



Gibberellin in Regulating Poplar Growth, Development, and Stress Responses

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1 **Gibberellin in Regulating Poplar Growth, Development, and Stress**

2 **Responses**

3 Lixia Zhang¹, Xiaoqi Zhou¹, Guanming Chen¹, Han Han^{1,*}

4 ¹Co-Innovation Center for Sustainable Forestry in Southern China, College of Life Science,
5 Nanjing Forestry University, Nanjing 210037, China

6 *Correspondence: hhan@njfu.edu.cn

7 **Abstract:** Gibberellic acid (GA) plays a central role in regulating growth, development, and stress
8 **responses**. Poplars exhibit woody-specific GA regulatory mechanisms due to their long-life cycle,
9 continuous vascular cambium activity, and seasonal dormancy. While the GA biosynthetic pathway is
10 highly conserved between herbaceous and woody plants, key poplar synthesis genes such as KS1 and
11 KS2 show vascular tissue-specific expression. Centered on the GID1-DELLA signaling pathway, GA
12 modulates downstream genes via ubiquitination and interacts synergistically or antagonistically with
13 hormones like IAA, ABA, and JA to regulate poplar growth and stress **responses**. Under abiotic stress,
14 poplars downregulate GA levels and accumulate DELLA proteins to enhance resistance. During biotic
15 stress, GA integrates with miRNAs and transcription factors, maintaining growth-defense balance
16 through the DELLA-MYC2 module. Addressing current gaps in holistic GA regulatory network studies
17 and weak understanding of biotic stress mechanisms, this review summarizes poplar GA synthesis,
18 metabolism, and signaling pathways, elucidating their roles in woody-specific traits and stress
19 **responses**. We aim to provide a theoretical support for GA molecular mechanism research in woody
20 plants and forest tree breeding.

21 **Keywords:** Gibberellic acid (GA); gibberellins; woody; signaling pathway; poplar; **stress responses**;
22 growth and development

23 **1. Introduction**

24 Poplar (*Populus spp.*), as a significant broadleaf fast-growing tree species with strong adaptability,
25 possesses both high economic and ecological value. It is widely utilized in industrial raw materials,
26 papermaking, engineered wood products, and furniture manufacturing. Beyond its role in ecological
27 construction—including wind erosion prevention, shifting sand fixation, water conservation, and
28 climate regulation—certain species also exhibit medicinal properties (Du et al., 2012; Xu et al., 2014).
29 Concurrently, poplars possess a compact genome and a well-established genetic transformation system.
30 They exhibit typical woody plant characteristics such as perennial growth, continuous vascular
31 cambium activity, and efficient asexual reproduction, making them a model species for studying woody
32 plant growth, development, and stress response mechanisms (Biselli et al., 2022).

33 Plant hormones serve as core regulators of growth, development, and environmental adaptation.
34 Among these, gibberellins (GAs)—a class of natural diterpene hormones—exhibit potent physiological
35 activity and are extensively involved in plant growth, development, and regulatory processes (Kende &
36 Zeevaart, 1997; Shah et al., 2023). To date, over 136 GAs have been identified, though most are
37 biosynthetic intermediates or inactive metabolites (Hedden & Sponsel, 2015). Only GA₁, GA₃, GA₄,
38 and GA₇ are confirmed to possess direct biological activity (L. Yang et al., 2021). During the “Green
39 Revolution” in mid-20th century, the application of GA-related genes in crop dwarfing breeding drove
40 global agricultural yield increases, demonstrating the immense potential of GA in breeding. Current
41 research extensively explores GA's functions, which span multiple stages of the plant life cycle. These
42 include promoting seed germination (Gong et al., 2022), fruit development and ripening (Fenn &
43 Giovannoni, 2021), stem and leaf growth and root elongation (Zluhan-Martínez et al., 2021). GAs also
44 participate in bud dormancy induction and release (Rinne et al., 2011), stress responses (Nagar et al.,
45 2021), and plant regeneration processes (Bassaganya-Riera et al., 2014). GA serves as an
46 environmentally friendly plant growth regulator widely applied in agricultural and forestry production
47 to enhance crop and fruit tree yield and quality (Kildegaard et al., 2021).

48 Early studies predominantly focused on annual herbaceous model plants like *Oryza sativa* and
49 *Arabidopsis thaliana*. Compared to herbaceous plants, woody plants' perennial nature (Busov et al.,
50 2006), seasonal dormancy (Rinne et al., 2016), and continuous secondary growth (Wei & Wei, 2023)
51 necessitate significant functional specificity for GA, making its regulatory mechanisms incompatible
52 with direct extrapolation from herbaceous plant research. Current research on gibberellin functions in
53 woody plants has primarily focused on poplar, thus our review specifically centered on poplar and
54 comprehensively detailing its gibberellin regulatory mechanisms, including the synthesis, metabolism,
55 and signal transduction mechanisms of GA. In recent years, key genes in GA synthesis, metabolism,
56 and signaling pathways (*GA20ox*, *GA3ox*, *GA2ox*, *GID1*, *DELLA*) have been progressively identified in
57 poplar. Their roles in growth processes such as apical dominance, vascular cambium development, and
58 dormancy release, as well as in responses to abiotic stresses like drought and salinity, have been
59 gradually elucidated (Zawaski & Busov, 2014; Zhang et al., 2024). However, significant gaps remain
60 in current research: First, the GA regulatory network is fragmented, lacking holistic integration of
61 synthesis-metabolism-signaling pathways, with unclear tissue-specific regulatory mechanisms. Second,
62 the interaction network between GA and other hormones has not been systematically elucidated, and
63 core interaction nodes remain undefined. Third, research on biological stress response mechanisms is
64 relatively weak, and the molecular regulatory logic of the growth-defense balance remains unclear.
65 Fourth, there is insufficient linkage between basic research and its application in molecular breeding of
66 poplar. This review elucidates GA's role in stress responses and hormone interaction networks, and
67 explores its potential applications in molecular breeding. We aim to provide theoretical support for
68 hormone regulation studies in woody plants and genetic improvement of poplar.

69 2. Biosynthesis, Metabolism, and Signaling Mechanisms of Gibberellin

70 2.1 Biosynthetic Pathway of Gibberellin

71 GA biosynthesis is a complex metabolic process involving multiple organelles and synergistic
72 enzyme participation (Figure 1), divided into three main stages sequentially completed in plastids,
73 endoplasmic reticulum, and cytoplasm. This pathway is highly conserved in both herbaceous and
74 woody plants (Hedden & Thomas, 2012). The first stage occurs in the plastids, primarily through the
75 interaction between the methylenepyruvate (MEP) pathway and the mevalonate (MVA) pathway to
76 generate isopentenyl pyrophosphate (IPP). IPP is further synthesized into geranylgeranyl
77 pyrophosphate (GGPP). GGPP is sequentially catalyzed by ent-caryophyllene diphosphate synthase
78 (*ent*-CPS) and ent-kaurene synthase (*ent*-KS) to yield *ent*-kaurene, a key intermediate for GA synthesis
79 (Shah et al., 2023). Notably, this stage exhibits significant specificity in poplar: the *KS1* and *KS2* genes
80 are highly expressed in vascular tissues, directly participating in xylem formation and secondary stem
81 growth—a core characteristic distinguishing poplar from herbaceous plants (Zhang et al., 2024). The
82 second stage occurs within the endoplasmic reticulum (ER). First, ent-kaurene is oxidized to GA₁₂-
83 aldehyde by ent-kaurene oxidase (KO) and ent-kaurenoic acid oxidase (KAO), catalyzed by members
84 of the cytochrome P450 monooxygenase family. This is further converted to GA₁₂ (Hartweck, 2008).
85 This process is conserved in both herbaceous and woody plants. The third stage occurs in the
86 cytoplasm, where GA₁₂ is catalyzed by GA20-oxidase (*GA20ox*) and GA3-β-hydroxylase (*GA3ox*),
87 yielding bioactive molecules such as GA₁ and GA₄ (Gou et al., 2011). *GA20ox* plays a key regulatory
88 role in GA precursor synthesis, with its expression directly influencing active GA levels. Concurrently,
89 active GA molecules exert negative feedback regulation by suppressing *GA20ox* and *GA3ox*
90 expression, thereby maintaining GA homeostasis. This feedback mechanism is highly conserved in
91 poplar and adapts to its continuous growth requirements. Given the high-specificity expression of
92 poplar *KS1/KS2* in vascular tissues, locally synthesized GA may be transported to the shoot apex or
93 roots via specific carrier proteins. NPF and SWEET family transporters have been identified in
94 Arabidopsis as efflux carriers for GA, participating in inter-tissue GA transport and regulating GA
95 concentration equilibrium (Binenbaum et al., 2018). It is speculated that a similar transport mechanism
96 may exist in poplar, which represents one of the core directions for future GA regulation research in
97 poplar.

98 2.2 Metabolic Inactivation of Gibberellin

99 The inactivation of gibberellins is primarily mediated by the 2-oxoglutarate-dependent
100 dioxygenase *GA2-oxidase* (*GA2ox*). This enzyme terminates the physiological effects of GA signaling
101 by hydroxylating bioactive GAs and converting them into inactive products (Song et al., 2024). The
102 *GA2ox* gene family is widely distributed across the plant kingdom. In 2001, Busov et al. first
103 demonstrated that overexpression of *PtaGA2ox1* causes dwarfism in poplar trees, highlighting its

104 significant research value in trees (Busov et al., 2003); In 2011, 11 poplar *GA2ox* genes were
105 identified, including seven C19 *GA2oxs* members and four C20 *GA2oxs* members. These genes not
106 only regulate shoot height and vascular development but also influence root development. In-depth
107 exploration of *GA2oxs* holds significant implications for research on the growth and development of
108 woody plants (Gou et al., 2011).

109 2.3 Gibberellin Signaling

110 The core mechanism of GA signal transduction is mediated by the GA receptor GID1 and the
111 transcription repressor DELLA protein, a process conserved in both herbaceous and woody plants. GID
112 belongs to the phytohormone receptor family and specifically recognizes bioactive GA molecules.
113 Upon binding to GA, GID1 undergoes a conformational change, forming the GA-GID1-DELLA
114 complex with DELLA proteins (Murase et al., 2008). This complex is recognized by F-box proteins
115 (e.g., SLY1/GID2) and recruited to the SCF ubiquitin ligase complex, triggering ubiquitin-mediated
116 degradation of DELLA proteins. This process releases their transcriptional repression of GA-
117 responsive genes (Shah et al., 2023). DELLA proteins act as key negative regulators in the GA
118 signalling pathway. In *Arabidopsis thaliana*, DELLA binds to transcription factors PIF4, BZR1, and
119 ARF6 to inhibit hypocotyl cell elongation responses (Oh et al., 2014). It also influences the expression
120 of key flowering regulators, such as SOC1 and FLC, which are involved in the regulation of
121 reproductive development (Li et al., 2016). In poplar, they interact with multiple transcription factors to
122 modulate the expression of genes associated with cell proliferation, elongation and differentiation
123 (Zhang et al., 2024). Similar functions have been observed in other woody species. For example, in
124 *Pinus tabulaeformis*, the interaction between the phytochrome-interacting factors (PIFs) and the DELLA
125 protein inhibits light-mediated signalling and elongation responses (Guo et al., 2024).

126 The GA signalling pathway exhibits characteristic feedback regulation mechanisms in both
127 herbaceous and woody plants. When GA levels are insufficient, the accumulation of DELLA proteins
128 simultaneously activates the transcription of GA synthesis-related genes (e.g. GA20ox and GA3ox),
129 thereby promoting GA biosynthesis. When GA levels are sufficient, GA-GID1-mediated degradation
130 of DELLA terminates the pathway that promotes GA synthesis, thus achieving steady-state regulation
131 of GA signalling (Busov et al., 2006; Hartweck, 2008). The synthesis, metabolism, and signal
132 transduction of GA form a highly coordinated regulatory network, providing the molecular basis for
133 GA-mediated growth and development in poplar trees.

134

135 3. Role of the GA signaling pathway in poplar growth and development

136 Gibberellic acid plays a central regulatory role in the growth and development of poplar trees
137 (Figure 2): On one hand, it promotes cell division and elongation, accelerates xylem development,

138 enhances stem elongation, and increases plant biomass accumulation (Su et al., 2025); On the other
139 hand, regulates cambial cell differentiation and regeneration through interactions with the auxin
140 signaling pathway, thereby promoting secondary growth processes (Zhang et al., 2024). These
141 mechanisms provide crucial theoretical foundations for breeding fast-growing, high-yielding, and
142 stress-tolerant poplar varieties.

143 3.1 Plant Height Regulation

144 GA is a key hormone regulating internode cell elongation in poplar, primarily promoting stem
145 internode elongation by facilitating cell wall relaxation, microtubule reorganization, and the expression
146 of related cell wall hydrolases. This process regulates plant height and canopy architecture (Eriksson et
147 al., 2000). Its regulatory effects can be precisely controlled through key genes involved in its synthesis,
148 metabolism, and signaling pathways, and it has been applied in dwarfing breeding and tree form
149 improvement of fast-growing poplars (Busov et al., 2006).

150 Controlling the expression of key enzymes and receptors involved in GA synthesis and signal
151 transduction pathways can be used to regulate the height of poplar trees. Overexpression of the GA
152 synthesis key gene *PtoKSI* enhances GA signaling, significantly promoting overall poplar growth
153 (Zhang et al., 2024); Similarly, overexpression of *PttGA20ox* and *PttGID1* both promote internode
154 elongation and xylem formation by enhancing the GA signaling pathway (Eriksson, 2000; Mauriat &
155 Moritz, 2009). Furthermore, overexpression of *PtGA3ox*, the terminal enzyme in GA synthesis,
156 significantly increases active GA levels, thereby enhancing both plant height and stem diameter in
157 poplar (Hu et al., 2022). However, it is important to note that enhanced GA signaling disrupts
158 development of other organs. For instance, overexpression *Pinus densiflora GA20ox* (*PdGA20ox*) in
159 poplar leads to elongated stems, but reduced leaf size, and poor rooting; suggesting tissue- or stage-
160 specific regulation of GA on secondary growth (Jeon et al., 2016).

161 In contrast, inhibiting GA activity or signalling significantly suppresses growth and produces
162 dwarf phenotypes. Poplars that overexpress genes degrading GA such as *PtaGA2ox* exhibit moderate
163 or semi-dwarf phenotypes (Zawaski & Busov, 2014); Similarly, the overexpression of *ClGA2ox12* in
164 hybrid poplar (*Populus tremula* × *Populus tremuloides*) resulted in reduced plant height and stem
165 diameter (Peng et al., 2024). In the GA signalling pathway, DELLA protein accumulation or the
166 overexpression is key to plant height regulation. *PtoGAI* overexpression severely inhibits cambial
167 proliferation, resulting in significantly reduced plant height and stem diameter (Zhang et al., 2024).
168 Consistently, the dwarfing phenotype in tetraploid 84K poplar (*P. alba* × *P. glandulosa*) is directly
169 correlated with decreased GA and IAA content, as well as the upregulation of DELLA proteins and the
170 downregulation of GID1 receptors (Ren et al., 2022).

171 3.2 Phase Transition, Flowering, Bud Formation and Dormancy Release

172 GA participates in the transition from juvenile to adult stages in poplar and regulates flowering
173 (Zawaski et al., 2011). Juvenile and adult trees are typically distinguished by their flowering capacity,
174 specifically adult poplars convert a portion of their axillary meristems into inflorescence meristems
175 during specific seasons (Sheng et al., 2023). The vegetative growth phase in trees can last from several
176 years to decades, thus early flowering techniques can effectively accelerate breeding and propagation
177 processes (Zawaski et al., 2011). Unlike in herbaceous plants such as *Arabidopsis* (Jang et al., 2009; Li
178 et al., 2008) and *Chrysanthemum* (*Chrysanthemum morifolium*) (Dong et al., 2017; Yang et al., 2014),
179 where GA promotes flowering, GA typically inhibits flowering in woody plants (Brunner & Nilsson,
180 2004). In poplar, overexpression of DELLA or GA degradation genes like *GA2ox* increases flowering
181 rate and promotes early flowering (Zawaski et al., 2011). In *Arabidopsis*, GA promotes flowering via
182 multiple pathways including *DELLA-GAF1-TPR* (Fukazawa et al., 2021), *DELLA-CO-FT*, and
183 *miR156-SPL* (Castro-Camba et al., 2022; Xu et al., 2016). In woody plants like apple, sweet orange,
184 and chestnut, GA primarily inhibits flowering by upregulating *MdTFL1* (S. Zhang et al., 2019),
185 suppressing *CiFT* (Muñoz-Fambuena et al., 2012), or affecting the *CmmiR156-SPL* pathway (Chen et
186 al., 2019). Only in a few species like *Jatropha curcas* (Hui et al., 2018) and Tree peony (*Paeonia*
187 *suffruticosa*) (Xue et al., 2018) does GA promote flowering or reblooming. Thus, GA participates in
188 phase transition and flowering initiation in poplar.

189 Plants respond to low temperatures and adverse environments during winter by entering
190 dormancy. Both the initiation and release of dormancy are finely regulated by environmental signals
191 and hormonal networks. Among these, GA serves as the core hormone promoting dormancy release
192 and bud germination, exhibiting a classic antagonistic relationship with abscisic acid (ABA). ABA
193 promotes dormancy maintenance by inducing GA degradation pathways, while GA accumulation
194 accelerates dormancy release and shoot elongation. The equilibrium between these two hormones
195 determines the seasonal growth rhythm of poplar trees (Chen et al., 2023; Ding et al., 2024; Zhang et
196 al., 2017). Together, they regulate the seasonal growth-dormancy cycle (Singh et al., 2016).

197 As a central gene regulating flowering, FT not only participates in floral timing regulation but also
198 serves as a key target for dormancy induction. The mechanism by which GA promotes dormancy
199 release and bud priming in poplar has been elucidated and is closely linked to the FT signaling
200 pathway: Rinne et al. (2011) revealed that GA breaks dormancy by enhancing 1,3- β -glucanase activity
201 to degrade callose, thereby opening sieve pathway channels to facilitate PttFT protein transport (Rinne
202 et al., 2011); Eriksson et al. (2015) further indicated that GA can promote bud germination
203 independently of the *FT2* pathway. Exogenous GA application significantly enhances bud germination,
204 regulating hybrid poplar bud elongation in parallel with the *FT2* pathway (Eriksson et al., 2015); The
205 cold-induced transcription factor *PttSVL* suppresses the expression of *PttFT1* and *PttGA20ox*,

206 antagonistically regulating bud germination through GA and ABA signaling. It serves as an integration
207 node between environmental signals and the hormone network (Singh et al., 2018). Concurrently, FT
208 signaling influences shoot growth by inversely regulating GA content. For instance, *PtaFT2* modulates
209 shoot apical meristem development and inhibits internode elongation via the GA13-hydroxylation
210 pathway (Gómez-Soto et al., 2022). GA also plays a crucial role in sustaining continuous shoot
211 elongation (Cao et al., 2023). Beyond FT signaling, *PtoHY5a* directly activates *PtoFT2* expression to
212 suppress short-day-induced growth arrest. Simultaneously, it reduces apical GA levels by upregulating
213 key GA inactivation genes and downregulating GA synthesis genes, thereby inhibiting bud emergence.
214 This *HY5a*-GA module adapts to the seasonal growth patterns regulated by photoperiod in woody
215 plants (Gao et al., 2024).

216 3.3 Development of the Vascular Cambium and Secondary Growth

217 The secondary growth of poplar trees primarily relies on the sustained activity of the vascular
218 cambium, which produces secondary xylem and secondary phloem through bidirectional
219 differentiation. Its activity directly determines wood yield and quality (Sun et al., 2025). Recent studies
220 indicate that GA signaling plays a central role in regulating cambial cell activity and xylem
221 differentiation by influencing processes such as cell division, elongation, and lignification. Its
222 regulatory mechanisms have been progressively elucidated through ongoing research. Israelsson et al.
223 (2005) first demonstrated that GA exerts a pivotal role during early wood formation, particularly in
224 regulating xylem differentiation and fiber cell elongation (Israelsson et al., 2005). Mauriat and Moritz
225 (2009) further revealed GA's dual role in xylem development through histological observations and
226 gene expression analysis: it enhances meristematic activity in cambial cells to initiate secondary xylem
227 formation, while simultaneously promoting elongation and cell wall thickening in mature xylem fiber
228 cells. Notably, its regulation of fiber cell length occurs independently of the IAA pathway (Mauriat &
229 Moritz, 2009).

230 Recent studies have progressively elucidated the molecular mechanisms by which the GA
231 signaling pathway regulates the development of the vascular cambium and secondary growth in poplar
232 trees: Du et al. (2024) discovered that *PdRabG3f* regulates internode elongation and xylem
233 development in poplar by interfering with endogenous GA levels (Du et al., 2024); Su et al. (2025)
234 further revealed that localized GA synthesis in stems is a key factor regulating xylem development,
235 clarifying that tissue-specific distribution of GA levels is essential for maintaining normal cambium
236 activity (Su et al., 2025). The synergistic regulation of GA and IAA constitutes the core mechanism
237 governing poplar cambium development: IAA forms a polar gradient in the cambium region via polar
238 transporters such as *PINI* (*PIN-FORMED 1*), with its maximum concentration located in the cambium
239 cell layer, thereby determining stem cell differentiation fate (Hartweck, 2008; Mäkilä et al., 2023).
240 Björklund et al. (2007) revealed that GA regulation of poplar cambium depends on IAA; GA alone

241 cannot induce cambial regeneration but significantly enhances IAA-induced expression of cambium-
242 related genes. The two exhibit marked synergistic effects, share multiple transcriptional regulatory
243 elements, and show highly overlapping downstream transcriptional responses (Björklund et al., 2007).
244 Zhang et al. (2024) further elucidated the molecular basis of this synergistic mechanism: the IAA
245 response factor ARF7 interacts with the DELLA protein RGL1 via its MR domain while
246 simultaneously binding to the *Aux/IAA* family member IAA9 through its PB domain. This forms the
247 ARF7-RGL1-IAA9 ternary complex, serving as a key platform for integrating GA and IAA signaling
248 (Zhang et al., 2024). GA promotes IAA accumulation in the cambium region by upregulating *PIN1*
249 expression and positively regulates *ARF7* and *WOX4* expression, thereby enhancing cambium cell
250 activity (Hu et al., 2022; Mäkilä et al., 2023). DELLA proteins negatively regulate *PIN1* expression,
251 forming a GA-IAA feedback loop that precisely controls the sustained activity of the cambium (Zhang
252 et al., 2024).

253 Multiple PIN family members exist in the poplar genome (Liu et al., 2014). Despite functional
254 redundancy, their tissue expression is highly differentiated. For example, *PttPIN1* and *PttPIN2* are
255 specifically expressed in the cambium and its derived xylem, participating in polar IAA transport
256 within vascular tissues (Schrader et al., 2003). The tissue-specific distribution of GA and expression of
257 its biosynthetic genes further safeguard vascular cambium development: active GA forms (e.g., GA₁
258 and GA₄) accumulate in xylem regions, while GA precursors (e.g., GA₉, GA₂₀) predominantly localize
259 in phloem (Israelsson et al., 2005), closely aligning with xylem differentiation functions. GA activity is
260 primarily regulated by three key enzymes: *PdGA20ox* overexpression significantly increases poplar
261 xylem cross-sectional width and cell number (Jeon et al., 2016); *GA3ox* expression levels directly
262 determine the accumulation of active GA (Israelsson et al., 2004); inhibiting *GA2ox* (e.g., *PtGA2ox4*,
263 *PtGA2ox5*) enhances meristem cell proliferation and promotes secondary growth (Gou et al., 2011).
264 These three enzymes synergistically regulate GA activity within vascular tissues, determining wood
265 formation efficiency.

266 3.4 Root Development and Nutrient Acquisition

267 Most poplars can reproduce asexually, and the ability to form adventitious roots (AR) through
268 cuttings is a key factor for their field establishment and survival, holding significant importance for
269 large-scale forestry seedling propagation (Bannoud & Bellini, 2021). Adventitious root formation
270 represents a bottleneck for efficient propagation in many woody plants. Elucidating the molecular
271 mechanisms by which plant hormones regulate adventitious root formation can help optimize asexual
272 propagation systems, holding significant value for forestry production (Zhang et al., 2023). Current
273 research indicates that IAA acts as a positive regulator in adventitious root induction, while cytokinins
274 (CK) and GA primarily exert inhibitory effects (Liu et al., 2024).

275 The molecular mechanism by which GA inhibits adventitious root formation in poplar has been
276 elucidated: binding of GA to its receptor *GID1* induces degradation of DELLA proteins, thereby
277 releasing DELLA's inhibition of polar IAA transport. This leads to disrupted IAA distribution in the
278 cutting base, ultimately suppressing adventitious root primordia formation (Zhang et al., 2023).
279 Consequently, enhanced GA signaling significantly inhibits rooting, while its suppression promotes
280 rooting. Mauriat et al. (2014) found that hybrid poplars overexpressing the Arabidopsis GA synthesis
281 gene *AtGA20ox1* exhibited accelerated plant growth rates but accompanied by a marked decrease in
282 rooting efficiency; Similarly, overexpression of *PttGID1.1* or *PttGID1.3* markedly suppressed
283 adventitious root formation. Consistently, exogenous application of GA significantly inhibits
284 adventitious root formation (Žiauka & Kuusienė, 2010). GA regulation of lateral roots (LR) mirrors its
285 effect on adventitious roots: GA-deficient (*35S:PcGA2ox1*) and GA-insensitive (*35S:rgl1*) poplar
286 plants exhibit markedly increased lateral root number and elongation alongside reduced plant height,
287 with these effects reversible upon exogenous GA treatment (Gou et al., 2009). Conversely, GA
288 synthesis inhibitors like paclobutrazol, when applied exogenously, promote adventitious root formation
289 in hybrid poplar while inhibiting secondary root and shoot growth. They are frequently used to aid the
290 *in vitro* rooting of hybrid poplar (Vaiciukyne et al., 2019). These studies collectively demonstrate GA's
291 negative regulatory role in poplar root development, with particularly pronounced inhibition during
292 adventitious root formation (Bannoud & Bellini, 2021). As the core organ for nutrient uptake and stress
293 responses, the root system's negative regulation by GA provides a key target for balancing
294 aboveground growth with belowground stress tolerance.

295 3.5 Biomass Accumulation and Wood Quality Formation

296 Genetically engineered plant hormone pathways represent a key direction in current molecular
297 breeding of forest trees. Molecular approaches can significantly shorten the cultivation cycles required
298 in traditional breeding while enabling precise control over specific traits. Current tree genetic
299 engineering research focuses on modifying the lignin biosynthesis pathway to reduce lignin content and
300 monomer composition, thereby optimizing wood processing properties and enhancing pulp conversion
301 efficiency. Research indicates that GA levels correlate with pulp production, and biofuel yield, offering
302 novel insights for genetic improvement in woody plants (Eriksson et al., 2000). GA not only regulates
303 cell elongation, xylem formation, and the expression of stress-related genes but also directly
304 participates in these processes, thereby influencing plant biomass accumulation (Lin et al., 2025).

305 GA exhibits distinct organ specificity in regulating material accumulation in poplar: it positively
306 regulates above-ground biomass accumulation by optimizing wood processing properties through
307 modulation of lignin content and monomer composition; conversely, it negatively regulates below-
308 ground root biomass, consistent with root development regulation. This characteristic provides precise
309 targets for breeding fast-growing, high-quality poplar varieties (Eriksson et al., 2000). Adjusting the

310 ratio of lignin monomers (S/G ratio) can reduce cell wall resistance while enhancing wood quality,
311 without affecting biomass accumulation (Tang et al., 2025). The core value of GA in regulating wood
312 quality has been validated: Field trials by Cho et al. (2019) confirmed that co-overexpressing
313 *PdGA20ox1* and *PtrMYB221* in poplar synergistically optimizes GA levels and the lignin synthesis
314 network. This resulted in above-ground biomass doubling compared to wild-type, significantly reduced
315 lignin content, increased total cellulose proportion, and approximately 8% higher saccharification
316 efficiency, without noticeable growth defects (Cho et al., 2019), representing a classic case of GA
317 application for wood quality improvement. GA signaling imbalance disrupts material accumulation and
318 xylem development: excessive suppression of above-ground GA signaling impairs xylem
319 differentiation, such as *CIGA2ox12* overexpression in poplar significantly inhibiting vessel
320 differentiation and reducing lignin deposition (Peng et al., 2024); Elevated GA levels resulting from
321 suppressed *PtGA2ox2* and *PtGA2ox7* activity in roots decrease root biomass (Gou et al., 2011), further
322 confirming its organ-specific regulatory characteristics.

323 **4. Role of the GA Signaling Pathway in Abiotic and Biotic Stress Responses**

324 GA not only regulates poplar growth and development but also mediates responses to abiotic and
325 biotic stresses by interacting with hormones and integrating transcription factor and non-coding RNA
326 networks. It establishes a dynamic equilibrium between growth and defense, playing a crucial role in
327 enhancing plant **stress response** to both biotic and abiotic stresses (Ding et al., 2016; Gou et al., 2009).

328 4.1 Abiotic Stress **Responses**

329 Drought and saline-alkali stress are two of the main abiotic factors that limit forestry production
330 (Fang et al., 2021; X. Yang et al., 2021). In poplar, GA plays a role in regulating abiotic stress by
331 modulating its own content, hormone interactions and transcription factor networks, and exhibits a
332 typical 'growth-stress trade-off' effect. Phenotypically, a trade-off is evident: Poplar trees that
333 overexpress GA exhibit accelerated growth and increased leaf area, but reduced drought tolerance. In
334 contrast, GA-deficient plants exhibit limited growth yet superior drought **stress responses** (Eriksson et
335 al., 2000; Zhang et al., 2024). As an evolutionary adaptation to drought, the heterophyllous trait in
336 *Populus euphratica* shows significant positive correlations between GA₃ content and leaf length and
337 spongy tissue thickness, reflecting species adaptation regulated by GA (Han et al., 2021).

338 Drought induces poplar to downregulate GA synthesis genes and upregulate metabolic genes,
339 resulting in lower active GA levels and increased accumulation of the protein DELLA. DELLA
340 proteins inhibit cell elongation, thereby reducing the transpiration area of the plant and lowering
341 stomatal aperture to minimize water loss, ultimately enhancing drought tolerance (Zawaski & Busov,
342 2014). Hormone interactions play a crucial role in this process. The primary plant hormone involved in
343 the response to drought, ABA, suppresses GA-mediated cell growth by promoting DELLA

344 accumulation, thereby enhancing stress **responses** (Liao et al., 2023).

345 Different transcription factors participate in GA-mediated drought tolerance: *PagKNAT2/6b*
346 suppresses GA synthesis by downregulating *PagGA20ox1*, altering poplar morphology to enhance
347 drought tolerance (Song et al., 2021); *PtoMYB142* binds the MBS element in the *PtoGA2ox4* promoter
348 to promote its expression, thereby reducing GA content while regulating leaf and stomatal structure to
349 enhance poplar drought **stress responses** (Song et al., 2024). Furthermore, in *Populus euphratica*, the
350 GA repressed B3-domain transcription factor *FUSCA3* (*FUS3*) coordinates IAA and ABA signaling to
351 maintain root growth under drought (Liu et al., 2025).

352 Compared to drought, research on GA regulatory mechanisms in salt stress in poplars remains less
353 studied. *PsnERF76* has been identified to enhance salt tolerance by upregulating ABA and GA
354 synthesis genes (X. Zhang et al., 2019). In other plants, nitrate regulates growth responses through GA-
355 mediated DELLA accumulation (Camut et al., 2021), and it will be interesting to explore whether
356 similar mechanisms exist in poplars. Given that global saline-alkali land spans 1.125 billion hectares
357 (Quamruzzaman et al., 2021), elucidating GA's regulatory role in poplar salt tolerance holds significant
358 implications for afforestation on marginal lands (Su et al., 2022).

359 4.2 Biotic Stress **Responses**

360 Research on GA in poplar responses to biotic stress is limited. Existing studies indicate that GA
361 plays a central role in regulating the growth-defense balance in poplars by integrating miRNA,
362 transcription factor, and hormone interaction networks, making it crucial for poplar environmental
363 adaptation. GA enhances insect **stress response** regulation by synergizing with the microRNA319a-
364 TCP module: miR319a enhances leaf trichome density and insect **stress response** by suppressing
365 expression of its target genes *PtTCPs*. Simultaneously, GA signaling inhibitor RGA interacts with
366 *PtmiR319a* to jointly suppress trichome differentiation mediated by the GL1-GL2 pathway. The
367 balance between these two factors determines insect **stress response** and growth rate (Fan et al., 2020).
368 In disease **stress response** regulation, transcription factor-mediated GA signaling balances immunity:
369 *PagWRKY33a/b* participates in GA signaling by activating NRG1.1 and GASA14 expression. Its
370 absence induces spontaneous immunity in poplar, enhancing **stress responses** to anthracnose but
371 causing growth inhibition, confirming GA's central role in balancing immunity and growth (Yu et al.,
372 2024). Additionally, GA significantly suppresses *PtrPARVUS2* transcription. Highly expressed in
373 vascular tissues and epidermis, *PtrPARVUS2* participates in cell wall biosynthesis, suggesting GA may
374 regulate defense structure formation via cell wall biosynthetic pathways (Wang & Coleman, 2024).

375 The interaction between GA and jasmonic acid (JA) constitutes a core molecular mechanism for
376 growth-defense balance: JA is a central hormone in plant defense responses (Zhao et al., 2021). When
377 GA levels are low, DELLA proteins can interact with MYC2, a core transcription factor in JA

378 signaling, enhancing JA-mediated defense responses: When GA levels increase, DELLA proteins are
379 degraded, weakening the JA pathway's defense capacity and exhibiting a classic 'growth-defense trade-
380 off effect' (Navarro et al., 2008). This mechanism adapts poplar to survival strategies of 'growth-
381 priority' under low-stress environments and 'defense-priority' under high-stress environments,
382 representing a core direction for future research.

383 **5. Discussion and Summary**

384 5.1 Integration of the Core GA Biology in Poplar

385 The poplar GA signaling pathway centers on the conserved 'GA-GID1-DELLA' pathway while
386 evolving unique regulatory mechanisms adapted to its perennial characteristics. Through complex
387 cross-interactions with hormones such as ABA, IAA, and JA, it achieves precise regulation of growth,
388 development, and stress responses. In-depth analysis of the molecular mechanisms and specificity
389 underlying these hormonal interactions not only refines the understanding of the GA signaling
390 regulatory network in poplar but also provides a crucial theoretical foundation for elucidating the
391 conservation and divergence in GA regulation between woody and herbaceous plants. By integrating
392 gene homology and functional differentiation characteristics, the GA biology in poplars can be
393 summarized from three dimensions: well-established mechanisms, mechanisms that can be safely
394 inferred to be conserved from herbaceous, and specialized mechanisms adapted to the woody perennial
395 lifestyle.

396 5.1.1 Well-established Mechanisms

397 Similar to the annual herbaceous model plant Arabidopsis, GA signaling in poplar relies on the
398 highly evolutionarily conserved GA-GID1-DELLA core pathway (Mauriat & Moritz, 2009).
399 Furthermore, the key enzyme families involved in GA biosynthesis and degradation are highly
400 homologous between herbaceous and woody plants. Among these, the GA20ox and GA3ox families
401 are responsible for the synthesis of active GAs, while the GA2ox family mediates the irreversible
402 inactivation of GAs (Busov et al., 2003). It is through the precise regulation of the expression and
403 activity of these core enzymes and signal transduction genes that GA mediates plant growth,
404 development, and stress responses. This constitutes the molecular basis for the conservation of GA
405 regulation between herbaceous and woody plants.

406 The signaling interactions between GA and auxin, as well as the functional division of labor
407 among GA metabolic enzymes, exert highly consistent regulatory roles in the basic growth and
408 development processes of herbaceous and woody plants. GA and IAA primarily exhibit synergistic
409 interactions, jointly regulating vascular cambium development (Zhang et al., 2024). GA and IAA
410 synergistically release the suppression of ARF family transcription factors, thereby activating vascular

411 cambium stem cell activity and promoting the directed differentiation and development of secondary
412 xylem and phloem (Ben-Targem et al., 2021; Zhang et al., 2024). GA and IAA also jointly regulate
413 apical dominance (Cao et al., 2023), yet show antagonistic effects in root development (Liu et al.,
414 2024), demonstrating tissue-specificity in hormone interactions. Furthermore, GA inhibits lateral root
415 formation by regulating polar IAA transporters (e.g., PtPIN9), with GA and ABA exhibiting synergistic
416 inhibition in this process (Gou et al., 2009).

417 Similar to Arabidopsis, GA interacts synergistically or antagonistically with multiple other
418 hormonal pathways to form a sophisticated regulatory network. GA and ABA exhibit extensive
419 antagonistic relationships involving bud dormancy (Singh et al., 2018), lateral root formation (Gou et
420 al., 2009), drought tolerance regulation (Liu et al., 2025), and other processes. The core mechanism
421 involves balancing growth and stress response through the accumulation of DELLA proteins. Under
422 adverse conditions such as drought and high salinity, both Arabidopsis and poplar reduce endogenous
423 gibberellin levels by upregulating *GA2ox* and downregulating *GA20ox/GA3ox*, while simultaneously
424 increasing ABA content (Shu et al., 2018), thereby achieving a trade-off between growth inhibition and
425 stress tolerance (Achard et al., 2006). Concurrently, IAA influences ABA synthesis and signaling
426 responses, thereby indirectly participating in the GA-ABA interaction network (Gou et al., 2009). In
427 Arabidopsis, the transcription factor DDF1 directly promotes *GA2ox* expression, further reducing GA
428 accumulation to enhance stress adaptation (Magome et al., 2008); this stress-GA metabolic regulation
429 pattern also holds true in woody plants.

430 5.1.2 Mechanisms that Can Be Safely Inferred to Be Conserved from Herbaceous

431 Due to the long growth cycles, complex genetic backgrounds, and high experimental difficulty
432 associated with woody plants, direct functional evidence for many regulatory mechanisms remains
433 lacking. Based on pathways already elucidated in Arabidopsis and the high homology of core genes in
434 the poplar genome, it is reasonable to infer that certain light and auxin regulatory modules are
435 potentially conserved in woody plants. In Arabidopsis, the DELLA-ABI4-HY5 module integrates light
436 and GA signaling to regulate hypocotyl elongation (Xiong et al., 2023). HY5 directly activates the
437 transcription of *GA2ox* genes, promoting the degradation of active GA and thereby inhibiting stem cell
438 elongation and internode growth (Gao et al., 2024). Furthermore, DBB1a increases active GA levels by
439 inhibiting the expression of GA degradation genes and inducing the expression of GA synthesis genes,
440 thereby promoting hypocotyl elongation (Wang et al., 2010). The core regulatory factors of this
441 pathway all possess direct homologs in the poplar genome (Wu et al., 2024), suggesting that this
442 mechanism is likely conserved in poplar.

443 Auxin works in concert with gibberellin signaling to shape root morphology by regulating the
444 transcriptional levels of *GA2ox* (Kubalová et al., 2025; Mauriat et al., 2014). In Arabidopsis, the
445 histone deacetylase HDT1/2 suppresses *GA2ox2* expression and maintains cell division activity in the

446 root apical meristem. Auxin can both regulate HDT-mediated epigenetic modifications and directly
447 activate *GA2ox2*, finely balancing proliferation in the root meristem and growth in the elongation zone
448 (Li et al., 2017). Given that GA signaling in poplars similarly relies on the interaction between DELLA
449 proteins and auxin, it is hypothesized that the IAA-HDT-*GA2ox*-GA regulatory module is conserved in
450 woody plants.

451 5.1.3 Specialized Mechanisms Adapted to the Perennial Habits of Woody Plants

452 Although the core GA signaling and metabolic pathways are conserved across species, woody
453 perennials such as poplars have evolved unique GA regulatory mechanisms to support their perennial
454 life cycles during their long-term adaptation to terrestrial environments and seasonal changes. These
455 specific regulatory mechanisms are primarily manifested in the unique perennial biological traits of
456 woody plants. Firstly, poplars possess a specialized pathway under long-day conditions in which *FT2*
457 reduces active GA levels by upregulating *GA2ox1* and downregulating *GA3ox2*, thereby specifically
458 limiting internode elongation and promoting apical meristem development (Gao et al., 2024). This FT-
459 dependent GA metabolic regulation pattern is completely absent in Arabidopsis, highlighting the
460 evolutionary differences in plant height regulation between herbaceous and woody plants. Secondly,
461 GA acting as a flowering-promoting signal in annual herbs which are characterized by rapid
462 generational turnover (Wilson et al., 1992). GA activates integrons such as *SOCI* and *LEAFY* to
463 accelerate the reproductive transition (Blazquez et al., 1998; Li et al., 2016). In contrast, in poplars, GA
464 inhibits flowering integrons, prioritizing stem elongation and secondary growth, and delaying the
465 reproductive transition to accumulate nutrients and resist frost damage (André et al., 2022). Thirdly,
466 herbaceous dormancy is confined to the seed stage and is regulated by the *DOG1*-ABA-GA pathway
467 (Bentsink et al., 2006; Hilhorst & Karssen, 1992); in contrast, woody plants maintain bud dormancy via
468 the *PttSVL*-FT-*GA2ox* pathway (Singh et al., 2018) and break dormancy via the *PtoHY5a*-FT-GA
469 pathway (Gao et al., 2024), adapting to annual growth cycle cycles (Ruttink et al., 2007). Fourthly, GA
470 in herbaceous plants primarily governs above-ground stem and leaf elongation, whereas in woody
471 plants, GA bidirectionally regulates the allocation of resources between above- and below-ground
472 parts; high GA levels promote wood deposition (Liao et al., 2025; Su et al., 2025), while low GA levels
473 facilitate root system development (Elias et al., 2012). Lastly, in herbaceous plants, GA is only
474 indirectly involved in JA pathway regulation (Hou et al., 2010; Mir et al., 2025), whereas woody plants
475 have evolved GA-specific defense modules. Through the *PtmiR319a*-*PtTCP19*-RGA pathway, they
476 promote trichome development (Fan et al., 2020), and the DELLA-MYC2-JA pathway to activate
477 immune responses (Navarro et al., 2008), thereby comprehensively enhancing the long-term resistance
478 of perennial plants. In poplars, GA and JA exhibit a bidirectional antagonistic relationship; both
479 regulate the plant growth-defense balance through the DELLA-MYC2 module (Zhao et al., 2021). GA
480 participates in JA signaling regulation by activating MYC2, which both inhibits AR formation and
481 implements negative feedback on JA signaling by upregulating GH3-like genes (Mauriat et al., 2014).

482 During root formation, high JA concentrations inhibit AR development via MYC2 (Gutierrez et al.,
483 2012). However, in Ussuri poplar (*Populus ussuriensis*), MYC2 promotes AR formation (Bannoud &
484 Bellini, 2021), indicating species-specificity in JA effects.

485 5.2 Future Research Directions

486 The functions of GA in poplar growth and development are now relatively well understood, but
487 the underlying molecular mechanisms are less revealed. Research on its role in stress responses
488 remains limited. Coordinating poplar growth and development with immune responses remains an
489 unresolved challenge (Yu et al., 2024). Building on current studies, future research on GA's role in
490 poplar should aim to deepen investigations into whether core GA signaling factors exhibit tissue-
491 specific functions, as well as GA's interaction networks with other hormones.

492 It will also be important to explore upstream/downstream genes interacting with the GA signaling
493 pathway and novel action mechanisms, including deep decipherment of the molecular basis of the GA-
494 DELLA interaction network, investigating the structural basis of DELLA-GA interactions, and
495 revealing downstream regulatory targets and signaling cascade reactions of DELLA (Dahal et al.,
496 2025). Furthermore, it is necessary to further elucidate the GA-mediated phase transition and flowering
497 regulation mechanisms in poplar. Although the regulatory role of GA in flowering has been extensively
498 studied in herbaceous plants, related knowledge in woody plants remains largely confined to fruit tree
499 species (Mutasa-Gottgens & Hedden, 2009). Since early flowering can significantly accelerate
500 breeding progress, elucidating the GA-dependent flowering mechanism in poplar is crucial for
501 developing early-flowering varieties, shortening the prolonged juvenile phase, expediting hybrid
502 breeding processes, and enhancing overall breeding efficiency (Zawaski et al., 2011). Such research
503 also provides valuable insights for exploring GA-regulated flowering mechanisms in other woody
504 plants.

505 In *Arabidopsis*, extensive research has been conducted on downstream effectors of the GA
506 signaling pathway. For instance, DELLA, a core GA signaling repressor, has been shown to interact
507 with the transparent TESTA protein GLABRA2 (TTG2) and components of the MYB-bHLH-WD40
508 (MBW) complex, thereby influencing pectin synthesis and plant development (Xu et al., 2025). In
509 *Arabidopsis*, GA promotes selective autophagic degradation of DELLA proteins through interaction
510 with ATG8, thereby enhancing seed germination and hypocotyl elongation (Zhang et al., 2025).
511 However, in poplar, the degradation of DELLA is currently known to follow only the classical 'GA-
512 GID1-DELLA' pathway. Therefore, whether the GA signaling pathway achieves precise and sustained
513 regulation of poplar root development through epigenetic modifications remains to be further
514 investigated.

515 At the same time, efforts should be made to further promote the practical application of GA
516 signaling mechanisms in the genetic improvement of forest trees. Field trials have confirmed that GA
517 regulation can be directly applied to poplar breeding: in development and stress tolerance breeding.
518 Reducing endogenous GA activity or accumulating DELLA proteins can lead to the development of
519 dwarfing, lodging-resistant, and high-density-planting-suitable cultivars. Overexpression of GA
520 degradation genes yields stably dwarfing poplars (Busov et al., 2003). GA can be used to selectively
521 improve wood traits precisely: overexpression of GA20ox enhances GA signaling, simultaneously
522 promoting internode elongation, xylem formation, and fiber elongation; overexpression of the GA
523 receptor GID1 accelerates xylem formation and trunk thickening (Eriksson, 2000; Mauriat & Moritz,
524 2009). GA can also promote cambium regeneration after ring barking in an auxin-dependent manner,
525 repairing stem damage and restoring secondary growth (Zhang et al., 2024). In vegetative propagation,
526 GA and auxin interact to negatively regulate root development; attenuating GA signaling significantly
527 promotes lateral root elongation, enhances rooting efficiency of cuttings, and accelerates seedling
528 propagation (Gou et al., 2009).

529 Furthermore, upregulating *GA2ox* or accumulating DELLA can enhance poplar drought tolerance
530 and mediate short-day bud dormancy regulation, thereby improving seasonal stress adaptation
531 (Eriksson et al., 2000; Zawaski & Busov, 2014). The GA-JA defense mechanism should be applied to
532 enhance the stress response of forest trees. Building on this foundation, we must further promote the
533 translation of fundamental GA theory into practical forest tree breeding. By leveraging CRISPR/Cas9
534 gene editing technology to target key sites in the GA pathway, we can efficiently transform existing
535 mechanistic research into practical, implementable molecular breeding strategies (Yao et al., 2023).

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550 **Conflict of interest**

551 The authors declare no conflict of interest.

552 **Reference**

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1041 **Figure 1. Overview of gibberellin biosynthesis, metabolism, and signal transduction.** GA
 1042 biosynthesis occurs in three stages: 1) In plastids, IPP is generated via the MEP pathway, while the MVA
 1043 pathway for IPP synthesis occurs in the cytoplasm, and GGPP synthesizes the key intermediate *ent*-
 1044 kaurene; 2) In the endoplasmic reticulum (ER), *ent*-kaurene is catalyzed by KO (*ent*-kaurene oxidase)
 1045 and KAO (*ent*-kaurenoic acid oxidase) to form GA₁₂; 3) In the cytoplasm, GA₁₂ is converted into active
 1046 GA (e.g., GA₁, GA₄) via *GA20ox* (*GA20-oxidase*) and *GA3ox* (*GA3-oxidase*). GA inactivation is
 1047 mediated by *GA2ox* (*GA2-oxidase*), which hydroxylates active GA into inactive forms (e.g., GA₈, GA₂₉).
 1048 In signal transduction, active GA binds to the receptor *GID1*, inducing a conformational change in *GID1*
 1049 that promotes the formation of a GA-*GID1*-DELLA complex. This complex triggers the ubiquitination
 1050 of DELLA proteins followed by their degradation via the 26S proteasome pathway, releasing their
 1051 transcriptional repression of GA-responsive genes, ultimately modulating plant growth, development,
 1052 and stress responses. Key enzymes/proteins and reaction sites involved in each step are labeled.

1053

1054 **Figure 2. GA signaling and its regulatory role in tree growth, development, and stress responses.**

1055 Schematic of GA-mediated pathways (via key biosynthetic enzymes *GA20ox/GA3ox* [GA activation]
 1056 and *GA2ox* [GA inactivation], and interacting factors) controlling multiple physiological processes in
 1057 trees, while interacting with other plant hormones (e.g., IAA, ABA, CK, JA): 1) Plant height regulation:
 1058 Key GA synthesis enzymes (*KS*, *GA20ox*, *GA3ox*) promote stem elongation by increasing GA content.
 1059 The *PtoHY5a-FT2* pathway induces *GA2ox* expression, thereby promoting GA inactivation and inducing
 1060 dwarfing phenotypes; 2) Dormancy Release and Bud Germination: Short-day conditions or low
 1061 temperatures promote *PttSVL* (by inhibiting *PttFT1* and *GA2ox*) to maintain dormancy; long-day (LD)
 1062 conditions or high temperatures induce *PtoHY5a-PtoFT2* (elevated GA) to trigger bud priming. ABA
 1063 antagonizes GA function in this process; 3) Vascular cambium development and secondary growth: GA
 1064 and IAA regulate DELLA and *Aux/IAAs* activity, respectively. Concurrently, DELLA forms complexes
 1065 with *ARF7* and *Aux/IAAs* to synergistically regulate cambial cell activity and xylem differentiation.
 1066 *GA20ox/GA3ox* promotes GA synthesis, enhancing vascular cambium activity. *GA2ox* reduces GA
 1067 content, inhibiting vascular cambium growth; 4) Root development and nutrient acquisition: Increasing
 1068 GA, *GID*, *GA20ox*, or *GA3ox* content, or decreasing DELLA content, inhibits adventitious and lateral
 1069 root growth. GA inactivation mediated by *GA2ox* promotes root development; 5) Biomass Accumulation
 1070 and Wood Quality Formation: GA positively regulates aboveground biomass accumulation and xylem
 1071 lignification with distinct organ specificity (promoting shoot growth while inhibiting root biomass
 1072 accumulation); 6) Abiotic/Biotic Stress Responses: *PsnERF76* enhances salt tolerance by elevating
 1073 GA/ABA levels; Drought induces upregulation of *GA20ox* and *GA3ox* while downregulating *GA2ox* to
 1074 modulate GA levels and improve drought tolerance; Transcription factor *PagKNAT2/6b* inhibits GA
 1075 synthesis by downregulating *PagGA20ox1*, enhancing drought **stress responses**; *PtoMYB142* promotes
 1076 *PtoGA2ox4* expression, reducing GA content and improving poplar drought tolerance. GA mediates

1077 growth-defense trade-offs by interacting with the miRNA319a–TCP module (regulating trichome
1078 development) and the DELLA–MYC2 complex (JA-mediated defense responses). Arrows indicate
1079 activation; blunt lines indicate inhibition. “*Pto*” denotes *Populus tomentosa*, “*Psn*” denotes *Populus*
1080 *simonii* × *P. nigra*, “*Pag*” denotes *Populus alba* × *Populus glandulosa* (84K poplar), “*Pm*” denotes
1081 *Populus tomentosa*, other genes are conserved across *Populus spp.* ABA (abscisic acid), BR
1082 (brassinolide), CK (cytokinin), IAA (indole-3-acetic acid), JA (jasmonic acid), DELLA (GA signal
1083 inhibitor), ARF7 (Auxin Response Factor 7).

For Peer Review

Gibberellin in Regulating Poplar Growth, Development, and Stress

Responses Resistance

Lixia Zhang¹, Xiaoqi Zhou¹, Guanming Chen¹, Han Han^{1,*}

¹Co-Innovation Center for Sustainable Forestry in Southern China, College of Life Science, Nanjing Forestry University, Nanjing 210037, China

*Correspondence: hhan@njfu.edu.cn

Abstract: Gibberellic acid (GA) plays a central role in regulating growth, development, and stress responses resistance. Poplars exhibit woody-specific GA regulatory mechanisms due to their long-life cycle, continuous vascular cambium activity, and seasonal dormancy. While the GA biosynthetic pathway is highly conserved between herbaceous and woody plants, key poplar synthesis genes such as KS1 and KS2 show vascular tissue-specific expression. Centered on the GID1-DELLA signaling pathway, GA modulates downstream genes via ubiquitination and interacts synergistically or antagonistically with hormones like IAA, ABA, and JA to regulate poplar growth and stress responses-resistance. Under abiotic stress, poplars downregulate GA levels and accumulate DELLA proteins to enhance resistance. During biotic stress, GA integrates with miRNAs and transcription factors, maintaining growth-defense balance through the DELLA-MYC2 module. Addressing current gaps in holistic GA regulatory network studies and weak understanding of biotic stress mechanisms, this review summarizes poplar GA synthesis, metabolism, and signaling pathways, elucidating their roles in woody-specific traits and stress responses-resistance. We aim to provide a theoretical support for GA molecular mechanism research in woody plants and forest tree breeding.

Keywords: Gibberellic acid (GA); gibberellins; woody; signaling pathway; poplar; stress responses-resistance; growth and development

1. Introduction

Poplar (*Populus spp.*), as a significant broadleaf fast-growing tree species with strong adaptability, possesses both high economic and ecological value. It is widely utilized in industrial raw materials, papermaking, engineered wood products, and furniture manufacturing. Beyond its role in ecological construction—including wind erosion prevention, shifting sand fixation, water conservation, and climate regulation—certain species also exhibit medicinal properties (Du et al., 2012; Xu et al., 2014). Concurrently, poplars possess a compact genome and a well-established genetic transformation system. They exhibit typical woody plant characteristics such as perennial growth, continuous vascular cambium activity, and efficient asexual reproduction, making them a model species for studying woody plant growth, development, and stress response mechanisms (Biselli et al., 2022).

33 Plant hormones serve as core regulators of growth, development, and environmental adaptation.
34 Among these, gibberellins (GAs)—a class of natural diterpene hormones—exhibit potent physiological
35 activity and are extensively involved in plant growth, development, and regulatory processes (Kende &
36 Zeevaart, 1997; Shah et al., 2023). To date, over 136 GAs have been identified, though most are
37 biosynthetic intermediates or inactive metabolites (Hedden & Sponsel, 2015). Only GA₁, GA₃, GA₄,
38 and GA₇ are confirmed to possess direct biological activity (L. Yang et al., 2021). During the “Green
39 Revolution” in mid-20th century, the application of GA-related genes in crop dwarfing breeding drove
40 global agricultural yield increases, demonstrating the immense potential of GA in breeding. Current
41 research extensively explores GA's functions, which span multiple stages of the plant life cycle. These
42 include promoting seed germination (Gong et al., 2022), fruit development and ripening (Fenn &
43 Giovannoni, 2021), stem and leaf growth and root elongation (Zluhan-Martínez et al., 2021). GAs also
44 participate in bud dormancy induction and release (Rinne et al., 2011), stress ~~responses~~response (Nagar
45 et al., 2021), and plant regeneration processes (Bassaganya-Riera et al., 2014). GA serves as an
46 environmentally friendly plant growth regulator widely applied in agricultural and forestry production
47 to enhance crop and fruit tree yield and quality (Kildegaard et al., 2021).

48 Early studies predominantly focused on annual herbaceous model plants like *Oryza sativa* and
49 *Arabidopsis thaliana*. Compared to herbaceous plants, ~~woody plants'~~poplar's perennial nature (Busov
50 et al., 2006), seasonal dormancy (Rinne et al., 2016), and continuous secondary growth (Wei & Wei,
51 2023) necessitate significant functional specificity for GA, making its regulatory mechanisms
52 incompatible with direct extrapolation from herbaceous plant research. Current research on gibberellin
53 functions in woody plants has primarily focused on poplar, thus our review specifically centered on
54 poplar and comprehensively detailing its gibberellin regulatory mechanisms, including the synthesis,
55 metabolism, and signal transduction mechanisms of GA. In recent years, key genes in GA synthesis,
56 metabolism, and signaling pathways (*GA20ox*, *GA3ox*, *GA2ox*, *GIDI*, *DELLA*) have been
57 progressively identified in poplar. Their roles in growth processes such as apical dominance, vascular
58 cambium development, and dormancy release, as well as in responses to abiotic stresses like drought
59 and salinity, have been gradually elucidated (Zawaski & Busov, 2014; Zhang et al., 2024). However,
60 significant gaps remain in current research: First, the GA regulatory network is fragmented, lacking
61 holistic integration of synthesis-metabolism-signaling pathways, with unclear tissue-specific regulatory
62 mechanisms. Second, the interaction network between GA and other hormones has not been
63 systematically elucidated, and core interaction nodes remain undefined. Third, research on biological
64 stress response mechanisms is relatively weak, and the molecular regulatory logic of the growth-
65 defense balance remains unclear. Fourth, there is insufficient linkage between basic research and its
66 application in molecular breeding of poplar. ~~This review. Given the central role of GA in poplar growth,~~
67 ~~development, and stress resistance regulation, coupled with the unique research value of woody plants,~~
68 ~~this paper focuses on the woody model plant poplar. It systematically reviews the synthesis,~~

69 ~~metabolism, and signal transduction mechanisms of GA, emphasizing its distinctive growth regulatory~~
70 ~~functions in woody plants. The study also~~ elucidates GA's role in stress responses and hormone
71 interaction networks, and explores its potential applications in molecular breeding. We aim to provide
72 theoretical support for hormone regulation studies in woody plants and genetic improvement of poplar.

73 2. Biosynthesis, Metabolism, and Signaling Mechanisms of Gibberellin

74 2.1 Biosynthetic Pathway of Gibberellin

75 GA biosynthesis is a complex metabolic process involving multiple organelles and
76 ~~diversesynergistic enzymes participation~~ (Figure 1), divided into three main stages sequentially
77 completed in plastids, endoplasmic reticulum, and cytoplasm. This pathway is highly conserved in both
78 herbaceous and woody plants (Hedden & Thomas, 2012). The first stage occurs in the plastids,
79 primarily through the interaction between the methylenepyruvate (MEP) pathway and the mevalonate
80 (MVA) pathway to generate isopentenyl pyrophosphate (IPP). IPP is further synthesized into
81 geranylgeranyl pyrophosphate (GGPP). GGPP is sequentially catalyzed by ent-caryophyllene
82 diphosphate synthase (*ent-CPS*) and ent-kaurene synthase (*ent-KS*) to yield *ent*-kaurene, a key
83 intermediate for GA synthesis (Shah et al., 2023). Notably, this stage exhibits significant specificity in
84 poplar: the *KS1* and *KS2* genes are highly expressed in vascular tissues, directly participating in xylem
85 formation and secondary stem growth—a core characteristic distinguishing poplar from herbaceous
86 plants (Zhang et al., 2024). The second stage occurs within the endoplasmic reticulum (ER). First, *ent*-
87 kaurene is oxidized to GA₁₂-aldehyde by *ent*-kaurene oxidase (KO) and *ent*-kaurenoic acid oxidase
88 (KAO), catalyzed by members of the cytochrome P450 monooxygenase family. This is further
89 converted to GA₁₂ (Hartweck, 2008). This process is conserved in both herbaceous and woody plants.
90 The third stage occurs in the cytoplasm, where GA₁₂ is catalyzed by GA20-oxidase (*GA20ox*) and
91 GA3-β-hydroxylase (*GA3ox*), yielding bioactive molecules such as GA₁ and GA₄ (Gou et al., 2011).
92 *GA20ox* plays a key regulatory role in GA precursor synthesis, with its expression directly influencing
93 active GA levels. Concurrently, active GA molecules exert negative feedback regulation by
94 suppressing *GA20ox* and *GA3ox* expression, thereby maintaining GA homeostasis. This feedback
95 mechanism is highly conserved in poplar and adapts to its continuous growth requirements. Given the
96 high-specificity expression of poplar *KS1/KS2* in vascular tissues, locally synthesized GA may be
97 transported to the shoot apex or roots via specific carrier proteins. NPF and SWEET family transporters
98 have been identified in Arabidopsis as efflux carriers for GA, participating in inter-tissue GA transport
99 and regulating GA concentration equilibrium (Binenbaum et al., 2018). It is speculated that a similar
100 transport mechanism may exist in poplar, which represents one of the core directions for future GA
101 regulation research in poplar.

102 2.2 Metabolic Inactivation of Gibberellin

103 The inactivation of gibberellins is primarily mediated by the 2-oxoglutarate-dependent
104 dioxygenase *GA2-oxidase* (*GA2ox*). This enzyme terminates the physiological effects of GA signaling
105 by hydroxylating bioactive GAs and converting them into inactive products (Song et al., 2024). The
106 *GA2ox* gene family is widely distributed across the plant kingdom. In 2001, Busov et al. first
107 demonstrated that overexpression of *PtaGA2ox1* causes dwarfism in poplar trees, highlighting its
108 significant research value in trees (Busov et al., 2003); In 2011, 11 poplar *GA2ox* genes were
109 identified, including seven C19 *GA2oxs* members and four C20 *GA2oxs* members. These genes not
110 only regulate shoot height and vascular development but also influence root development. In-depth
111 exploration of *GA2oxs* holds significant implications for research on the growth and development of
112 woody plants (Gou et al., 2011).

113 2.3 Gibberellin Signaling

114 The core mechanism of GA signal transduction is mediated by the GA receptor *GID1* and the
115 transcription repressor *DELLA* protein, a process conserved in both herbaceous and woody plants. *GID1*
116 belongs to the phytohormone receptor family and specifically recognizes bioactive GA molecules.
117 Upon binding to GA, *GID1* undergoes a conformational change, forming the *GA-GID1-DELLA*
118 complex with *DELLA* proteins (Murase et al., 2008). This complex is recognized by F-box proteins
119 (e.g., *SLY1/GID2*) and recruited to the SCF ubiquitin ligase complex, triggering ubiquitin-mediated
120 degradation of *DELLA* proteins. This process releases their transcriptional repression of GA-
121 responsive genes (Shah et al., 2023). *DELLA* proteins act as key negative regulators in the GA
122 signalling pathway. In *Arabidopsis thaliana*, *DELLA* binds to transcription factors *PIF4*, *BZR1*, and
123 *ARF6* to inhibit hypocotyl cell elongation responses (Oh et al., 2014). It also influences the expression
124 of key flowering regulators, such as *SOC1* and *FLC*, which are involved in the regulation of
125 reproductive development (Li et al., 2016). In poplar, they interact with multiple transcription factors to
126 modulate the expression of genes associated with cell proliferation, elongation and differentiation
127 (Zhang et al., 2024). Similar functions have been observed in other woody species. For example, in
128 *Pinus tabulaeformis*, the interaction between the phytochrome-interacting factors (*PIFs*) and the *DELLA*
129 protein inhibits light-mediated signalling and elongation responses (Guo et al., 2024).

130 The GA signalling pathway exhibits characteristic feedback regulation mechanisms in both
131 herbaceous and woody plants. When GA levels are insufficient, the accumulation of *DELLA* proteins
132 simultaneously activates the transcription of GA synthesis-related genes (e.g. *GA20ox* and *GA3ox*),
133 thereby promoting GA biosynthesis. When GA levels are sufficient, *GA-GID1*-mediated degradation
134 of *DELLA* terminates the positive feedback pathway that promotes GA synthesis, thus achieving
135 steady-state regulation of GA signalling (Busov et al., 2006; Hartweck, 2008). The synthesis,
136 metabolism, and signal transduction of GA form a highly coordinated regulatory network, providing
137 the molecular basis for GA-mediated growth and development in poplar trees.

138

139 3. Role of the GA signaling pathway in poplar growth and development

140 Gibberellic acid plays a central regulatory role in the growth and development of poplar trees
141 (Figure 2): On one hand, it promotes cell division and elongation, accelerates xylem development,
142 enhances stem elongation, and increases plant biomass accumulation (Su et al., 2025); On the other
143 hand, regulates cambial cell differentiation and regeneration through interactions with the auxin
144 signaling pathway, thereby promoting secondary growth processes (Zhang et al., 2024). These
145 mechanisms provide crucial theoretical foundations for breeding fast-growing, high-yielding, and
146 stress-tolerant poplar varieties.

147 3.1 Plant Height Regulation

148 GA is a key hormone regulating internode cell elongation in poplar, primarily promoting stem
149 internode elongation by facilitating cell wall relaxation, microtubule reorganization, and the expression
150 of related cell wall hydrolases. This process regulates plant height and canopy architecture (Eriksson et
151 al., 2000). Its regulatory effects can be precisely controlled through key genes involved in its synthesis,
152 metabolism, and signaling pathways, and it has been applied in dwarfing breeding and tree form
153 improvement of fast-growing poplars (Busov et al., 2006).

154 Controlling the expression of key enzymes and receptors involved in GA synthesis and signal
155 transduction pathways can be used to regulate the height of poplar trees. Overexpression of the GA
156 synthesis key gene *PtoKSI* enhances GA signaling, significantly promoting overall poplar growth
157 (Zhang et al., 2024); Similarly, overexpression of *PttGA20ox* and *PttGID1* both promote internode
158 elongation and xylem formation by enhancing the GA signaling pathway (Eriksson, 2000; Mauriat &
159 Moritz, 2009). Furthermore, overexpression of *PtGA3ox*, the terminal enzyme in GA synthesis,
160 significantly increases active GA levels, thereby enhancing both plant height and stem diameter in
161 poplar (Hu et al., 2022). However, it is important to note that enhanced GA signaling disrupts
162 development of other organs. For instance, overexpression *Pinus densiflora GA20ox* (*PdGA20ox*) in
163 poplar leads to elongated stems, but reduced leaf size, and poor rooting; suggesting tissue- or stage-
164 specific regulation of GA on secondary growth (Jeon et al., 2016).

165 In contrast, inhibiting GA activity or signalling significantly suppresses growth and produces
166 dwarf phenotypes. Poplars that overexpress genes degrading GA such as *PtaGA2ox* exhibit moderate
167 or semi-dwarf phenotypes (Zawaski & Busov, 2014); Similarly, the overexpression of *ClGA2ox12* in
168 hybrid poplar (*Populus tremula* × *Populus tremuloides*) resulted in reduced plant height and stem
169 diameter (Peng et al., 2024). In the GA signalling pathway, DELLA protein accumulation or the
170 overexpression is key to plant height regulation. *PtoGAI* overexpression severely inhibits cambial

171 proliferation, resulting in significantly reduced plant height and stem diameter (Zhang et al., 2024).
172 Consistently, the dwarfing phenotype in tetraploid 84K poplar (*P. alba* × *P. glandulosa*) is directly
173 correlated with decreased GA and IAA content, as well as the upregulation of DELLA proteins and the
174 downregulation of GID1 receptors (Ren et al., 2022).

175 3.2 Phase Transition, Flowering, Bud Formation and Dormancy Release and Bud Formation

176 GA also participates in the transition from juvenile to mature stages in poplar trees and regulates
177 flowering (Zawaski et al., 2011). Juvenile and adult trees are typically distinguished by their flowering
178 capacity, that adult poplars convert a portion of their axillary meristems into inflorescence meristems
179 during specific seasons (Sheng et al., 2023). The vegetative growth phase in trees can last from several
180 years to decades, thus early flowering techniques can effectively accelerate breeding and propagation
181 processes (Zawaski et al., 2011). Unlike in herbaceous plants such as *Arabidopsis* (Jang et al., 2009; Li
182 et al., 2008) and *Chrysanthemum* (*Chrysanthemum morifolium*) (Dong et al., 2017; Yang et al., 2014),
183 where GA promotes flowering, GA typically inhibits flowering in woody plants (Brunner & Nilsson,
184 2004). In poplar, overexpression of DELLA or GA degradation genes like *GA2ox* increases flowering
185 rate and promotes early flowering (Zawaski et al., 2011). In *Arabidopsis*, GA promotes flowering via
186 multiple pathways including *DELLA-GAF1-TPR* (Fukazawa et al., 2021), *DELLA-CO-FT*, and
187 *miR156-SPL* (Castro-Camba et al., 2022; Xu et al., 2016). In woody plants like apple, sweet orange,
188 and chestnut, GA primarily inhibits flowering by upregulating *MdTFL1* (S. Zhang et al., 2019),
189 suppressing *CiFT* (Muñoz-Fambuena et al., 2012), or affecting the *CmmiR156-SPL* pathway (Chen et
190 al., 2019). Only in a few species like *Jatropha curcas* (Hui et al., 2018) and Tree peony (*Paeonia*
191 *suffruticosa*) (Xue et al., 2018) does GA promote flowering or reblooming. Thus, GA participates in
192 phase transition and flowering initiation in poplar.

193 Plants respond to low temperatures and adverse environments during winter by entering
194 dormancy. Both the initiation and release of dormancy are finely regulated by environmental signals
195 and hormonal networks. Among these, GA serves as the core hormone promoting dormancy release
196 and bud germination, exhibiting a classic antagonistic relationship with abscisic acid (ABA). ABA
197 promotes dormancy maintenance by inducing GA degradation pathways, while GA accumulation
198 accelerates dormancy release and shoot elongation. The equilibrium between these two hormones
199 determines the seasonal growth rhythm of poplar trees (Chen et al., 2023; Ding et al., 2024; Zhang et
200 al., 2017). Together, they regulate the seasonal growth-dormancy cycle (Singh et al., 2016).

201 As a central gene regulating flowering, FT not only participates in floral timing regulation but also
202 serves as a key target for dormancy induction. The mechanism by which GA promotes dormancy
203 release and bud priming in poplar has been elucidated and is closely linked to the FT signaling
204 pathway: Rinne et al. (2011) revealed that GA breaks dormancy by enhancing 1,3-β-glucanase activity

205 to degrade callose, thereby opening sieve pathway channels to facilitate PttFT protein transport (Rinne
206 et al., 2011); Eriksson et al. (2015) further indicated that GA can promote bud germination
207 independently of the *FT2* pathway. Exogenous GA application significantly enhances bud germination,
208 regulating hybrid poplar bud elongation in parallel with the *FT2* pathway (Eriksson et al., 2015); The
209 cold-induced transcription factor *PttSVL* suppresses the expression of *PttFT1* and *PttGA20ox*,
210 antagonistically regulating bud germination through GA and ABA signaling. It serves as an integration
211 node between environmental signals and the hormone network (Singh et al., 2018). Concurrently, FT
212 signaling influences shoot growth by inversely regulating GA content. For instance, *PtaFT2* modulates
213 shoot apical meristem development and inhibits internode elongation via the GA13-hydroxylation
214 pathway (Gómez-Soto et al., 2022). GA also plays a crucial role in sustaining continuous shoot
215 elongation (Cao et al., 2023). Beyond FT signaling, *PtoHY5a* directly activates *PtoFT2* expression to
216 suppress short-day-induced growth arrest. Simultaneously, it reduces apical GA levels by upregulating
217 key GA inactivation genes and downregulating GA synthesis genes, thereby inhibiting bud emergence.
218 This *HY5a*-GA module adapts to the seasonal growth patterns regulated by photoperiod in woody
219 plants (Gao et al., 2024).

220 3.3 Development of the Vascular Cambium and Secondary Growth

221 The secondary growth of poplar trees primarily relies on the sustained activity of the vascular
222 cambium, which produces secondary xylem and secondary phloem through bidirectional
223 differentiation. Its activity directly determines wood yield and quality (Sun et al., 2025). Recent studies
224 indicate that GA signaling plays a central role in regulating cambial cell activity and xylem
225 differentiation by influencing processes such as cell division, elongation, and lignification. Its
226 regulatory mechanisms have been progressively elucidated through ongoing research. Israelsson et al.
227 (2005) first demonstrated that GA exerts a pivotal role during early wood formation, particularly in
228 regulating xylem differentiation and fiber cell elongation (Israelsson et al., 2005). Mauriat and Moritz
229 (2009) further revealed GA's dual role in xylem development through histological observations and
230 gene expression analysis: it enhances meristematic activity in cambial cells to initiate secondary xylem
231 formation, while simultaneously promoting elongation and cell wall thickening in mature xylem fiber
232 cells. Notably, its regulation of fiber cell length occurs independently of the IAA pathway (Mauriat &
233 Moritz, 2009).

234 Recent studies have progressively elucidated the molecular mechanisms by which the GA
235 signaling pathway regulates the development of the vascular cambium and secondary growth in poplar
236 trees: Du et al. (2024) discovered that *PdRabG3f* regulates internode elongation and xylem
237 development in poplar by interfering with endogenous GA levels (Du et al., 2024); Su et al. (2025)
238 further revealed that localized GA synthesis in stems is a key factor regulating xylem development,
239 clarifying that tissue-specific distribution of GA levels is essential for maintaining normal cambium

240 activity (Su et al., 2025). The synergistic regulation of GA and IAA constitutes the core mechanism
241 governing poplar cambium development: IAA forms a polar gradient in the cambium region via polar
242 transporters such as *PINI* (*PIN-FORMED 1*), with its maximum concentration located in the cambium
243 cell layer, thereby determining stem cell differentiation fate (Hartweck, 2008; Mäkilä et al., 2023).
244 Björklund et al. (2007) revealed that GA regulation of poplar cambium depends on IAA; GA alone
245 cannot induce cambial regeneration but significantly enhances IAA-induced expression of cambium-
246 related genes. The two exhibit marked synergistic effects, share multiple transcriptional regulatory
247 elements, and show highly overlapping downstream transcriptional responses (Björklund et al., 2007).
248 Zhang et al. (2024) further elucidated the molecular basis of this synergistic mechanism: the IAA
249 response factor ARF7 interacts with the DELLA protein RGL1 via its MR domain while
250 simultaneously binding to the *Aux/IAA* family member IAA9 through its PB domain. This forms the
251 ARF7-RGL1-IAA9 ternary complex, serving as a key platform for integrating GA and IAA signaling
252 (Zhang et al., 2024). GA promotes IAA accumulation in the cambium region by upregulating *PINI*
253 expression and positively regulates *ARF7* and *WOX4* expression, thereby enhancing cambium cell
254 activity (Hu et al., 2022; Mäkilä et al., 2023). DELLA proteins negatively regulate *PINI* expression,
255 forming a GA-IAA feedback loop that precisely controls the sustained activity of the cambium (Zhang
256 et al., 2024).

257 Multiple PIN family members exist in the poplar genome (Liu et al., 2014). Despite functional
258 redundancy, their tissue expression is highly differentiated. For example, *PttPIN1* and *PttPIN2* are
259 specifically expressed in the cambium and its derived xylem, participating in polar IAA transport
260 within vascular tissues (Schrader et al., 2003). The tissue-specific distribution of GA and expression of
261 its biosynthetic genes further safeguard vascular cambium development: active GA forms (e.g., GA₁
262 and GA₄) accumulate in xylem regions, while GA precursors (e.g., GA₉, GA₂₀) predominantly localize
263 in phloem (Israelsson et al., 2005), closely aligning with xylem differentiation functions. GA activity is
264 primarily regulated by three key enzymes: *PdGA20ox* overexpression significantly increases poplar
265 xylem cross-sectional width and cell number (Jeon et al., 2016); *GA3ox* expression levels directly
266 determine the accumulation of active GA (Israelsson et al., 2004); inhibiting *GA2ox* (e.g., *PtGA2ox4*,
267 *PtGA2ox5*) enhances meristem cell proliferation and promotes secondary growth (Gou et al., 2011).
268 These three enzymes synergistically regulate GA activity within vascular tissues, determining wood
269 formation efficiency.

270 3.4 Root Development and Nutrient Acquisition

271 Most poplars can reproduce asexually, and the ability to form adventitious roots (AR) through
272 cuttings is a key factor for their field establishment and survival, holding significant importance for
273 large-scale forestry seedling propagation (Bannoud & Bellini, 2021). Adventitious root formation
274 represents a bottleneck for efficient propagation in many woody plants. Elucidating the molecular

275 mechanisms by which plant hormones regulate adventitious root formation can help optimize asexual
276 propagation systems, holding significant value for forestry production (Zhang et al., 2023). Current
277 research indicates that IAA acts as a positive regulator in adventitious root induction, while cytokinins
278 (CK) and GA primarily exert inhibitory effects (Liu et al., 2024).

279 The molecular mechanism by which GA inhibits adventitious root formation in poplar has been
280 elucidated: binding of GA to its receptor *GID1* induces degradation of DELLA proteins, thereby
281 releasing DELLA's inhibition of polar IAA transport. This leads to disrupted IAA distribution in the
282 cutting base, ultimately suppressing adventitious root primordia formation (Zhang et al., 2023).
283 Consequently, enhanced GA signaling significantly inhibits rooting, while its suppression promotes
284 rooting. Mauriat et al. (2014) ~~demonstrated found that the inhibitory effect of enhanced GA signaling~~
285 ~~on rooting, finding that~~ hybrid poplars overexpressing the Arabidopsis GA synthesis gene *AtGA20ox1*
286 exhibited accelerated plant growth rates but accompanied by a marked decrease in rooting efficiency;
287 Similarly, overexpression of *PttGID1.1* or *PttGID1.3* also markedly suppressed adventitious root
288 formation (Mauriat et al., 2014). ~~Conversely, GA synthesis inhibitors like paclobutrazol, when applied~~
289 ~~exogenously, promote adventitious root formation in hybrid poplar while inhibiting secondary root and~~
290 ~~shoot growth. They are frequently used for in vitro rooting of hybrid poplar (Vaiciukyne et al., 2019).~~
291 Consistently~~In contrast~~, exogenous application of GA significantly inhibits adventitious root formation
292 (Žiauka & Kuusienė, 2010). GA regulation of lateral roots (LR) mirrors its effect on adventitious roots:
293 GA-deficient (*35S:PcGA20ox1*) and GA-insensitive (*35S:rg11*) poplar plants exhibit markedly increased
294 lateral root number and elongation alongside reduced plant height, with these effects reversible upon
295 exogenous GA treatment (Gou et al., 2009). Conversely, GA synthesis inhibitors like paclobutrazol,
296 when applied exogenously, promote adventitious root formation in hybrid poplar while inhibiting
297 secondary root and shoot growth. They are frequently used for in vitro rooting of hybrid poplar
298 (Vaiciukyne et al., 2019). These studies collectively demonstrate GA's negative regulatory role in
299 poplar root development, with particularly pronounced inhibition during adventitious root formation
300 (Bannoud & Bellini, 2021). As the core organ for nutrient uptake and stress responses~~resistance~~, the
301 root system's negative regulation by GA provides a key target for balancing aboveground growth with
302 belowground stress tolerance.

303 3.5 Biomass Accumulation and Wood Quality Formation

304 Genetically engineered plant hormone pathways represent a key direction in current molecular
305 breeding of forest trees. Molecular approaches can significantly shorten the cultivation cycles required
306 in traditional breeding while enabling precise control over specific traits. Current tree genetic
307 engineering research focuses on modifying the lignin biosynthesis pathway to reduce lignin content and
308 monomer composition, thereby optimizing wood processing properties and enhancing pulp conversion
309 efficiency. Research indicates that GA levels correlate with ~~forestry breeding~~, pulp production, and

310 biofuel yield, offering novel insights for genetic improvement in woody plants (Eriksson et al., 2000).
311 GA not only regulates cell elongation, xylem formation, and the expression of stress-related genes but
312 also directly participates in these processes, thereby influencing plant biomass accumulation (Lin et al.,
313 2025).

314 GA exhibits distinct organ specificity in regulating material accumulation in poplar: it positively
315 regulates above-ground biomass accumulation by optimizing wood processing properties through
316 modulation of lignin content and monomer composition; conversely, it negatively regulates below-
317 ground root biomass, consistent with root development regulation. This characteristic provides precise
318 targets for breeding fast-growing, high-quality poplar varieties (Eriksson et al., 2000). Adjusting the
319 ratio of lignin monomers (S/G ratio) can reduce cell wall resistance while enhancing wood quality,
320 without affecting biomass accumulation (Tang et al., 2025). The core value of GA in regulating wood
321 quality has been validated: Field trials by Cho et al. (2019) confirmed that co-overexpressing
322 *PdGA20ox1* and *PtrMYB221* in poplar synergistically optimizes GA levels and the lignin synthesis
323 network. This resulted in above-ground biomass doubling compared to wild-type, significantly reduced
324 lignin content, increased total cellulose proportion, and approximately 8% higher saccharification
325 efficiency, without noticeable growth defects (Cho et al., 2019), representing a classic case of GA
326 application for wood quality improvement. GA signaling imbalance disrupts material accumulation and
327 xylem development: excessive suppression of above-ground GA signaling impairs xylem
328 differentiation, such as *CIGA2ox12* overexpression in poplar significantly inhibiting vessel
329 differentiation and reducing lignin deposition (Peng et al., 2024); Elevated GA levels resulting from
330 suppressed *PtGA2ox2* and *PtGA2ox7* activity in roots decrease root biomass (Gou et al., 2011), further
331 confirming its organ-specific regulatory characteristics.

332

333 4. Role of the GA Signaling Pathway in Abiotic and Biotic Stress Responses~~Resistance~~ 334 Regulation

335 GA not only regulates poplar growth and development but also mediates responses to abiotic and
336 biotic stresses by interacting with hormones and integrating transcription factor and non-coding RNA
337 networks. It establishes a dynamic equilibrium between growth and defense, playing a crucial role in
338 enhancing plant stress response~~resistance~~ to both biotic and abiotic stresses (Ding et al., 2016; Gou et
339 al., 2009).

340 4.1 Abiotic Stress Response

341 Drought and saline-alkali stress are two of the main abiotic factors that limit forestry production
342 (Fang et al., 2021; X. Yang et al., 2021). In poplar, GA plays a role in regulating abiotic stress by

343 modulating its own content, hormone interactions and transcription factor networks, and exhibits a
344 typical “growth-stress trade-off” effect. Phenotypically, a trade-off is evident: Poplar trees that
345 overexpress GA exhibit accelerated growth and increased leaf area, but reduced drought tolerance. In
346 contrast, GA-deficient plants exhibit limited growth yet superior drought ~~stress response-resistance~~
347 (Eriksson et al., 2000; Zhang et al., 2024). As an evolutionary adaptation to drought, the heterophyllous
348 trait in *Populus euphratica* shows significant positive correlations between GA₃ content and leaf length
349 and spongy tissue thickness, reflecting species adaptation regulated by GA (Han et al., 2021).

350 Drought induces poplar to downregulate GA synthesis genes and upregulate metabolic genes,
351 resulting in lower active GA levels and increased accumulation of the protein DELLA. DELLA
352 proteins inhibit cell elongation, thereby reducing the transpiration area of the plant and lowering
353 stomatal aperture to minimise water loss, ultimately enhancing drought tolerance (Zawaski & Busov,
354 2014). Hormone interactions play a crucial role in this process. The primary plant hormone involved in
355 the response to drought, ABA, suppresses GA-mediated cell growth by promoting DELLA
356 accumulation, thereby enhancing stress ~~response-resistance~~ (Liao et al., 2023).

357 Different transcription factors participate in GA-mediated drought tolerance: *PagKNAT2/6b*
358 suppresses GA synthesis by downregulating *PagGA20ox1*, altering poplar morphology to enhance
359 drought tolerance (Song et al., 2021); *PtoMYB142* binds the MBS element in the *PtoGA2ox4* promoter
360 to promote its expression, thereby reducing GA content while regulating leaf and stomatal structure to
361 enhance poplar drought ~~stress response-resistance~~ (Song et al., 2024). Furthermore, in *Populus*
362 *euphratica*, the GA repressed B3-domain transcription factor *FUSCA3* (*FUS3*) coordinates IAA and
363 ABA signaling to maintain root growth under drought (Liu et al., 2025).

364 Compared to drought, research on GA regulatory mechanisms in salt stress in poplars remains less
365 studied. *PsnERF76* has been identified to enhance salt tolerance by upregulating ABA and GA
366 synthesis genes (X. Zhang et al., 2019). In other plants, nitrate regulates growth responses through GA-
367 mediated DELLA accumulation (Camut et al., 2021), and it will be interesting to explore whether
368 similar mechanisms exist in poplars. Given that global saline-alkali land spans 1.125 billion hectares
369 (Quamruzzaman et al., 2021), elucidating GA's regulatory role in poplar salt tolerance holds significant
370 implications for afforestation on marginal lands (Su et al., 2022).

371 4.2 Biotic Stress ~~Responses~~

372 Research on GA in poplar responses to biotic stress is limited. Existing studies indicate that GA
373 plays a central role in regulating the growth-defense balance in poplars by integrating miRNA,
374 transcription factor, and hormone interaction networks, making it crucial for poplar environmental
375 adaptation. GA enhances insect ~~stress response-resistance~~ regulation by synergizing with the
376 microRNA319a-TCP module: miR319a enhances leaf trichome density and insect ~~stress response-~~

377 **resistance** by suppressing expression of its target genes *PtTCPs*; simultaneously, GA signaling inhibitor
 378 RGA interacts with *PtmiR319a* to jointly suppress trichome differentiation mediated by the GL1-GL2
 379 pathway. The balance between these two factors determines insect **stress response** and growth
 380 rate (Fan et al., 2020). In disease **resistance** regulation, transcription factor-mediated
 381 GA signaling balances immunity: *PagWRKY33a/b* participates in GA signaling by activating NRG1.1
 382 and GASA14 expression. Its absence induces spontaneous immunity in poplar, enhancing **stress**
 383 **response** to anthracnose but causing growth inhibition, confirming GA's central role in
 384 balancing immunity and growth (Yu et al., 2024). Additionally, GA significantly suppresses
 385 *PtrPARVUS2* transcription. Highly expressed in vascular tissues and epidermis, *PtrPARVUS2*
 386 participates in cell wall biosynthesis, suggesting GA may regulate defense structure formation via cell
 387 wall biosynthetic pathways (Wang & Coleman, 2024).

388 The interaction between GA and jasmonic acid (JA) constitutes a core molecular mechanism for
 389 growth-defense balance: JA is a central hormone in plant defense responses (Zhao et al., 2021). When
 390 GA levels are low, DELLA proteins can interact with MYC2, a core transcription factor in JA
 391 signaling, enhancing JA-mediated defense responses: When GA levels increase, DELLA proteins are
 392 degraded, weakening the JA pathway's defense capacity and exhibiting a classic “growth-defense trade-
 393 off effect” (Navarro et al., 2008). This mechanism adapts poplar to survival strategies of “growth-
 394 priority” under low-stress environments and “defense-priority” under high-stress environments,
 395 representing a core direction for future research.

396 5. Discussion and Summary

397 5.1 Integration of the Core GA Biology in Poplar ~~Core Integration of the GA Signaling Regulatory-~~ 398 ~~Network in Popla~~

399 The poplar GA signaling pathway centers on the conserved ‘GA–GID1–DELLA’ pathway while
 400 evolving unique regulatory mechanisms adapted to its perennial characteristics. Through complex
 401 cross-interactions with hormones such as ABA, IAA, and JA, it achieves precise regulation of growth,
 402 development, and stress responses. In-depth analysis of the molecular mechanisms and specificity
 403 underlying these hormonal interactions not only refines the understanding of the GA signaling
 404 regulatory network in poplar but also provides a crucial theoretical foundation for elucidating the
 405 conservation and divergence in GA regulation between woody and herbaceous plants. By integrating
 406 gene homology and functional differentiation characteristics, the GA biology in poplars can be
 407 summarized from three dimensions: well-established mechanisms, mechanisms that can be safely
 408 inferred to be conserved from herbaceous, and specialized mechanisms adapted to the woody perennial
 409 lifestyle.

410 5.1.1 Well-established Mechanisms

411 Similar to the annual herbaceous model plant Arabidopsis, GA signaling in poplar relies on the
412 highly evolutionarily conserved GA-GID1-DELLA core pathway (Mauriat & Moritz, 2009).
413 Furthermore, the key enzyme families involved in GA biosynthesis and degradation are highly
414 homologous between herbaceous and woody plants. Among these, the GA20ox and GA3ox families
415 are responsible for the synthesis of active GAs, while the GA2ox family mediates the irreversible
416 inactivation of GAs (Busov et al., 2003). It is through the precise regulation of the expression and
417 activity of these core enzymes and signal transduction genes that GA mediates plant growth,
418 development, and stress responses. This constitutes the molecular basis for the conservation of GA
419 regulation between herbaceous and woody plants.

420 The signaling interactions between GA and auxin, as well as the functional division of labor
421 among GA metabolic enzymes, exert highly consistent regulatory roles in the basic growth and
422 development processes of herbaceous and woody plants. GA and IAA primarily exhibit synergistic
423 interactions, jointly regulating vascular cambium development (Zhang et al., 2024). GA and IAA
424 synergistically release the suppression of ARF family transcription factors, thereby activating vascular
425 cambium stem cell activity and promoting the directed differentiation and development of secondary
426 xylem and phloem (Ben-Targem et al., 2021; Zhang et al., 2024). GA and IAA also jointly regulate
427 apical dominance (Cao et al., 2023), yet show antagonistic effects in root development (Liu et al.,
428 2024), demonstrating tissue-specificity in hormone interactions. Furthermore, GA inhibits lateral root
429 formation by regulating polar IAA transporters (e.g., PtPIN9), with GA and ABA exhibiting synergistic
430 inhibition in this process (Gou et al., 2009).

431 Similar to Arabidopsis, GA interacts synergistically or antagonistically with multiple other
432 hormonal pathways to form a sophisticated regulatory network (Weiss & Ori, 2007). GA and ABA
433 exhibit extensive antagonistic relationships involving bud dormancy (Singh et al., 2018), lateral root
434 formation (Gou et al., 2009), drought tolerance regulation (Liu et al., 2025), and other processes. The
435 core mechanism involves balancing growth and stress response through the accumulation of DELLA
436 proteins. Under adverse conditions such as drought and high salinity, both Arabidopsis and poplar
437 reduce endogenous gibberellin levels by upregulating GA2ox and downregulating GA20ox/GA3ox,
438 while simultaneously increasing ABA content (Shu et al., 2018), thereby achieving a trade-off between
439 growth inhibition and stress tolerance (Achard et al., 2006). Concurrently, IAA influences ABA
440 synthesis and signaling responses, thereby indirectly participating in the GA-ABA interaction network
441 (Gou et al., 2009). In Arabidopsis, the transcription factor DDF1 directly promotes GA2ox expression,
442 further reducing GA accumulation to enhance stress adaptation (Magome et al., 2008); this stress-GA
443 metabolic regulation pattern also holds true in woody plants.

444 5.1.2 Mechanisms that Can Be Safely Inferred to Be Conserved from Herbaceous

445 Due to the long growth cycles, complex genetic backgrounds, and high experimental difficulty

446 associated with woody plants, direct functional evidence for many regulatory mechanisms remains
447 lacking. Based on pathways already elucidated in Arabidopsis and the high homology of core genes in
448 the poplar genome, it is reasonable to infer that certain light and auxin regulatory modules are
449 potentially conserved in woody plants. In Arabidopsis, the DELLA-ABI4-HY5 module integrates light
450 and GA signaling to regulate hypocotyl elongation (Xiong et al., 2023). HY5 directly activates the
451 transcription of *GA2ox* genes, promoting the degradation of active GA and thereby inhibiting stem cell
452 elongation and internode growth (Gao et al., 2024). Furthermore, DBB1a increases active GA levels by
453 inhibiting the expression of GA degradation genes and inducing the expression of GA synthesis genes,
454 thereby promoting hypocotyl elongation (Wang et al., 2010). The core regulatory factors of this
455 pathway all possess direct homologs in the poplar genome (Wu et al., 2024), suggesting that this
456 mechanism is likely conserved in poplar.

457 Auxin works in concert with gibberellin signaling to shape root morphology by regulating the
458 transcriptional levels of *GA2ox* (Kubalová et al., 2025; Mauriat et al., 2014). In Arabidopsis, the
459 histone deacetylase *HDT1/2* suppresses *GA2ox2* expression and maintains cell division activity in the
460 root apical meristem. Auxin can both regulate HDT-mediated epigenetic modifications and directly
461 activate *GA2ox2*, finely balancing proliferation in the root meristem and growth in the elongation zone
462 (Li et al., 2017). Given that GA signaling in poplars similarly relies on the interaction between DELLA
463 proteins and auxin, it is hypothesized that the IAA-HDT-*GA2ox*-GA regulatory module is conserved in
464 woody plants.

465 5.1.3 Specialized Mechanisms Adapted to the Perennial Habits of Woody Plants

466 Although the core GA signaling and metabolic pathways are conserved across species, woody
467 perennials such as poplars have evolved unique GA regulatory mechanisms to support their perennial
468 life cycles during their long-term adaptation to terrestrial environments and seasonal changes. These
469 specific regulatory mechanisms are primarily manifested in the unique perennial biological traits of
470 woody plants. Firstly, poplars possess a specialized pathway under long-day conditions in which *FT2*
471 reduces active GA levels by upregulating *GA2ox1* and downregulating *GA3ox2*, thereby specifically
472 limiting internode elongation and promoting apical meristem development (Gao et al., 2024). This FT-
473 dependent GA metabolic regulation pattern is completely absent in Arabidopsis, highlighting the
474 evolutionary differences in plant height regulation between herbaceous and woody plants. Secondly,
475 GA acting as a flowering-promoting signal in annual herbs which are characterized by rapid
476 generational turnover (Wilson et al., 1992). GA activates integrons such as *SOCI* and *LEAFY* to
477 accelerate the reproductive transition (Blazquez et al., 1998; Li et al., 2016). In contrast, in poplars, GA
478 inhibits flowering integrons, prioritizing stem elongation and secondary growth, and delaying the
479 reproductive transition to accumulate nutrients and resist frost damage (André et al., 2022). Thirdly,
480 herbaceous dormancy is confined to the seed stage and is regulated by the *DOG1*-ABA-GA pathway

481 (Bentsink et al., 2006; Hilhorst & Karszen, 1992); in contrast, woody plants maintain bud dormancy via
482 the *PttSVL-FT-GA2ox* pathway (Singh et al., 2018) and break dormancy via the *PtoHY5a-FT-GA*
483 pathway (Gao et al., 2024), adapting to annual growth cycle cycles (Ruttink et al., 2007). Fourthly, GA
484 in herbaceous plants primarily governs above-ground stem and leaf elongation, whereas in woody
485 plants, GA bidirectionally regulates the allocation of resources between above- and below-ground
486 parts; high GA levels promote wood deposition (Liao et al., 2025; Su et al., 2025), while low GA levels
487 facilitate root system development (Elias et al., 2012). Lastly, in herbaceous plants, GA is only
488 indirectly involved in JA pathway regulation (Hou et al., 2010; Mir et al., 2025), whereas woody plants
489 have evolved GA-specific defense modules. Through the *PtmiR319a-PtTCP19-RGA* pathway, they
490 promote trichome development (Fan et al., 2020), and the DELLA-MYC2-JA pathway to activate
491 immune responses (Navarro et al., 2008), thereby comprehensively enhancing the long-term resistance
492 of perennial plants. In poplars, GA and JA exhibit a bidirectional antagonistic relationship; both
493 regulate the plant growth-defense balance through the DELLA-MYC2 module (Zhao et al., 2021). GA
494 participates in JA signaling regulation by activating MYC2, which both inhibits AR formation and
495 implements negative feedback on JA signaling by upregulating GH3-like genes (Mauriat et al., 2014).
496 During root formation, high JA concentrations inhibit AR development via MYC2 (Gutierrez et al.,
497 2012). However, in Ussuri poplar (*Populus ussuriensis*), MYC2 promotes AR formation (Bannoud &
498 Bellini, 2021), indicating species-specificity in JA effects.†

499 GA signaling does not act alone but forms a complex network of hormone interactions with
500 various plant hormones, collectively regulating plant growth, development, and stress responses (Weiss
501 & Ori, 2007). This study systematically reviews hormones co-regulating poplar growth and
502 development with GA, including ABA and IAA, as well as the stress-related hormone JA: GA and
503 ABA exhibit extensive antagonistic relationships involving bud dormancy (Singh et al., 2018), lateral
504 root formation (Gou et al., 2010), drought tolerance regulation (Liu et al., 2025), and other processes.
505 The core mechanism involves balancing growth and stress resistance through the accumulation of
506 DELLA proteins. GA and IAA primarily exhibit synergistic interactions, jointly regulating vascular
507 cambium development (Zhang et al., 2024), they also jointly regulate apical dominance in *Pisum*
508 *sativum* L (Cao et al., 2022), yet show antagonistic effects in root development (Liu et al., 2024),
509 demonstrating tissue-specificity in hormone interactions; Furthermore, GA inhibits lateral root
510 formation by regulating polar IAA transporters (e.g., PtPIN9), with GA and ABA exhibiting synergistic
511 inhibition in this process (Gou et al., 2010). Concurrently, IAA influences ABA synthesis and signaling
512 responses, thereby indirectly participating in the GA-ABA interaction network (Gou et al., 2009). GA
513 and JA exhibit a bidirectional trade-off relationship, regulating the growth-defense balance through the
514 DELLA-MYC2 module (Zhao et al., 2021). GA participates in JA signaling regulation by activating
515 MYC2, which both inhibits AR formation and implements negative feedback on JA signaling by
516 upregulating GH3-like genes (Mauriat et al., 2014). During root formation, high JA concentrations

517 inhibit AR development via MYC2 (Gutierrez et al., 2012). However, in Ussuri poplar (*Populus*
518 *ussuriensis*), MYC2 promotes AR formation (Bannoud & Bellini, 2021), indicating species-specificity
519 in JA effects. The above findings highlight the complexity and specificity of plant hormone regulatory
520 networks. In-depth analysis of hormone interaction networks provides a foundation for elucidating
521 hormone action mechanisms.

522 5.2 Future Research Directions

523 The functions of GA in poplar growth and development are now relatively well understood, but
524 the underlying molecular mechanisms are less revealed. Research on its role in stress
525 responses/resistance, particularly biological stress,—remains limited. Coordinating poplar growth and
526 development with immune responses remains an unresolved challenge (Yu et al., 2024). Building on
527 current studies, future research on GA's role in poplar should aim to focus on: dDeepening
528 investigations into whether core GA signaling factors exhibit tissue-specific functions, as well as GA's
529 interaction networks with other hormones.

530 It will also be important to explore upstream/downstream genes interacting with the GA signaling
531 pathway and novel action mechanisms, including dwhether core GA signaling factors exhibit tissue-
532 specificity; translating GA signaling effects into forest tree breeding—e.g., applying CRISPR/Cas9 to
533 GA-signal-based breeding improvements, converting fundamental GA pathway knowledge into
534 practical breeding strategies (Yao et al., 2023); Exploration of upstream/downstream genes interacting
535 with the GA signaling pathway and novel action mechanisms: Deeply deciphering the molecular basis
536 of the GA–DELLA interaction network, investigating the structural basis of DELLA–GA interactions,
537 and revealing downstream regulatory targets and signaling cascade reactions of –DELLA (Dahal et al.,
538 2025). Furthermore, it is necessary to further elucidate the GA-mediated phase transition and flowering
539 regulation mechanisms in poplar. Although the regulatory role of GA in flowering has been extensively
540 studied in herbaceous plants, related knowledge in woody plants remains largely confined to fruit tree
541 species (Mutasa-Gottgens & Hedden, 2009). Since early flowering can significantly accelerate
542 breeding progress, elucidating the GA-dependent flowering mechanism in poplar is crucial for
543 developing early-flowering varieties, shortening the prolonged juvenile phase, expediting hybrid
544 breeding processes, and enhancing overall breeding efficiency (Zawaski et al., 2011). Such research
545 also provides valuable insights for exploring GA-regulated flowering mechanisms in other woody
546 plants.

547 In *Arabidopsis*, extensive research has been conducted on downstream effectors of the GA
548 signaling pathway. For instance, DELLA, a core GA signaling repressor, has been shown to interact
549 with the transparent TESTA protein GLABRA2 (TTG2) and components of the MYB-bHLH-WD40
550 (MBW) complex, thereby influencing pectin synthesis and plant development (Xu et al., 2025). In

551 Arabidopsis, GA promotes selective autophagic degradation of DELLA proteins through interaction
552 with ATG8, thereby enhancing seed germination and hypocotyl elongation (Zhang et al., 2025).
553 However, in poplar, the degradation of DELLA is currently known to follow only the classical ‘GA-
554 GID1-DELLA’ pathway. Therefore, whether the GA signaling pathway achieves precise and sustained
555 regulation of poplar root development through epigenetic modifications remains to be further
556 investigated.

557 At the same time, efforts should be made to further promote the practical application of GA
558 signaling mechanisms in the genetic improvement of forest trees. Field trials have confirmed that GA
559 regulation can be directly applied to poplar breeding: in development and stress tolerance breeding.
560 Reducing endogenous GA activity or accumulating DELLA proteins can lead to the development of
561 dwarfing, lodging-resistant, and high-density-planting-suitable cultivars. Overexpression of GA
562 degradation genes yields stably dwarfing poplars (Busov et al., 2003). GA can be used to selectively
563 improve wood traits precisely: overexpression of GA20ox enhances GA signaling, simultaneously
564 promoting internode elongation, xylem formation, and fiber elongation; overexpression of the GA
565 receptor GID1 accelerates xylem formation and trunk thickening (Eriksson, 2000; Mauriat & Moritz,
566 2009). GA can also promote cambium regeneration after ring barking in an auxin-dependent manner,
567 repairing stem damage and restoring secondary growth (Zhang et al., 2024). In vegetative propagation,
568 GA and auxin interact to negatively regulate root development: attenuating GA signaling significantly
569 promotes lateral root elongation, enhances rooting efficiency of cuttings, and accelerates seedling
570 propagation (Gou et al., 2009).

571 Furthermore, upregulating GA2ox or accumulating DELLA can enhance poplar drought tolerance
572 and mediate short-day bud dormancy regulation, thereby improving seasonal stress adaptation
573 (Eriksson et al., 2000; Zawaski & Busov, 2014). The GA-JA defense mechanism should be applied to
574 enhance the stress response of forest trees. Building on this foundation, we must further promote the
575 translation of fundamental GA theory into practical forest tree breeding. By leveraging CRISPR/Cas9
576 gene editing technology to target key sites in the GA pathway, we can efficiently transform existing
577 mechanistic research into practical, implementable molecular breeding strategies (Yao et al.,
578 2023). DELLA degradation currently follows the classical “GA-GID1-DELLA” pathway. Whether the
579 gibberellin signaling pathway achieves precise and sustained regulation of poplar root growth through
580 epigenetic modification pathways warrants further investigation.

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1060 List of figure legends:

1061 **Figure 1. Overview of gibberellin biosynthesis, metabolism, and signal transduction.** GA biosynthesis occurs
1062 in three stages: 1) In plastids, IPP is generated via the MEP pathway, while the MVA pathway for IPP
1063 synthesis occurs in the cytoplasm, and GGPP synthesizes the key intermediate *ent*-kaurene; 2) In the
1064 endoplasmic reticulum (ER), *ent*-kaurene is catalyzed by KO (*ent*-kaurene oxidase) and KAO (*ent*-
1065 kaurenoic acid oxidase) to form GA₁₂; 3) In the cytoplasm, GA₁₂ is converted into active GA (e.g., GA₁,
1066 GA₄) via *GA20ox* (*GA20-oxidase*) and *GA3ox* (*GA3-oxidase*). GA inactivation is mediated by *GA2ox*
1067 (*GA2-oxidase*), which hydroxylates active GA into inactive forms (e.g., GA₈, GA₂₉). In signal
1068 transduction, active GA binds to the receptor GID1, inducing a conformational change in GID1 that
1069 promotes the formation of a GA-GID1-DELLA complex. This complex triggers the ubiquitination of
1070 DELLA proteins followed by their degradation via the 26S proteasome pathway, releasing their
1071 transcriptional repression of GA-responsive genes, ultimately modulating plant growth, development,
1072 and stress responses. Key enzymes/proteins and reaction sites involved in each step are labeled.

1073

1074 **Figure 2. GA signaling and its regulatory role in tree growth, development, and stress resistance.** Schematic
1075 of GA-mediated pathways (via key biosynthetic enzymes *GA20ox/GA3ox* [GA activation] and *GA2ox* [GA
1076 inactivation], and interacting factors) controlling multiple physiological processes in trees, while interacting with
1077 other plant hormones (e.g., IAA, ABA, CK, JA): 1) Plant height regulation: Key GA synthesis enzymes (*KS*, *GA20ox*,
1078 *GA3ox*) promote stem elongation by increasing GA content. The *PtoHY5a-FT2* pathway induces *GA2ox* expression,
1079 thereby promoting GA inactivation and inducing dwarfing phenotypes; 2) Dormancy Release and Bud Germination:
1080 Short-day conditions or low temperatures promote *PttSVL* (by inhibiting *PttFT1* and *GA2ox*) to maintain dormancy;
1081 long-day (LD) conditions or high temperatures induce *PtoHY5a-PtoFT2* (elevated GA) to trigger bud priming. ABA
1082 antagonizes GA function in this process; 3) Vascular cambium development and secondary growth: GA and IAA
1083 regulate DELLA and *Aux/IAAs* activity, respectively. Concurrently, DELLA forms complexes with *ARF7* and
1084 *Aux/IAAs* to synergistically regulate cambial cell activity and xylem differentiation. *GA20ox/GA3ox* promotes GA
1085 synthesis, enhancing vascular cambium activity. *GA2ox* reduces GA content, inhibiting vascular cambium growth;
1086 4) Root development and nutrient acquisition: Increasing GA, GID, *GA20ox*, or *GA3ox* content, or decreasing

1087 DELLA content, inhibits adventitious and lateral root growth. GA inactivation mediated by *GA2ox* promotes root
1088 development; 5) Biomass Accumulation and Wood Quality Formation: GA positively regulates aboveground
1089 biomass accumulation and xylem lignification with distinct organ specificity (promoting shoot growth while
1090 inhibiting root biomass accumulation); 6) Abiotic/Biotic Stress Responses: *PsnERF76* enhances salt tolerance by
1091 elevating GA/ABA levels; Drought induces upregulation of *GA20ox* and *GA3ox* while downregulating *GA2ox* to
1092 modulate GA levels and improve drought tolerance; Transcription factor *PagKNAT2/6b* inhibits GA synthesis by
1093 downregulating *PagGA20ox1*, enhancing drought resistance; *PtoMYB142* promotes *PtoGA2ox4* expression,
1094 reducing GA content and improving poplar drought tolerance. GA mediates growth-defense trade-offs by interacting
1095 with the miRNA319a–TCP module (regulating trichome development) and the DELLA–MYC2 complex (JA-
1096 mediated defense responses). Arrows indicate activation; blunt lines indicate inhibition. “*Pto*” denotes *Populus*
1097 *toomentosa*, “*Psn*” denotes *Populus simonii* × *P. nigra*, “*Pag*” denotes *Populus alba* × *Populus glandulosa* (84K
1098 poplar), “*Pm*” denotes *Populus tomentosa*, other genes are conserved across *Populus spp.* ABA (abscisic acid), BR
1099 (brassinolide), CK (cytokinin), IAA (indole-3-acetic acid), JA (jasmonic acid), DELLA (GA signal inhibitor), ARF7
1100 (Auxin Response Factor 7).

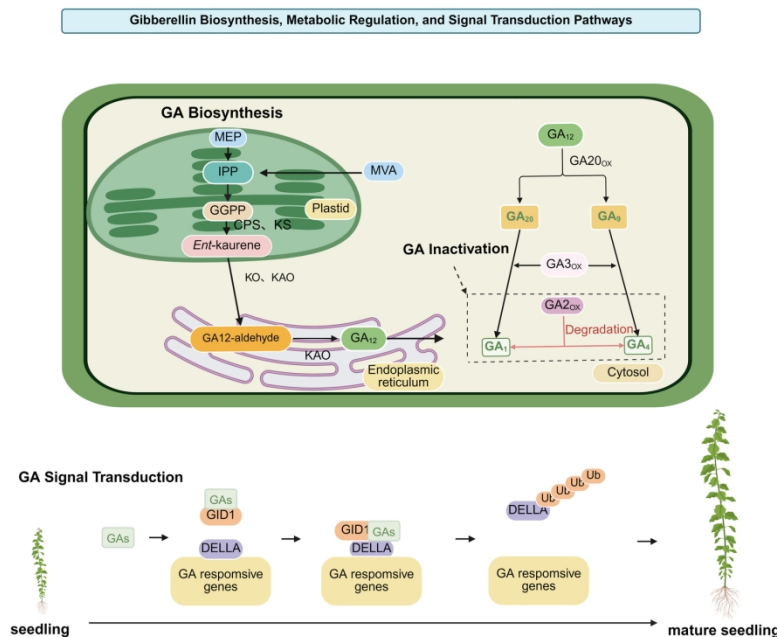


Figure 1. Overview of gibberellin biosynthesis, metabolism, and signal transduction. GA biosynthesis occurs in three stages: 1) In plastids, IPP is generated via the MEP pathway, while the MVA pathway for IPP synthesis occurs in the cytoplasm, and GGPP synthesizes the key intermediate ent-kaurene; 2) In the endoplasmic reticulum (ER), ent-kaurene is catalyzed by KO (ent-kaurene oxidase) and KAO (ent-kaurenoic acid oxidase) to form GA₁₂; 3) In the cytoplasm, GA₁₂ is converted into active GA (e.g., GA₁, GA₄) via GA₂₀ox (GA₂₀-oxidase) and GA₃ox (GA₃-oxidase). GA inactivation is mediated by GA₂ox (GA₂-oxidase), which hydroxylates active GA into inactive forms (e.g., GA₈, GA₂₉). In signal transduction, active GA binds to the receptor GID1, inducing a conformational change in GID1 that promotes the formation of a GA-GID1-DELLA complex. This complex triggers the ubiquitination of DELLA proteins followed by their degradation via the 26S proteasome pathway, releasing their transcriptional repression of GA-responsive genes, ultimately modulating plant growth, development, and stress responses. Key enzymes/proteins and reaction sites involved in each step are labeled.

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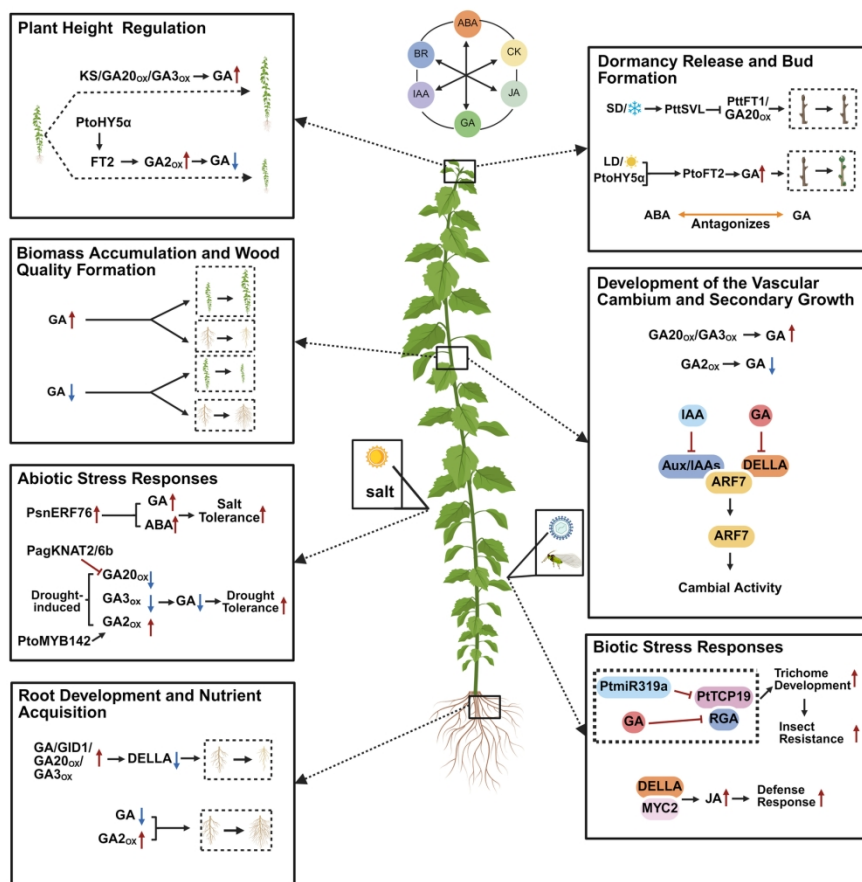


Figure 2. GA signaling and its regulatory role in tree growth, development, and stress responses. Schematic of GA-mediated pathways (via key biosynthetic enzymes GA20ox/GA3ox [GA activation] and GA2ox [GA inactivation], and interacting factors) controlling multiple physiological processes in trees, while interacting with other plant hormones (e.g., IAA, ABA, CK, JA): 1) Plant height regulation: Key GA synthesis enzymes (KS, GA20ox, GA3ox) promote stem elongation by increasing GA content. The PtoHY5a-FT2 pathway induces GA2ox expression, thereby promoting GA inactivation and inducing dwarfing phenotypes; 2) Dormancy Release and Bud Germination: Short-day conditions or low temperatures promote PttSVL (by inhibiting PttFT1 and GA2ox) to maintain dormancy; long-day (LD) conditions or high temperatures induce PtoHY5a-PtoFT2 (elevated GA) to trigger bud priming. ABA antagonizes GA function in this process; 3) Vascular cambium development and secondary growth: GA and IAA regulate DELLA and Aux/IAAs activity, respectively. Concurrently, DELLA forms complexes with ARF7 and Aux/IAAs to synergistically regulate cambial cell activity and xylem differentiation. GA20ox/GA3ox promotes GA synthesis, enhancing vascular cambium activity. GA2ox reduces GA content, inhibiting vascular cambium growth; 4) Root development and nutrient acquisition: Increasing GA, GID1, GA20ox, or GA3ox content, or decreasing DELLA content, inhibits adventitious and lateral root growth. GA inactivation mediated by GA2ox promotes root development; 5) Biomass Accumulation and Wood Quality Formation: GA positively regulates aboveground biomass accumulation and xylem lignification with distinct organ specificity (promoting shoot growth while inhibiting root biomass accumulation); 6) Abiotic/Biotic Stress Responses: PsnERF76 enhances salt tolerance by elevating GA/ABA levels; Drought induces upregulation of GA20ox and GA3ox while downregulating GA2ox to modulate GA levels and improve drought tolerance; Transcription factor PagKNAT2/6b inhibits GA synthesis by downregulating PagGA20ox1, enhancing drought stress responses; PtoMYB142 promotes PtoGA2ox4 expression, reducing GA content and improving poplar drought tolerance. GA mediates growth-defense trade-offs by interacting with the miRNA319a-TCP module (regulating trichome development) and the DELLA-MYC2 complex (JA-mediated defense responses). Arrows indicate activation; blunt lines indicate inhibition.

inhibition. "Pto" denotes *Populus tomentosa*, "Psn" denotes *Populus simonii* × *P. nigra*, "Pag" denotes *Populus alba* × *Populus glandulosa* (84K poplar), "Pm" denotes *Populus tomentosa*, other genes are conserved across *Populus* spp. ABA (abscisic acid), BR (brassinolide), CK (cytokinin), IAA (indole-3-acetic acid), JA (jasmonic acid), DELLA (GA signal inhibitor), ARF7 (Auxin Response Factor 7).

169x155mm (300 x 300 DPI)

Reviewer: 1

Comments to the Author

This review summarizes the state of the knowledge, future directions and potential applications of gibberellins in tree breeding with focus on poplar because the majority of the knowledge is derived from this species. The review is highly appropriate for the journal and covers aspects that are now very well reviewed to my knowledge although the authors should probably indicate this in the introduction section.

Responses: Thank you for your comment. We have added this statement in the Introduction (line 52-55).

The structure of the paper is logical with several sections describing the state of the knowledge of GA metabolism and signaling followed by what is known about these mechanisms in processes unique to tree biology. The paper is organized by different traits and processes unique to woody perennials. Generally, the paper covers well almost all areas with the prominent exceptions of reproductive biology and phase transition. Literature is probably weak in these areas but there are bits and pieces, and the authors should probably highlight these areas as a future direction.

Responses: Thank you for your comment. We have incorporated content related to flowering and phase transitions (juvenile-to-adult transition) in Section 3.2 (Phase Transition, Flowering, Bud Formation and Dormancy Release) (line 172-188). We have also discussed this topic in Section 5.2 Future Research Directions (line 495-503).

The biotic section on stress response is underdeveloped, and this may be linked to lack of literature. This section is also called 'Resistance' but also captures the abiotic stress studies. I find this confusing and they probably will need to change by explicitly say biotic and abiotic stress resistance. In addition, I would probably use response to stress because resistance, avoidance etc. mean different things. This also refers to the title and throughout text, including abstract.

Responses: Thank you for your comment. We have uniformly replaced the term 'stress resistance' with 'stress responses' throughout the manuscript, including the title, abstract, main text, and all figures and tables, to eliminate conceptual ambiguity.

Future directions are on the weak side, and they have to be reinforced both on the biological and application front.

Responses: Thank you for your comment. We have expanded Section 5.2 (Future Research Directions) both on the biological and application front.

I would also recommend the authors attempt a stronger conceptual GA biology synthesis in woody perennials by using a combination of well-characterized mechanisms, ones that can be safely inferred to be conserved from herbaceous and hypothesized ones that will serve the woody perennial adaptations.

Responses: Thank you for your comment. We revised the Section 5.1 titled 'Integration of the Core GA Signaling Regulatory Network in Poplar'. This section provides a progressive summary of the three modules 'Well-established', 'Inferable', and 'Tree-Specific' and

integrates both conserved and tree-specific mechanisms in poplar (line 383-483).

Finally, I would recommend some language improvements.

Responses: Thank you for your comment. We have carefully revised and polished the entire manuscript in accordance with your suggestions.

Reviewer: 2

Comments to the Author

The manuscript at hand "Gibberellin in Regulating Poplar Growth, Development, and Stress Resistance" outlines the current state of knowledge of gibberellin (GA) research of poplar trees, and makes an inventory of research needs as well as possibilities for future biotechnological approaches. Overall, the manuscript is well written and provides a clear and informative overview of the subject.

Reviewer: 1

Citations: Yes

Reviewer: 2

Citations: Yes

Reviewer: 1

Citation details:

Reviewer: 2

Citation details: I think the citations are fine, perhaps I would have cited the older literature a bit more. However, it is a matter of style and not critical.

Responses: Thank you for your comment. We have included early classic literature on GA research, such as Hilhorst & Karssen, 1992, and Kende & Zeevaart, 1997.