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Phytohormone and transcriptome analyses reveal the mechanisms underlying branch angle formation in narrow-crowned *Chamaecyparis hodginsii*

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Abstract

The narrow-crown form of *Chamaecyparis hodginsii* has ornamental, greening, and timber value, making it promising for forestry. To identify superior narrow-crown provenances and elucidate mechanisms of branch inclination angle variation, we measured growth traits, branch angles, and phytohormones in axillary buds from 14 provenances, followed by multivariate analyses. A narrow-crown (provenance 3) and a wide-crown (provenance 6) provenance were selected for transcriptome sequencing. Significant variation in traits and hormone levels was found. Provenance 4 had the lowest branch angle (20.4% below mean), and provenance 2 the highest proportion of narrow-crown individuals (21.7%). Zeatin was highest in provenance 2 (42.8% higher), auxin lowest in provenance 14 (27.6% lower). Comprehensive evaluation identified provenances 3 and 4 as superior. Branch angle negatively correlated with zeatin and auxin, with auxin showing strong negative direct effect. Transcriptome analysis revealed 2272 differentially expressed genes, including 27 in hormone pathways. Six up- and three down-regulated auxin-responsive genes showed unique patterns in the narrow-crown provenance. Cytokinin regulators had opposite expression; gibberellin receptor was down-regulated while

growth repressor up-regulated. Salicylic and jasmonic acid signaling were suppressed, whereas abscisic acid regulator decreased and ethylene signaling increased. These findings indicate auxin and auxin-responsive genes regulate branch inclination angle, and provenances 3 and 4 are superior narrow-crown sources, providing insights for early selection and molecular breeding.

Keyword

Chamaecyparis hodginsii, narrow-crown architecture, branch inclination angle, phytohormone signaling, transcriptome analysis

1 Introduction

Branch inclination angle is a key determinant of crop yield and ideal plant architecture. The magnitude of branch inclination angle directly influences crown architecture, photosynthetic efficiency, and stress resistance [1]. Despite its importance, the mechanisms governing branch inclination angle formation remain insufficiently understood [2]. Plants with larger branch inclination angles typically develop a more dispersed canopy structure, which can reduce photosynthetic efficiency and hinder mechanized operations [3]. In contrast, smaller branch inclination angles promote a more compact and dense plant architecture, which is generally associated with improved productivity [4]. For example, in peach cultivation, trees with narrower crowns and smaller branch inclination angles produce fewer lateral branches and are easier to train and prune, thereby reducing labour inputs [5]. The establishment of axillary meristems and the subsequent growth of axillary buds are the two main developmental processes involved in branch development. Phytohormones play a key regulatory role in the intricate interactions between genetic factors, environmental conditions, and axillary meristem formation, ultimately leading to the initiation and development of axillary buds [6]. Subsequent axillary bud growth is a critical determinant of branch inclination angle, thereby exerting a fundamental influence on overall plant architecture [7].

Genetic factors, environmental conditions, phytohormones, and nutritional availability jointly regulate branch inclination angle development [8]. From a hormonal perspective, branch inclination angle formation depends on the interactions and spatiotemporal dynamics of many phytohormone signaling pathways. Among them, auxin is a key regulator [9, 10]. Auxin gradients are established through local biosynthesis mediated by flavin monooxygenases of the YUCCA family [11], polar transport facilitated by carrier proteins such as PIN transporters [12], and signal transduction via TIR1/AFB receptors and ARF transcription factors [13]. This coordinated regulatory network generates asymmetric auxin distribution within tissues, thereby modulating gravitropic growth and branch inclination angle [14]. Strigolactones further interact with auxin to regulate branch inclination angle through conserved biosynthetic pathways involving *MAX*, *D*, and *RMS* genes [15]. In addition, other hormones—including cytokinins [16], brassinosteroids [17], gibberellins [18], ethylene [19] and abscisic acid [20]—participate in this process by modulating cell elongation and gravitropic responses. At the genetic level, several key genes controlling branch inclination angle have been cloned [21]. Expression of the *LAZY1* gene is negatively correlated with branch inclination angle. Previous studies suggest that *LAZY1* interacts with genes involved in auxin signaling at both the plasma membrane and the nucleus [22, 23], and may regulate branch inclination angle by repressing the expression of auxin-responsive genes [22]. In contrast, *TAC1* functions antagonistically to *LAZY1*. Loss of the conserved C-terminal domain V may impair the ability of *TAC1* to bind to actin filaments, thereby modulating branch inclination angle by suppressing *LAZY1*-induced gravitropic responses [24-26]. The *LPA1* gene participates in amyloplast sedimentation during gravity perception [27], whereas *PROG1*, a domestication-related gene, plays a critical role in regulating plant architecture in rice [28]. Additionally, branch inclination angle is dynamically regulated by environmental cues, including gravity and light, which can lead to induce uneven distribution of phytohormones [29, 30]. Gravitational stimuli trigger amyloplast sedimentation and downstream signal transduction, thereby influencing branch inclination angle

formation [31]. Similarly, unilateral light induces differential auxin distribution through photoreceptor-mediated pathways, resulting in phototropic bending [32].

Chamaecyparis hodginsii is listed as a nationally protected species in China and possesses substantial ecological, economic, and ornamental value. In recent years, research on *C. hodginsii* has expanded across multiple aspects, including germplasm morphology [33, 34], physiological ecology [35, 36], stand management [37], and cultivation regulation [38, 39]. These studies have provided an increasingly systematic scientific basis for the cultivation and utilization of this species. The narrow-crown form of *C. hodginsii* represents a naturally occurring variant characterized by desirable timber properties as well as landscape and ornamental value, and therefore holds considerable promise for forestry and horticultural applications. Current studies on narrow-crown *C. hodginsii* have primarily focused on morphological differences between narrow- and normal-crown types. For instance, compared with the standard variety, the narrow-crown form exhibits greater tree height and diameter at breast height, but smaller crown dimensions, including crown length, width, and crown ratio. In addition, the two forms show pronounced stage-dependent and trait-specific differences in branching rate, branch and leaf morphology, and leaf area [40]. Despite these advances, the mechanisms mechanisms that govern branch inclination angle formation in *C. hodginsii* remain poorly known. Considering the critical role of branch inclination angle in determining crown architecture and ornamental value, a deeper understanding of the endogenous processes that regulate branch inclination angle development is required.

In our study, 14 provenances of *C. hodginsii* were selected to identify superior narrow-crown sources characterized by smaller branch inclination angles, cylindrical crown architecture, and multilayered leaf arrangement, which together indicate strong natural self-pruning ability. The study aimed to elucidate the hormonal and molecular mechanisms underlying variation in branch inclination angle. By integrating endogenous phytohormone profiling with transcriptome analysis, we identified key genes and phytohormones

signalling pathways involved in regulating branch inclination angle development in *C. hodginsii*. These findings have substantial implications for selecting and developing superior narrow-crown cultivars. Furthermore, they establish a scientific basis for molecular design breeding aimed at optimizing tree architecture and enhancing both the economic and ecological value of forest stands. Collectively, this work contributes to the efficient utilization and industrial development of this multifunctional tree species.

2 Materials and Methods

2.1 Overview of Experimental Conditions

The Feng Tian State-owned Forest Farm in Hutou Town, Anxi County, Fujian Province, China (25°18′ N, 118°0′ E) was the study site. It has a subtropical monsoon climate, an elevation of 350-550 m, and an annual average temperature of 21 °C. The rainfall is 1600 mm, and the frost-free period lasts 330 days. The provenance trial plantation is dominated by yellow–red soils with relatively high organic matter content and favorable physicochemical properties, providing suitable conditions for the growth of a wide range of forest tree species. The main understory vegetation includes *Blechnum orientale*, *Maesa japonica*, and *Ophiopogon bodinieri*.

2.2 Experimental Materials

2.2.1 Experimental design

Seeds of *C. hodginsii* collected from 14 different provenances were used as experimental materials. Seedlings were initially raised under forest canopy conditions in 2015. During the early introduction and cultivation phase, individuals exhibiting vigorous growth were preliminarily selected. In 2016, seedlings of similar height were transplanted from the nursery stage to an experimental site with comparable site characteristics. The trial consisted of seven plots in the provenance trial. Five trees from each provenance were planted in each plot, for a total of 35 trees per provenance. Trees were planted 2 m × 2 m apart. During both nursery establishment and afforestation, a single row of *C. hodginsii* was planted around the experimental

plantation as a protective row. The provenance trial plantation was distributed across upper-, middle-, and lower-slope positions of the mountain. Standard silvicultural management practices, including fertilization, irrigation, and weed control, were conducted twice annually. Germplasm evaluation was carried out again during the young stand stage.

At present, the provenance trial plantation at Feng Tian State-owned Forest Farm in Anxi County, Fujian Province, consists mainly of 7-year-old *C. hodginsii* trees. Detailed information on the provenance origins of *C. hodginsii* is presented in Fig. 1 and Table 1.

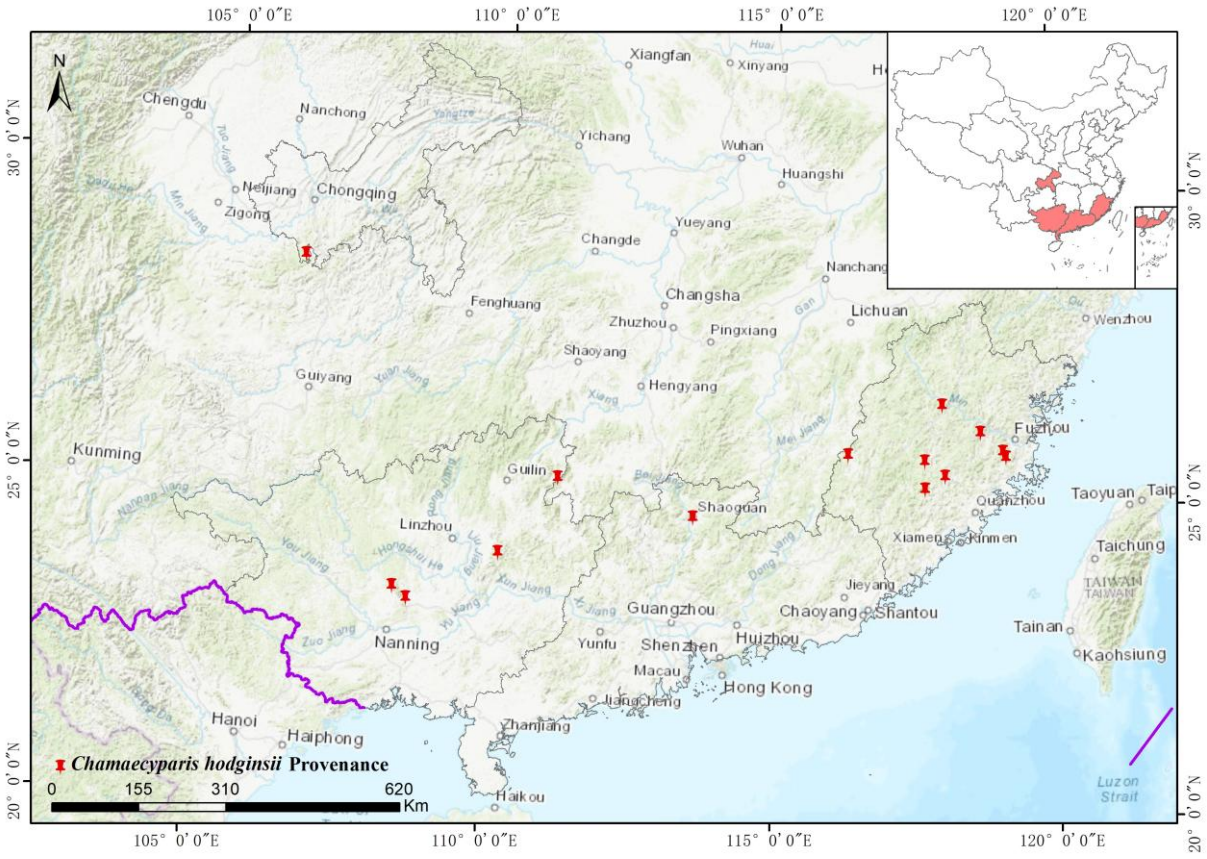


Figure 1. Geographical information of *C. hodginsii* from different provenances.

Note: P1, Wuming District, Nanning, Guangxi Zhuang Autonomous Region, China; P2, Shanglin County, Nanning, Guangxi Zhuang Autonomous Region, China; P3, Minqing County, Fuzhou, Fujian Province, China; P4, Jiangjin District, Chongqing, China; P5, Ruyuan Yao Autonomous County, Shaoguan, Guangdong Province, China; P6, Changting County, Longyan, Fujian Province, China; P7, Anxi County, Quanzhou, Fujian Province, China; P8, Yongchun County, Quanzhou, Fujian Province, China; P9, Shanghang County, Longyan, Fujian

Province, China; P10, Yongtai County, Fuzhou, Fujian Province, China; P11, Hua'an County, Zhangzhou, Fujian Province, China; P12, Xianyou County, Putian, Fujian Province, China; P13, Jinxiu Yao Autonomous County, Laibin, Guangxi Zhuang Autonomous Region, China; P14, Guanyang County, Guilin, Guangxi Zhuang Autonomous Region, China.

Table2 . Basic information of different provenances of *C. hodginsii.*

Provenance	Longitude	Latitude	Elevation (m)	Annual average temperature (℃)	Annual precipitation (mm)	Sunshine duration (h)	Relative humidity (%)
P1	108.38	23.51	1000	21.7	1500	1660	78
P2	108.63	23.33	800	20.9	1500	1576	81
P3	106.68	26.19	400	19.7	1700	1515	83
P4	106.35	28.58	1300	18.4	1001	1141	90
P5	113.59	24.80	1500	17.7	1705	1234	84
P6	116.32	25.84	400	18.3	1700	1936	84
P7	118.05	25.49	340	20.0	1600	1843	79
P8	117.69	25.29	500	20.4	1850	1908	79
P9	118.00	26.64	1300	20.1	1646	1801	77
P10	119.08	25.88	1000	17.0	1500	1755	75
P11	117.69	25.74	1300	19.0	1700	2000	75
P12	119.13	25.79	600	20.6	1800	1833	76
P13	110.19	24.13	550	17.0	1648	1269	83
P14	111.18	25.37	1150	18.0	1583	1171	69

2.2.2 Sample collection and trait measurements

(1) Sample collection

A tree-by-tree survey was conducted in April 2023 in each plot. A hypsometer was used to measure the tree height (TH), and diameter at breast height (DBH) at 1.3 meters above ground was measured with a diameter tape. Crown width (CW) was determined using a measuring tape. From the base upward, three branch inclination angle （BIA） was measured using an electronic goniometer, and the mean BIA was calculated for each individual. The proportion of narrow-crown individuals within each provenance was defined as the percentage of *C. hodginsii* trees with an average branch inclination angle smaller than 35°.

Axillary buds at the third and fourth nodes from the base during the early spring bud-burst stage were collected, together with leaf and stem tissues (reserved for further analyses). Samples from the same provenance and tissue position across the seven plots were pooled. All Samples were immediately frozen in liquid nitrogen and stored at −80 °C.

(2) Determination of endogenous phytohormones

Axillary buds from the 14 provenances of *C. hodginsii* were sampled with three biological replicates. Phytohormones, including indole-3-acetic acid (IAA), abscisic acid (ABA), gibberellin (GA_3), and Zeatin (ZT), in the axillary buds of *C. hodginsii* were quantified by HPLC (Shimadzu LCMS-2010) [41].

(3) Transcriptome sequencing

RNA extraction, library construction, de novo transcriptome sequencing, and subsequent bioinformatic analyses were performed by Novogene Co., Ltd. (Beijing, China).

To assess the reliability of the transcriptome data, quantitative real-time PCR (qRT-PCR) was used for validation. Total RNA was isolated from the axillary buds of several *C. hodginsii* provenances and reverse transcribed into cDNA. Six genes related to branch development were randomly selected for qRT-PCR validation, with Actin as the internal reference gene. The primer sequences are presented in Table 2.

Table2 . Primer sequences

Gene ID	Primer sequences	Length
Actin	F:GGAGGTTCCACCATGTTTCC R:GTGCTGAGCGAAGCGAGAAT	90
SAU39 (EVM_prediction_ctg10659.17)	F:GACTTGGAAGCAAAGTGCAGA R:AAATGCCCACGTAGACTGCC	84
SAUR71 (EVM_prediction_ctg5845.47)	F:TTGGAAGGCTCACTTTGGCA R:AGGAACCCTCGCTGACATTG	118
*SAUR*50 (EVM_prediction_ctg7038.48)	F:CTGGTCATTTGCCTGTGTGTG R:AGGAGCTCCCTAAACAGGGG	94
DUF659 (EVM_prediction_ctg4425.1)	F:ACCAGGAGTGCTTTATGGGC R:AGGAAAGAGCTTGTTCGGCA	98

*ETR*2 (EVM_prediction_ctg5771.74)	F:TGAACCGTGAAATGAGGGCA R:CAGCTGTTCAGCATTCAGGC	86
PR1C (EVM_prediction_ctg6256.2)	F:TAAACGCAAGGGGGACTGTG R:ATCAGCAGGCGTGAATTCCT	94

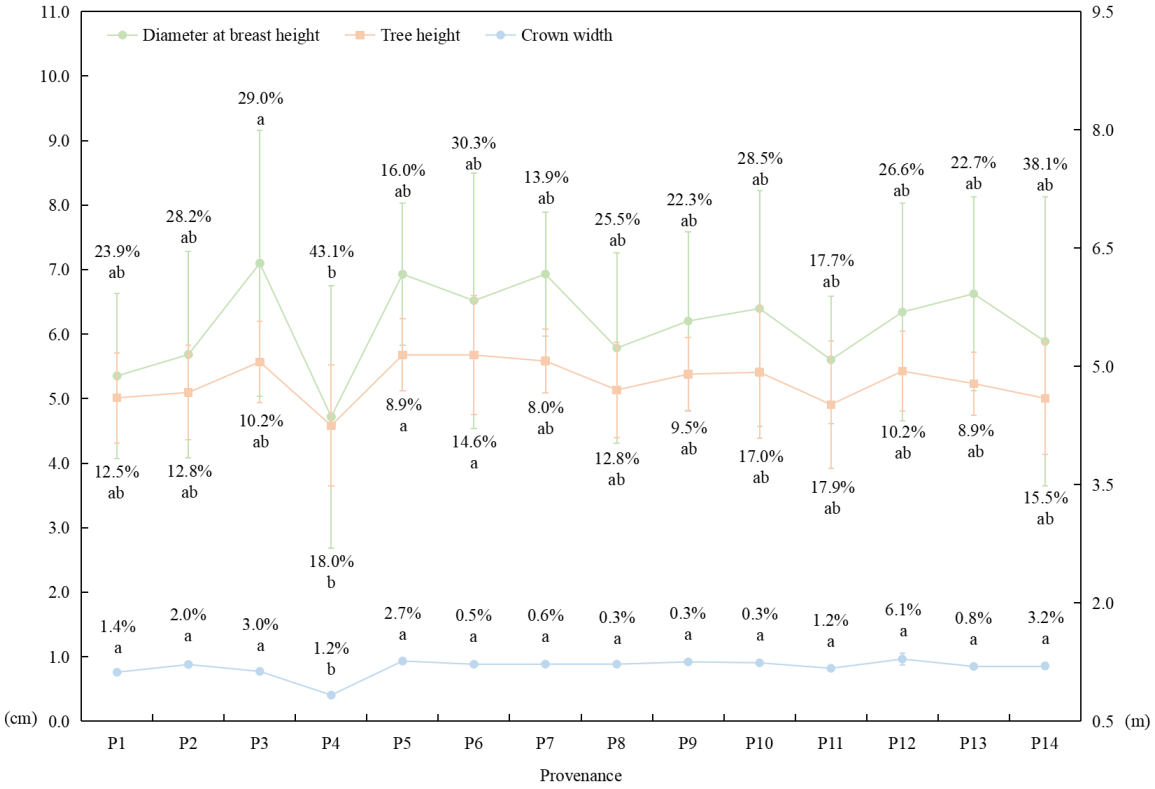
2.2.3 Statistical Analysis

Excel 2019 and SPSS 25.0 were used to analyze the data. One-way ANOVA with LSD testing ($P < 0.05$) was used to evaluate group differences; the findings are shown as mean ± SD. Multivariate analyses were conducted using PCA, Pearson correlation, and R-based heatmaps. Canoco 5.0 was used to do RDA of *C. hodginsii* growth attributes and environmental conditions.

3 Results

3.1 Variation in morphological traits of *C. hodginsii*

Across all provenances, the average DBH, TH, and CW of *C. hodginsii* were 4.8 cm, 6.1 m, and 1.2 m, respectively. Provenance No. 3 exhibited the largest DBH, which was 15.5% higher than the overall mean, whereas provenance No. 4 showed the smallest DBH, 23.2% lower than the mean, and displayed the highest coefficient of variation (43.1%). A significant difference was observed between these two provenances ($P < 0.05$). TH varied significantly among provenances. Provenance No. 5 had the greatest TH, exceeding the mean by 7.0%, whereas provenance No. 4 exhibited the smallest value, 11.6% lower than the mean, with the highest coefficient of variation (18.0%). Compared with provenances No. 5 and No. 6, provenance No. 4 had a significantly lower TH ($P < 0.05$). For CW, provenance No. 12 showed the largest value, which was 8.7% higher than the mean and had the highest coefficient of variation (6.1%). In contrast, provenance No. 4 exhibited significantly smaller CW than the other provenances ($P < 0.05$), being 29.8% lower than the overall mean.



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171 **Figure 2.** Analysis of differences in diameter at breast height, tree height and crown width of *C. hodginsii* from different provenances.

172 Note: Different lowercase letters indicate significant differences between provenances ($p < 0.05$), the same below. The diameter at

173 breast height represents the index on the left side of the Y axis, and the tree height and crown width represent the index on the right side of

174 the Y axis. The provenance is represented on the X axis.

175 The mean BIA across all *C. hodginsii* provenances was 58.1°. Provenance No. 6 exhibited the largest BIA,

176 which was 11.6% higher than the overall mean and significantly greater than those of provenances No. 3 and No.

177 4 ($P < 0.05$). In contrast, provenance No. 4 showed the smallest BIA, 20.4% lower than the mean, and was

178 significantly smaller than those of provenances No. 1, 5, 6, 7, 8, 10, 11, 12 and 14 ($P < 0.05$). Provenance No. 14

179 displayed the highest coefficient of variation, reaching 23.6%. Regarding crown architecture, provenance No. 2

180 had the highest proportion of narrow-crown individuals (21.7%), followed by provenances No. 3 and No. 13

181 (11.5%). No narrow-crown individuals were observed in provenances No. 1, 5, 6, 8, 10, 11 or 12.

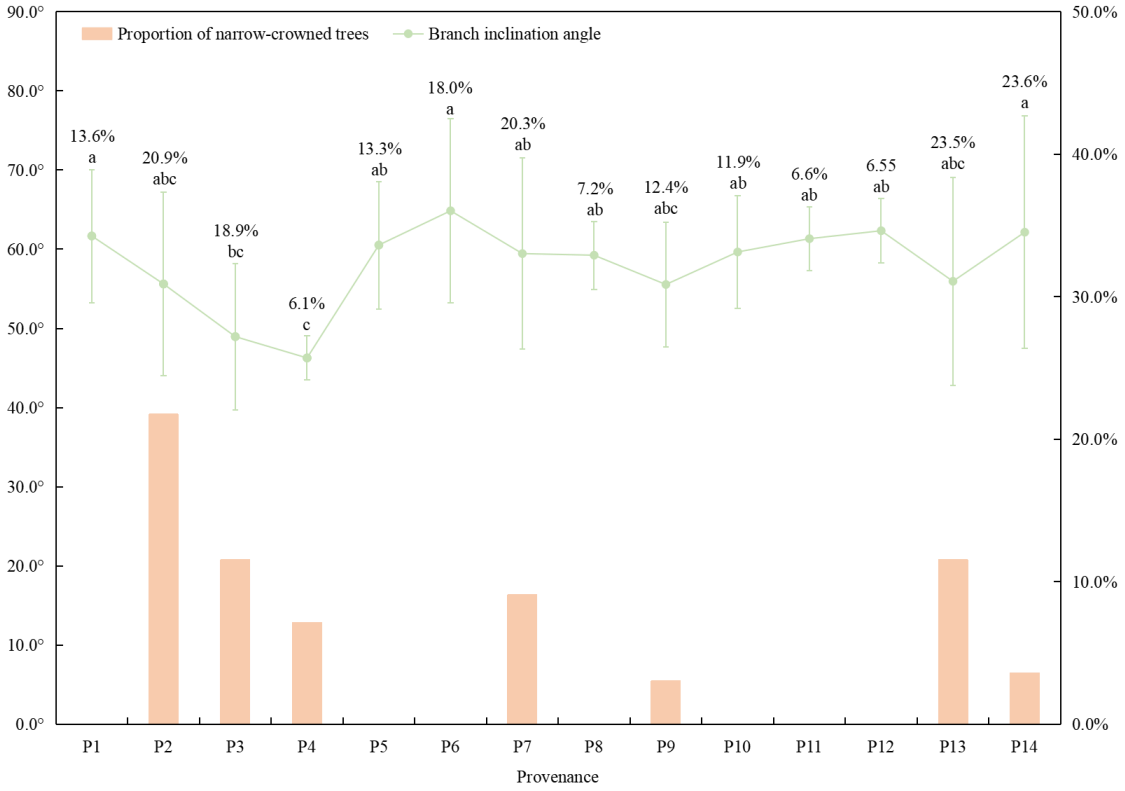


Figure 3. Analysis of differences in branch inclination angle and proportion of narrow-crowned trees of *C. hodginsii* from different provenances.

Note: The branch inclination angle represents the index on the left side of the Y axis, and the proportion of narrow-crowned trees represents the index on the right side of the Y axis. The provenance is represented on the X axis.

3.2 Variation in endogenous phytohormone concentrations in axillary buds of *C. hodginsii*

The mean concentrations of ZT, IAA, GA_3, and ABA in axillary buds of *C. hodginsii* across all provenances were 4.5, 190.8, 3072.8, and 22.0 ng g^{-1}, respectively. Significant variation in phytohormone levels was observed among provenances. Provenance No. 2 exhibited the highest ZT concentration, which was 42.8% higher than the overall mean and significantly greater than those of most other provenances ($P < 0.05$), whereas provenance No. 14 showed the lowest ZT concentration, 33.7% lower than the mean, and significantly lower than those of provenances No. 2, 3, 4, 5, 7, 12, and 13 ($P < 0.05$). For IAA, provenance No. 7 had the highest concentration, 9.5% higher than the mean and significantly greater than those of provenances No. 1, 6, 11, 12, and 14 ($P < 0.05$).

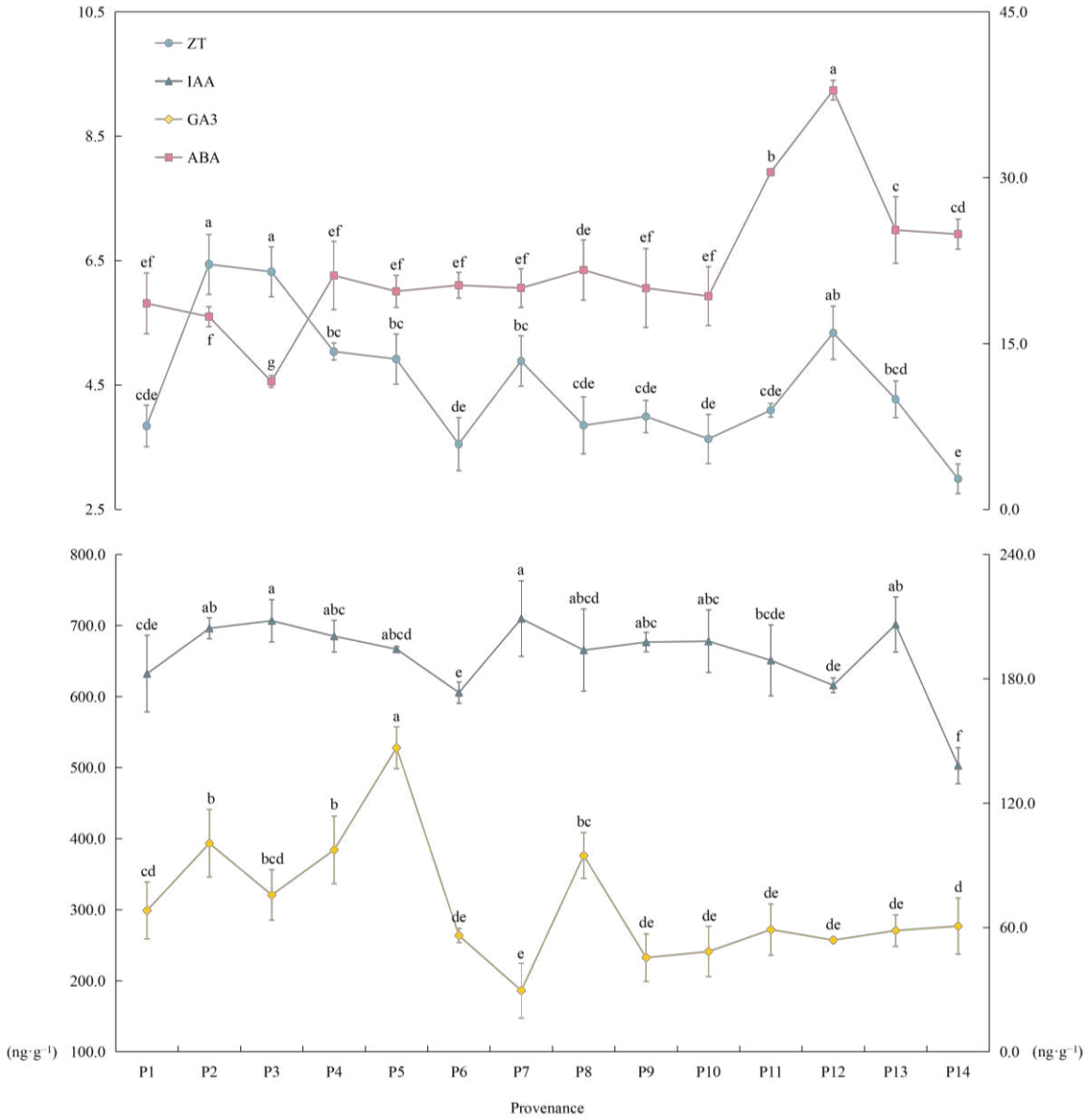


Figure 4. Analysis of differences in endogenous hormone content of axillary buds of *C. hodginsii* from different provenances.

Note: The contents of ZT and GA_3 represent the index on the left side of the Y axis, and the contents of IAA and ABA represent the index on the right side of the Y axis. The provenance is represented on the X axis.

In contrast, provenance No. 14 exhibited the lowest IAA level, 27.6% lower than the mean, and significantly lower than those of all other provenances ($P < 0.05$). GA_3 concentrations also differed significantly among provenances. Provenance No. 5 showed the highest GA_3 concentration, exceeding the mean by 71.8% and significantly higher than that of all other provenances ($P < 0.05$). Conversely, provenance No. 7 exhibited the lowest GA_3 level, which was 39.4% lower than the mean and significantly lower than those of provenances

No. 1, 2, 3, 4, 5, 8, and 14 ($P < 0.05$). For ABA, provenance No. 12 had the highest concentration, 72.2% higher than the mean and significantly greater than those of the other provenances ($P < 0.05$), whereas provenance No. 3 showed the lowest ABA level, 47.5% lower than the mean and significantly lower than those of the other provenances ($P < 0.05$). The ZT/IAA ratio in axillary buds ranged from 0.018 to 0.032, while the GA_3/ABA ratio ranged from 6.8 to 27.2 (Table 3).

Table3 . Variation in phytohormone ratios of *C. hodginsii* from different provenances.

Phytohormone ratio	Provenance													
	P1	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**	**P11**	**P12**	**P13**	**P14**
ZT/IAA	0.021	0.032	0.030	0.025	0.025	0.020	0.023	0.020	0.020	0.018	0.022	0.030	0.021	0.022
GA_3/ABA	16.0	22.6	27.7	18.2	26.8	13.0	9.3	17.4	11.6	12.5	8.9	6.8	10.7	11.1

3.3 Principal component analysis and comprehensive evaluation of phenotypic traits among *C. hodginsii* provenances

Using the criteria of eigenvalues > 1 and cumulative contribution ⩾ 65%, two principal components were retained, explaining 67.85% of the variation in *C. hodginsii* phenotypic traits (Table 4). These two components were therefore considered sufficient to capture most of the variation in phenotypic traits and were subsequently used for the comprehensive evaluation of narrow-crown *C. hodginsii* provenances. The results indicated that P3, P4, and P2 were identified as the superior provenances, whereas P14, P6, and P12 were ranked as the least favorable (Table 5).

CW and BIA were the major contributors to PC1. To further assess the provenances, a second principal component analysis concentrating on narrow-crown characteristics was carried out in light of these findings. The total contribution rate rose to 84.46% in our analysis (Table 4). According to the comprehensive evaluation scores, P4 and P3 continued to be the best-performing provenances, whereas P6 and P12 were the worst (Table 5).

224 **Table 4.** Initial factor loading matrix, eigenvector, and principal component contribution rate.

Index	Principal component 1		Eigenvector 1		Principal component 2	Eigenvector 2
	1-1	1-2	1-1	1-2		
Diameter at breast height	−0.571	0.758	−0.332	0.482		
Tree height	−0.640	0.721	−0.372	0.459		
Branch inclination angle	0.863	0.306	0.502	0.195	0.919	0.707
Crown width	0.862	−0.290	0.501	−0.184	0.919	0.707
ZT	−0.469	−0.635	−0.273	−0.404		
IAA	0.451	0.682	0.262	0.434		
GA3	0.419	0.177	0.244	0.113		
ABA	−0.366	−0.547	−0.213	−0.348		
Eigenvalue	2.957	2.471	2.957	2.471	1.689	1.689
Contribution %	36.96	30.89	36.96	30.89	84.46	84.46
Cumulative contribution %	36.96	67.85	36.96	67.85	84.46	84.46

225 **Table 5.** The principal component value and comprehensive value of *C. hodginsii* with different provenance.

Provenance	Principal Component Score 1		Comprehensive Score 1	Sort 1·	Principal Component Score 2	Sort 2·
	F1	F2	F		FF	
P1	0.02	0.19	0.10	10	0.38	6
P2	0.36	0.87	0.59	3	0.46	4
P3	0.28	1.45	0.82	1	0.85	2
P4	1.17	0.17	0.71	2	1.41	1
P5	−0.27	1.10	0.36	4	0.21	11
P6	−0.66	0.59	−0.08	13	0.11	13
P7	−0.35	1.03	0.28	5	0.30	12
P8	−0.06	0.45	0.17	8	0.31	8
P9	−0.19	0.69	0.22	7	0.41	5
P10	−0.34	0.68	0.13	9	0.27	9
P11	−0.10	0.12	0.00	11	0.32	7
P12	−0.54	0.49	−0.07	12	0.11	13
P13	−0.11	0.72	0.27	6	0.49	3
P14	−0.45	−0.14	−0.30	14	0.24	10

3.4 Cluster analysis of *C. hodginsii* provenances

Hierarchical cluster analysis was conducted using squared Euclidean distance based on the comprehensive scores of narrow-crown *C. hodginsii* provenances. At a Euclidean distance of 5, different provenances of *C. hodginsii* could be divided into three separate groups. Among these groups, provenances P3 and P4 were identified as superior sources. Provenances P2, P9, and P13 were categorized as intermediate, whereas provenances P1, P5, P6, P7, P8, P10, P11, P12, and P14 were classified as inferior.

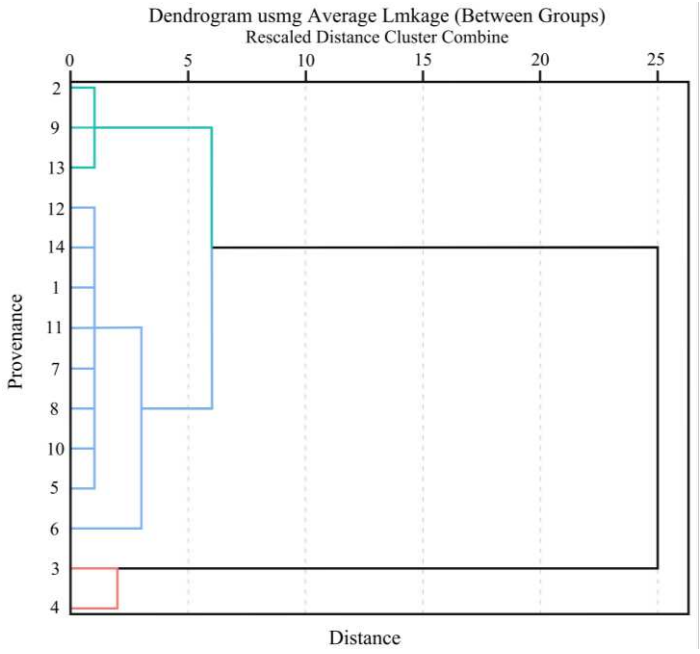


Figure 5. Cluster analysis results of comprehensive evaluation of narrow crown *C. hodginsii* provenance.

3.5 Correlation between morphological traits and endogenous phytohormone concentrations in *C. hodginsii*

Pearson correlation analysis revealed four significant correlations ($P < 0.05$) and three highly significant correlations ($P < 0.01$; Fig. 6). BIA was significantly negatively correlated with ZT ($r = -0.56$) and IAA ($r = -0.57$). In contrast, ZT was positively correlated with IAA ($r = 0.58$). CW showed a significant positive correlation with DBH ($r = 0.64$). Highly significant positive correlations were observed between BIA and CW ($r = 0.69$), as well as between TH and DBH ($r = 0.92$) and CW ($r = 0.69$).

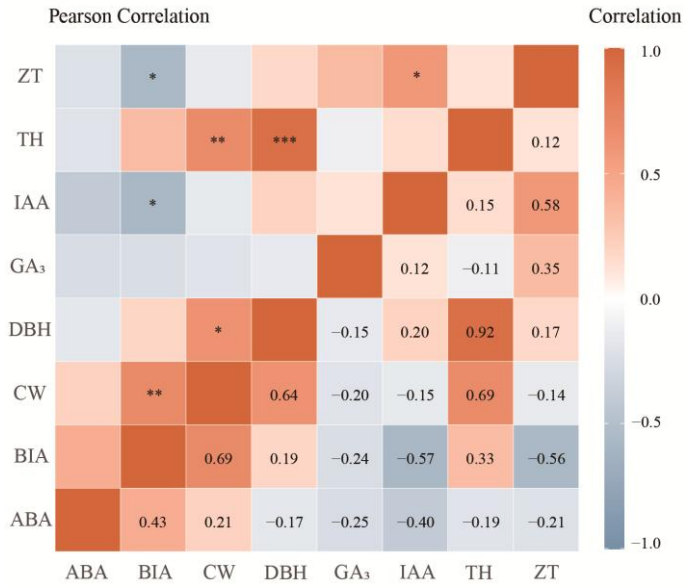


Figure 6. Heatmap analysis of morphological characteristics and endogenous hormones content of *C. hodginsii*.

Note: DBH, TH, CW and BIA represent the diameter at breast height, tree height, crown width and branch inclination angle, and ZT, GA_3, IAA and ABA represent the contents of zeatin, gibberellin 3, indoleacetic acid and abscisic acid.

Based on the variables that contributed most strongly to PC1 and PC2, namely CW, TH, and DBH, together with the results of the Pearson correlation analysis, traits showing strong collinearity were excluded and a path analysis model was constructed to evaluate the factors influencing BIA (Fig. 7). The goodness-of-fit indices indicated that the model fit the data well ($\chi^2/df = 1.17 < 3$, $P = 0.304 > 0.05$, $CFI = 0.980 \geq 0.95$, $TLI = 0.980 \geq 0.95$). The path analysis revealed that IAA exerted a highly significant negative direct effect on BIA. ZT indirectly influenced BIA through its highly significant effect on IAA. Among morphological traits, CW had a highly significant direct effect on BIA. DBH significantly affected TH, which in turn significantly influenced CW, thereby indirectly affecting BIA. Overall, these results indicate that IAA and CW act as key determinants of BIA, jointly regulating BIA with other traits. Notably, higher IAA concentrations were associated with smaller branch inclination angles.

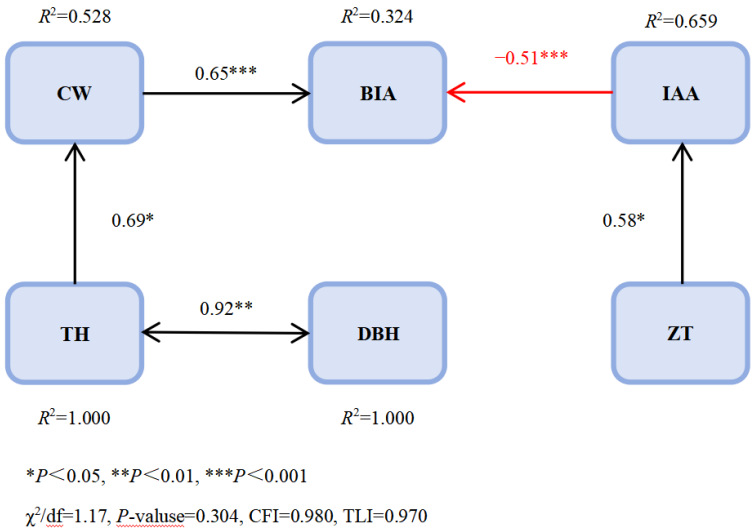


Figure 7. The results of the path analysis.

3.6 Transcriptome analysis of different *C. hodginsii* provenances

3.6.1 Differential gene expression analysis

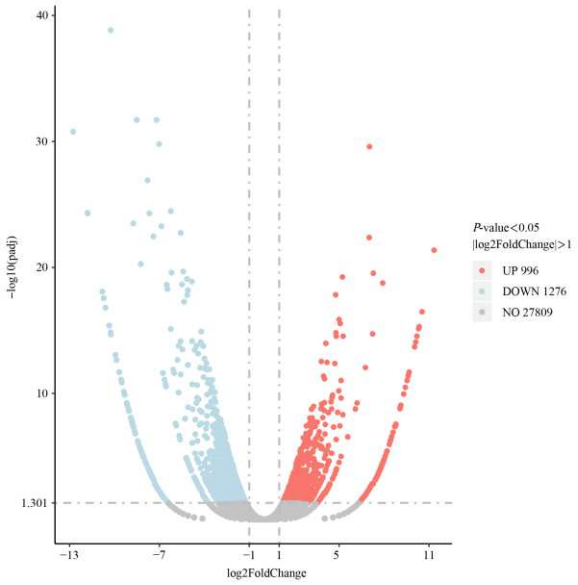
Based on the results of the comprehensive evaluation and cluster analysis, transcriptomic comparisons were performed between provenance P3 (narrow-crown type with smaller branch inclination angle) and provenance P6 (wider crown type). Strict statistical criteria ($|\log_2 FoldChange| \geq 1$ and $P < 0.05$) were used to identify differentially expressed genes (DEGs). Between the two provenances, 2272 DEGs were found, including 1276 down-regulated genes (DRGs) and 996 up-regulated genes (URGs) in P3 relative to P6 (Fig. 8a).

According to Gene Ontology (GO) enrichment analysis, URGs were primarily enriched in cellular component categories including nuclear outer membrane–endoplasmic reticulum membrane network, endoplasmic reticulum membrane, and actin cytoskeleton (Fig. 8b). In contrast, DRGs were enriched in cell periphery, proton-transporting two-sector ATPase complex, and monolayer-surrounded lipid storage body (Fig. 8c).

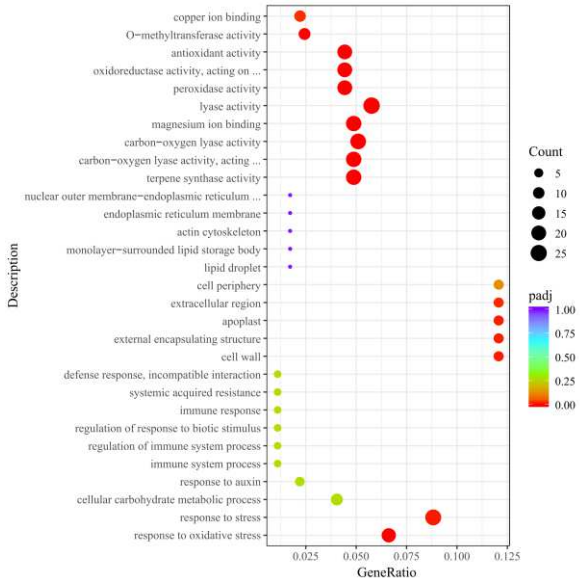
Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway enrichment analysis further showed that URGs were mainly associated with pathways related to endoplasmic reticulum organization and cytoskeleton

structure, whereas DRGs were enriched in pathways associated with membrane-associated cellular processes and energy metabolism (Fig. 8d-e).

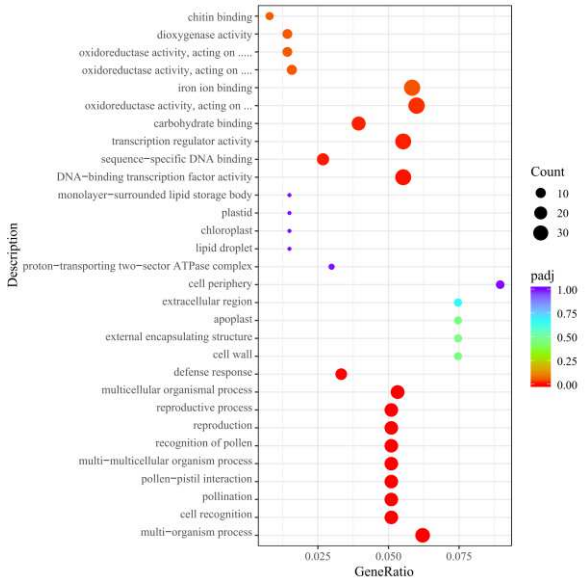
Taken together, the GO and KEGG enrichment results suggest that cellular structural organization and membrane-associated processes may play important roles in regulating branch inclination angle development in young shoots of *C. hodginsii.*



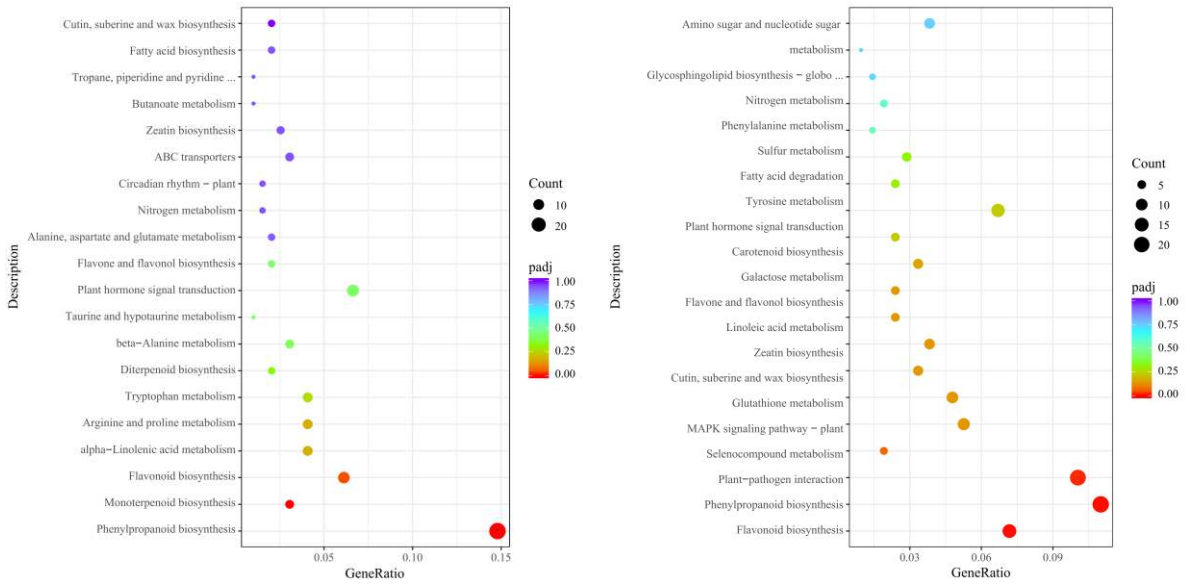
(a)



(b)



(c)



(d) (e)

Figure 8. Volcanic map, GO, and KEGG enrichment analysis for DEGs. (A) Volcanic map of differentially expressed genes. (B) GO enrichment analysis of up-regulated genes. (C) GO enrichment analysis of down-regulated genes. (D) KEGG enrichment analysis of up-regulated genes. (E) KEGG enrichment analysis of down-regulated genes.

Note: In panel A, the y-axis represents the statistical significance of differential gene expression, and the x-axis indicates the fold change in gene expression levels. Red dots represent significantly up-regulated genes, blue dots represent significantly down-regulated genes, and grey dots represent genes with no significant differential expression.

3.6.2 Phytohormone-related gene expression patterns

To discover genes involved in phytohormone-mediated regulation of branch inclination angle, phytohormones-related DEGs were screened using GO enrichment analysis. Nine genes from the *SAUR* (Small Auxin Up RNA) family were identified, which may participate in auxin biosynthesis and polar auxin transport. Among these genes, six were significantly up-regulated in provenance P3, including: *SAUR39* (EVM_prediction_ctg10659.17), *SAUR50* (EVM_prediction_ctg3240.76, EVM_prediction_ctg3240.75, EVM_prediction_ctg3240.73, EVM_prediction_ctg3240.53) and *SAUR32* (EVM_prediction_ctg374.90), (Fig. 9a). Conversely, three genes were significantly down-regulated, including: *SAUR50*

(EVM_prediction_ctg3233.30), *SAUR72* (EVM_prediction_ctg7012.33) and *SAUR32* (EVM_prediction_ctg9820.36), (Fig. 9b).

Notably, the six up-regulated genes showed markedly higher expression levels in provenance P3, which exhibited a smaller branch inclination angle, whereas the three down-regulated genes were suppressed in this provenance. This coordinated expression pattern suggests activation of auxin signalling in P3, which may contribute to the reduction of branch inclination angle. In contrast, the opposite expression pattern observed in provenance P6 may be associated with its larger branch inclination angle phenotype.

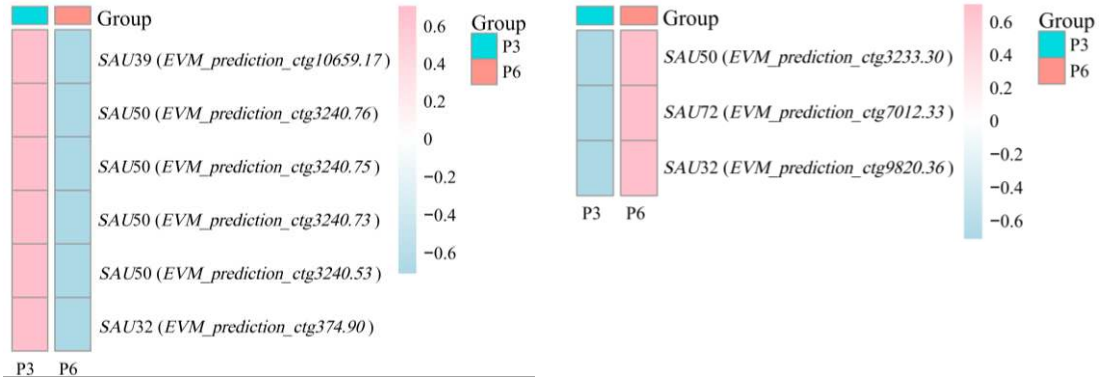


Figure 9. Heatmap of differential gene expression related to plant endogenous hormone regulation.

Note: A: heat map of the expression levels of up-regulated differential genes; B: heat map of the expression levels of down-regulated differential genes.

3.6.3 Phytohormones signalling pathways and associated genes related to branch inclination angle regulation

Differentially expressed genes involved in phytohormones signal transduction were further analysed to explore their potential roles in regulating branch inclination angle in *C. hodginsii*. A total of 27 DEGs associated with phytohormone signalling pathways were identified, representing 14 protein families across several phytohormones pathways, including auxin, cytokinin, gibberellin, abscisic acid, ethylene, jasmonic acid, and salicylic acid (Fig. 10). Among these, two or more genes were identified in the AUX/IAA (auxin-responsive IAA protein), *SAUR* family proteins, protein phosphatase 2C (PP2C), jasmonate ZIM domain-containing proteins

(JAZ), TGA transcription factors, and pathogenesis-related protein 1 (PR-1) families.

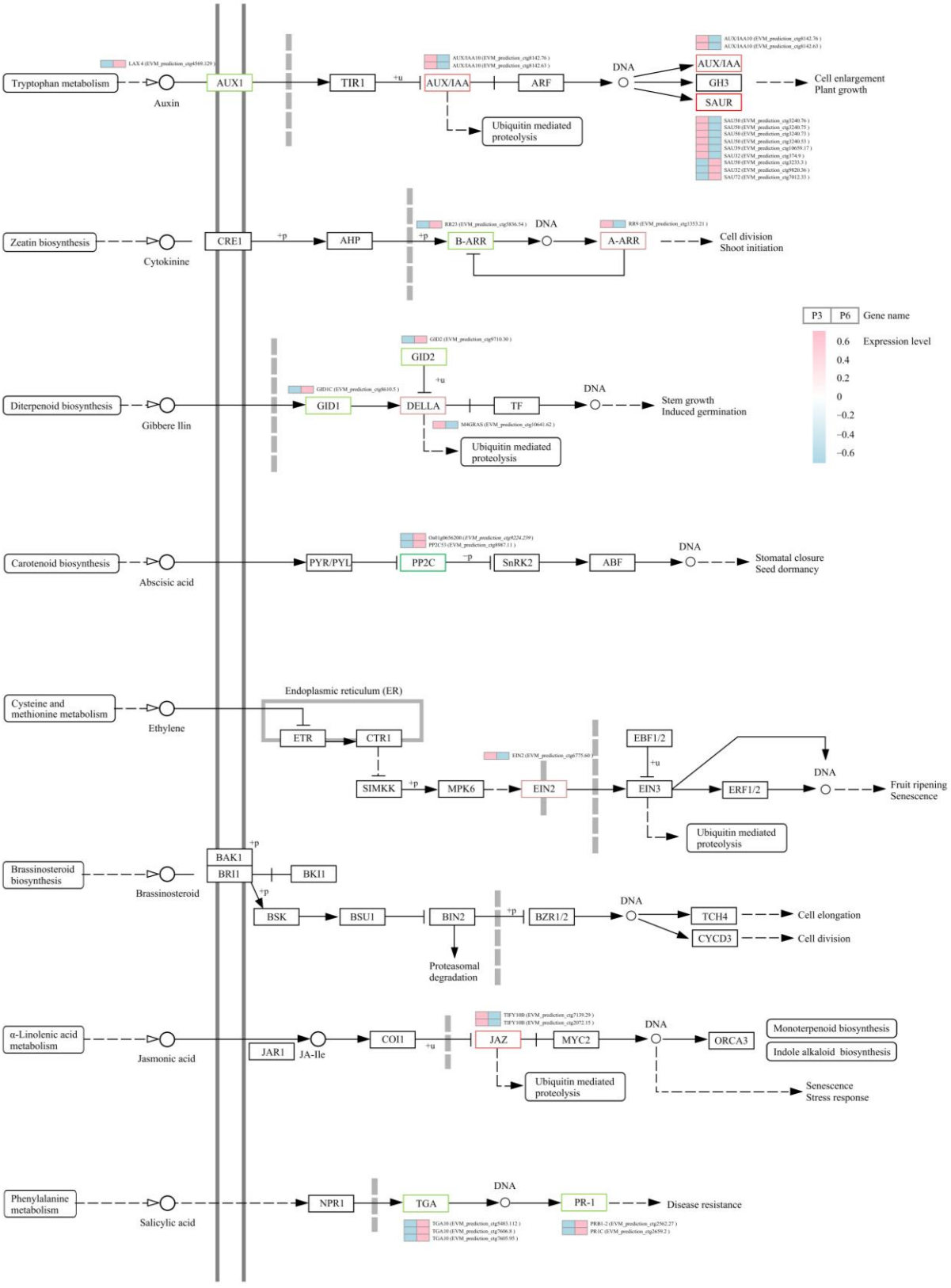


Figure 10. Plant hormone signal transduction pathway and related unigenes expression.

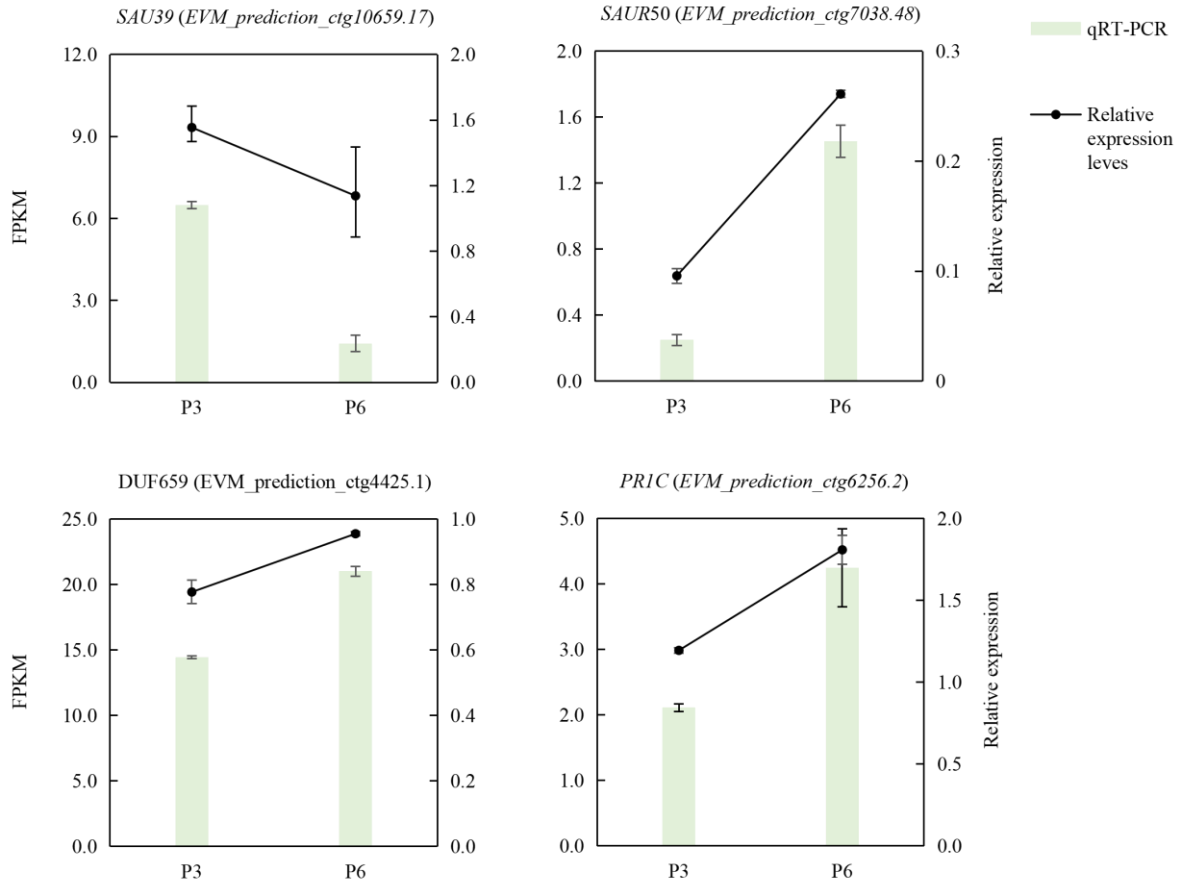
Note: In plant hormone signaling pathways, key components include AUX1 (auxin influx carrier), TIR1 (transport inhibitor response 1), AUX/IAA (auxin-responsive IAA protein), ARF (auxin response factor), GH3 (auxin-responsive GH3 gene family), and SAUR (SAUR family protein) for auxin signaling. Cytokinin signaling involves CRE1 (cytokinin receptor), AHP (histidine-containing phosphotransfer protein), B-ARR (two-component response regulator ARR-B family), and A-ARR (two-component response regulator ARR-A family). For gibberellin, key players are GID1 (gibberellin receptor GID1), GID2 (F-box protein GID2), DELLA (DELLA protein), and TF (phytochrome-interacting factor 4). Abscisic acid signaling includes PYR/PYL (abscisic acid receptor PYR/PYL family), PP2C (protein phosphatase 2C), SnRK2 (serine/threonine-protein kinase SRK2), and ABF (ABA responsive element binding factor). Brassinosteroid signaling involves BAK1 (brassinosteroid insensitive 1-associated receptor kinase 1), BRI1 (protein brassinosteroid insensitive 1), BKI1 (BRI1 kinase inhibitor 1), BSK (BR-signaling kinase), BSU1 (serine/threonine-protein phosphatase BSU1), BIN2 (shaggy-related protein kinase, also known as protein brassinosteroid insensitive 2), BZR1/2 (brassinosteroid resistant 1/2), TCH4 (xyloglucan:xyloglucosyl transferase TCH4), and CYCD3 (plant cyclin D3). Jasmonic acid signaling components are JAR1 (jasmonic acid-amino synthetase), JA-Ile ((-)-jasmonoyl-L-isoleucine), COI1 (coronatine-insensitive protein 1), JAZ (jasmonate ZIM domain-containing protein), MYC2 (transcription factor MYC2), ORCA3 (AP2-domain DNA-binding protein ORCA2/3), NPR1 (regulatory protein NPR1), TGA (transcription factor TGA), and PR1 (pathogenesis-related protein 1).

The down-regulation of one auxin influx carrier gene (*AUX1/LAX* family) in axillary buds may promote the up-regulation of two downstream early auxin-responsive genes, such as *SAUR* and *Aux/IAA* genes. Interestingly, six genes in the *SAUR* family were up-regulated while three were down-regulated, suggesting a complex regulatory mechanism in auxin signalling output. In the cytokinin signalling pathway, one gene each from the A-type ARR (*A-ARR*) and B-type ARR (*B-ARR*) families was identified, showing opposite expression patterns. Furthermore, the gibberellin receptor *GID1* and F-box protein *GID2* were down-regulated in the gibberellin signaling pathway, whereas the core repressor DELLA protein was up-regulated. These findings imply that the cytokinin and gibberellin signalling pathways in axillary bud cells may be suppressed.

Regarding defence-related phytohormoness, the gene encoding JAZ protein in the jasmonic acid signalling pathway was up-regulated, whereas genes encoding TGA transcription factors and PR proteins in the salicylic acid pathway were down-regulated, indicating reduced signalling output from these defence-related phytohormones pathways. Furthermore, the negative regulator of abscisic acid signalling (*PP2C*) was down-regulated, while the core positive regulator of ethylene signalling (*EIN2*) was up-regulated, suggesting potential enhancement of abscisic acid signalling and activation of ethylene signalling.

3.6.4 Validation of differentially expressed genes by qRT-PCR

For qRT-PCR validation, six differentially expressed genes were selected (Fig. 11). The accuracy of the transcriptome analysis was confirmed by the qRT-PCR results, which agreed with the RNA-seq data.



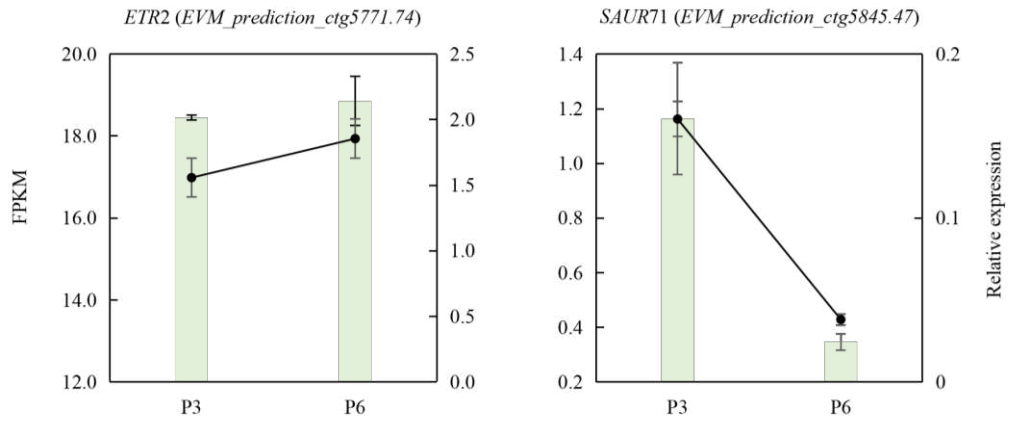


Figure 11. Expression profile of differentially expressed genes in axillary buds of *C. hodginsii*.

4 Discussion

4.1 Phenotypic variation among narrow-crown *C. hodginsii* provenances and selection of superior sources

Provenance selection is one of the fundamental approaches in forest genetic improvement [42]. After the introduction and cultivation of *C. hodginsii* from different provenances, clear differences in morphological traits were observed. Among the evaluated traits, provenance P3 exhibited the largest DBH, P5 showed the greatest TH, P12 had the widest CW, P6 displayed the largest branch inclination angle, and P2 presented the highest proportion of narrow-crown individuals. In contrast, provenance P4 performed the poorest in DBH, TH, and CW. Considering crown architecture traits, provenances P2, P3, and P13 showed relatively desirable narrow-crown characteristics. These differences are likely associated with genetic variation among provenances, which is known to influence trait variability in forest trees [43]. Tree morphological traits are jointly influenced by genetic and environmental factors. During the early stages of plantation establishment, environmental conditions may obscure genetic differences among provenances, resulting in relatively small phenotypic variation [44]. However, the present study was conducted in a seven-year-old provenance trial plantation. With increasing stand age, trees gradually adapt to the local environment, allowing intrinsic genetic differences among provenances to become more evident [45]. This shows that the narrow-crown phenotype results from genetic variation, with genetic variables driving phenotypic variance among *C. hodginsii* provenances. Moreover, the coefficients of variation

for DBH and BIA were 38.1% and 23.6%, respectively. The coefficient of variation indicates both the degree of variation and the genetic potential of the associated traits [46]. Traits with higher coefficients of variation generally exhibit greater breeding potential [47], suggesting that DBH and BIA could serve as key indicators for selecting superior provenances.

Plant metabolism produces endogenous signalling molecules called phytohormones, which are essential for regulating the plant growth processes [48, 49]. In this study, significant differences in phytohormone concentrations in axillary buds were observed among *C. hodginsii* provenances, further indicating that genetic factors contribute to variation in phytohormones levels. Prior research has demonstrated that whereas ABA inhibits growth and causes bud dormancy, IAA, ZT, and GA_3 promote plant growth [50]. In the present study, the relatively high GA_3/ABA ratio suggests that the axillary buds may be transitioning from dormancy to the bud-break stage [51]. Meanwhile, the relatively low ZT/IAA ratio indicates that the buds are likely preparing for sprouting but have not yet entered the rapid elongation phase [52].

Principal component analysis further indicated that provenances P3, P4, and P12 exhibited relatively good growth performance, whereas provenances P14, P6, and P12 showed comparatively poorer growth. Considering the overall evaluation results, provenance P3 displayed strong environmental adaptability and desirable narrow-crown characteristics, suggesting high economic and ornamental value. Other provenances with favorable narrow-crown traits but moderate growth performance, such as P13, may be suitable for landscape and ornamental applications.

4.2 Regulation of branch inclination angle by endogenous phytohormones in *C. hodginsii*

Auxin biosynthesis, transport, and signaling, together with its polar transport and uneven distribution, contribute to the development and regulation of branch inclination angle [10]. *SAUR* (Small Auxin Up RNA) family genes in *Arabidopsis thaliana* promote cell elongation and regulate plant growth [53, 54], and auxin

induces the expression of approximately two-thirds of these genes [55, 56]. Auxin synthesized at the shoot apex is transported basipetally and accumulates at the base of branches. Asymmetric auxin distribution triggers transcription factors such as ARF7/19, which in turn induce preferential expression of *SAUR* genes on the lower side of the branch when exposed to environmental cues including gravity and light [57]. Highly expressed SAUR proteins activate plasma membrane H^+-ATPases, leading to cell wall acidification [53] and enhanced cell elongation on the lower side of the branch, thereby promoting more vertical growth [57]. IAA concentrations in leaves, axillary buds, and stems are significantly higher in plant lines with narrower branch inclination angles, according to earlier research [58]. Our finding is consistent with the current investigation, which found that IAA significantly reduces branch inclination angle. In addition, nine members of the *SAUR* gene family identified in this study have previously been associated with auxin biosynthesis and polar transport, further supporting this regulatory relationship.

Interestingly, ZT showed a regulatory trend similar to that of IAA in influencing branch inclination angle. Cytokinins may regulate auxin distribution by altering the expression of several auxin transport components, thereby affecting intercellular auxin transport [59]. Collectively, these results suggest that branch inclination angle in *C. hodginsii* is primarily regulated by auxin signalling. The higher concentrations of IAA and ZT in the axillary buds of provenance P3 likely contribute to its smaller branch inclination angle, whereas the opposite trend observed in provenance P6 may explain its larger branch inclination angle phenotype. In contrast, GA_3 and ABA did not show significant regulatory effects on branch inclination angle in our study, suggesting that these phytohormoness may primarily influence branch growth vigor rather than directly determining branch architecture [60].

Regulation of auxin biosynthesis is also critical for branch growth [61]. In general, plant cells increase auxin signalling input by up-regulating AUX1 transporters and down-regulating AUX/IAA repressors, resulting

in *SAUR* gene expression [62]. However, the present results suggest a putative negative feedback regulatory mechanism, in which six *SAUR* genes were up-regulated while *AUX1* expression was decreased. During early spring, plants typically allocate limited resources preferentially to the apical bud and roots to maintain apical dominance and enhance resource acquisition, resulting in the suppression of axillary bud growth [63, 64]. The up-regulation of *SAUR* genes observed here may indicate that environmental cues, such as low temperature or changes in photoperiod, triggered a reactivation process in axillary buds. Following an initial burst of auxin signalling, a negative feedback loop may be activated, characterized by down-regulation of *AUX1* to reduce further auxin influx and up-regulation of *AUX/IAA* to suppress signal transduction, thereby restoring signalling homeostasis and preventing excessive responses [65]. Meanwhile, signalling pathways of two other growth-promoting phytohormoness, cytokinin and gibberellin, were suppressed in axillary buds [66, 67], suggesting that the buds were transitioning from a suppressed dormant state toward a potentially activated growth state. In addition, the signalling outputs of defence-related phytohormoness, jasmonic acid and salicylic acid, were also reduced [68-70]. This pattern indicates that axillary bud cells may be operating under a low metabolic state with a simplified transcriptional programme, in which stress-response pathways related to wounding and pathogen defence are temporarily attenuated [66]. Such a change may allow the buds to reallocate resources from defence to development. Additionally, the up-regulation of the ethylene signaling regulator *EIN2* [71] and the down-regulation of *PP2C*, a negative regulator of abscisic acid signaling [72], imply that axillary buds may perceive environmental cues like low temperature, fluctuations in water availability, or mechanical stress [73]. These signals may induce moderate abscisic acid and ethylene responses, helping to maintain water balance and adjust cellular metabolism during bud activation [66].

5 Conclusion

In summary, our results identified provenances P3 and P4 as superior narrow-crown sources of *C. hodginsii*,

characterized by smaller branch inclination angles and narrower crown architecture. Branch inclination angle was directly and negatively regulated by IAA, while ZT indirectly influenced branch inclination angle through its interaction with IAA. Transcriptome analysis further revealed clear expression differentiation of the *SAUR* gene family between provenances with contrasting branch inclination angles, with six genes up-regulated and three down-regulated. These findings suggest that *SAUR*-mediated auxin signalling plays a central role in regulating branch inclination angle formation, while multiple phytohormones signalling pathways act coordinately to shape the narrow-crown architecture.

Overall, this study provides a multi-level understanding of the mechanisms underlying branch inclination angle variation in narrow-crown *C. hodginsii*. Future research should focus on functional validation of key *SAUR* genes and the development of molecular markers to facilitate early identification and breeding of narrow-crown germplasm. In addition, vegetative propagation and regional cultivation trials of the selected superior provenances will further support their application in forestry production and landscape greening.

Author contributions

The roles and contributions of each author must be described in the subsequent manner: The authors confirm contribution to the paper as follows: study conception and design: Xing Cai and Tianyu Gao; data collection: Lingyan Chen, Jundong Rong and Liguang Chen; analysis and interpretation of results: Xing Cai and Zhitao Chen; draft manuscript preparation: Xing Cai. conducted an investigation: Jiali Bai, Jihong Xiao, Jiaying Liu, Bingbing Lu, Yuchen Lin and Yuchun Lin. administration and supervision of the project: Yushan Zheng. funding acquisition: Tianyou He. All authors reviewed the results and approved the final version of the manuscript. An author name can appear multiple times, and each author name must appear at least once.

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Declarations

a. Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

b. Availability of data and materials

Data available on request from the corresponding author.

c. Ethics approval and consent to participate

Not applicable.

d. Consent for publication

Not applicable.

Reference

1. Wang B, Smith SM, Li J: **Genetic Regulation of Shoot Architecture**. *ANNU REV PLANT BIOL* 2018, **69**(1):437-468.

2. Zhu M, Hu YJ, Tong AZ, Yan BW, Lv YP, Wang SY, Ma WH, Cui ZB, Wang XX: **LAZY1 Controls Tiller Angle and Shoot Gravitropism by Regulating the Expression of Auxin Transporters and Signaling Factors in Rice.** *Plant & Cell Physiology* 2020, **61**(12):2111-2125.

3. Wang WG, Gao HB, Yan L, Li JY, Wang YH: **Molecular Basis Underlying Rice Tiller Angle: Current Progress and Future Perspectives.** *MOL PLANT* 2021, **15**(1):125-137.

4. Zhao JZ, Wang JQ, Liu J, Zhang PH, Kudoyarova G, Liu CJ, Zhang KW: **Spatially Distributed Cytokinins: Metabolism, Signaling, and Transport.** *PLANT COMMUN* 2024, **5**(7):100936.

5. Liu MM, Tan B, Zheng XB, Ye X, Li JD, Feng JC: **Several Key Genes and Its Regulation Mechanisms Affecting the Plant Branching Angle**. *Molecular Plant Breeding* 2017, **15**(07):2815-2822.

6. ERameau C, EBertheloot J, ELEDUC N, EAndrieu B, ESAKR S, EFoucher F: **Multiple Pathways Regulate Shoot Branching**. *FRONT PLANT SCI* 2015, **5**:741.

7. Wang M, Le Moigne MA, Bertheloot J, Crespel L, Garcia MDP, Ogé L, Mainard SD, Hamama L, Davière JM, Sakr S: **BRANCHED1: A Key Hub of Shoot Branching**. *FRONT PLANT SCI* 2019, **10**:76.

8. Liu DX, Yan GB, Wang SB, Yu LQ, Lin W, Lu SP, Guo L, Yang QY, Dai C: **Comparative Transcriptome Profiling Reveals the Multiple Levels of Crosstalk in Phytohormone Networks in Brassica napus.** *PLANT BIOTECHNOL J* 2023, **21**(8):1611-1627.

9. Manvi S, Mohan S, Muhammed JK, Ashverya L: **Jasmonic Acid Coordinates with Light, Glucose and Auxin signalling in Regulating Branching Angle of Arabidopsis Lateral Roots.** *Plant, Cell & Environment* 2022, **45**(5):1554-1572.

10. Li SF, Lin L, Wang YP, Wu J: **The Branching Angle Regulation Mechanism in Plants**. *Molecular Plant Breeding* 2022:1-10.

11. Xu HF, Chen Y: **Current Opinions on Auxin Research and Its Application in Soybean Breeding**.

Scientia Sinica(Vitae) 2024, **54**(02):247-259.

12. Maciek A, Jiří F: **PIN-dependent Auxin Transport: Action, Regulation, and Evolution.** *The Plant cell* 2015, **27**(1):20-32.

13. Meirav L, Mark E: **Mechanisms of Auxin Signaling.** *Development (Cambridge, England)* 2016, **143**(18):3226-3229.

14. Hu PP, Zhang XF, Zhao X, Li G, Zhao FL, Li LJ, Zhou HC: **Relation betweenship Strigolactones and Branching in Strawberry**. *Journal of Fruit Science* 2019, **36**(05):578-589.

15. Su WN, Zang JF: **Research Progress on Biological Functions of Strigolactone**. *Shandong Agricultural Sciences* 2022, **54**(05):159-164.

16. Hanaé R, Tiffanie G, François B, Thomas P, Nathalie B, Aleš P, Ondřej N, Alain V, Soulaiman S, Jérémy L *et al*: **Cytokinins Are Initial Targets of Light in the Control of Bud Outgrowth.** *PLANT PHYSIOL* 2016, **172**(1):489-509.

17. Fang ZM, Ji YY, Hu J, Guo RK, Sun SY, Wang XL: **Strigolactones and Brassinosteroids Antagonistically Regulate the Stability of the D53 – OsBZR1 Complex to Determine FC1 Expression in Rice Tillering**. *MOL PLANT* 2020, **13**(4):586-597.

18. Jutarou F, Takeshi I, Yuji K, Shinjiro Y, Yohsuke T: **Binding of GID1 to DELLAs Promotes Dissociation of GAF1 from DELLA in GA Dependent Manner.** *PLANT SIGNAL BEHAV* 2015, **10**(10):e1052923.

19. Cox MCH, Benschop JJ, Vreeburg RAM, Wagemaker CAM, Moritz T, Peeters AJM, Voesenek LACJ: **The Roles of Ethylene, Auxin, Abscisic Acid, and Gibberellin in the Hyponastic Growth of Submerged Rumex palustris Petioles.** *PLANT PHYSIOL* 2004, **136**(2):2948-2960, 3001.

20. Ali F, Qanmber G, Li FG, Wang Z: **Updated Role of ABA in Seed Maturation, Dormancy, and Germination**. *J ADV RES* 2022, **35**:199-214.

21. Li PJ, Wang YH, Qian Q, Fu ZM, Wang M, Zeng DL, Li BH, Wang XJ, Li JY: **LAZY1 Controls Rice Shoot Gravitropism Through Regulating Polar Auxin Transport.** *CELL RES* 2007, **17**(5):402-410.

22. Zhang N, Yu H, Yu H, Cai YY, Huang LZ, Xu C, Xiong GS, Meng XB, Wang JY, Chen HF *et al*: **A Core Regulatory Pathway Controlling Rice Tiller Angle Mediated by the LAZY1-dependent Asymmetric Distribution of Auxin.** *The Plant Cell* 2018, **30**(7):1461-1475.

23. Hollender CA, Pascal T, Tabb A, Hadiarto T, Srinivasan C, Wang WP, Liu ZC, Scorza R, Dardick C: **Loss of A Highly Conserved Sterile Alpha Motif Domain Gene (WEEP) Results in Pendulous Branch Growth in Peach Trees.** *P NATL ACAD SCI USA* 2018, **115**(20):E4690-E4699.

24. Sasaki S, Yamamoto KT: **Arabidopsis LAZY1 Is A Peripheral Membrane Protein of Which the Carboxy-terminal Fragment Potentially Interacts with Microtubules**. *PLANT BIOTECHNOL-NAR* 2015, **32**(1):103-108.

25. Chris D, Ann C, Renate H, B RK, Tetyana Z, Courtney H, Michael W, Albert A, Ralph S: **PpeTAC1 Promotes the Horizontal Growth of Branches in Peach Trees and Is A Member of A Functionally Conserved Gene Family Found in Diverse Plants Species.** *The Plant Journal : for Cell and Molecular Biology* 2013, **75**(4):618-630.

26. Takeshi Y, P SE, Moritoshi I: **AtLAZY1 Is A Signaling Component Required for Gravitropism of the Arabidopsis thaliana Inflorescence.** *The Plant Journal : for Cell and Molecular Biology* 2013, **74**(2):267-279.

27. Wu XR, Tang D, Li M, Wang KJ, Cheng ZK: **Loose Plant Architecture1, An INDETERMINATE DOMAIN Protein Involved in Shoot Gravitropism, Regulates Plant Architecture in Rice.** *PLANT PHYSIOL* 2013, **161**(1):317-329.

28. Tan LB, Li XR, Liu FX, Sun XY, Li CG, Zhu ZF, Fu YC, Cai HW, Wang XK, Xie DX *et al*: **Control of A Key Transition from Prostrate to Erect Growth in Rice Domestication.** *NAT GENET* 2008, **40**(11):1360-1364.

29. Li LY, He Y, Li J, Jiang DG: **Research Advances of Rice Gravitropism**. *Genomics and Applied Biology* 2022, **41**(03):639-647.

30. Waite JM, Dardick C: **TILLER ANGLE CONTROL 1 Modulates Plant Architecture in Response to Photosynthetic Signals.** *J EXP BOT* 2018, **69**(20):4935-4944.

31. Zhou XM, Fu CM, Chang L, Wang XJ, Zhao CZ: **Research Progress of Molecular Regulation of Branching of Crops**. *Biotechnology Bulletin* 2021, **37**(03):107-114.

32. Zhang L, Yue JJ, Zhang J: **Research Advance of Phototropism in Plants**. *Molecular Plant Breeding* 2018, **16**(06):2015-2027.

33. Li BJ, Deng M, Pan YM, Chen WC, Rong JD, Chen LG, Zheng YS: **Differences in Photosynthetic Characteristics and Enzyme Activities of Fokienia hodginsii Families under Heterogeneous Nutrient Environments**. *Journal of Northwest A & F University (Natural Science Edition)* 2024, **52**(07):29-41.

34. Li BJ, Cai ZM, Liu P, Rong JD, Chen LG, Zheng YS: **Site Classification and Evaluation of Fokienia hodginsii Plantation in Fujian Province**. *Journal of Northwest Forestry University* 2023, **38**(05):86-92.

35. Liu K, Chen Q, Wang XX, Wang GB, Shen QS, Rong JD, Zheng YS, Chen LG: **Dynamics of Soil Nutrients in Fokienia hodginsii-Pinus massoniana Mixed Forest and Fokienia hodginsii Pure Forest at Different Ages**. *Journal of Fujian Agriculture and Forestry University (Natural Science Edition)* 2022, **51**(02):185-194.

36. Chen Q, Liu K, Wang XX, Huang X, Wang GB, Rong JD, He TY, Chen LG, Zheng YS: **Correlation between Main Soil Physiochemical Properties and Soil Water Content under Fokienia hodginsii Mixed Forests**. *Journal of Fujian Agriculture and Forestry University (Natural Science Edition)* 2021, **50**(06):771-780.

37. Li BJ, Liu P, Han YZ, Rong J, Chen LG, Zheng YS: **Evaluation of Site Quality of Fokienia hodginsii Plantation Based on Site Index Method**. *Journal of Nanjing Forestry University (Natural Sciences Edition)* 2024, **48**(02):191-198.

38. Li BJ, Deng M, Pan YM, Chen WC, Rong JD, He TY, Chen LG, Zheng YS: **Responses of Growth and Root Vitality of Fokienia hodginsii Seedling to the Neighbor Competition in Different Heterogeneous Nutrient Environments**. *FORESTS* 2023, **14**(12).

39. Deng M, Li BJ, Pan YM, Rong JD, Li YS, Zheng YS: **Effects of Different Nutrient Patches on Photosynthetic and Physiological Characteristics of Fokienia hodginsii Families**. *Journal of Forest and Environment* 2023, **43**(06):622-633.

40. Huang YP, Fan FR, Su SJ, Wang BF, Zhou DX, Wu JL: **Architectural Analysis of Fokienia hodginsii and Its Variant Types at Different Growth Stages**. *Forest and Grassland Resources Research* 2015(05):67-69.

41. Chen R, Chen JP, Yang WX, Deng ZY, Cheng WH: **HPLC Method for Determination of Endogenous Polyamines in Rosa multiflora Thunb. and Its Changes in Different Tissues**. *Journal of Anhui University(Natural Science Edition)* 2022, **46**(02):101-108.

42. Kang XY: **Rethinking the Issues That Need to Be Taken Seriously in Forest Tree Breeding, Seed Production of Improved Variety and Their Application in China**. *Scientia Silvae Sinicae* 2025, **61**(06):224-231.

43. Hong Z, Yang ZJ, Zhang NN, Guo JY, Liu XJ, Cui ZY, Xu DP: **Variation and Provenance Juvenile Selection of Growth and Wood Characters for Dalbergia odorifera**. *Journal of Nanjing Forestry University (Natural Sciences Edition)* 2020, **44**(01):11-17.

44. Liu JH, Li ZX, Zhang HG, Song LX, Yang Y: **Analysis of Variation in Growth Traits of Different Species and Families of Juglans mandshurica**. *Journal of Northeast Forestry University* 2023, **51**(08):9-17.

45. Fang YF, Xu LF, Zhang Q, Wu XW, Fu YQ, Lin W, Song LX: **Variation and Selection in Growth and Seed Traits among Different Provenances of Juglans mandshurica**. *Journal of Nanjing Forestry University (Natural Sciences Edition)* 2025:1-10.

578 46. Wang F, Zhang Q, Tian Y, Yang S, Wang H, Wang L, Li Y, Zhang P, Zhao X: **Comprehensive Assessment of**
579 **Growth Traits and Wood Properties in Half-sib Pinus koraiensis Families**. *EUPHYTICA* 2018, **214**(11):1-15.
580 47. Li ZX: **Analysis and Evaluation on Seeds and Fruits, Nutritional Characters Variation of**
581 **Juglansmandshurica Natural Populations**. *博士*.: Northeast Forestry University; 2022.
582 48. Su T, Zhang YH, Xia L, Peng ML, Ni XM, Xu JQ: **Advances in Molecular Regulation Mechanism of**
583 **Lateral Branch Development in Plants**. *Plant Physiology Journal* 2021, **57**(08):1609-1616.
584 49. Zheng XL, Zhou JQ, Teng Y, Zhang LP, Shao YF, Hu PS, Wei XJ: **Difference in Yield-related Traits of**
585 **Grains in Various Parts of Panicle in japonica Rice and Its Correlation with Endogenous Hormones**.
586 *Chinese Journal of Rice Science* 2022, **36**(01):43-54.
587 50. Ruth E, Luke R, Patrick S: **Hormones as Go-betweens in Plant Microbiome Assembly.** *The Plant Journal :*
588 *for Cell and Molecular Biology* 2020, **105**(2).
589 51. Veerabagu M, Christiaan VDS, Turečková V, Tarkowská D, Strnad M, Rinne PLH: **Light on Perenniality:**
590 **Para-dormancy Is Based on ABA-GA Antagonism And Endo-dormancy on the Shutdown of GA**
591 **Biosynthesis.** *Plant, Cell & Environment* 2023, **46**(6):1785-1804.
592 52. Zhang H, Yang FS, Hu WB, Sun HJ, Li HL: **Changes of Endogenous Hormone Content During Growth**
593 **of Pitaya**. *Jiangsu Agricultural Sciences* 2022, **50**(10):110-116.
594 53. Sun N, Wang JJ, Gao ZX, Dong J, He H, Terzaghi W, Wei N, Deng XW, Chen HD: **Arabidopsis SAURs Are**
595 **Critical for Differential Light Regulation of the Development of Various Organs.** *P NATL ACAD SCI USA*
596 2016, **113**(21):6071-6076.
597 54. Ren H, Gray WM: **SAUR Proteins as Effectors of Hormonal and Environmental Signals in Plant**
598 **Growth**. *MOL PLANT* 2015, **8**(8):1153-1164.
599 55. Bargmann BOR, Vanneste S, Krouk G, Nawy T, Efroni I, Shani E, Choe G, Friml J, Bergmann DC, Estelle M

et al: **A Map of Cell Type-specific Auxin Responses.** *MOL SYST BIOL* 2013, **9**(1):688.

56. Chapman EJ, Greenham K, Castillejo C, Sartor R, Bialy A, Sun TP, Estelle M: **Hypocotyl Transcriptome Reveals Auxin Regulation of Growth-promoting Genes through GA-Dependent and -Independent Pathways.** *PLOS ONE* 2012, **7**(5):e36210.

57. Marian B, Hilda VM, Jose M M, Cristina F, Kerstin K, Gerco C A: **FRUITFULL Controls SAUR10 Expression and Regulates Arabidopsis Growth and Architecture.** *J EXP BOT* 2017, **68**(13):3391-3403.

58. Wang H, Cheng HT, Wang WX, Liu J, Hao MY, Mei DS, Zhou RJ, Fu L, Hu Q: **Identification of BnaYUCCA6 as A Candidate Gene for Branch Angle in Brassica napus by QTL-seq.** *SCI REP-UK* 2016, **6**(1):38493.

59. Kamil R, Mária S, Jerome D, Jan P, Eva Z, Sibu S, Jirí F, Van Montagu Marc C E, Eva B: **Cytokinin Regulates Root Meristem Activity Via Modulation of the Polar Auxin Transport.** *P NATL ACAD SCI USA* 2009, **106**(11):4284-4289.

60. Singh SK, Kumari P, Sharma S, Nath V: **The Endogenous Hormonal and Biochemical Status of Shoots Decide Transition from Vegetative to Reproductive Phases in Litchi (Litchi chinensis Sonn.)**. *J PLANT GROWTH REGUL* 2026(prepublish):1-16.

61. Tian YT, Wang JN, Guo HP, Qu K, Xu D, Hou LL, Li JH: **Transcriptome Analysis of Active Axillary Buds from Narrow-crown and Broad-crown Poplars Provides Insight into the Phytohormone Regulatory Network for Branching Angle**. *PLANT MOL BIOL REP* 2021, **39**(3):1-12.

62. Ni ZY, Liang D, Gao F, Hu RP, Xia H: **Advances in Transcriptome Research on Plant Response to Drought**. *Molecular Plant Breeding* 2018, **16**(08):2460-2465.

63. Lin ZH, Yao J, Teng GX, Sheng JH, Fan JH, Du KJ, Zhou ZC, Zhang R: **Analysis of Lateral Branches Formation in Schima superba and Exploration of Related Genes**. *Forest Research* 2025, **38**(05):37-48.

64. Kebrom TH: **A Growing Stem Inhibits Bud Outgrowth – The Overlooked Theory of Apical Dominance**. *FRONT PLANT SCI* 2017, **8**:1874.

65. Fu XQ, Zhong L, Wang H, He HH, Chen XR: **Elucidation of the Mechanism of Rapid Growth Recovery in Rice Seedlings after Exposure to Low-Temperature Low-Light Stress: Analysis of Rice Root Transcriptome, Metabolome, and Physiology**. *International Journal of Molecular Sciences* 2023, **24**(24).

66. Yu J, Zhou YH, Xu CT, Wang F, Zheng YL: **Transcriptome Analysis Reveals Plant Hormone Signal Transduction Mechanisms Underlying Freezing Stress Responses in Cycas panzhihuaensis.** *BMC PLANT BIOL* 2025, **26**(1):66.

67. Jeon J, Cho C, Lee MR, Van Binh N, Kim J: **CYTOKININ RESPONSE FACTOR2 (CRF2) and CRF3 Regulate Lateral Root Development in Response to Cold Stress in Arabidopsis.** *The Plant Cell* 2016, **28**(8):1828-1843.

68. Baiyin B, Xiang Y, Shao Y, Hu JT, Son JE, Tagawa K, Yamada S, Yang QC: **Nutrient Flow Environment as A Eustress That Promotes Root Growth by Regulating Phytohormone Synthesis and Signal Transduction in Hydroponics**. *PLANT STRESS* 2024, **12**:100428.

69. Zhang YL, Li X: **Salicylic Acid: Biosynthesis, Perception, and Contributions to Plant Immunity**. *CURR OPIN PLANT BIOL* 2019, **50**:29-36.

70. Thireault C, Shyu C, Yoshida Y, St Aubin B, Campos ML, Howe GA: **Repression of Jasmonate Signaling by A Non-TIFY JAZ Protein in Arabidopsis.** *The Plant Journal : for Cell and Molecular Biology* 2015, **82**(4):669-679.

71. Danquah A, de Zelicourt A, Colcombet J, Hirt H: **The Role of ABA and MAPK Signaling Pathways in Plant Abiotic Stress Responses**. *BIOTECHNOL ADV* 2014, **32**(1):40-52.

72. Zhao H, Yin CC, Ma B, Chen SY, Zhang JS: **Ethylene Signaling in Rice and Arabidopsis: New regulators**

644 **and Mechanisms.** *J INTEGR PLANT BIOL* 2020, **63**(1):102-125.

645 73. ShangGuan LF, Tang M, Song SY, Fang XW, Xi C, Xu WD, Fan HH, Fang JG: **Advances in Bud**

646 **Dormancy-breaking Techniques and Regulatory Mechanisms of Dormancy in Grapevine**. *Journal of*

647 *Nanjing Agricultural University* 2025:1-12.

648