thaliana	20°C vs. 45°C	Increased JA levels in leaves, unchanged JA levels in apices, and decreased in roots	Prerostova et al., 2020
	Cotton	28-34°C day/22-27°C night vs. 39-41°C day/22-27°C night and 28-34 °C day/29-31 °C night	Decreased JA levels leading to reduced flower size, decreased filament length and increased pollen sterility	Khan et al., 2020
Ethylene	Lettuce	20°C vs. 35°C	Decreased ethylene biosynthetic gene expression	Argyris et al., 2008
	Pea	19°C /17°C vs. 33-35°C /17°C	Increased ethylene level in pre-pollinated ovaries but decreased levels in ovaries, stigma, style and petals after pollination	Savada et al., 2017
	A. thaliana	22°C vs. 27°C	Increased ethylene level	Fei et al., 2017
	Tomato	25°C vs. 45°C	Increased ethylene level and biosynthetic gene expression	Jegadeesan et al., 2018
	A. thaliana	20°C vs. 45°C	Unchanged ethylene levels in apices and roots, but induced in leaves	Prerostova et al., 2020

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Table 2. Regulation of plant hormone biosynthesis and accumulation at low temperatures.

Plant Hormone	Species	Temperature Comparison	Observation at Low Temperature	Reference
Auxin	*Arabidopsis thaliana*	22°C vs. 4°C	Decreased basipetal auxin transport and PIN3 intracellular cycling	Shibasaki et al., 2009
	A. thaliana	22°C vs. 16°C	Decreased auxin levels, auxin biosynthetic gene expression and PIN1/3 levels due to ARR1/2	Zhu et al., 2015
Brassinosteroid (BR)	*A. thaliana*	22°C vs. 4°C	Increased BR biosynthetic gene *DWF4* and *DET2* expression by cold stratification	Kim et al., 2019
Cytokinin (CK)	*A. thaliana*	26°C vs. 4°C	Increased CK levels	Todorova et al., 2005
	A. thaliana	23°C vs. 1°C	Unchanged CK levels at 4h	Jeon et al., 2010
Strigolactone (SL)	Rose	20°C vs. 5°C	Induced acropetal gradient of SL biosynthetic gene *RwMAX1* expression leading to increased quiescent medial and proximal buds	Djennane et al., 2014
Gibberellin (GA)	Wheat	25°C vs. 10°C	Decreased endogenous GA(1) levels leading to temperature-dependent leaf elongation	Pinthus et al., 1989
	A. thaliana	22°C vs. 4°C	Increased bioactive GA levels and biosynthetic gene *GA3ox1* expression in seeds	Yamauchi et al., 2004
	A. thaliana	22°C vs. 4°C	Decreased bioactive GA levels due to increased *GA 2-oxidase* gene expression in leaves	Achard et al., 2008
	Rice	27°C-19.4°C (fluctuating) vs. 19°C	Decreased bioactive GA(4) and GA(7) levels and biosynthetic gene *GA20ox3* and *GA3ox1* expression	Sakata et al., 2014
	Rice	30°C vs. 15°C	Decreased GA levels leading to delayed germination	Wang et al., 2018
	Tomato	20°C vs. 10°C and 15°C	Increased bioactive GA levels due to downregulated *SlGA2ox* gene expression	Li et al., 2019
	Salix babylonica, Ginkgo biloba, Acer mono, Cotinus coggygria	Year-round temperature comparison	Increased GA(3) and GA(4) levels that regulates timing of senescence	Zhang et al., 2020
Abscisic acid (ABA)	Rice	30°C vs. 15°C	Increased ABA levels leading to delayed germination	Wang et al., 2018
	Grape	25°C vs. 15°C	Decreased ABA levels	Gao-Takai et al., 2019
	Salix babylonica, Ginkgo biloba, Acer mono, Cotinus coggygria	Year-round temperature comparison	Increased ABA levels in leaves to directly trigger senescence	Zhang et al., 2020
Salicylic acid (SA)	*A. thaliana*	22°C vs. 4°C	Increased SA levels due to loss of *ICS1* gene repression by CAMTAs	Kim et al., 2013
	A. thaliana	22°C vs. 4°C	Increased SA levels due to loss of repression via the CAMTA N-terminal repression module	Kim et al., 2017
	A. thaliana	22-23°C vs. 4°C	Increased SA biosynthetic gene expression and decreased SA catabolic gene expression	Wu et al., 2019
	A. thaliana	22°C vs. 16°C	Increased basal SA levels due to decreased inhibition by ethylene	Li et al., 2020B
	Maize	22°C vs. 15°C and 5°C	Increased SA levels	Pál et al., 2020

	A. thaliana	22°C vs. 16°C	Increased, decreased or unchanged basal SA levels depending on accessions – not dependent on ICS1/PBS3 but mediated by bHLH059	Bruessow et al., 2021
Jasmonic acid (JA)	*A. thaliana*	22°C vs. 4°C	Increased JA levels	Hu et al., 2013
	Artemisia annua	25°C vs. -7°C	Increased JA levels and biosynthetic gene expression	Liu et al., 2017
	Maize	22°C vs. 15°C and 5°C	Decreased JA levels in leaves but increased in roots	Pál et al., 2020
	Tea	25°C vs. 15°C	Increased JA levels leading to enhanced indole biosynthesis	Zhou et al., 2020
	Salix babylonica, Ginkgo biloba, Acer mono, Cotinus coggygria	Year-round temperature comparison	Decreased MeJA levels	Zhang et al., 2020
Ethylene	*A. thaliana*	22°C vs. 4°C	Decreased ethylene levels in wild-type and *eto1* mutant	Shi et al., 2012
	A. thaliana	22°C day/12°C night vs. 12°C day/22°C night	Decreased ethylene levels and biosynthetic gene expression in petioles at cooler photoperiods	Bours et al., 2013
	A. thaliana	20°C vs. 4°C	Decreased stability of the biosynthetic enzyme ACS leading to restrained ethylene biosynthesis	Catalá et al., 2014
	Grapefruit	20°C vs. 8-10°C	Very low ethylene levels and biosynthetic gene expression	Lado et al., 2015
	Apple	24°C vs. -10°C	Increased ethylene levels and biosynthetic gene expression	Wang et al., 2021

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7 **Table 3. Regulation of plant hormone signaling at high temperatures.**

| Plant Hormone	Species	Temperature Comparison	Observation at High Temperature	Reference
Auxin	*Arabidopsis thaliana*	20°C vs. 29°C	Increased auxin-inducible gene (*IAA4*) expression	Gray et al., 1998
	Tobacco	32°C vs. 38°C	Decreased auxin-responsive gene expression in protoplasts	Dong et al., 2007
	A. thaliana	20°C vs. 28°C	Increased auxin signaling through the temperature-induced monothiol glutaredoxin AtGRXS17	Cheng et al., 2011
	A. thaliana	20°C vs. 28°C	Increased auxin-inducible gene (*SAUR*) expression	Franklin et al., 2011
	A. thaliana	22°C vs. 29°C	Increased accumulation of the auxin TIR1 receptor due to HSP90 stabilization	Wang et al., 2016
	Cotton	28–35°C/20–28°C day/night vs. 39 ± 2°C/29 ± 2°C day/night	Increased auxin response factor *ARF10* and *ARF17* gene expression in high temperature-tolerant 84021 strain but decreased in high temperature-sensitive strain in H05.	Ding et al., 2017
	A. thaliana	22°C vs. 28°C	Decreased auxin-induced gene expression in response to ethylene	Jin et al., 2018
Brassinosteroid (BR)	*A. thaliana*	20°C vs. 28°C	Increased BR signaling and response through the synergistic interaction of BZR1 and PIF4	Oh et al., 2012
	A. thaliana	21°C vs. 26°C	Decreased BR receptor BRI1 protein levels and BR metabolism genes (*BAS1/CYP72B1* and *SOB7/CYP72C1*), but increased BR response genes (*CPD* and *STE1/DWF7*)	Martins et al., 2017
	A. thaliana	20°C vs. 28°C	Increased BZR1 accumulation in the nucleus to promote *PIF4* gene expression	Ibañez et al., 2018
	A. thaliana	20°C vs. 28°C	Increased BR signaling and hypocotyl elongation by mobile auxin transport and BZR1 activation	Bellstaedt et al., 2019
Cytokinin (CK)	*A. thaliana*	21°C vs. 35°C	AHK2/3 enhances while CKX2 reduces temperature-sensitive hypocotyl elongation	Cerný et al., 2014
Strigolactone (SL)	*A. thaliana*	24°C vs. 32°C	SL signaling is required for decreased sensitivity to seed thermoinhibition.	Toh et al., 2012
	Tall fescue	22/18°C vs. 35/30°C	Increased basal levels of SL receptor D14 and increased SL-induced *D3* gene expression	Hu et al., 2019
Gibberellin (GA)	Carrizo citrange	17/12 °C vs. 32/27 °C	Increased GA-mediated seedling elongation	Vidal et al., 2003
	A. thaliana	23°C vs. 29°C	Increased GA-mediated petiole and hypocotyl elongation	Ferrero et al., 2019
	Wheat	13°C vs. 28°C	Increased GA signaling gene expression	Tuan et al., 2020
Abscisic acid (ABA)	Rice	29°C/23°C vs. 35°C/29°C	Increased expression of ABA-responsive genes	Cohen et al., 2017
	Rice	30°C vs. 40°C	ABA signaling is required for heat tolerance	Li et al., 2020A
	Wheat	13°C vs. 28°C	Decreased ABA signaling gene expression	Tuan et al., 2020
Salicylic acid (SA)	*A. thaliana*	22°C vs. 28°C	Decreased basal *PR1* gene expression in wild-type and autoimmune mutant	Zhu et al., 2010
	A. thaliana	23°C vs. 30°C	Decreased expression of SA-responsive *PR1* gene expression, but SA-mediated protection via NPR1 is intact	Huot et al., 2017
	Rice	29°C/23°C vs. 35°C/29°C	Decreased expression of SA-responsive genes	Cohen et al., 2017

	A. thaliana	22°C vs. 27°C	Decreased basal *PR1* gene expression in an autoimmune mutant that is dependent on PIF4	Gangappa et al., 2017
	A. thaliana	22°C vs. 27°C	Decreased basal *PR1* gene expression in an autoimmune mutant that is dependent on COP1 and DET1	Gangappa and Vinod Kumar 2018
	A. thaliana	22°C vs. 28°C	Decreased basal *PR1* gene expression in an autoimmune mutant that is dependent on SIZ1	Hammoudi et al., 2018
	A. thaliana	22°C vs. 28°C	SA-mediated stomatal closure via NPR1 is intact	Yan et al., 2019
Jasmonic acid (JA)	*A. thaliana*	22°C vs. 38°C	JA receptor COI1 is required for basal thermotolerance of an autoimmune mutant	Clarke et al., 2009
	Aquilaria sinensis (heartwood tree)	25°C vs. 50°C	Increased JA signaling gene expression leading to increased sesquiterpene accumulation	Xu et al., 2016
	A. thaliana	23°C vs. 30°C	Increased JA signaling gene expression after *Pst* DC3000 infection and BTH treatment	Huot et al., 2017
	A. thaliana	23°C vs. 42°C	Increased JA-associated gene expression	Balfagón et al., 2019
	Tomato	25°C/20°C vs. 35°C/30°C	Altered JA-responsive gene expression in stamens and pistils	Pan et al., 2019
	Tomato	28°C/18°C vs. 38°C/28°C	Increased JA receptor COI1 levels due to HSP90 stabilization	Havko et al., 2020A
	A. thaliana	22°C vs. 29°C	Increased JA-responsive *VSP3* gene expression but decreased *LOX3* gene expression in response to wounding	Havko et al., 2020B
Ethylene	Lettuce	20°C vs. 35°C	Increased or decreased ethylene response factor *ERF1* gene expression depending on the genotype	Yoong et al., 2016
	A. thaliana	22°C vs. 27°C	Increased ethylene receptor *ETR1* gene expression but decreased *EIN2* gene expression	Fei et al., 2017
	Tomato	25°C vs. 45°C	Increased ethylene receptor *ETR3* and signaling gene *CTR2* expression	Jegadeesan et al., 2018
	A. thaliana	22°C vs. 28°C	Decreased ethylene-triggered hook formation	Jin et al., 2018
	A. thaliana	22°C vs. 37°C	Increased interaction between ERF95 and ERF97 to promote *HSFA2* and other heat-responsive gene expression	Huang et al., 2020
	A. thaliana	22°C vs. 28°C	Increased ethylene signaling through EIN3 stabilization and EBF1/2 degradation	Hao et al., 2021

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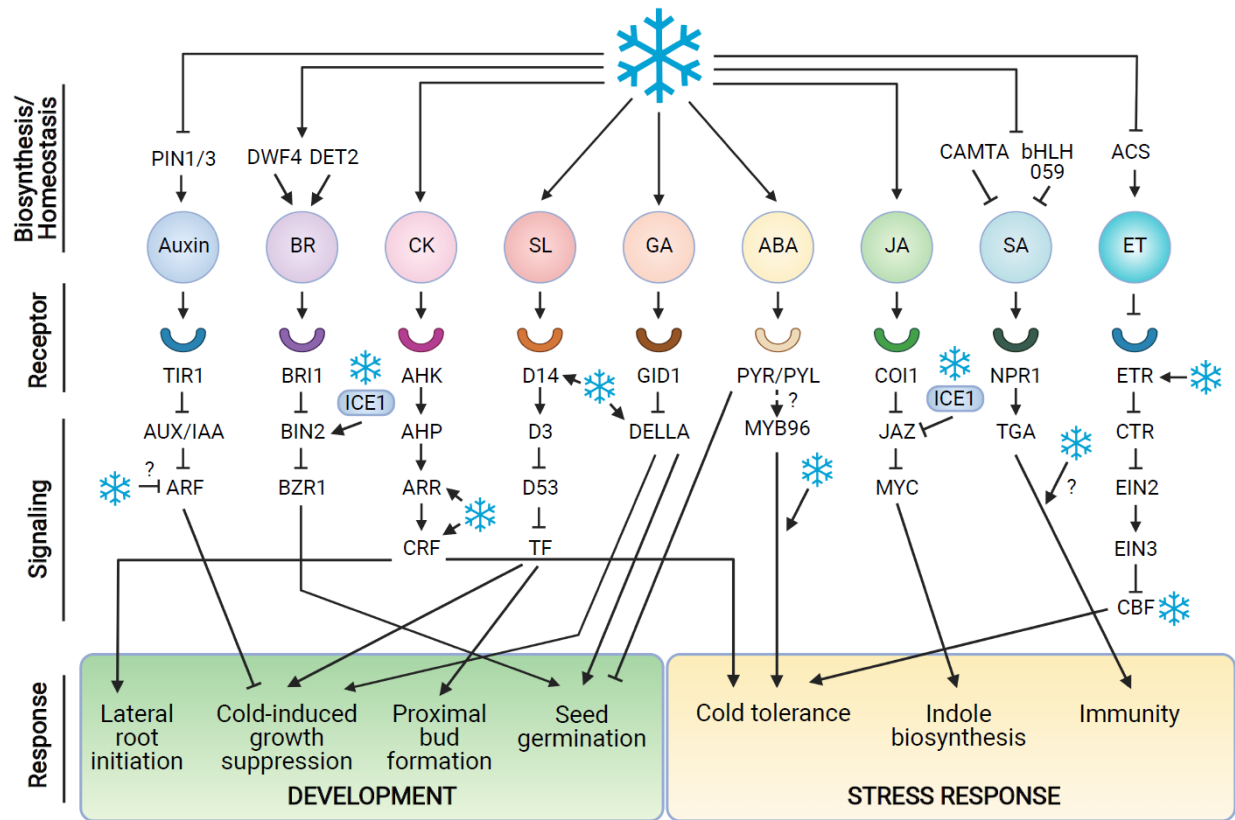9   **Table 4. Regulation of plant hormone signaling at low temperatures.**

Plant Hormone	Species	Temperature Comparison	Observation at Low Temperature	Reference
Auxin	Tulip	17°C vs. 5°C	Increased auxin sensitivity	Rietveld et al., 2009
	Arabidopsis thaliana	22°C vs. 16°C	Decreased auxin signaling levels due to ARR1/2	Zhu et al., 2015
Brassinosteroid (BR)	*A. thaliana*	20°C vs. 10°C	BEE1 is required for cold-modulated phenylpropanoid accumulation and anthocyanin biosynthetic gene expression	Petridis et al., 2016
	A. thaliana	22°C vs. 4°C	BR receptor BRI1 is required for cold stratification release from dormancy	Kim et al., 2019
	A. thaliana	22°C vs. 4/9°C	Enhanced interaction between BIN2 and ICE1 to promote ICE1 degradation	Ye et al., 2019
Cytokinin (CK)	*A. thaliana*	23°C vs. 1°C	Increased A-type *ARR* gene expression; unaffected AHK gene expression but freezing tolerance is enhanced by *ahk* mutants	Jeon et al., 2010
	A. thaliana	21°C vs. 5°C	Cytokinin modulated temperature shock proteins	Cerný et al., 2014
	A. thaliana	22°C vs. 16°C	ARR1/2 regulates reduction of auxin levels, auxin biosynthetic gene expression and PIN1/3 levels	Zhu et al., 2015
	A. thaliana	22°C vs. 4°C	Increased *CRF4* gene expression in roots and shoots leads to better freezing tolerance	Zwack et al., 2016
	A. thaliana	22°C vs. 1°C	Increased *CRF2* and *CRF3* gene expression to regulate cold-induced lateral root initiation	Jeon et al., 2016
Strigolactone (SL)	Rose	20°C vs. 5°C	Induced acropetal gradient of SL receptor gene *RwMAX2* expression leading to increased quiescent medial and proximal buds	Djennane et al., 2014
	Pea	25°C day/20°C night vs. 4°C	Reduced photosynthetic carbon assimilation in SL signaling mutants	Cooper et al., 2018
	A. thaliana	25°C day/20°C night vs. 4°C	SL signaling is required for cold reduction of leaf area	Cooper et al., 2018
Gibberellin (GA)	*A. thaliana*	22°C vs. 4°C	Increased GA-inducible gene expression in seeds	Yamauchi et al., 2004
	A. thaliana	22°C vs. 4°C	Increased accumulation of the GA signaling repressors DELLAs leading to restrained growth	Achard et al., 2008
Abscisic acid (ABA)	*Physcomitrium patens*	4°C vs. -3°C, -6°C and -9°C	ABA signaling is required for freezing tolerance after cold acclimation	Bhyan et al., 2012
	A. thaliana	23°C vs. 4°C	ABA signaling and cold signaling are integrated by MYB96	Lee and Seo 2015
	P. patens	25°C vs. 10°C	Increased ABA signaling gene expression	Tan et al., 2017
Salicylic acid (SA)	Pepper	24°C vs. 20°C	Increased SA levels and immunity	Koeda et al., 2011
	A. thaliana	22°C vs. 4°C	Increased SA-mediated immunity	Kim et al., 2013
	A. thaliana	22°C vs. 4°C	Increased SA receptor NPR1 accumulation in the nucleus and interaction with HSFA1	Olate et al., 2018
	A. thaliana	22-23°C vs. 4°C	Increased SA-mediated immunity	Wu et al., 2019
	A. thaliana	22°C vs. 16°C	Increased SA-mediated immunity	Li et al., 2020B

	A. thaliana	22°C vs. 16°C	Increased SA-mediated immunity	Bruessow et al., 2021
Jasmonic acid (JA)	A. thaliana	22°C vs. 4°C	Increased JA signaling leading to loss of ICE1 repression by JAZ proteins	Hu et al., 2013
	Tea	25°C vs. 15°C	Increased JA-responsive gene expression due to ICE1-JAZ interaction to relieve MYC2 repression	Zhou et al., 2020
Ethylene	A. thaliana	22°C vs. -4°C	Ethylene signaling negatively regulates freezing stress tolerance through negative regulation of CBF gene expression by EIN3	Shi et al., 2012
	A. thaliana	20°C vs. 8-10°C	Increased ethylene receptor gene ETR1 and ETR3 expression	Lado et al., 2015
	Grapevine	26°C vs. 4°C	Increased ethylene response factor ERF057 gene expression	Sun et al., 2016
	Pear	20°C vs. 0°C	Increased ethylene signaling gene expression	Yao et al., 2018
	Soybean	22°C vs. 5°C	Enhanced ethylene signaling inhibits the CBF/DREB1 pathway through EIN3	Robison et al., 2019
	A. thaliana	22°C vs. 16°C	Decreased ethylene signaling through EIN3 degradation and EBF1/2 stabilization	Hao et al., 2021
	Apple	24°C vs. -10°C	Increased ethylene response factor MdERF1b gene expression leading to increased cold tolerance	Wang et al., 2021

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Figures
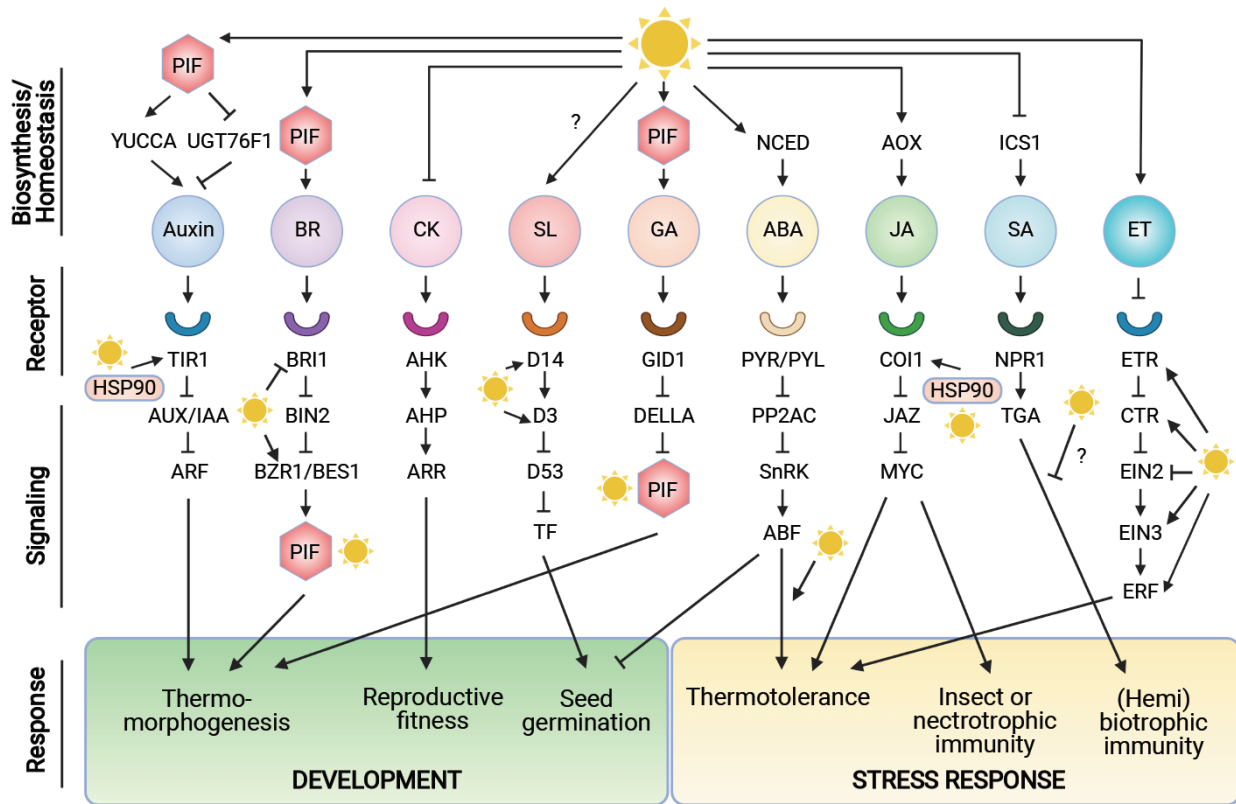
Fig. 1 Regulation of plant hormone production and signaling at high temperature.
High temperatures influence plant hormone pathways by suppressing or activating key molecular hubs, including biosynthetic/catabolic enzymes, hormone transport proteins, receptor proteins, signaling components and/or downstream transcriptional regulators. Temperature regulation of certain hormone pathways can be linked to the known phyB-PIF thermosensing mechanism. Mechanistically connecting other hormone pathways to direct temperature perception is still outstanding. Ultimately, the impacts of high temperature on these hormone pathways manifest in altered developmental, defense and stress responses. Pointed arrows represent activation, while blunt-end arrows represent repression or inhibition. The artwork was generated using BioRender (https://biorender.com/).

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Fig. 2 Regulation of plant hormone production and signaling at low temperatures.
Low temperatures influence plant hormone pathways by suppressing or activating key
molecular hubs, including biosynthetic/catabolic enzymes, hormone transport proteins,
receptor proteins, signaling components and/or downstream transcriptional regulators.
Temperature regulation of certain hormone pathways can be linked to the known ICE1-CBF
cold response module. Mechanistically connecting hormone pathways to direct cold
perception is still outstanding. Ultimately, the impacts of low temperature on these hormone
pathways manifest in altered developmental, defense and stress responses. Pointed arrows
represent activation, while blunt-end arrows represent repression or inhibition. The artwork
was generated using BioRender (https://biorender.com/).