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Forest Adaptation to Climate Change: Altitudinal Response and Wood Variation in Natural-Growth *Cunninghamia lanceolata* in the Context of Climate Change

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Abstract: This research delves into the impact of climate change on the wood traits of *Cunninghamia lanceolata* across various altitudinal gradients, aiming to understand the influence of altitude and climatic factors like temperature and precipitation on key wood characteristics. Employing a comprehensive approach, samples were collected from different altitudes for detailed phenotypic analysis. Methods included Pearson correlation, principal component analysis, cluster analysis, and random forest analysis. Results revealed significant variations in wood traits such as heartwood ratio, tracheid length, and width across altitudes. Notably, wood traits in lower- and middle-elevation populations exhibited higher variability compared to higher elevations, indicating greater environmental diversity and genetic adaptability at these altitudes. Climatic factors, particularly temperature and precipitation, were found to increasingly influence wood trait variation with altitude. The research concludes that the adaptation of *Cunninghamia lanceolata* to climate change is significantly influenced by both altitudinal and climatic factors, highlighting their importance in forest genetic breeding and conservation strategies amidst global climate change.

Keywords: *Cunninghamia lanceolata*; wood traits; altitude; climatic adaptation; random forest analysis

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1. Introduction

Cunninghamia lanceolata, endemic to China, is a predominant afforestation species in southern China. It covers one-fourth of the country's artificial arboreal forests in area and one-third in volume, amounting to 9.87 million hectares and 755 million cubic meters, respectively, leading the nation in both aspects [1]. With a long history of cultivation and a wide range of applications, natural occurrences of *Cunninghamia lanceolata* have become exceedingly rare due to prolonged human interference and high levels of gene flow, resulting in minimal genetic differentiation among different sources of *Cunninghamia lanceolata* [2]. This suggests a potential weakening of adaptability against the backdrop of climate change [3]. In 2012, our research team discovered a natural population of *Cunninghamia lanceolata* in the Xiaoxi National Nature Reserve in Hunan Province, a narrowly distributed ecotype. Locally known as "Iron-Heart *Cunninghamia lanceolata*", this variant is distinguished by its dense texture, good rot resistance, high heartwood ratio, and brownish heartwood [4]. Its mechanical properties, such as bending strength, compressive strength, and shrinkage, are significantly superior to other populations of *Cunninghamia lanceolata* [5]. The quality of wood is a crucial indicator for timber forest cultivation [6]. With the shift in China's timber market demand, developing precious native timber species is a key step towards modernizing forestry [7]. The superior wood quality of this regional *Cunninghamia lanceolata* has attracted widespread attention. Extensive research has been conducted on its wood physical properties [4,8], seed traits [9], breeding population construction [10,11], and spatial genetic structure [12]. To further explore the excellent germplasm resources of *Cunninghamia lanceolata* and enhance the sustainable utilization and management of these resources, our research focuses on wood properties of natural populations of *Cunninghamia lanceolata* and their correlation with altitudinal climate change.

Genetic diversity, encompassing the genetic variation within biological populations and individuals [13], forms the foundation of species diversity and represents the core of biodiversity. It reflects the genetic richness of species and determines their potential to adapt to environmental changes [14,15]. Phenotypic diversity, as the external manifestation of genetic diversity, results from the interplay of genes and the environment [16]. The phenotypic variation among individuals within a species is influenced not only by specific habitat conditions but also by historical processes and phylogeny [17]. In different environmental settings, populations of the same plant species may undergo varying selective pressures, leading to genetic and phenotypic distinctions among populations [18]. Thus, researching the phenotypic diversity of forest tree populations in diverse ecological environments not only unveils the extent of genetic variation but also aids in understanding the evolutionary level and environmental adaptability of plants [19,20]. Studies have demonstrated that wood traits are significantly influenced by environmental factors such as geographic location (latitude and longitude) [21], altitude [22], light [23], soil [24], and climate [25,26].

According to relevant statistics, by 2020, the global temperature had risen by approximately 0.99 °C compared to the pre-industrial era (1850–1900), leading to an increase in extreme weather events worldwide [27]. Global climate change is accelerating its impact on forest disturbance mechanisms and adaptability [28], with effects on forests being dual-natured; they can be either positive or negative [29]. The adaptive capacity of tree populations to climate change depends on intraspecific genetic variation and phenotypic plasticity [30]. Altitude, a pivotal ecological factor, influences plant growth through gradient changes in temperature, precipitation, light, soil, and other factors [31]. This contributes to adaptive variation in plant phenotypic traits, making altitude an ideal subject for researching genetic variation [32,33]. While previous research has explored wood trait variation across altitudinal gradients from ecological [34,35], physiological [36–38], and dendrochronological perspectives [39,40], there remains a gap in understanding the genetic variation of these traits and their impact on the environmental adaptability of trees, particularly from a genetic standpoint. The upper limit of the vertical distribution of *Cunninghamia lanceolata* often varies with different topographical and climatic conditions. In the high-latitude Dabie Mountains, it grows below an altitude of 700 m, while in the lower latitude region of Dali, Yunnan, it can be found at elevations as high as 2500 m [41]. Investigating the variation of *Cunninghamia lanceolata* across different altitudinal gradients and the influence of altitudinal climatic factors on wood traits can provide insights into the species' response to climate change and the role of the environment in shaping traits [42].

Wood traits encompass a range of characteristics, primarily including anatomical traits such as tracheids and microfibril angles, physical traits like wood density, shrinkage and swelling properties, mechanical properties, and chemical traits involving the content of cellulose, hemicellulose, lignin, and various metabolites [43]. Wood density is a pivotal factor affecting plant ecological strategies, influenced by vascular traits and tree growth rates [44,45]. Denser wood is not only harder and more decay-resistant but also exhibits greater wind resistance [46]. In this research, seven representative wood traits were meticulously selected for comprehensive analysis. The annual ring width, indicative of the wood layer formed during a tree's one-year growth cycle, serves not only as a crucial indicator of growth rate [47] but also mirrors historical climate changes, ecosystem dynamics, and trees' adaptability to environmental shifts [48]. The heartwood ratio, wood density, and water absorption rate are pivotal in assessing wood quality. The heartwood ratio often signifies wood quality, while wood density and water absorption directly influence wood's processing performance, strength, and durability [49]. Wood with high water absorption is susceptible to swelling, deformation, and biodegradation [50]. Moreover, variations in wood density, a vital attribute in trees' carbon storage strategy, emerge as significant indicators for climate change assessment [51,52]. Lastly, the dimensions, shape, and arrangement of tracheids, crucial xylem cells in gymnosperms responsible for water and nutrient transport, not only impact the wood's physical and mechanical properties [53] but also reflect the plant's adaptability to its growth environment [54].

In this research, wood core samples were meticulously collected from four distinct altitudinal populations of *Cunninghamia lanceolata* within its natural habitat. We conducted a thorough analysis of phenotypic variation in seven key wood traits. The objective was to unravel the patterns of phenotypic differentiation and variation in *Cunninghamia lanceolata* wood traits along altitudinal gradients and to investigate the correlations between these traits and corresponding climatic factors at different altitudes. The findings of this research significantly enhance our understanding of the growth characteristics and adaptive mechanisms of *Cunninghamia lanceolata* across various altitudes. This is crucial for the discovery and conservation of high-quality germplasm resources of *Cunninghamia lanceolata*, as well as for bolstering its conservation and sustainable utilization. Furthermore, in the context of global climate change, these insights are pivotal in forecasting future shifts in forest ecosystems and elucidating the mechanisms through which trees adapt to environmental changes.

2. Materials and Methods

2.1. Overview of the Research Area

Xiaoxi National Nature Reserve (hereinafter referred to as Xiaoxi) is located in Xiangxi Tujia and Miao Autonomous Prefecture of Hunan Province (Figure 1), east of the Yunnan–Guizhou Plateau and the central part of the Wuling Mountain Range, which is the intersection of China's second and third ladders, with the highest altitude of 1327.1 m, and latitude and longitude of 110°6′50″–110°21′35″ E, 28°42′15″–28°53′55″ N. The climate is a subtropical humid monsoon climate, a warm and humid climate with abundant rainfall and an annual average temperature of 13~15 °C, annual precipitation of 1300~1400 mm, and relative humidity of 79%. The soil in Xiaoxi shows distinct zonal characteristics: below 400 m in altitude, there are mountain red soils; between 400 m and 500 m, mountain yellow–red soils; from 500 m to 800 m, mountain yellow soils; and above 800 m, mountain yellow–brown soils. Due to the diversity of habitats in Xiaoxi, the area boasts an exceptionally rich variety of plant species. According to surveys and analyses, there are a total of 2252 species of seed plants in Xiaoxi, including 20 species of gymnosperms and 2232 species of angiosperms. The reserve is home to 43 species of nationally protected plants of Classes I and II, such as *Manglietia decidua*, *Davidia involucrata Baill*, *Taxus wallichiana var. mairei*, and *Bretschneidera sinensis* [55]. *Cunninghamia lanceolata* predominantly exists as scattered individuals in primary and secondary forests, mainly distributed at altitudes between 500 m and 1200 m.

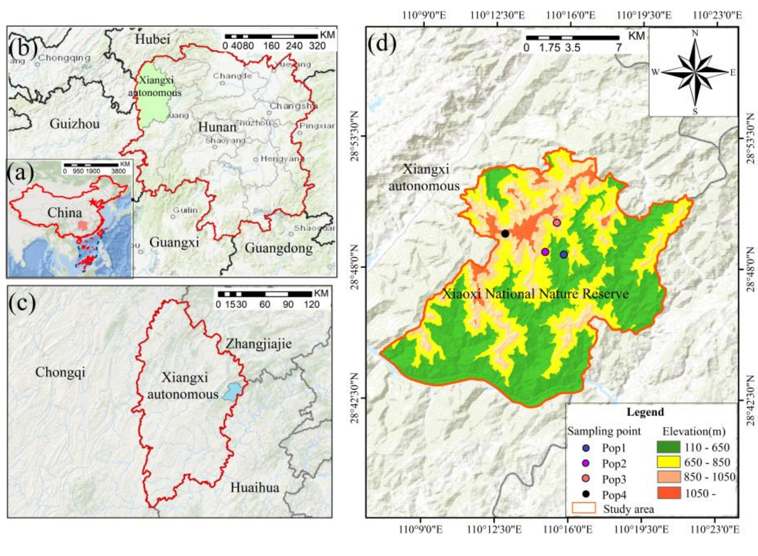

Figure 1. Schematic map of the sampling research area of *Cunninghamia lanceolata* at different altitudes. (**a**) Administrative map of China; (**b**) Administrative map of Hunan; (**c**) Tujia–Miao autonomous continent of Xiangxi Prefecture; (**d**) Xiaoxi National Nature Reserve.

2.2. Sample Collection

In November 2022, a comprehensive field survey was conducted on the naturally grown *Cunninghamia lanceolata* in the Xiaoxi National Nature Reserve. The species was categorized into four altitudinal populations, each separated by an interval of 200 m: population 1 (Pop1) at 550 m, population 2 (Pop2) at 750 m, population 3 (Pop3) at 950 m, and population 4 (Pop4) at 1150 m. For each population, 30 adult individual plants exhibiting normal growth and free from apparent pests and diseases were selected, with a consistent diameter at breast height (DBH, 1.3 m). Due to prior human interference and the species' altitudinal distribution limits, only 8 sample trees were collected for Pop4. A minimum distance of 100 m was maintained between each plant. Using a 5 mm growth cone, a core sample was extracted through the pith from south to north at a height of 1.3 m from the target tree. The core was then placed into a PVC pipe and numbered for subsequent wood trait analysis. Concurrently, the DBH and height of each sample tree were measured, and GPS coordinates were recorded to locate the sample sites. Detailed information about the sample sites and associated meteorological factors is presented in Table S1.

2.3. Measurement of Traits

Wood properties assessed in this research encompass seven key attributes: average annual ring width (Rb), heartwood ratio (P), basic wood density (WHD), water absorption (Hy), tracheid length (L), tracheid width (D), and the tracheid length-to-width ratio (L/D).

As per the technical guidelines, the wood core was first smoothed with 600# sandpaper. A line was drawn perpendicular to the annual rings in the radial direction, and the total width of the complete annual rings was measured along this line. The total width was precisely measured to 0.01 mm using a ruler, and the number of annual rings within the measurement range was counted. The average width of the annual rings was then calculated by dividing the total width by the number of rings [56]. The heartwood ratio (P) was determined by dividing the disc area, calculated using the radius from the edge of the heartwood to the pith, by the total disc area. This was carried out by measuring the length of the heartwood and the cores, with P calculated as $r^2/R^2 \times 100\%$, where r and R represent the lengths of the heartwood and the core, respectively (Figure 2a). Basic wood density (WHD) was measured using the saturated drainage method. The cores were immersed in water, with water changes every two days, and weighed periodically until a constant saturated water content weight (W1) was achieved. The cores were then dried in an oven at 103 + 2 °C to a constant weight (W2); WHD was calculated as $1(W1/W2 - 0.346)$, and Hy as $(W1 - W2)/W2$. The cores were divided radially into three sections (near the pith, middle section, near the bark) and dissociated using a mixture of glacial acetic acid and 30% hydrogen peroxide solution. The dissociated samples were then observed under a bio-digital microscope (model OLYMPUS-BX51) to analyze the tracheids' morphological characteristics (Figure 2b). The lengths and widths of the tracheids were measured 20 times for each sample using Photoshop 2022 software, with the average of these measurements from the three samples taken as the final value. Finally, the tracheid length-to-width ratio was calculated [57].

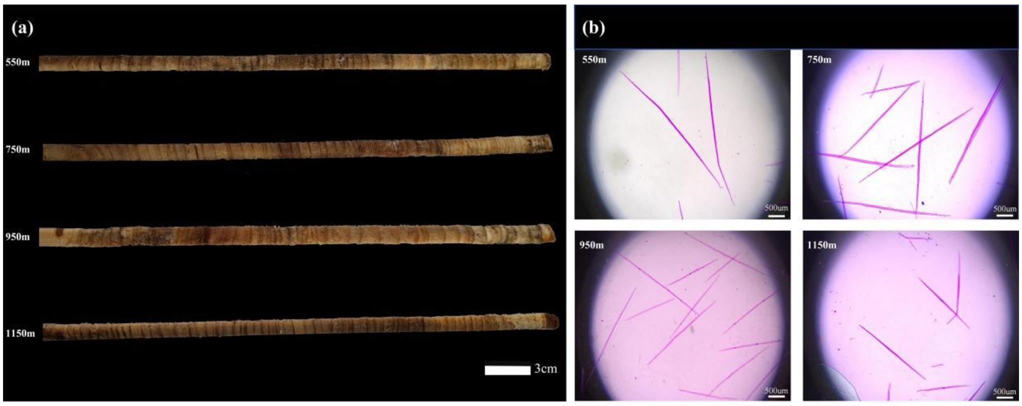

Figure 2. Schematic diagrams of *Cunninghamia lanceolata* cores and tracheids at different altitudes; 550 m, 750 m, 950 m, and 1150 m from Pop1, Pop2, Pop3, and Pop4 populations, respectively, representing the average altitude sampled, (**a**) *Cunninghamia lanceolata* cores collected from different altitudes; (**b**) tracheids under the bio-digital microscope.

2.4. Data Processing and Analysis

Preliminary processing of the measured data was carried out using Excel, and the population mean, standard deviation, intra- and interpopulation coefficients of variation, and Nestle's analysis of variance (ANOVA) were calculated for each trait using SPSS 27.

(1) Inter- and intrapopulation variation was analyzed based on Nestle's ANOVA model (significance tests were performed using the Duncan method of multiple comparisons), with a linear model of:

$$Y_{ijk} = \mu + \tau_i + \delta_{j(i)} + \varepsilon_{ijk} \tag{1}$$

where: Y_{ijk} is the kth observation of the jth monoculture in the ith population, μ is the overall mean, τ_i is the between-population effect value, $\delta_{j(i)}$ is the within-population monoculture random effect value, and ε_{ijk} is the random error.

(2) The coefficient of variation (CV) between populations was calculated using the following formula:

$$CV = \delta/\overline{x} \tag{2}$$

where: δ and $\overline{x}$ represent the standard deviation and mean of the trait, respectively.

The climate data for this research were sourced from the World Climate Database (https://worldclim.org/data/worldclim21.html, accessed on 26 October 2023). This database primarily compiles climate observation records from weather stations globally, spanning from 1950 to 2000. The data were generated through interpolation, utilizing a global climate database with a spatial resolution of 30′ [58]. Utilizing ArcGIS 10.2 software, we obtained estimated meteorological data for each altitudinal sampling point. Subsequently, six representative meteorological factors were extracted from a total of nineteen climatic factors through principal component analysis. These factors included the annual mean temperature (BIO1), the average temperature of the wettest season (BIO8), the average temperature of the driest season (BIO9), the annual precipitation (BIO12), the precipitation of the wettest season (BIO16), and the precipitation of the driest season (BIO17). The specifics of these factors are detailed in Table S1.

Data processing and analysis in this research were conducted within the R language environment. Principal component analysis (PCA) was executed using the FactoMineR package, complemented by graphical presentations created with the factoextra and ggplot2 packages. Cluster analysis employed the Euclidean distance matrix, computed via the ape package, and hierarchical clustering was performed using the Ward.D method, with graphical outputs generated by the RColorBrewer package. The linkET package facilitated correlation analysis, calculating Pearson correlation coefficients and significance *p*-values, which were further validated through the Mantel test. Data processing and transformation were adeptly handled by the dplyr and magrittr packages, with all graphs being plotted using ggplot2.

To uncover the primary drivers of wood trait variation, four traits—heartwood ratio, tracheid length, tracheid width, and tracheid aspect ratio—showing significant correlations with altitudinal climatic factors, were selected based on correlation analysis results. These traits were then subjected to random forest (RF) analysis [59], utilizing the randomForest package to calculate feature importance. The contribution rate of altitudinal climatic factors to the variation of these four wood traits was determined based on this feature importance. The contributions were then visualized using Origin 2022 software.

3. Results

3.1. Analysis of Variance of Wood Traits of *Cunninghamia lanceolata* at Different Altitudes

Nested ANOVA conducted on the wood traits of *Cunninghamia lanceolata* across different altitudes revealed significant variations (refer to Table 1). There were highly significant differences observed among *Cunninghamia lanceolata* populations in terms of heartwood ratio, tracheid length, and tracheid length-to-width ratio ($p < 0.001$). Notable differences were also evident in the average annual ring width and tracheid width ($p < 0.05$). However, no significant differences were found in basic wood density and water absorption rate. The within-population ANOVA indicated a lack of significant differences across all seven wood traits.

Table 1. Nested ANOVA of wood property traits of natural populations of *Cunninghamia lanceolata* at different altitudes.

Wood Property Traits	Mean Square			F	
	Among Populations	Within Populations	Random Error	Among Populations	Within Populations
R_b, mm	207.6424	53.2672	67.8218	3.0616 *	0.7854
P	1031.1240	102.7945	63.9987	16.1116 ***	1.0662
WBD, gm^3	0.0023	0.0014	0.0024	0.9622	0.5977
Hy, %	763.9594	492.2978	820.6657	0.9309	0.5999
L, um	1,076,974.1572	68,727.2615	64,557.9490	16.6823 ***	1.0646
D, um	59.0698	21.0064	20.0651	2.9439 *	1.0469
L/D	385.5733	44.5341	78.5751	4.9071 ***	0.5668

Note: * $p < 0.05$; *** $p > 0.001$. Rb, Average Annual Ring Width; P, Heartwood Ratio; WBD, Basic Wood Density; Hy, Water Absorption Rate; L, Tracheid Length; D, Tracheid Width; L/D, Tracheid Length-to-Width Ratio.

Multiple comparisons and comparing the mean values of wood traits at different altitudes (Table 2) showed that the basic wood density, tracheid length, tracheid width, and tracheid length-to-width ratio were the largest in Pop1, reaching 0.42 g/cm^3, 2888.06 mm, 45.22 mm, and 67.45, respectively; and they were the smallest in Pop4, with 0.39 g/cm^3, 2283.09 mm, 40.99 mm, and 58.20. The mean heartwood ratio and water absorption were the largest in Pop3, reaching 30.51 mm, and the smallest in Pop1, with only 24.35 mm. The average annual ring width was the largest in Pop3, reaching 30.51 mm, and the smallest in Pop1, only 24.35 mm. Heartwood ratio and water absorption were the largest in Pop3, 77.51% and 191.9%, respectively, and the smallest in Pop1, only 53.95% and 174.97%, respectively.

The variation of each wood trait showed (see Table 2) that the coefficient of variation of wood traits was 13.55% on average, and the level of variation of different wood traits varied greatly, with the average variation of each trait ranging from 9.40% to 24.31%, with the smallest variation being in tracheid length (9.40%) and the largest being in the average annual ring width (24.31%). The magnitude of variation of wood traits within populations at different altitudes was also significantly different, with the largest magnitude of variation in Pop3 (9.4%~36.38%) and the smallest magnitude of variation in Pop4 (7.81%~13.38%). In terms of the average coefficient of variation of wood traits within the populations, the largest and smallest coefficients of variation were found in Pop3 (15.14%) and Pop4 (10.27%), respectively.

Table 2. Variations of wood property traits of natural populations of *Cunninghamia lanceolata* at different altitudes.

Wood Property Traits	Population I		Population Pop2		Population Pop3		Population Pop4		Among Populations	
	Mean ± SD	CV (%)	Mean ± SD	CV (%)	Mean ± SD	CV (%)	Mean ± SD	CV (%)	Mean ± SD	CV (%)
R_b, mm	24.35 ± 6.66b	27.35	28.01 ± 5.88ab	20.99	30.51 ± 11.1a	36.38	29.21 ± 3.61ab	12.36	28.02 ± 6.81	24.31
P	53.95 ± 7.58c	14.04	57.963 ± 8.99c	15.51	63.58 ± 9.64b	15.15	77.51 ± 7.95a	10.25	63.05 ± 8.54	13.50
WBD, g/cm^3	0.42 ± 0.05a	11.90	0.42 ± 0.05a	11.90	0.41 ± 0.04a	9.76	0.39 ± 0.04a	10.26	0.41 ± 0.05	10.98
Hy, %	174.97 ± 27.86a	15.92	177.64 ± 28.43a	16.00	180.61 ± 24.25a	13.43	191.90 ± 25.67a	13.38	181.28 ± 26.55	14.65
L, um	2888.06 ± 266.18a	9.22	2589.22 ± 215.29b	8.31	2503.64 ± 296.24b	11.83	2283.09 ± 187.22c	8.20	2629.51 ± 241.23	9.40
D, um	45.22 ± 4.54a	10.04	44.65 ± 4.92a	11.02	43.21 ± 4.32ab	10.00	40.99 ± 3.2b	7.81	43.52 ± 4.25	9.75
L/D	67.45 ± 10.06a	14.91	61.08 ± 9b	14.73	59.14 ± 5.56b	9.40	58.20 ± 5.60b	9.62	61.47 ± 7.56	12.29
average value	-	14.77	-	14.07	-	15.14	-	10.27	-	13.55

Note: SD, standard deviation; CV, coefficient of variation. The underline represents the maximum value and the letters a, b, and c represent the results of multiple comparisons. Rb, Average Annual Ring Width; P, Heartwood Ratio; WBD, Basic Wood Density; Hy, Water Absorption Rate; L, Tracheid Length; D, Tracheid Width; L/D, Tracheid Length-to-Width Ratio.

3.2. *Principal Component Analysis and Cluster Analysis of Wood Traits of Cunninghamia lanceolata at Different Altitudes*

3.2.1. Principal Component Analysis of *Cunninghamia lanceolata* Wood Traits at Different Altitudes

The principal component analysis (PCA) conducted on the *Cunninghamia lanceolata* populations at different altitudes identified three principal components with eigenvalues exceeding 1. The cumulative contribution rate of these first three principal components to the variance in the seven wood traits was 79.79% (as shown in Figure 3, Tables S2 and S3), effectively encapsulating most of the information pertinent to the characteristic variables of the wood traits. The first principal component, accounting for 37.98% of the total variance, included key variables such as water absorption rate, basic wood density, average annual ring width, and the aspect ratio of *Cunninghamia lanceolata*. The second principal component, encompassing tracheid length and heartwood ratio, explained 23.14% of the total variance. The third principal component, comprising tracheid width and tracheid aspect ratio, accounted for 10.82% of the total variance. The cumulative contributions of these principal components, in descending order of significance, were for tracheid width, basic wood density, water absorption, tracheid aspect ratio, tracheid length, mean annual ring width, and heartwood ratio.

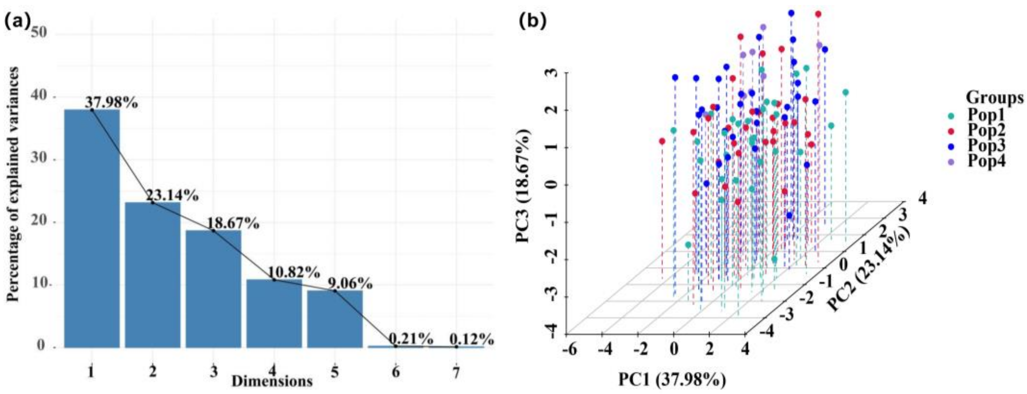

Figure 3. (**a**) Fragmentation plot; (**b**) Principal component analysis 3D plot. Pop1, Pop2, Pop2, Pop4 represent four *Cunninghamia lanceolata* populations at different elevations.

3.2.2. Cluster Analysis of Wood Traits of *Cunninghamia lanceolata* at Different Altitudes

The clustering analysis of 12 wood traits from four *Cunninghamia lanceolata* populations at different altitudes revealed distinct clusters, as illustrated in Figure 4. The analysis categorized the 98 samples into four clusters. Cluster I comprised 27 samples, representing 27.55% of the total, predominantly including 16 samples from Pop1 and 7 from Pop2. Cluster II, with the fewest samples, contained 10 samples, accounting for 12.20% of the total, mainly from Pop3. Cluster III encompassed 20 samples, constituting 20.41% of the total, primarily including eight samples from Pop3 and six from Pop4. Cluster IV, the largest population, contained 41 samples, making up 41.84% of the total, with 16 samples from Pop2, 13 from Pop1, and 12 from Pop3.

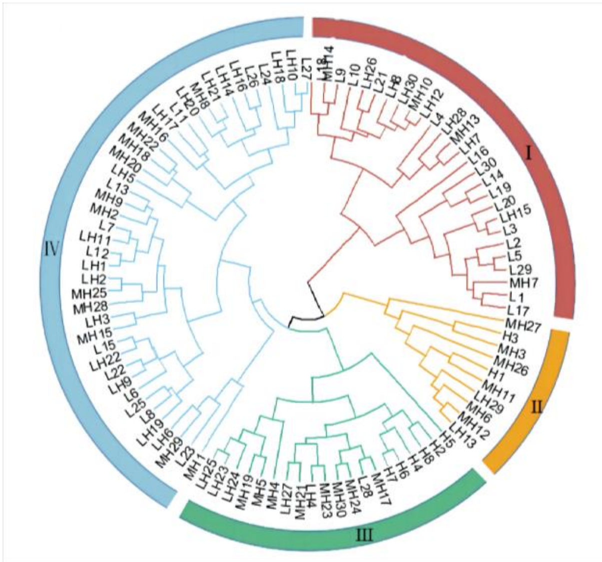

Figure 4. Cluster analysis diagram. L1–L30 represent 30 samples from Pop1; LH1–LH30 represent 30 samples from Pop2; MH1–MH30 represent 30 samples from Pop1; H1–H8 represent 8 samples from Pop4.

3.3. Correlation between Cunninghamia lanceolata Wood Traits and Altitude Climate Factors at Different Altitudes

3.3.1. Correlation Analysis between Wood Traits of *Cunninghamia lanceolata* at Different Altitudes

Pearson's correlation analysis was conducted among various wood traits of *Cunninghamia lanceolata* (as depicted in Figure 5 and detailed in the accompanying Table S4). The analysis revealed that the mean annual ring width was significantly negatively correlated with the tracheid aspect ratio (−0.2449 *) and tracheid length (−0.2363 *). It also showed a significant negative correlation with wood density (r = −0.4641 ***) and a significant positive correlation with water absorption rate (r = 0.4668 ***). The heartwood ratio exhibited a significant negative correlation with the tracheid aspect ratio (−0.3011 **) and a highly significant negative correlation with tracheid length (−0.3525 ***). Wood density was found to have a significant positive correlation with the tracheid aspect ratio (0.2182 *) and a highly significant negative correlation with water absorption (−0.9908 ***). The tracheid aspect ratio demonstrated a highly significant negative correlation with water absorption (−0.2280 *) and tracheid width (−0.4466 ***), indicating significant and highly significant negative correlations, respectively. Furthermore, tracheid length showed a highly significant positive correlation with tracheid width (0.3570 ***) and the tracheid length-to-width ratio (0.6573 ***).

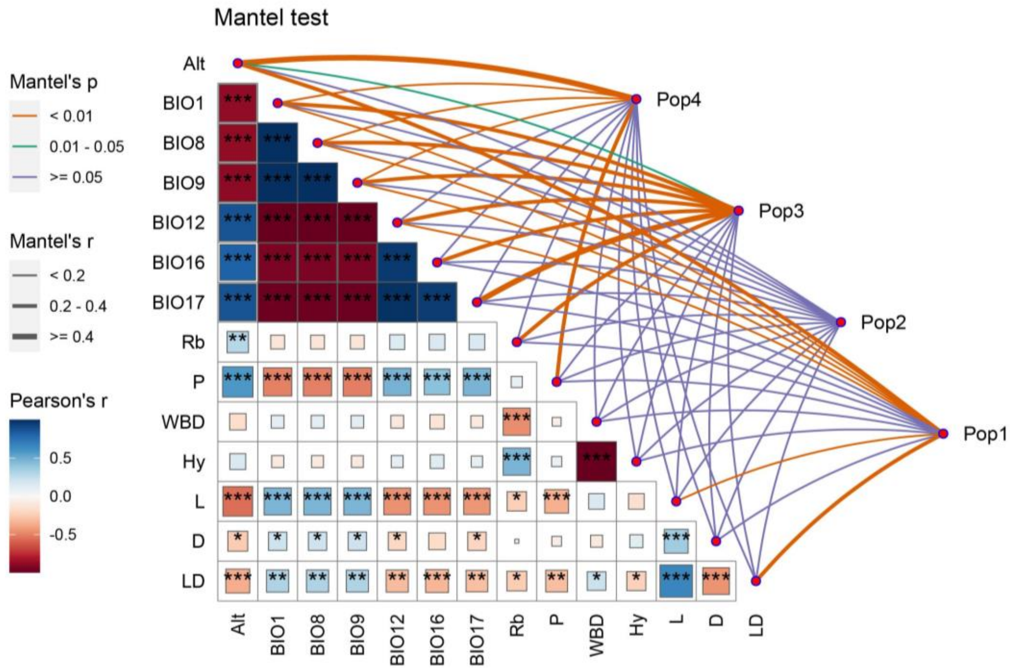

Figure 5. Correlation analysis and Mantel test between altitude climatic factors and wood traits. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. BIO1, Mean Annual Temperature; BIO8, Mean Wettest Season Temperature; BIO9, Mean Driest Season Temperature; BIO12, Annual Precipitation; BIO16, Wettest Season Precipitation; BIO17, Driest Season Precipitation. Rb, Average Annual Ring Width; P, Heartwood Ratio; WBD, Basic Wood Density; Hy, Water Absorption Rate; L, Tracheid Length; D, Tracheid Width; L/D, Tracheid Length-to-Width Ratio.

3.3.2. Correlation Analysis of Wood Traits of *Cunninghamia lanceolata* at Different Altitudes with Altitude Climatic Factors

The correlation analysis between wood traits and altitudinal–climatic factors revealed highly significant correlations for three traits: heartwood ratio, tracheid length, and tracheid length–width ratio (Figure 5 and Table S4). The results of detailed analyses are as follows: there was a significant positive correlation between the average annual ring width and altitude (0.2852 *). A highly significant positive correlation was observed between the heartwood ratio and altitude (0.5793 ***), annual precipitation (0.4752 ***), precipitation of the wettest season (0.4153 ***), and precipitation of the driest season (0.4687 ***), along with a highly significant negative correlation with annual average temperature (−0.5019 ***), average temperature of the wettest season (−0.5004 ***), and average temperature of the driest season (−0.5061 ***). Tracheid length demonstrated a highly significant negative correlation with altitude (−0.5525 ***), annual precipitation (−0.4516 ***), precipitation of the wettest season (−0.4497), and precipitation of the driest season (−0.4369 ***) and a highly significant positive correlation with annual average temperature (0.4634 ***), average temperature of the wettest season (0.4626 ***), and average temperature of the driest season (0.4630 ***). Tracheid width showed a significant negative correlation with altitude (−0.2488 *), annual precipitation (−0.2030 *), and precipitation of the driest season (−0.2123 *) and a significant positive correlation with annual average temperature (0.2111 *), average temperature of the wettest season (0.2103 *), and average temperature of the driest season (0.2135 *). The tracheid length–width ratio exhibited a highly significant negative correlation with altitude (−0.3608 ***) and precipitation of the wettest season (−0.3303), a significant negative correlation with annual precipitation (−0.3100 *) and precipitation of the driest season (−0.2960 *), and a significant positive correlation with annual average temperature (0.3095 **), average temperature of the wettest season (0.3095 **), and average temperature of the driest season (0.3080 **). Notably, wood density and water absorption rate showed no significant correlation with altitudinal–climatic factors.

3.3.3. Mantel Test of *Cunninghamia lanceolata* Populations at Different Altitudes with Altitudinal Climatic Factors

The Mantel test conducted on the wood traits of *Cunninghamia lanceolata* at different altitudes in relation to altitudinal climatic factors revealed (as shown in Figure 5, Table S5) a highly significant correlation between the wood traits of the Pop3 population and the driest seasonal precipitation (BIO17). Additionally, a highly significant correlation was observed between the wood traits of the Pop4 population and altitude. The wood traits of the Pop3 population exhibited significant or highly significant correlations with altitudinal climate factors. In contrast, the wood traits of Pop1 and Pop4 populations showed partial significant correlations with these factors, whereas the wood traits of the Pop2 population did not display any significant correlation with altitudinal climate factors.

3.4. Random Forest Analysis of Wood Traits of Cunninghamia lanceolata at Different Altitudes

Random forest analysis results (illustrated in Figure 6a) suggested that the altitude factor predominantly influenced the variation of four wood traits: heartwood ratio, tracheid length, tracheid width, and tracheid length-to-width ratio, with contribution rates of 48.81%, 45.71%, 61.94%, and 60.92%, respectively. The variances of these four wood traits were differentially impacted by climatic factors. For instance, the average temperature during the wettest season was the most influential climatic factor for the heartwood ratio (10.18%), tracheid length (9.97%), and tracheid length-to-width ratio (7.13%). In contrast, the precipitation during the driest season had the most significant impact on tracheid width (7.55%). Additionally, the cumulative contributions of temperature factors (BIO1, BIO8, BIO9) to the heartwood ratio, tracheid length, tracheid width, and tracheid length-to-width ratio were 29.72%, 28.22%, 19.53%, and 20.70%, respectively. These were higher than the cumulative contributions of precipitation factors (BIO12, BIO16, and BIO17) to the four wood traits, which were 21.46%, 26.07%, 18.53%, and 18.38%, respectively. This indicates that among the climatic factors, temperature had a greater contribution to the variation of wood traits compared to precipitation.

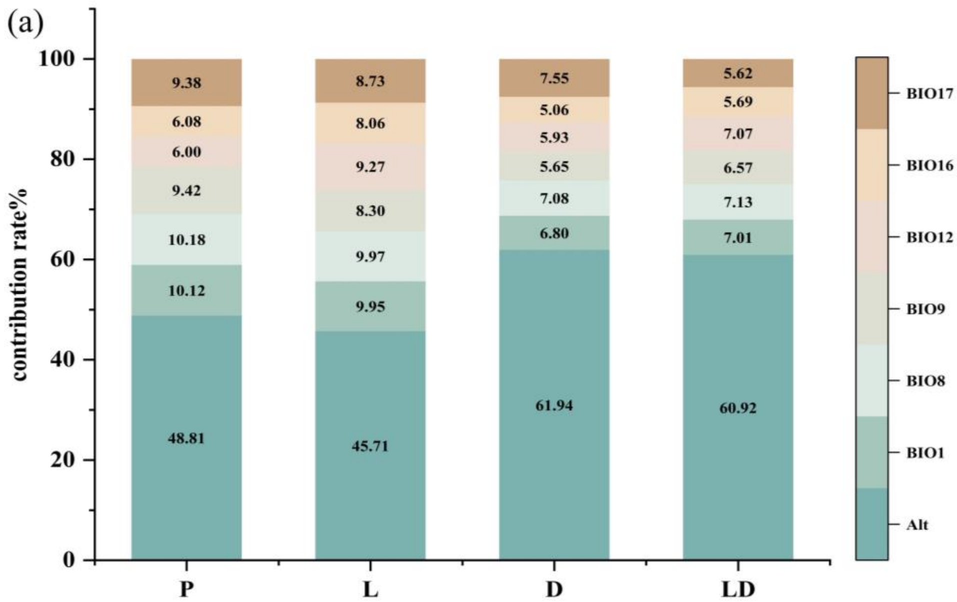

Figure 6. *Cont*.

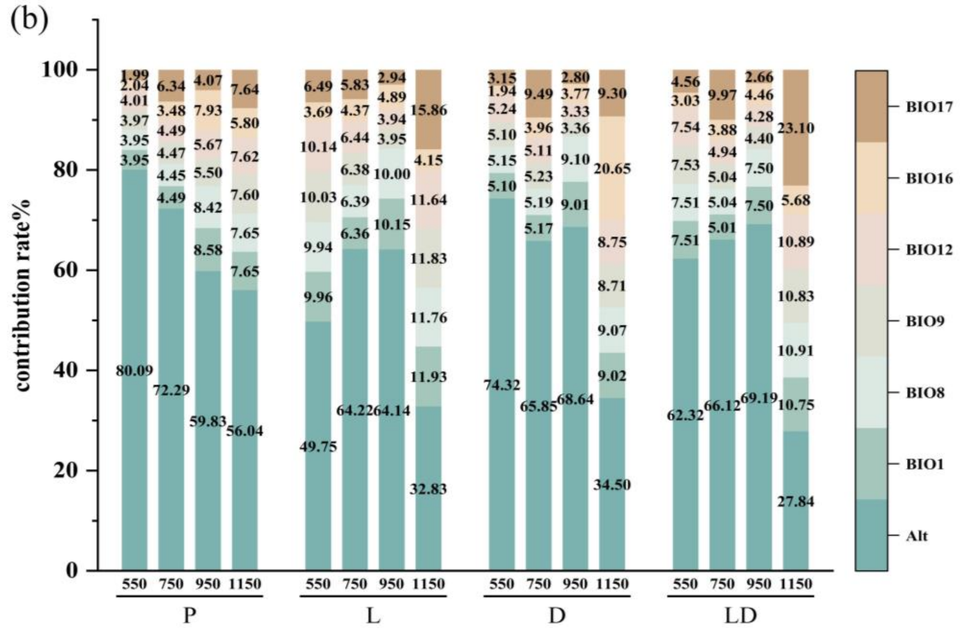

Figure 6. (**a**) Stacked diagram of the sources of variation in wood traits. (**b**) Stacked diagram of the sources of variation in wood traits at different altitudes. Random forest analysis. Values represent the contribution of altitudinal climatic factors to variation in wood traits. BIO1, Mean Annual Temperature; BIO8, Mean Wettest Season Temperature; BIO9, Mean Driest Season Temperature; BIO12, Annual Precipitation; BIO16, Wetter Season Precipitation; BIO17, Driest Season Precipitation; P, Heartwood Ratio; L, Tracheid Length; D, Tracheid Width; L/D, Tracheid Length-to-Width Ratio; 550, 750, 950, 1150 for different altitudes.

Further analysis revealed significant differences in the contribution of altitudinal climatic factors to the variability of four wood traits across the altitudinal gradient (as shown in Figure 6b). In the middle- and low-altitude gradients (populations Pop1, Pop2, and Pop3), the altitude factor was the predominant influence on the variation of the four wood traits. However, with increasing altitude, the influence of the altitude factor on the variance of heartwood ratio decreased, while its effects on tracheid length and tracheid aspect ratio initially increased and then decreased. The impact on tracheid width showed an overall decreasing trend. This decrease in the influence of the altitude factor was accompanied by an increased impact of the climatic factor on the four wood traits. Notably, except for the heartwood ratio, the cumulative contribution of climatic factors to tracheid length, tracheid width, and tracheid aspect ratio was greater than that of the altitude factor at higher altitudes (population Pop4), reaching 67.17%, 65%, and 72.16%, respectively. These factors became the primary influences on the wood traits at higher altitudes.

4. Discussion

4.1. Analysis of Variation in Wood Traits of Cunninghamia lanceolata at Different Altitudes

Plant phenotypic traits, resulting from the interplay between genetics and environment, not only mirror genetic diversity but are also pivotal in identifying superior germplasm resources [12]. This research delved into the variation of wood traits in *Cunninghamia lanceolata* across different altitudes, examining the influence of altitudinal climatic factors. Nested ANOVA results indicated highly significant differences ($p < 0.001$) in heartwood ratio, tracheid length, and tracheid length-to-width ratio among various altitudes. Mean annual ring width and tracheid width also showed significant differences ($p < 0.05$). These findings align with Elif Topaloğlu et al.'s research [60] on the anatomical properties of oriental beech wood, underscoring the variability of wood traits across altitudes. However, basic wood density and water absorption rate did not exhibit significant differences across altitudes, suggesting a stronger genetic influence on these traits, with a lesser role for environmental factors [61]. The within-population ANOVA revealed no significant differences in any of the seven wood traits, contrasting with Hongjing Duan et al.'s findings [57], which showed significant within-population variation in *Cunninghamia lanceolate* wood traits from different seed sources. This discrepancy might stem from factors like similar selection pressures [62], inbreeding [63], gene flow [64], and human interference [65] in *Cunninghamia lanceolata* populations in the same altitudinal gradient. The variability of *Cunninghamia lanceolata* wood traits across altitudes ranged from 9.40% to 24.31%, relatively modest compared to the variability (6.43% to 45.55%) in *Cunninghamia lanceolate* wood traits from different seed sources [57]. The coefficients of variation for middle- and low-altitude populations (Pop1, Pop2, Pop3) were comparable, yet significantly higher than the 10.27% for the high-altitude population Pop4. This could reflect the more complex and diverse habitats at middle and low altitudes, while the high-altitude region might offer more severe and uniform environmental conditions, constraining phenotypic variation [66].

To delve deeper into the contribution of the seven wood traits to overall variance, we conducted a principal component analysis (PCA). This analysis identified the key variables of *Cunninghamia lanceolata* wood traits at various altitudes and quantified their contributions to total variance. This approach offers valuable insights into the adaptation and growth characteristics of *Cunninghamia lanceolata* across different altitudinal ranges. The PCA results indicated that the first three principal components accounted for a cumulative contribution of 79.79% to the total variance. The order of contribution of the seven wood traits, from highest to lowest, was tracheid width, basic wood density, water absorption, tracheid length-to-width ratio, tracheid length, average annual ring width, and heartwood ratio. This analysis underscored the principal factors influencing wood traits [67], providing a deeper understanding of *Cunninghamia lanceolata*'s adaptation and growth at different altitudes [68] and aiding in the selection of superior germplasm resources [69].

Cluster analysis of *Cunninghamia lanceolata* wood traits across different altitudes revealed that the 98 samples were categorized into four taxa. Interestingly, these clusters did not align strictly with altitude, suggesting that while traits like heartwood ratio, tracheid length, and tracheid length-to-width ratio varied significantly among altitudes, these variations were not solely altitude-dependent. This indicates the potential influence of genetic factors or other environmental elements beyond altitude on wood trait formation. For instance, studies on wood traits in species such as the spruce *Picea asperata* [70], Japanese larch [71], and poplar [72] have demonstrated that traits like tracheid size and wood density are strongly genetically controlled. Additionally, environmental factors like temperature [73], precipitation [74], soil [75], and their interactions [76] also significantly impact wood traits. Therefore, the variation in *Cunninghamia lanceolata* wood traits could be attributed to a combination of factors, including but not limited to altitude.

4.2. Variation Patterns of Wood Traits and Ecological Adaptations of Cunninghamia lanceolata at Different Altitudes

Mountains, as unique ecosystems, exhibit high habitat heterogeneity and climatic diversity. Environmental factors such as temperature, light, moisture, and soil exhibit gradient variations with altitude [77]. This gradient provides a distinctive setting for investigating species' genetic variation and their responses to climate change [78]. As altitude increases, plant growth and development are constrained by temperature and moisture, leading to notable changes in adaptive traits, which in turn influence the wood traits of trees [79,80].

In our Pearson correlation analysis of *Cunninghamia lanceolata* wood traits at different altitudes, we observed intricate relationships among wood traits and between wood traits and climatic factors at various altitudes. These relationships highlight the significance of quantitative traits in trees, where correlations between two traits might be due to strong linkage disequilibrium or pleiotropic effects of related genes [81]. Our findings revealed that the mean annual ring width was significantly negatively correlated with tracheid length and aspect ratio and highly significantly negatively correlated with wood density. Conversely, it showed highly significant positive correlations with water absorption. These results align with previous studies that underscore the interplay between wood traits and environmental influences [57,82]. Notably, the significant negative correlation between heartwood ratio and tracheid aspect ratio and the highly significant negative correlation with tracheid length suggest a robust connection between heartwood formation and the morphological characteristics of tracheids. Moreover, wood density exhibited a significant positive correlation with tracheid aspect ratio and a highly significant negative correlation with water absorption, underscoring the pivotal role of wood density in determining wood traits.

Further examination of the correlation between wood traits and climatic factors at different altitudes revealed that the heartwood ratio exhibited highly significant positive correlations with altitude, annual precipitation, and precipitation during the wettest and driest seasons and highly significant negative correlations with mean annual air temperature and mean air temperature during the wettest and driest seasons. This pattern suggests that heartwood formation is smaller in environments with higher temperatures and lower precipitation, reflecting the adaptive survival strategies of trees under varying hydrothermal conditions. These observations align with Almeida et al.'s findings [83] regarding the impact of climate on eucalyptus heartwood. Additionally, a significant positive correlation was observed between tracheid length, width, and aspect ratio and altitude and air temperature, indicating an increase in tracheid structural dimensions with rising altitude and air temperature. This trend might be attributed to the influence of climatic conditions on plant growth at higher altitudes [84], as suggested by Fonti et al. [85], where a warming climate is conducive to tracheid growth. Conversely, tracheid structure showed a significant negative correlation with annual precipitation and precipitation during the wettest and driest seasons, implying that excessive moisture may inhibit tracheid growth, highlighting the regulatory role of water conditions on plant cell structure. These insights corroborate previous studies [86,87], underscoring the critical role of environmental factors in shaping plant cell structure. Nonetheless, it is essential to consider the variability across different tree species, geographical locations, and environmental conditions [88,89].

4.3. Analysis of the Contribution Rate of Altitude Climatic Factors to the Variation of Wood Traits of Cunninghamia lanceolata

Random forest analysis results underscored the significant impact of altitude on the variability of wood traits like heartwood ratio and tracheid length, width, and aspect ratio, with respective contribution rates of 48.81%, 45.71%, 61.94%, and 60.92%. This evidence points to the pivotal role of altitude in shaping wood traits, particularly in middle and lower altitudinal gradients where it emerges as the dominant environmental influence. Additionally, the analysis revealed that temperature's contribution to wood trait variability surpassed that of precipitation, aligning with Castagneri et al. [90] and Dang, Haishan et al. [34], who highlighted temperature's limiting role in tree growth at higher altitudes.

As altitude increases, the influence of altitude factors on wood trait variation diminishes, while climatic factors become more pronounced. At higher altitudes, climatic factors' cumulative contribution to tracheid length, width, and aspect ratio surpasses that of altitude, becoming the primary determinants of wood traits. This shift could be attributed to low temperatures and altered precipitation patterns at higher altitudes significantly impacting tree growth and wood traits. For instance, low temperatures may restrict cell division and elongation, influencing tracheid formation and size [91]. Changes in precipitation, on the other hand, can affect trees' water use efficiency and growth rates [92], thereby altering wood quality and structure. These physiological responses indicate trees' adaptive adjustments to their environment. At higher altitudes, temperature and precipitation's limiting effects on tree growth become more evident, making wood traits more sensitive to these climatic factors [93]. Research has shown that at the upper limits of a species' altitudinal distribution, low temperatures during the growing season can limit metabolic processes like photosynthesis fixation, subsequently affecting cell differentiation and xylem formation [22,90].

5. Conclusions

In this research, the phenotypic variation in wood traits of *Cunninghamia lanceolata* across diverse altitudinal gradients was meticulously analyzed. Our findings revealed significant differences in traits like heartwood ratio, tracheid length, and tracheid length-to-width ratio among various elevations, with mean annual ring width and tracheid width also exhibiting notable variations. This underscores the substantial variability in *Cunninghamia lanceolata* wood traits across different elevation zones. Notably, the coefficients of variation for these wood traits were markedly higher in populations at middle and lower elevations compared to those at higher elevations, suggesting a greater influence of diverse environmental conditions and enhanced genetic adaptability at these altitudes.

Principal component analysis identified key variables influencing wood trait variation, with tracheid width, basic wood density, and water absorption emerging as significant contributors to overall variability. These insights are crucial for comprehending the adaptation and growth dynamics of *Cunninghamia lanceolata* at varying altitudes and are instrumental in identifying superior germplasm resources. Cluster analysis further revealed that wood trait variation is influenced not only by altitude but also by an interplay of genetic and other environmental factors.

Pearson correlation analysis delineated intricate relationships among wood traits and between these traits and climatic factors at different altitudes. These relationships highlight the significance of quantitative traits in trees, where correlations between traits could be attributed to strong linkage disequilibrium or pleiotropic effects of associated genes. Random forest analysis underscored the pivotal role of elevation in influencing wood traits such as heartwood ratio, tracheid length, width, and aspect ratio. As elevation increases, the influence of elevation factors on wood trait variation diminishes, while climatic factors, particularly temperature, play an increasingly limiting role in tree growth at higher elevations.

These findings offer novel perspectives on tree adaptation to climate change and bear significant implications for forest genetic breeding and resource conservation. The pronounced variability observed in populations at lower and middle elevations presents a wealth of genetic resources for breeding programs. Concurrently, preserving high-elevation populations is essential for maintaining their unique adaptive traits. In the context of global climate change, these insights are vital for anticipating future shifts in forest ecosystems.

Future research should delve into the specific mechanisms through which different environmental factors, such as soil and light, impact wood traits in *Cunninghamia lanceolata*. Understanding how these variations influence the ecological functions and ecosystem services of these trees will enrich our knowledge of forest ecology and genetics, guiding future forest management and conservation strategies.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15030411/s1, Table S1: Basic information of sampling population of different altitudes of Cunninghamia lanceolata; Table S2: Principal component analysis of wood traits of *Cunninghamia lanceolata* at different altitudes; Table S3: Contribution of variation in wood traits of *Cunninghamia lanceolata* at different elevations; Table S4: Correlation coefficients between wood traits of *Cunninghamia lanceolata* at different elevations and climatic factors at elevation; Table S5: Mantel test for wood traits of *Cunninghamia lanceolata* at different elevations in relation to climatic factors at elevation.

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