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Gibberellin in Regulating Poplar Growth, Development, and Stress Responses

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Abstract: Gibberellic acid (GA) plays a central role in regulating growth, development, and stress responses. 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. 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. 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; 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).

Plant hormones serve as core regulators of growth, development, and environmental adaptation. Among these, gibberellins (GAs)—a class of natural diterpene hormones—exhibit potent physiological activity and are extensively involved in plant growth, development, and regulatory processes (Kende & Zeevaart, 1997; Shah et al., 2023). To date, over 136 GAs have been identified, though most are biosynthetic intermediates or inactive metabolites(Hedden & Sponsel, 2015). Only GA_1, GA_3, GA_4, and GA_7 are confirmed to possess direct biological activity (L. Yang et al., 2021). During the "Green Revolution" in mid-20th century, the application of GA-related genes in crop dwarfing breeding drove global agricultural yield increases, demonstrating the immense potential of GA in breeding. Current research extensively explores GA's functions, which span multiple stages of the plant life cycle. These include promoting seed germination (Gong et al., 2022), fruit development and ripening (Fenn & Giovannoni, 2021), stem and leaf growth and root elongation (Zluhan-Martínez et al., 2021). GAs also participate in bud dormancy induction and release (Rinne et al., 2011), stress responses (Nagar et al., 2021), and plant regeneration processes (Bassaganya-Riera et al., 2014). GA serves as an environmentally friendly plant growth regulator widely applied in agricultural and forestry production to enhance crop and fruit tree yield and quality (Kildegaard et al., 2021).

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

2. Biosynthesis, Metabolism, and Signaling Mechanisms of Gibberellin

2.1 Biosynthetic Pathway of Gibberellin

GA biosynthesis is a complex metabolic process involving multiple organelles and synergistic enzyme participation (Figure 1), divided into three main stages sequentially completed in plastids, endoplasmic reticulum, and cytoplasm. This pathway is highly conserved in both herbaceous and woody plants (Hedden & Thomas, 2012). The first stage occurs in the plastids, primarily through the interaction between the methylenepyruvate (MEP) pathway and the mevalonate (MVA) pathway to generate isopentenyl pyrophosphate (IPP). IPP is further synthesized into geranylgeranyl pyrophosphate (GGPP). GGPP is sequentially catalyzed by ent-caryophyllene diphosphate synthase (*ent*-CPS) and ent-kaurene synthase (*ent*-KS) to yield *ent*-kaurene, a key intermediate for GA synthesis (Shah et al., 2023). Notably, this stage exhibits significant specificity in poplar: the *KS1* and *KS2* genes are highly expressed in vascular tissues, directly participating in xylem formation and secondary stem growth—a core characteristic distinguishing poplar from herbaceous plants (Zhang et al., 2024). The second stage occurs within the endoplasmic reticulum (ER). First, ent-kaurene is oxidized to GA_{12}-aldehyde by ent-kaurene oxidase (KO) and ent-kaurenoic acid oxidase (KAO), catalyzed by members of the cytochrome P450 monooxygenase family. This is further converted to GA_{12} (Hartweck, 2008). This process is conserved in both herbaceous and woody plants. The third stage occurs in the cytoplasm, where GA_{12} is catalyzed by GA20-oxidase (*GA20ox*) and GA3-β-hydroxylase (*GA3ox*), yielding bioactive molecules such as GA_1 and GA_4 (Gou et al., 2011). *GA20ox* plays a key regulatory role in GA precursor synthesis, with its expression directly influencing active GA levels. Concurrently, active GA molecules exert negative feedback regulation by suppressing *GA20ox* and *GA3ox* expression, thereby maintaining GA homeostasis. This feedback mechanism is highly conserved in poplar and adapts to its continuous growth requirements. Given the high-specificity expression of poplar *KS1*/*KS2* in vascular tissues, locally synthesized GA may be transported to the shoot apex or roots via specific carrier proteins. NPF and SWEET family transporters have been identified in Arabidopsis as efflux carriers for GA, participating in inter-tissue GA transport and regulating GA concentration equilibrium (Binenbaum et al., 2018). It is speculated that a similar transport mechanism may exist in poplar, which represents one of the core directions for future GA regulation research in poplar.

2.2 Metabolic Inactivation of Gibberellin

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

2.3 Gibberellin Signaling

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

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

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

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

3.1 Plant Height Regulation

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

Controlling the expression of key enzymes and receptors involved in GA synthesis and signal transduction pathways can be used to regulate the height of poplar trees. Overexpression of the GA synthesis key gene *PtoKS1* enhances GA signaling, significantly promoting overall poplar growth (Zhang et al., 2024); Similarly, overexpression of *PttGA20ox* and *PttGID1* both promote internode elongation and xylem formation by enhancing the GA signaling pathway (Eriksson, 2000; Mauriat & Moritz, 2009). Furthermore, overexpression of *PtGA3ox*, the terminal enzyme in GA synthesis, significantly increases active GA levels, thereby enhancing both plant height and stem diameter in poplar (Hu et al., 2022). However, it is important to note that enhanced GA signaling disrupts development of other organs. For instance, overexpression *Pinus densiflora GA20ox* (*PdGA20ox*) in poplar leads to elongated stems, but reduced leaf size, and poor rooting; suggesting tissue- or stage-specific regulation of GA on secondary growth (Jeon et al., 2016).

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

3.2 Phase Transition, Flowering, Bud Formation and Dormancy Release

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

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

As a central gene regulating flowering, FT not only participates in floral timing regulation but also serves as a key target for dormancy induction. The mechanism by which GA promotes dormancy release and bud priming in poplar has been elucidated and is closely linked to the FT signaling pathway: Rinne et al. (2011) revealed that GA breaks dormancy by enhancing 1,3-β-glucanase activity to degrade callose, thereby opening sieve pathway channels to facilitate PttFT protein transport (Rinne et al., 2011); Eriksson et al. (2015) further indicated that GA can promote bud germination independently of the *FT2* pathway. Exogenous GA application significantly enhances bud germination, regulating hybrid poplar bud elongation in parallel with the *FT2* pathway (Eriksson et al., 2015); The cold-induced transcription factor *PttSVL* suppresses the expression of *PttFT1* and *PttGA20ox*, antagonistically regulating bud germination through GA and ABA signaling. It serves as an integration node between environmental signals and the hormone network (Singh et al., 2018). Concurrently, FT signaling influences shoot growth by inversely regulating GA content. For instance, *PtaFT2* modulates shoot apical meristem development and inhibits internode elongation via the GA13-hydroxylation pathway (Gómez-Soto et al., 2022). GA also plays a crucial role in sustaining continuous shoot elongation (Cao et al., 2023). Beyond FT signaling, *PtoHY5a* directly activates *PtoFT2* expression to suppress short-day-induced growth arrest. Simultaneously, it reduces apical GA levels by upregulating key GA inactivation genes and downregulating GA synthesis genes, thereby inhibiting bud emergence. This *HY5a*-GA module adapts to the seasonal growth patterns regulated by photoperiod in woody plants (Gao et al., 2024).

3.3 Development of the Vascular Cambium and Secondary Growth

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

Recent studies have progressively elucidated the molecular mechanisms by which the GA signaling pathway regulates the development of the vascular cambium and secondary growth in poplar trees: Du et al. (2024) discovered that *PdRabG3f* regulates internode elongation and xylem development in poplar by interfering with endogenous GA levels (Du et al., 2024); Su et al. (2025) further revealed that localized GA synthesis in stems is a key factor regulating xylem development, clarifying that tissue-specific distribution of GA levels is essential for maintaining normal cambium activity (Su et al., 2025). The synergistic regulation of GA and IAA constitutes the core mechanism governing poplar cambium development: IAA forms a polar gradient in the cambium region via polar transporters such as *PIN1(PIN-FORMED 1)*, with its maximum concentration located in the cambium cell layer, thereby determining stem cell differentiation fate (Hartweck, 2008; Mäkilä et al., 2023). Björklund et al. (2007) revealed that GA regulation of poplar cambium depends on IAA; GA alone cannot induce cambial regeneration but significantly enhances IAA-induced expression of cambium-related genes. The two exhibit marked synergistic effects, share multiple transcriptional regulatory elements, and show highly overlapping downstream transcriptional responses (Björklund et al., 2007). Zhang et al. (2024) further elucidated the molecular basis of this synergistic mechanism: the IAA response factor ARF7 interacts with the DELLA protein RGL1 via its MR domain while simultaneously binding to the *Aux/IAA* family member IAA9 through its PB domain. This forms the ARF7-RGL1-IAA9 ternary complex, serving as a key platform for integrating GA and IAA signaling (Zhang et al., 2024). GA promotes IAA accumulation in the cambium region by upregulating *PIN1* expression and positively regulates *ARF7* and *WOX4* expression, thereby enhancing cambium cell activity (Hu et al., 2022; Mäkilä et al., 2023). DELLA proteins negatively regulate *PIN1* expression, forming a GA-IAA feedback loop that precisely controls the sustained activity of the cambium (Zhang et al., 2024).

Multiple PIN family members exist in the poplar genome (Liu et al., 2014). Despite functional redundancy, their tissue expression is highly differentiated. For example, *PttPIN1* and *PttPIN12* are specifically expressed in the cambium and its derived xylem, participating in polar IAA transport within vascular tissues (Schrader et al., 2003). The tissue-specific distribution of GA and expression of its biosynthetic genes further safeguard vascular cambium development: active GA forms (e.g., GA_1 and GA_4) accumulate in xylem regions, while GA precursors (e.g., GA_9, GA_{20}) predominantly localize in phloem (Israelsson et al., 2005), closely aligning with xylem differentiation functions. GA activity is primarily regulated by three key enzymes: *PdGA20ox* overexpression significantly increases poplar xylem cross-sectional width and cell number (Jeon et al., 2016); *GA3ox* expression levels directly determine the accumulation of active GA (Israelsson et al., 2004); inhibiting *GA2ox* (e.g., *PtGA2ox4*, *PtGA2ox5*) enhances meristem cell proliferation and promotes secondary growth (Gou et al., 2011). These three enzymes synergistically regulate GA activity within vascular tissues, determining wood formation efficiency.

3.4 Root Development and Nutrient Acquisition

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

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

3.5 Biomass Accumulation and Wood Quality Formation

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

GA exhibits distinct organ specificity in regulating material accumulation in poplar: it positively regulates above-ground biomass accumulation by optimizing wood processing properties through modulation of lignin content and monomer composition; conversely, it negatively regulates below-ground root biomass, consistent with root development regulation. This characteristic provides precise targets for breeding fast-growing, high-quality poplar varieties (Eriksson et al., 2000). Adjusting the ratio of lignin monomers (S/G ratio) can reduce cell wall resistance while enhancing wood quality, without affecting biomass accumulation (Tang et al., 2025). The core value of GA in regulating wood quality has been validated: Field trials by Cho et al. (2019) confirmed that co-overexpressing *PdGA20ox1* and *PtrMYB221* in poplar synergistically optimizes GA levels and the lignin synthesis network. This resulted in above-ground biomass doubling compared to wild-type, significantly reduced lignin content, increased total cellulose proportion, and approximately 8% higher saccharification efficiency, without noticeable growth defects (Cho et al., 2019), representing a classic case of GA application for wood quality improvement. GA signaling imbalance disrupts material accumulation and xylem development: excessive suppression of above-ground GA signaling impairs xylem differentiation, such as *ClGA2ox12* overexpression in poplar significantly inhibiting vessel differentiation and reducing lignin deposition (Peng et al., 2024); Elevated GA levels resulting from suppressed *PtGA2ox2* and *PtGA2ox7* activity in roots decrease root biomass (Gou et al., 2011), further confirming its organ-specific regulatory characteristics.

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

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

4.1 Abiotic Stress Responses

Drought and saline-alkali stress are two of the main abiotic factors that limit forestry production (Fang et al., 2021; X. Yang et al., 2021). In poplar, GA plays a role in regulating abiotic stress by modulating its own content, hormone interactions and transcription factor networks, and exhibits a typical ‘growth-stress trade-off’ effect. Phenotypically, a trade-off is evident: Poplar trees that overexpress GA exhibit accelerated growth and increased leaf area, but reduced drought tolerance. In contrast, GA-deficient plants exhibit limited growth yet superior drought stress responses (Eriksson et al., 2000; Zhang et al., 2024). As an evolutionary adaptation to drought, the heterophyllous trait in *Populus euphratica* shows significant positive correlations between GA_3 content and leaf length and spongy tissue thickness, reflecting species adaptation regulated by GA (Han et al., 2021).

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

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

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

4.2 Biotic Stress Responses

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

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

5. Discussion and Summary

5.1 Integration of the Core GA Biology in Poplar

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

5.1.1 Well-established Mechanisms

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

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

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

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

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

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

5.1.3 Specialized Mechanisms Adapted to the Perennial Habits of Woody Plants

Although the core GA signaling and metabolic pathways are conserved across species, woody perennials such as poplars have evolved unique GA regulatory mechanisms to support their perennial life cycles during their long-term adaptation to terrestrial environments and seasonal changes. These specific regulatory mechanisms are primarily manifested in the unique perennial biological traits of woody plants. Firstly, poplars possess a specialized pathway under long-day conditions in which *FT2* reduces active GA levels by upregulating *GA2ox1* and downregulating *GA3ox2*, thereby specifically limiting internode elongation and promoting apical meristem development (Gao et al., 2024). This FT-dependent GA metabolic regulation pattern is completely absent in Arabidopsis, highlighting the evolutionary differences in plant height regulation between herbaceous and woody plants. Secondly, GA acting as a flowering-promoting signal in annual herbs which are characterized by rapid generational turnover (Wilson et al., 1992). GA activates integrons such as *SOC1* and *LEAFY* to accelerate the reproductive transition (Blazquez et al., 1998; Li et al., 2016). In contrast, in poplars, GA inhibits flowering integrons, prioritizing stem elongation and secondary growth, and delaying the reproductive transition to accumulate nutrients and resist frost damage (André et al., 2022). Thirdly, herbaceous dormancy is confined to the seed stage and is regulated by the *DOG1*-ABA-GA pathway (Bentsink et al., 2006; Hilhorst & Karssen, 1992); in contrast, woody plants maintain bud dormancy via the *PttSVL*-FT-*GA2ox* pathway (Singh et al., 2018) and break dormancy via the *PtoHY5a*-FT-GA pathway (Gao et al., 2024), adapting to annual growth cycle cycles (Ruttink et al., 2007). Fourthly, GA in herbaceous plants primarily governs above-ground stem and leaf elongation, whereas in woody plants, GA bidirectionally regulates the allocation of resources between above- and below-ground parts; high GA levels promote wood deposition (Liao et al., 2025; Su et al., 2025), while low GA levels facilitate root system development (Elias et al., 2012). Lastly, in herbaceous plants, GA is only indirectly involved in JA pathway regulation (Hou et al., 2010; Mir et al., 2025), whereas woody plants have evolved GA-specific defense modules. Through the *PtmiR319a-PtTCP19*-RGA pathway, they promote trichome development (Fan et al., 2020), and the DELLA-MYC2-JA pathway to activate immune responses (Navarro et al., 2008), thereby comprehensively enhancing the long-term resistance of perennial plants. In poplars, GA and JA exhibit a bidirectional antagonistic relationship; both regulate the plant growth-defense balance through the DELLA-MYC2 module (Zhao et al., 2021). GA participates in JA signaling regulation by activating MYC2, which both inhibits AR formation and implements negative feedback on JA signaling by upregulating GH3-like genes (Mauriat et al., 2014).

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

5.2 Future Research Directions

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

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

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

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

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

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Authors' Contributions

L. Z. and H. H.: study conception and design, manuscript writing and revision. X. Z. and G. C: manuscript revision.

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Conflict of interest

The authors declare no conflict of interest.

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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 GA_{12}; 3) In the cytoplasm, GA_{12} is converted into active GA (e.g., GA_1, GA_4) 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., GA_8, GA_{29}). 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.

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, GID, *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. "*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).

Gibberellin in Regulating Poplar Growth, Development, and Stress Responses~~Resistance~~

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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).

Plant hormones serve as core regulators of growth, development, and environmental adaptation. Among these, gibberellins (GAs)—a class of natural diterpene hormones—exhibit potent physiological activity and are extensively involved in plant growth, development, and regulatory processes (Kende & Zeevaart, 1997; Shah et al., 2023). To date, over 136 GAs have been identified, though most are biosynthetic intermediates or inactive metabolites (Hedden & Sponsel, 2015). Only GA_1, GA_3, GA_4, and GA_7 are confirmed to possess direct biological activity (L. Yang et al., 2021). During the "Green Revolution" in mid-20th century, the application of GA-related genes in crop dwarfing breeding drove global agricultural yield increases, demonstrating the immense potential of GA in breeding. Current research extensively explores GA's functions, which span multiple stages of the plant life cycle. These include promoting seed germination (Gong et al., 2022), fruit development and ripening (Fenn & Giovannoni, 2021), stem and leaf growth and root elongation (Zluhan-Martínez et al., 2021). GAs also participate in bud dormancy induction and release (Rinne et al., 2011), stress responses~~response~~ (Nagar et al., 2021), and plant regeneration processes (Bassaganya-Riera et al., 2014). GA serves as an environmentally friendly plant growth regulator widely applied in agricultural and forestry production to enhance crop and fruit tree yield and quality (Kildegaard et al., 2021).

Early studies predominantly focused on annual herbaceous model plants like *Oryza sativa* and *Arabidopsis thaliana*. Compared to herbaceous plants, woody plants' ~~poplar's~~ perennial nature (Busov et al., 2006), seasonal dormancy (Rinne et al., 2016), and continuous secondary growth (Wei & Wei, 2023) necessitate significant functional specificity for GA, making its regulatory mechanisms incompatible with direct extrapolation from herbaceous plant research. Current research on gibberellin functions in woody plants has primarily focused on poplar, thus our review specifically centered on poplar and comprehensively detailing its gibberellin regulatory mechanisms, including the synthesis, metabolism, and signal transduction mechanisms of GA. In recent years, key genes in GA synthesis, metabolism, and signaling pathways (*GA20ox, GA3ox, GA2ox, GID1, DELLA*) have been progressively identified in poplar. Their roles in growth processes such as apical dominance, vascular cambium development, and dormancy release, as well as in responses to abiotic stresses like drought and salinity, have been gradually elucidated (Zawaski & Busov, 2014; Zhang et al., 2024). However, significant gaps remain in current research: First, the GA regulatory network is fragmented, lacking holistic integration of synthesis-metabolism-signaling pathways, with unclear tissue-specific regulatory mechanisms. Second, the interaction network between GA and other hormones has not been systematically elucidated, and core interaction nodes remain undefined. Third, research on biological stress response mechanisms is relatively weak, and the molecular regulatory logic of the growth-defense balance remains unclear. Fourth, there is insufficient linkage between basic research and its application in molecular breeding of poplar. This review ~~Given the central role of GA in poplar growth, development, and stress resistance regulation, coupled with the unique research value of woody plants, this paper focuses on the woody model plant poplar. It systematically reviews the synthesis,~~

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

2. Biosynthesis, Metabolism, and Signaling Mechanisms of Gibberellin

2.1 Biosynthetic Pathway of Gibberellin

GA biosynthesis is a complex metabolic process involving multiple organelles and diverse~~synergistic~~ enzymes~~ participation~~ (Figure 1), divided into three main stages sequentially completed in plastids, endoplasmic reticulum, and cytoplasm. This pathway is highly conserved in both herbaceous and woody plants (Hedden & Thomas, 2012). The first stage occurs in the plastids, primarily through the interaction between the methylenepyruvate (MEP) pathway and the mevalonate (MVA) pathway to generate isopentenyl pyrophosphate (IPP). IPP is further synthesized into geranylgeranyl pyrophosphate (GGPP). GGPP is sequentially catalyzed by ent-caryophyllene diphosphate synthase (*ent*-CPS) and ent-kaurene synthase (*ent*-KS) to yield *ent*-kaurene, a key intermediate for GA synthesis (Shah et al., 2023). Notably, this stage exhibits significant specificity in poplar: the *KS1* and *KS2* genes are highly expressed in vascular tissues, directly participating in xylem formation and secondary stem growth—a core characteristic distinguishing poplar from herbaceous plants (Zhang et al., 2024). The second stage occurs within the endoplasmic reticulum (ER). First, ent-kaurene is oxidized to GA_{12}-aldehyde by ent-kaurene oxidase (KO) and ent-kaurenoic acid oxidase (KAO), catalyzed by members of the cytochrome P450 monooxygenase family. This is further converted to GA_{12} (Hartweck, 2008). This process is conserved in both herbaceous and woody plants. The third stage occurs in the cytoplasm, where GA_{12} is catalyzed by GA20-oxidase (*GA20ox*) and GA3-β-hydroxylase (*GA3ox*), yielding bioactive molecules such as GA_1 and GA_4 (Gou et al., 2011). *GA20ox* plays a key regulatory role in GA precursor synthesis, with its expression directly influencing active GA levels. Concurrently, active GA molecules exert negative feedback regulation by suppressing *GA20ox* and *GA3ox* expression, thereby maintaining GA homeostasis. This feedback mechanism is highly conserved in poplar and adapts to its continuous growth requirements. Given the high-specificity expression of poplar *KS1*/*KS2* in vascular tissues, locally synthesized GA may be transported to the shoot apex or roots via specific carrier proteins. NPF and SWEET family transporters have been identified in Arabidopsis as efflux carriers for GA, participating in inter-tissue GA transport and regulating GA concentration equilibrium (Binenbaum et al., 2018). It is speculated that a similar transport mechanism may exist in poplar, which represents one of the core directions for future GA regulation research in poplar.

2.2 Metabolic Inactivation of Gibberellin

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

2.3 Gibberellin Signaling

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

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

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

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

3.1 Plant Height Regulation

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

Controlling the expression of key enzymes and receptors involved in GA synthesis and signal transduction pathways can be used to regulate the height of poplar trees. Overexpression of the GA synthesis key gene *PtoKS1* enhances GA signaling, significantly promoting overall poplar growth (Zhang et al., 2024); Similarly, overexpression of *PttGA20ox* and *PttGID1* both promote internode elongation and xylem formation by enhancing the GA signaling pathway (Eriksson, 2000; Mauriat & Moritz, 2009). Furthermore, overexpression of *PtGA3ox*, the terminal enzyme in GA synthesis, significantly increases active GA levels, thereby enhancing both plant height and stem diameter in poplar (Hu et al., 2022). However, it is important to note that enhanced GA signaling disrupts development of other organs. For instance, overexpression *Pinus densiflora GA20ox* (*PdGA20ox*) in poplar leads to elongated stems, but reduced leaf size, and poor rooting; suggesting tissue- or stage-specific regulation of GA on secondary growth (Jeon et al., 2016).

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

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

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

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

As a central gene regulating flowering, FT not only participates in floral timing regulation but also serves as a key target for dormancy induction. The mechanism by which GA promotes dormancy release and bud priming in poplar has been elucidated and is closely linked to the FT signaling pathway: Rinne et al. (2011) revealed that GA breaks dormancy by enhancing 1,3-β-glucanase activity to degrade callose, thereby opening sieve pathway channels to facilitate PttFT protein transport (Rinne et al., 2011); Eriksson et al. (2015) further indicated that GA can promote bud germination independently of the *FT2* pathway. Exogenous GA application significantly enhances bud germination, regulating hybrid poplar bud elongation in parallel with the *FT2* pathway (Eriksson et al., 2015); The cold-induced transcription factor *PttSVL* suppresses the expression of *PttFT1* and *PttGA20ox*, antagonistically regulating bud germination through GA and ABA signaling. It serves as an integration node between environmental signals and the hormone network (Singh et al., 2018). Concurrently, FT signaling influences shoot growth by inversely regulating GA content. For instance, *PtaFT2* modulates shoot apical meristem development and inhibits internode elongation via the GA13-hydroxylation pathway (Gómez-Soto et al., 2022). GA also plays a crucial role in sustaining continuous shoot elongation (Cao et al., 2023). Beyond FT signaling, *PtoHY5a* directly activates *PtoFT2* expression to suppress short-day-induced growth arrest. Simultaneously, it reduces apical GA levels by upregulating key GA inactivation genes and downregulating GA synthesis genes, thereby inhibiting bud emergence. This *HY5a*-GA module adapts to the seasonal growth patterns regulated by photoperiod in woody plants (Gao et al., 2024).

3.3 Development of the Vascular Cambium and Secondary Growth

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

Recent studies have progressively elucidated the molecular mechanisms by which the GA signaling pathway regulates the development of the vascular cambium and secondary growth in poplar trees: Du et al. (2024) discovered that *PdRabG3f* regulates internode elongation and xylem development in poplar by interfering with endogenous GA levels (Du et al., 2024); Su et al. (2025) further revealed that localized GA synthesis in stems is a key factor regulating xylem development, clarifying that tissue-specific distribution of GA levels is essential for maintaining normal cambium activity (Su et al., 2025). The synergistic regulation of GA and IAA constitutes the core mechanism governing poplar cambium development: IAA forms a polar gradient in the cambium region via polar transporters such as *PIN1(PIN-FORMED 1)*, with its maximum concentration located in the cambium cell layer, thereby determining stem cell differentiation fate (Hartweck, 2008; Mäkilä et al., 2023). Björklund et al. (2007) revealed that GA regulation of poplar cambium depends on IAA; GA alone cannot induce cambial regeneration but significantly enhances IAA-induced expression of cambium-related genes. The two exhibit marked synergistic effects, share multiple transcriptional regulatory elements, and show highly overlapping downstream transcriptional responses (Björklund et al., 2007). Zhang et al. (2024) further elucidated the molecular basis of this synergistic mechanism: the IAA response factor ARF7 interacts with the DELLA protein RGL1 via its MR domain while simultaneously binding to the *Aux/IAA* family member IAA9 through its PB domain. This forms the ARF7-RGL1-IAA9 ternary complex, serving as a key platform for integrating GA and IAA signaling (Zhang et al., 2024). GA promotes IAA accumulation in the cambium region by upregulating *PIN1* expression and positively regulates *ARF7* and *WOX4* expression, thereby enhancing cambium cell activity (Hu et al., 2022; Mäkilä et al., 2023). DELLA proteins negatively regulate *PIN1* expression, forming a GA-IAA feedback loop that precisely controls the sustained activity of the cambium (Zhang et al., 2024).

Multiple PIN family members exist in the poplar genome (Liu et al., 2014). Despite functional redundancy, their tissue expression is highly differentiated. For example, *PttPIN1* and *PttPIN12* are specifically expressed in the cambium and its derived xylem, participating in polar IAA transport within vascular tissues (Schrader et al., 2003). The tissue-specific distribution of GA and expression of its biosynthetic genes further safeguard vascular cambium development: active GA forms (e.g., GA_1 and GA_4) accumulate in xylem regions, while GA precursors (e.g., GA_9, GA_{20}) predominantly localize in phloem (Israelsson et al., 2005), closely aligning with xylem differentiation functions. GA activity is primarily regulated by three key enzymes: *PdGA20ox* overexpression significantly increases poplar xylem cross-sectional width and cell number (Jeon et al., 2016); *GA3ox* expression levels directly determine the accumulation of active GA (Israelsson et al., 2004); inhibiting *GA2ox* (e.g., *PtGA2ox4*, *PtGA2ox5*) enhances meristem cell proliferation and promotes secondary growth (Gou et al., 2011). These three enzymes synergistically regulate GA activity within vascular tissues, determining wood formation efficiency.

3.4 Root Development and Nutrient Acquisition

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

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

3.5 Biomass Accumulation and Wood Quality Formation

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

GA exhibits distinct organ specificity in regulating material accumulation in poplar: it positively regulates above-ground biomass accumulation by optimizing wood processing properties through modulation of lignin content and monomer composition; conversely, it negatively regulates below-ground root biomass, consistent with root development regulation. This characteristic provides precise targets for breeding fast-growing, high-quality poplar varieties (Eriksson et al., 2000). Adjusting the ratio of lignin monomers (S/G ratio) can reduce cell wall resistance while enhancing wood quality, without affecting biomass accumulation (Tang et al., 2025). The core value of GA in regulating wood quality has been validated: Field trials by Cho et al. (2019) confirmed that co-overexpressing *PdGA20ox1* and *PtrMYB221* in poplar synergistically optimizes GA levels and the lignin synthesis network. This resulted in above-ground biomass doubling compared to wild-type, significantly reduced lignin content, increased total cellulose proportion, and approximately 8% higher saccharification efficiency, without noticeable growth defects (Cho et al., 2019), representing a classic case of GA application for wood quality improvement. GA signaling imbalance disrupts material accumulation and xylem development: excessive suppression of above-ground GA signaling impairs xylem differentiation, such as *ClGA2ox12* overexpression in poplar significantly inhibiting vessel differentiation and reducing lignin deposition (Peng et al., 2024); Elevated GA levels resulting from suppressed *PtGA2ox2* and *PtGA2ox7* activity in roots decrease root biomass (Gou et al., 2011), further confirming its organ-specific regulatory characteristics.

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

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

4.1 Abiotic Stress Response

Drought and saline-alkali stress are two of the main abiotic factors that limit forestry production (Fang et al., 2021; X. Yang et al., 2021). In poplar, GA plays a role in regulating abiotic stress by modulating its own content, hormone interactions and transcription factor networks, and exhibits a typical "growth-stress trade-off" effect. Phenotypically, a trade-off is evident: Poplar trees that overexpress GA exhibit accelerated growth and increased leaf area, but reduced drought tolerance. In contrast, GA-deficient plants exhibit limited growth yet superior drought stress response~~resistance~~ (Eriksson et al., 2000; Zhang et al., 2024). As an evolutionary adaptation to drought, the heterophyllous trait in *Populus euphratica* shows significant positive correlations between GA_3 content and leaf length and spongy tissue thickness, reflecting species adaptation regulated by GA (Han et al., 2021).

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

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

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

4.2 Biotic Stress Responses

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

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

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

5. Discussion and Summary

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

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

5.1.1 Well-established Mechanisms

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

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

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

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

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

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

5.1.3 Specialized Mechanisms Adapted to the Perennial Habits of Woody Plants

Although the core GA signaling and metabolic pathways are conserved across species, woody perennials such as poplars have evolved unique GA regulatory mechanisms to support their perennial life cycles during their long-term adaptation to terrestrial environments and seasonal changes. These specific regulatory mechanisms are primarily manifested in the unique perennial biological traits of woody plants. Firstly, poplars possess a specialized pathway under long-day conditions in which *FT2* reduces active GA levels by upregulating *GA2ox1* and downregulating *GA3ox2*, thereby specifically limiting internode elongation and promoting apical meristem development (Gao et al., 2024). This FT-dependent GA metabolic regulation pattern is completely absent in Arabidopsis, highlighting the evolutionary differences in plant height regulation between herbaceous and woody plants. Secondly, GA acting as a flowering-promoting signal in annual herbs which are characterized by rapid generational turnover (Wilson et al., 1992). GA activates integrons such as *SOC1* and *LEAFY* to accelerate the reproductive transition (Blazquez et al., 1998; Li et al., 2016). In contrast, in poplars, GA inhibits flowering integrons, prioritizing stem elongation and secondary growth, and delaying the reproductive transition to accumulate nutrients and resist frost damage (André et al., 2022). Thirdly, herbaceous dormancy is confined to the seed stage and is regulated by the *DOG1*-ABA-GA pathway

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

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

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

5.2 Future Research Directions

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

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

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

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

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

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

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Authors' Contributions

L. Z. and H. H.: study conception and design, manuscript writing and revision. X. Z. and G. C: manuscript revision.

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Conflict of interest

The authors declare no conflict of interest.

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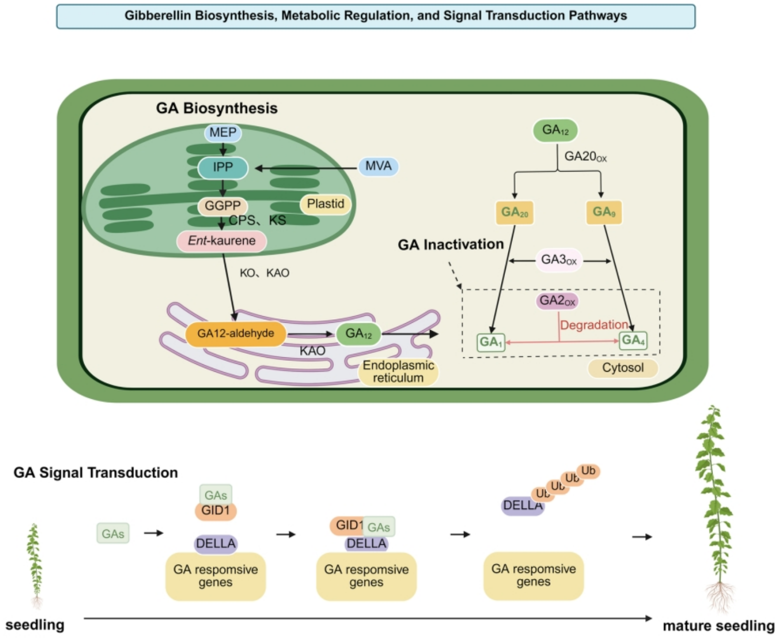
List of figure legends:

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 GA_{12}; 3) In the cytoplasm, GA_{12} is converted into active GA (e.g., GA_1, GA_4) 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., GA_8, GA_{29}). 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.

Figure 2. GA signaling and its regulatory role in tree growth, development, and stress resistance. 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, GID, *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 resistance; *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. "*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).



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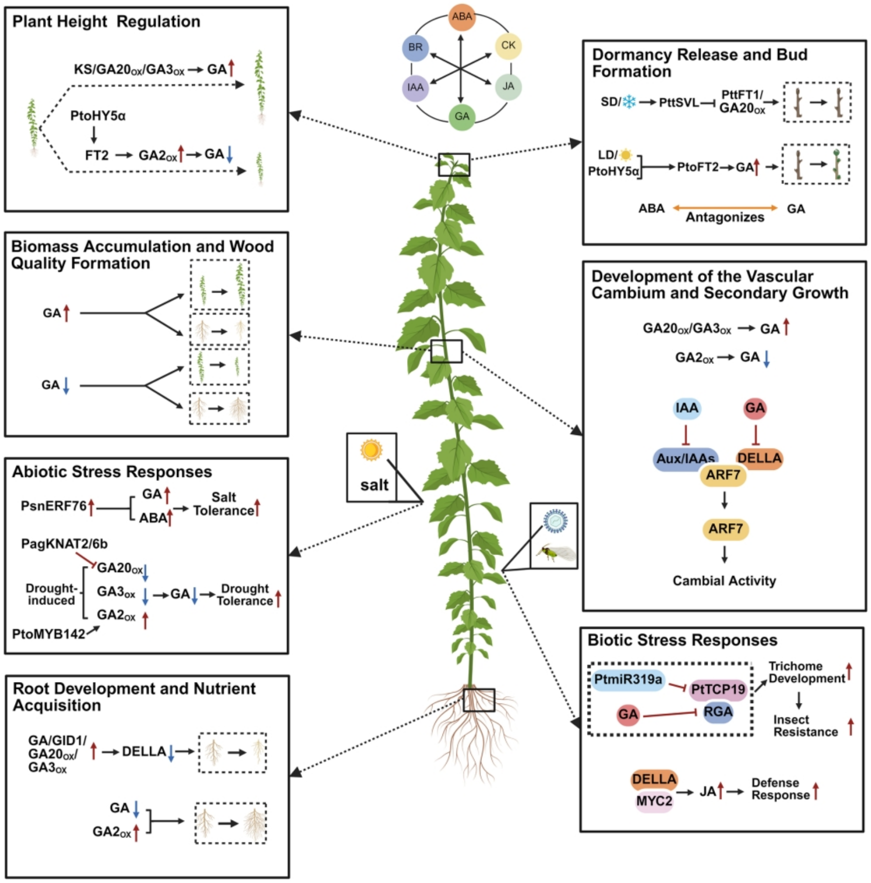

Figure 2. GA signaling and its regulatory role in tree growth, development, and stress responses. Schematic of GA-mediated pathways (via key biosynthetic enzymes GA20ox/GA3ox [GA activation] and GA2ox [GA inactivation], and interacting factors) controlling multiple physiological processes in trees, while 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, GID, 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

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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.