

Review

Research Progress on Woody Plants with Narrow Crown Phenotype

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Highlights

What are the main findings?

- We systematically summarized biological characteristics and formation mechanisms of narrow crown phenotype in woody plants, clarifying regulatory roles of plant hormones and key functional genes controlling branch angle traits.
- We analyzed multi-field practical applications of narrow crown woody germplasm, covering timber cultivation, orchard management, ornamental tree breeding and forest genetic improvement.
- We concluded recent research advances and put forward promising future research directions for narrow crown phenotype and branch angle regulation in woody plants.

What is the implication of the main finding?

- This review supplies integrated theoretical references for exploring the molecular regulation network of branch angle formation in woody plants.
- It supports the genetic breeding, popularization and industrial application of narrow-crown tree varieties in forestry and horticultural production.

Abstract

The narrow crown, a distinct form of canopy architecture and a specialized phenotypic expression of branch angle traits in woody plants, significantly influences key physiological processes such as photosynthesis, transpiration, and biomass accumulation. This phenotype holds substantial application value in forestry production. This article aims to elucidate the biological traits and formation mechanisms of the narrow-crown phenotype in woody plants by analyzing the contributions of plant hormones, their related genes, and specific key genes to the formation and determination of branch angles. Furthermore, the review explores applications of the narrow-crown phenotype in timber forestry, orchard production, breeding of new ornamental woody varieties, and forest tree genetic improvement. Finally, we summarize recent advances in research on narrow-crowned woody plants. On this basis, the future research directions of woody plants with narrow-crown phenotype were prospected, in order to provide reference for promoting the study of branching angle formation of woody plants and the production and application of woody plants with narrow-crown phenotype.



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1. Introduction

In the past, research on plant architecture has focused on herbaceous plants, which are mainly crops, such as rice [1], maize [2], etc. Compact strain types can increase the planting density of crops, so that they can make full use of the light energy to maximize the yield [3].

In 1968, Colin Malcolm Donald (C. M. Donald) first proposed the concept of ideal plant type, which refers to minimizing competition between individual plants by cultivating ideal plant types, allowing individual plants to make full use of their limited living environment without encroaching on the living environment of other individuals [4].

In 1985, Donald Ivan Dickmann (D. I. Dickmann) first introduced the concept of ideal tree form into the field of forest tree genetic breeding [5], and in 1996, he and Daniel Elden Keathley (D. E. Keathley) jointly proposed the ideal tree form for fast-growing and high-yielding poplar plantations under conditions of high density, no irrigation, and intensive management [6]. The ideal tree form should have branches that grow upward and form a small angle with the trunk, resulting in a long and narrow crown.

Against the backdrop of global climate change, rising atmospheric vapor pressure deficit and frequent seasonal drought exacerbate water limitation in planted forests, threatening stand productivity and stability [7,8]. Compact narrow-crown phenotypes represent promising architectural traits for climate-resilient forest cultivation. Compared with broad-crown individuals, narrow-crown trees possess reduced crown width, thinner lateral branches, and stronger natural pruning capacity, which effectively lower whole-stand transpiration and alleviate canopy competition under high-density planting [9]. Such traits help reconcile the pursuit of high biomass yield and water balance in intensive plantations, making narrow-crown variants valuable germplasm resources for breeding climate-adapted tree varieties [10]. Nevertheless, the physiological and molecular adaptive mechanisms of narrow-crown phenotypes under changing climatic conditions remain insufficiently understood.

At present, existing studies concerning woody plant narrow-crown phenotypes remain fragmented. Published reviews mostly focus on general tree ideotype theories, while systematic summaries specifically targeting narrow-crown traits are still lacking, and the range of investigated woody species needs further expansion.

Based on the above research gaps, this paper reviews the progress of research on narrow-crown phenotypes in woody plants, with a view to providing theoretical references for further studies on branch angle regulation, crown developmental pathways and the genetic improvement of climate-adaptive tree materials.

2. Biological Characteristics of Narrow-Crown Woody Plants

A narrow crown is a special phenotype of tree branching angle traits, which exhibits significant differences from the traditional wide crown type. These differences are manifested not only in the external morphology of the trees but also in their resource utilization.

Narrow-crowned trees exhibit stronger stem growth capacity and higher nutrient utilization efficiency. The narrow-crowned Fujian cypress (*Fokienia hodginsii* (Dunn) Henry et Thomas f. *columnaris* Z.F. Li et D.X. Zhou, forma nov) has significantly taller tree height and larger diameter at breast height (DBH) than the original Fujian cypress [11], exhibiting higher stem biomass. Additionally, the narrow-crowned Fujian cypress has a more uniform vertical distribution of trunk volume, a straighter and rounder trunk, and a higher timber outturn rate [12]. Narrow-crowned loblolly pine (*Pinus taeda*) exhibits higher leaf nutrient

utilization efficiency than the broad-crowned type, achieving comparable stem growth even under low leaf nutrient content [13]. The radius of the stem, number of vascular rays, lignin content, number of fiber cells, and average fiber length of the erect sand willow (*Salix psammophila*) are all higher than those of the spreading sand willow, indicating that the erect sand willow has stronger lateral nutrient transport capacity and greater mechanical strength of cell walls, which together promote the erect growth of the stem [14]. The size of the branching angle of branches of the drought-tolerant willow (*Salix matsudana*) is highly significantly negatively correlated with tree height and annual tree height growth, and significantly negatively correlated with annual trunk diameter growth. Overall, smaller branching angles accelerate both radial and longitudinal growth rates of trees [15].

Compared to their wide-canopy counterparts, narrow-canopy fruit trees such as apple and peach exhibit higher photosynthetic rates, greater light-use efficiency, and stronger transpiration. Concurrently, their lower light compensation and saturation points confer greater shade tolerance, which in turn enhances fruit yield and quality [16–18].

3. Causes of Narrow Crown Phenotype Formation in Woody Plants

The narrow-crown phenotype in woody plants arises from the synergistic regulation of genetic, hormonal, and environmental factors. Most existing studies, however, have focused on individual regulatory elements, leaving systematic analyses of multi-component networks largely unexplored. In fact, crown architecture development relies on the integrated action of hormone signal gradients, auxin polar transport, and *IGT* family-mediated responses to gravity and light signaling [1,19,20]. While basal branching angle is genetically determined and relatively stable, plastic traits such as branch spatial orientation and crown expansion are further shaped by hormonal crosstalk and genetic interaction networks [21,22]. This review integrates hormonal signals, auxin transport processes, and *IGT*-dependent gravitropic and light-signaling pathways to establish a unified framework for understanding narrow-crown formation in woody plants.

3.1. Role of Auxin, Gibberellin, and Associated Gene Regulation in Narrow-Crown Phenotype Formation

Endogenous plant hormones are crucial regulators of plant growth and development. Plant hormones are transported in planta and regulate downstream gene expression through signaling cascades, thereby affecting cell division and differentiation, organ development, and plant responses to environmental stimuli [23]. Among various phytohormones, auxin and gibberellin serve as the core hormones regulating tree branching angles and crown architecture [24–26]. Accumulating studies have confirmed that asymmetric hormone gradient distribution acts as an important initiating signal driving branch angle differentiation within this regulatory cascade [26,27]. Genes related to hormone transport and signal response can further amplify such spatial signal differences, ultimately shaping crown morphology [23,28].

3.1.1. Synergistic Effects of Growth Factors and Gibberellins

Indole-3-acetic acid (IAA) promotes plant cell division and differentiation and drives the growth and development of plant tissues and organs. Gibberellic acid (GA) stimulates stem elongation and plays pleiotropic roles in plant development [25]. The synergistic interaction between GA and IAA facilitates the development of plant secondary xylem [25,29], and GA alone exerts a significant regulatory effect on branch development [25]. GA₃ treatment in *Prunus spachiana* can induce tension wood formation in the upper branches, promote upright branch growth, and alter the weeping branch phenotype [30]. Differences in the content and spatial distribution of IAA and GA in upper and lower branch tissues

significantly affect branching angle formation and further regulate crown development patterns [31,32].

For *Populus* ‘Zhaiguan II’, the IAA and GA concentrations in the lower tissues of branch bases and branch tips are significantly higher than those in the upper tissues. Comparison of different crown-type poplar varieties reveals that a greater difference in upper–lower IAA and GA distribution corresponds to a more distinct variation in branching angle [24]. These findings suggest that the asymmetric distribution of IAA and GA may generate differential mechanical support between upper and lower branch tissues, thereby enhancing negative gravitropic growth and contributing to narrow-crown formation [24]. However, the precise mechanisms by which these hormonal asymmetries translate into morphological outputs remain to be fully elucidated.

3.1.2. Regulation of Plant Crown Shape and Branching by Auxin- and Gibberellin-Related Genes

Variations in hormone concentrations are essentially regulated by genes involved in hormone synthesis, transport, signal transduction, and other pathways. In woody plants, the PIN protein family, which is a key transporter for polar auxin transport, plays an important role [33]. *PIN* family genes reshape auxin polar transport and lateral redistribution to establish tissue auxin concentration gradients, serving as critical intermediate modules linking upstream hormonal signals and downstream crown development [34,35]. Phloem analyses at branch junctions of different peach tree types (*Prunus persica*) revealed that the expression levels of the *PpPIN2* gene in columnar peaches were significantly lower than those in standard peaches, while the expression levels of the *PpPIN13* gene were significantly higher than those in standard peaches. These significant differences in gene expression significantly influenced the formation of branch angles in peach branches [36].

During the early spring budding period, the expression levels of PIN protein family members in the axillary buds of 5-year-old *Populus* ‘Zhaiguanheibaiyang’ (narrow-crowned black–white poplar) were higher than those in broad-crowned poplar trees, whereas IAA levels were significantly lower than in the broad-crowned poplar. These findings indicate higher polar auxin transport efficiency in *Populus* ‘Zhaiguanheibaiyang’, with increased auxin efflux leading to reduced auxin levels within axillary buds, thereby promoting lateral bud emergence and forming a more branched phenotype [37]. However, the IAA content in the axillary buds of 7-year-old *Populus* ‘Zhaiguanheibaiyang’ was significantly higher than that in wide-crowned poplar trees, contrary to the previous findings [38], but this is consistent with the research results on narrow-crowned tail-leaf eucalyptus (*Eucalyptus urophylla*) [39]. These results indicate that tree endogenous hormone distribution patterns dynamically change with developmental stages, leading to variations in branching angle and crown morphology, while the specific regulatory mechanism remains unclear.

Differential regulation of gibberellin metabolism and signaling pathways shapes plant architecture, and GA-associated genes participate in governing internode growth and crown morphology [40,41]. The columnar mutant ‘McIntosh Wijcik’ of *Malus × domestica* exhibits a compact crown trait controlled by a dominant Columnar (*Co*) allele on chromosome 10 [42]. Transcriptome analyses have revealed that the *Co* locus alters the expression of numerous genes related to hormone metabolism and signal transduction [43,44]. *MdCo31* (also named *MdDOX-Co*), the key candidate gene within the *Co* interval, reduces bioactive gibberellin levels upon ectopic overexpression, thereby inducing shortened internodes and compact columnar crown architecture [45,46].

3.2. Regulation of Plant Crown Shape and Branching by *Lazy1* and *Tac1* Genes

The formation of the narrow-crowned phenotype in woody plants is also regulated by certain specific genes. The *IGT* gene family plays an important role in the gravitropism

and directed growth of plant lateral organs, including key genes such as *LAZY1*, *TILLER ANGLE CONTROL1 (TAC1)*, and *DEEPER ROOTING1 (DRO1)*. The first two have been confirmed to be key regulators in the regulation of plant branching angle [1,47,48]. Overall, the expression levels of the *LAZY1* gene are negatively correlated with plant branching angle, while those of the *TAC1* gene are positively correlated with plant branching angle [6]. The two genes differentially regulate plant branching angles via functional divergence.

3.2.1. Differences in the *LAZY1* and *TAC1* Gene Promoters

Analysis of the promoters of the *LAZY1* and *TAC1* genes revealed that the types of cis-elements in their promoters are associated with gene functional expression. In apple trees, the cis-elements of the *MdoTAC1* and *MdoLAZY1* gene promoters are primarily associated with plant hormones (such as gibberellin, salicylic acid, and methyl jasmonate response elements), abiotic stress, and light responses [49]. Similar results have been reported in studies on tea plants (*Camellia sinensis*) [50]. Comparative analysis of promoter sequences across apple varieties identified fragment deletions in *MdTAC1a*. These deletions were most pronounced in short-branched and weeping-branched varieties relative to standard and columnar types [51], which is also one of the factors contributing to the diverse branching angles observed in apple varieties.

In various plant species, the promoters of *LAZY* and *TAC* genes drive β -glucuronidase (*GUS*) activity in distinct tissues. These two genes modify plant branch angles by regulating the growth and development of different tissue regions. The expression patterns of the promoters from *PzTAC* and *PzLAZY* were examined in transgenic *Populus × euramericana* ‘Neva’. *GUS* activity driven by the *PzTAC* and *PzLAZY* promoters was detected in mature leaves, leaf axils, and vascular tissues of roots. Specifically, the *PzTAC* promoter showed dominant activity in leaf veins, while the *PzLAZY* promoter was mainly active in mesophyll cells and root tips. Transgenic 35S::*PzTAC* plants exhibited a larger average branch angle than transgenic 35S::*PzLAZY* lines. Differences in the active regions of these two gene promoters affect vascular tissue development, thus altering branch angles [52].

In *Salix psammophila*, the *SpsLAZY1* promoter was mainly active in the endodermis and phloem of stems. The promoters of the *SpsLAZY1a* and *SpsLAZY1b* genes were non-tissue-specific promoters, and there were differences in the activity of the promoters of these two genes. The *GUS* activity driven by the *SpsLAZY1a* promoter was stronger than that of the *SpsLAZY1b* promoter. In terms of expression patterns, the expression levels of both genes were higher in erect-type *S. psammophila* than in spreading-type *S. psammophila* [53,54]. By summarizing previous research results, the expression sites and patterns of *LAZY1* and *TAC1* genes in different woody plants were organized (Table 1).

Table 1. Expression characteristics of *IGT* family genes in woody plants.

Species	Genetics	Place of Expression	Mode of Expression	Reference
poplar <i>Populus × zhaiguanheibaiyang</i> <i>Populus deltoides</i>	<i>PzTAC</i>	Leaf blades, annual branches	Expression was higher in branches of wide-canopied poplar than in narrow-canopied poplar; overexpression of <i>PzTAC</i> increased branching angle.	[52]
	<i>PzLAZY</i>	Annual branches, axillary buds	There was no significant difference in expression in wide- and narrow-crowned poplars; overexpression of <i>PzLAZY</i> decreased branching angle.	[52]

Table 1. Cont.

Species	Genetics	Place of Expression	Mode of Expression	Reference
salix <i>Salix psammophila</i>	<i>SpsTAC1</i>	Stems, leaf axils	Expression was highest in stems, followed by leaf axils, and lowest in roots.	[55]
	<i>SpsTAC2</i>	Mature leaves, phloem	Overexpression of <i>SpsTAC2</i> and increased branching angle.	[56]
	<i>SpsLAZY1a</i> <i>SpsLAZY1b</i>	Stems, leaf axils	Expression was higher in erect salal than in open-disperse salal.	[53]
pineapple <i>Prunus persica</i>	<i>PpeTAC1</i>	In or around actively growing nutritive and reproductive tissues	No expression detected in branches of columnar peach varieties; expression was lower in erect peaches than in standard peaches.	[57]
		stem	Expression was highest in standard peach and lowest in columnar peach; expression was negatively correlated with growth hormone concentration in the branches.	[58]
European plum <i>Prunus domestica</i>	<i>PdoTAC1 (PpeTAC1)</i>	stem tip	RNAi silencing of <i>PpeTAC1</i> in Li: branching angle decreased, branches grew vertically and showed a distinct columnar growth habit, branch length increased, upper branches fluctuated and twisted, and stem diameter increased; Overexpression of <i>PpeTAC1</i> in plum resulted in increased branching angle, horizontal branching growth, increased branching diameter, increased overall tree height, and increased stem diameter.	[59]
pomegranate <i>Malus domestica</i>	<i>MdTAC1a</i> <i>MdTAC1b</i>	Stem tip, axillary buds	The highest expression levels were found in the stem tip and axillary buds of pendant apples, followed by standard apples, and the lowest expression levels were found in column apples; <i>MdTAC1a</i> expression was higher than <i>MdTAC1b</i> in stem tips and axillary buds; Overexpression of <i>MdTAC1a</i> and <i>MdTAC1b</i> and increased leaf angle.	[51]
	<i>MdoLAZY1</i> <i>MdoLAZY2</i>	Mature leaves, stem tips, axillary buds	Expression is lower in column apples than in other tree types.	[49]
rugosa rose (shrub) (<i>Rosa rugosa</i>) <i>Rosa rugosa</i>	<i>RrLAZY1</i>	stalk	Overexpression of <i>RrLAZY1</i> and reduced branching angle; Expression was significantly higher in columnar roses than in flat-lying roses.	[60]
sweet orange (<i>Citrus sinensis</i>) <i>Citrus sinensis</i>	<i>CsTAC1</i>	be in harmony	CRISPR/Cas9 silencing of <i>CsTAC1</i> reduced branching angle, reduced leaf growth angle, and reduced internode length.	[61]

Table 1. Cont.

Species	Genetics	Place of Expression	Mode of Expression	Reference
teas <i>Camellia sinensis</i>	<i>CsLAZY1</i>	stalk	There was no significant difference in expression in upright and open tea plants; overexpressing <i>CsLAZY1</i> , plants showed negative geotropic growth.	[50]
	<i>CsLAZY2</i>	florid	Highly expressed in fruit, very low expression in rootstock leaf bud fruit.	[50]
	<i>CsLAZY3</i>	be in harmony	Highly expressed in the second leaf and to a lesser extent in the third leaf.	[50]
	<i>CsIGT-1</i>	Old leaves, stem phloem	Expression is highest in old leaves and second highest in stem phloem.	[48]
	<i>CsIGT-2</i>	newly grown leaves	Highly expressed only in young leaves.	[48]
	<i>CsIGT-3</i>	stem phloem	Expression was highest in stem phloem, followed by stem xylem.	[48]
	<i>CsIGT-4</i>	Old leaves, young leaves	Expression was significantly higher in leaves than in other tissues.	[48]

3.2.2. Response Relationships of *LAZY1* and *TAC1* Genes to Gravity and Light

Genes *TAC1* and *LAZY1* of the IGT family exert opposite yet vital functions in regulating the growth orientation of lateral branches in vascular plants. The expression of *TAC1* is upregulated under light conditions, which promotes outward growth of lateral branches by generating wider branch or tiller angles. *LAZY1* functions in the gravity response pathway upstream of lateral auxin transport and facilitates upward growth of lateral branches by producing narrower branch or tiller angles [62]. When subjected to anti-gravity treatment under either light or dark conditions, transgenic *Arabidopsis thaliana* plants overexpressing *CsLAZY1* exhibited more pronounced responses than wild-type plants, indicating that *CsLAZY1* plays a critical role in modulating stem gravitropism in tea plants [50]. Notably, loss of *TAC1* exerts no detectable effect on the gravitropic bending response of branches in *Arabidopsis thaliana*. *TAC1* may promote outward outgrowth of lateral buds by negatively regulating *LAZY1*. Nevertheless, the regulatory effects of *TAC1* and *LAZY1* on lateral bud orientation are more complex than a simple direct negative regulatory pathway. Further research is required to elucidate the genetic interaction between these two genes and the direct linkage between *TAC1* and gravity responses [62].

3.3. Interaction Between Endogenous Hormones and the *Lazy1* and *Tac1* Genes

Altered expression of *LAZY1* and *TAC1* regulates both branch angle architecture and modulates the endogenous hormone content of plants and the expression abundance of their related genes.

3.3.1. Interaction with Auxin

Genes of the IGT family function in regulating auxin distribution and signaling in plants. *LAZY1* modulates asymmetric auxin distribution by controlling polar auxin transport, whereas *TAC1* mediates hormone homeostasis primarily via transcriptional pathways [47]. In peach trees, *TAC1* transcript abundance is inversely correlated with auxin concentrations in branches; expression is highest in standard trees and lowest in colum-

nar trees [58]. Loss-of-function mutation of *TAC1* elevates auxin concentration, facilitates upright shoot growth, and narrows branching angles. In contrast, *TAC1* overexpression promotes wider, horizontally oriented branches. The columnar phenotype of peach trees is tightly linked to repressed *TAC1* expression. Columnar peaches with low *PpeTAC1* expression possess significantly higher auxin and cytokinin levels than standard peaches [58]. By comparison, *CsTAC1*-silenced sweet orange (*Citrus sinensis*) lines exhibit increased cytokinin levels but reduced auxin abundance [61]. These conflicting hormonal responses may stem from intrinsic physiological differences between evergreen and deciduous tree species, and the precise regulatory mechanisms await further investigation.

LAZY1 and *TAC1* display functional differentiation and cooperatively shape branch architecture by modulating the expression of genes involved in auxin biosynthesis, polar transport, and signal transduction. Heterologous overexpression of *RrLAZY1* from *Rosa rugosa* represses transcript levels of auxin transporter genes *AtAUX1* and *AtPIN3* in *Arabidopsis*, thereby altering gravitropic characteristics of branches [60]. Heterologous overexpression of apple *MdTAC1a* upregulates auxin response genes *ARF2* and *ARF3*, together with the gibberellin catabolic gene *GA2ox* [51]. Variation in the expression of these hormone-related genes modulates branching angles and ultimately shapes plant crown shape.

3.3.2. Interactions with Other Hormones

Plant architecture is coordinately regulated by multiple phytohormones, such as gibberellins (GAs), cytokinins, and strigolactones (SLs). GAs facilitate upright shoot growth and inhibit branch bending; cytokinins act as key regulators of aerial branching; strigolactones mainly modulate shoot branching [63]. Studies in rice have demonstrated that strigolactones modify local auxin homeostasis, thereby regulating plant gravitropism and shoot architecture [64].

Direct experimental evidence linking cytokinins or strigolactones to *LAZY1* and *TAC1* remains limited in woody species. Existing studies confirm that *LAZY1* is highly evolutionarily conserved among woody plants, and hormonal signals exert central control over tree architectural development [48]. It is hypothesized that various phytohormones may cooperate with *LAZY1* and *TAC1* via indirect pathways to shape woody plant architecture, yet the underlying regulatory networks require further experimental validation.

3.4. A Proposed Conceptual Model for Narrow-Crown Formation Regulated by *LAZY1* and *TAC1*

Integrating findings from herbaceous model species and woody plants, we propose a conceptual model illustrating how the IGT-family *LAZY1* and *TAC1* coordinate environmental signals, auxin transport, and gibberellin signaling to govern crown architecture differentiation (Figure 1). *LAZY1* perceives gravity signals to trigger PIN repolarization and strengthen lateral IAA gradients within branches. Light induces *TAC1* expression, which may weaken the *LAZY1*–PIN pathway and attenuate lateral IAA asymmetry. Asymmetric IAA cooperates with GA to control differential cell elongation of branches. Enhanced lateral IAA gradients reduce branch angles and produce narrow-crown phenotypes; attenuated IAA asymmetry enlarges branch angles, leading to wide crowns.

There is no evidence of direct protein interaction between *LAZY1* and *TAC1*. Their opposite effects on branch angle are achieved through indirect pathway regulation. In addition, the crosstalk of cytokinins and strigolactones with this module remains insufficiently studied in trees. This framework is hypothetical and requires further experimental validation in woody plants.

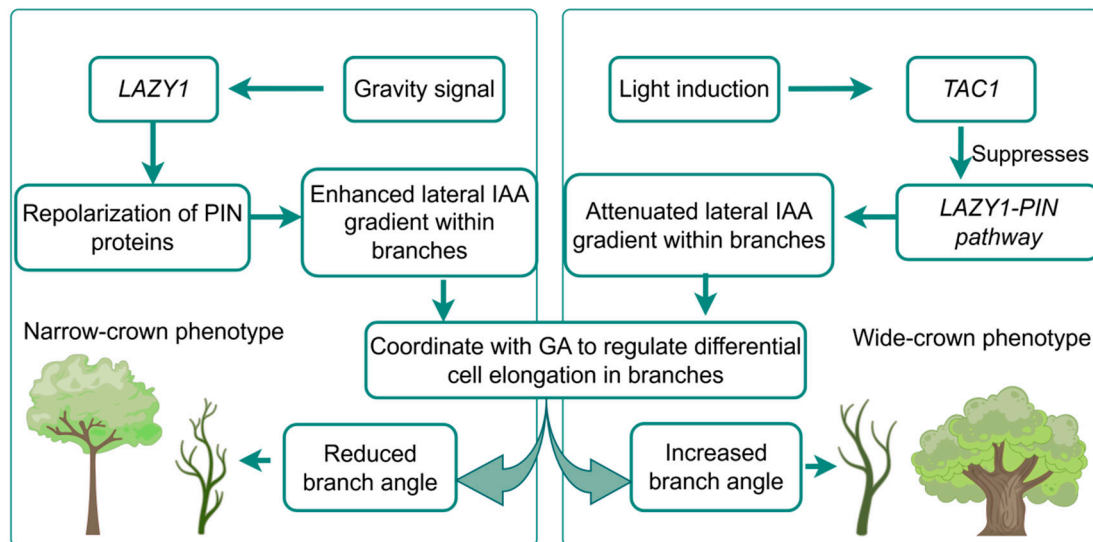


Figure 1. Molecular mechanism model for canopy architecture formation in woody plants. *LAZY1* perceives gravity signals and triggers repolarization of PIN proteins, enhancing lateral IAA gradients within branches to form narrow-crown phenotypes with reduced branch angles. Light-induced *TAC1* may weaken the *LAZY1*–PIN cascade and attenuate lateral IAA gradients, potentially forming wide-crown phenotypes with larger branch angles. The asymmetric IAA gradient coordinates with GA to regulate differential cell elongation and determines branch angle. The gravity signal arrow denotes signal perception by *LAZY1*, not transcriptional induction. Direct physical interaction between *TAC1* and *LAZY1* has not been identified.

4. Applications of Narrow-Crowned Woody Plants

The unique phenotypic merits of narrow-crowned woody plants confer broad application prospects in timber plantations, orchard cultivation, ornamental germplasm innovation and forest tree genetic improvement. Compared with conventional broad-crown ideotypes, narrow-crown varieties exhibit distinct morphological and physiological advantages that support dense planting, mechanized management and improved resource-use efficiency [65].

4.1. Application in Timber Forests

Timber forests are forest stands managed primarily for wood production. Species selection prioritizes “fast-growing, high-quality, and productive” as the starting point, which requires that the tree species have straight and complete trunks, small crowns, small branches, and a strong ability to natural pruning. Tree crown architecture significantly affects the profitability of timber forests and wood properties, and trees with narrow crowns are more advantageous.

Narrow-crown phenotypes possess compact canopies suitable for high-density planting, which enhances space utilization and boosts stand volume per unit land area. Compared with larger growing space, stem growth and fiber length of narrow-crowned Norway spruce (*Picea abies* f. *pendula*) were significantly improved under tight spacing with reduced phenotypic variation [66,67]. Compared with common black locust, narrow-crowned black locust (*Robinia pseudoacacia* cl. ‘Zhaiguan’) displays higher survival rates for root cuttings, stronger adaptability to infertile mountain soils and wider cultivation suitability, enabling the establishment of high-yield fast-growing plantations in northern temperate regions [68–70]. Such advantages highlight the potential of narrow-crown materials to facilitate the transition from traditional low-density silviculture to intensive, high-output plantation systems.

4.2. Applications in Orchard Cultivation

Fruit tree cultivation pursues balanced fruit yield and quality, and crown architecture governs aboveground plant structure, mediating photosynthetic efficiency and biomass partitioning [65,71,72]. Therefore, crown morphology represents a core agronomic trait for fruit tree breeding and orchard management.

Narrow-crown cultivars reduce pruning labor and operational costs, and high-density planting substantially lifts economic returns [73]. In Southwest China, columnar training systems are widely adopted in simplified pear orchards owing to compact canopy structure, early high bearing potential, superior fruit quality, and compatibility with mechanical harvesting [74]. Narrow-crown trees also facilitate diversified agroforestry management [75]. For instance, compact almond (*Prunus dulcis*) maintains stable fruit load while improving canopy light penetration, making it suitable for intercropping with wheat [76]. In recent decades, targeted breeding has released multiple narrow-crown fruit cultivars, including columnar peach (*Prunus persica*) ‘Pillar’ and narrow-crown sour cherry (*Prunus cerasus*) ‘JAC Him’ [77,78]. Given the global trend toward mechanized, labor-saving orchards, narrow-crown columnar ideotypes are expected to occupy an increasingly important position in future fruit tree improvement programs.

4.3. Application in the Selection of New Varieties of Woody Ornamental Plants

Canopy architecture is a core aesthetic trait of woody ornamentals. Branch angle shapes landscape performance and horticultural applicability, forming distinct visual effects. Narrow-crown cultivars usually present upright, fusiform growth habits with compact canopies, and exhibit unique ornamental value when combined with flowering and fruiting traits [78,79].

Many narrow-crowned ornamental cultivars have been developed via resource screening and artificial breeding, including crabapple and ornamental peach. Morphological traits of these cultivars are listed in Table 2 [80–85]. Rising demand for urban vertical greening and intensive planting increases the application potential of narrow-crown germplasm. Most existing cultivars are derived from conventional phenotypic selection, and further utilization of narrow-crown ideotypes relies on molecular genetic research and precision breeding technologies.

Table 2. Morphological characteristics of representative narrow-crown woody ornamental cultivars.

Cultivar	Tree Age	Crown Width	Key Morphological Traits	Reference
<i>Malus</i> ‘Juan Zhulian’	3-year-old	0.5 m	Compact narrow-crown crabapple	[81]
<i>Malus</i> ‘Hongyi’	4-year-old	0.5 m	Columnar upright narrow-crown crabapple	[80]
<i>Malus</i> ‘Fen Balei’	6-year-old	1.2 m	Upright narrow-crown crabapple	[82]
<i>Malus</i> ‘Zi Dieer’	4-year-old	1.0 m	Upright narrow-crown crabapple	[83]
<i>Malus spectabilis</i> ‘Duojiang’	-	0.84–1.07 m	Height of 2.24–2.80 m, narrow-crown yellow-leaf crabapple	[84]
<i>Prunus persica</i> ‘Sahonglongzhu’	5-year-old	ca. 1.0 m	Compact upright columnar growth habit	[85]

4.4. Application in Genetic Breeding of Forest Trees

Traditional crossbreeding has realized preliminary selection of narrow-crowned woody plants. However, long generation cycles, complex polygenic inheritance, and obstacles to early phenotypic screening restrict breeding efficiency. Advances in molecular biology facilitate dissection of the genetic basis of branch angles and promote precision breeding for narrow crown architecture. Early research used SRAP markers to analyze genetic diversity of narrow-crowned poplar and optimize crossbreeding schemes [86]. cDNA-AFLP

screening detected differentially expressed *STPK* related to heterosis in narrow-crowned hybrid poplar, which is speculated to regulate branch angle development [87]. Integration of SLAF sequencing and QTL mapping constructed genetic linkage maps and uncovered candidate genes controlling branch angle in narrow-crowned poplar [88]. Nevertheless, conventional phenotypic selection and screening relying on traditional molecular markers hardly enable rapid early identification of ideal genotypes at the seedling stage.

4.4.1. Molecular Marker-Assisted Selection and Genomic Selection

Marker-assisted selection (MAS) and genome-wide association studies (GWAS) provide powerful tools to accelerate narrow-crowned breeding [89]. Utilizing validated trait-linked SNP, InDel, and SSR markers, breeders can conduct genotype identification at the seedling stage rather than waiting for mature canopy phenotypic expression, thereby drastically shortening breeding cycles [90]. In apple, InDel markers associated with *MdTAC1a* promoter variation can distinguish varieties with divergent branch angles [51]. In peach, molecular markers tightly linked to columnar growth habit have been developed to screen upright ideotypes in hybrid progenies [91]. For poplar, QTL and GWAS resources for crown traits support the implementation of genomic selection, which exhibits potential to predict breeding values for narrow crown architecture in juvenile poplar populations [90]. Molecular markers targeting *LAZY1*, *TAC1*, and *PIN* family genes and hormone-related genes can be exploited as core selective markers for screening narrow-crowned germplasm [92]. Despite these prospects, the polygenic nature of branch angle and strong genotype-by-environment ($G \times E$) interaction still restrict the universal application of single molecular markers across different genetic backgrounds [89].

4.4.2. Prospects of CRISPR/Cas-Mediated Genome Editing

CRISPR/Cas genome editing achieves targeted modification of key regulatory genes and represents a revolutionary strategy for creating novel narrow-crowned woody germplasm. Functional studies in poplar have confirmed that CRISPR-mediated knockout of poplar *TAC1* homologs can induce upright growth and reduced branch angles under experimental conditions, consistent with the functional model of *LAZY1* and *TAC1* regulating gravitropism and shoot architecture described above [47,93]. Targeted editing of *IGT* family members, *PIN* auxin transporters and GA metabolic genes represents promising candidate strategies to remodel branch angle and crown morphology [92]. However, large-scale application in trees faces prominent obstacles: many woody species suffer low genetic transformation efficiency and poor plant regeneration capacity; additionally, strict biosafety regulations limit field trials of edited perennial woody plants [94]. At present, CRISPR editing in forest trees is mostly confined to model poplar clones, and multi-generation field verification of edited narrow-crowned materials remains scarce [94].

4.4.3. Integrated Breeding Schemes for Intensive Production Systems

Future narrow-crown breeding should build an integrated pipeline oriented toward intensive plantation and orchard systems. The workflow can be summarized as: (1) excavating natural narrow-crown variants from wild populations and germplasm repositories; (2) utilizing GWAS and QTL mapping to mine superior alleles of *LAZY1*, *TAC1* and downstream hormone-related genes; (3) establishing efficient MAS and genomic selection systems for early seedling screening; (4) generating new germplasm via crossbreeding or precise gene editing; and (5) conducting multi-site field trials to evaluate crown morphology, growth performance, wood quality or fruit productivity under high-density cultivation conditions [90].

5. Future Prospects

Narrow-crown phenotypes of woody plants have broad application prospects in timber forest cultivation, high-density planting of orchards, agroforestry systems, and ornamental plant landscaping. At present, studies on woody plants with narrow-canopy phenotypes mainly focus on the regulation of branch angles by biological characteristics, plant hormones, and specific genes. Such research broadens the research perspectives of tree canopy architecture, enriches relevant research achievements concerning canopy traits of woody plants, lays a foundation for the breeding of new narrow-canopy woody plant cultivars, and facilitates the utilization of the advantages of narrow-canopy phenotype plants in forestry production. Based on the current status of domestic and international research in this field, the research on narrow-crowned woody plants can be strengthened in the following three aspects in the future:

- (1) Elucidate the interactive regulatory mechanisms governing crown architecture in plants. The regulation of plant growth and development constitutes an intricately coordinated process, where individual hormones and genes exhibit limited functionality, necessitating crosstalk among diverse regulatory factors, which can affect and interact with each other; similarly, crown architecture represents a multifaceted process involving dynamic interactions between various determinants. Systematic investigation of these interacting entities and their operational pathways will establish a theoretical framework for targeted breeding of woody plants with optimized crown architectures.
- (2) Investigating the genetic basis of branching angle traits is fundamental to advancing woody plant improvement. This requires integrating multi-omics approaches (genomics, metabolomics, and transcriptomics) with modern molecular biology techniques and conducting comparative analyses across populations and species to elucidate the genetic principles underlying crown architecture. We will develop high-density genetic linkage maps for branching angle traits to characterize their genomic architecture and inheritance patterns and identify candidate genes regulating branching angle through functional genomics. These efforts will establish a genetic framework for precision breeding of superior tree varieties.
- (3) Investigating the biological properties of narrow-crown woody plants is essential. As plant phenotypic expression results from genotype–environment interactions, comprehensive characterization of narrow-crown phenotypes' biological impacts, including responses to biotic/abiotic stressors and environmental adaptation mechanisms, will enable optimized deployment of narrow-crown genotypes to enhance silvicultural productivity and sustainable forest management.

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