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Morphological characteristics of tree crowns of *Cunninghamia lanceolata* var. *Luotian*

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Abstract The structural characteristics of the tree crowns of *Cunninghamia lanceolata* var. *Luotian* (herein, Luotian), a natural variety of *C. lanceolata* (Chinese-fir, herein Lanceolata) in China, were analyzed using trunk and branch measurements and biomass determinations. Samples from two typical cultivated varietal populations were collected, including twenty-six 15–23-year-old trees of Luotian from a plantation, and nine 16–23-year-old trees of Lanceolata. Our results show that Luotian and Lanceolata samples differed significantly in crown structure, morphological indices, and biomass: (1) the oldest live branches on Luotian trees were 5–6 years old and 8–11 years old on Lanceolata. The ages of the live branches were not affected by the ages of the Luotian trees, while live branch ages increased with ages of Lanceolata trees; (2) the maximum

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branching order of Luotian was level two. Compared to Lanceolata, the average number of first-order lateral branches (i.e., branches emerging from the trunk) and the number of first-order lateral branch whorls per sample tree were 12.9% and 32.2% lower, respectively, in Luotian. However, the average number of branches within a single whorl was 21.8% greater in Luotian; the average number of branch whorls at crown height was 51.1% greater. Thus, the Luotian variety has thicker branches; (3) the average lateral branch angles in Luotian and Lanceolata sample trees were 105.2° and 61.4°, respectively. The branch angles in 53.0% of lateral branches on Luotian ranged from 105° to 135°, but 30° to 90° in 96% of the lateral branches on Lanceolata. Within the same crown layer, the average branch angle was 1.6–2.2 times greater in Luotian, and the angle was directly proportional to crown thickness; (4) the average base diameter and branch length on Luotian were 1.3 cm and 75.8 cm, respectively, and 1.6 cm and 112.2 cm for Lanceolata. For individual trees, branch growth differed significantly ($p < 0.01$) between Luotian and Lanceolata. However, the lateral branches grew at a similar rate among Luotian trees of different ages; (5) the average height to the lowest live branch on Luotian was 128.3% greater than on Lanceolata, resulting in a significant difference ($p < 0.01$) in crown size. Compared to the crowns on Lanceolata, the Luotian crowns were 45.3% higher and 41.1% wider, and the surface area, volume, and growth of the crown were 27.0%, 11.4%, and 2.4 times greater than for Lanceolata, respectively; and, (6) the biomass of Luotian and Lanceolata sample trees also differed significantly. The mean crown, branch, and leaf biomass for Luotian was 40.0%, 25.2%, and 54.1% of those for Lanceolata, respectively. However, the leaf biomass in each layer of the Luotian crown was higher than

that of Lanceolata, and leaf biomass increased with crown thickness.

Introduction

Cunninghamia lanceolata (Lamb.) Hook. (Chinese-fir, denoted as Lanceolata), is an important commercial tree species in southern China. It has been cultivated for more than 1000 years in the Yangtze River Basin (Zheng 1983). Approximately 11.26 million hectares and 734.09 million cubic meters of Chinese-fir were distributed over 10 provinces in southern China in 2010 (Xu et al. 2015). Affected by complex eco-environmental and human factors, natural populations of *C. lanceolata* have evolved different genetic traits to adapt to different environments (Wu 1984). *C. lanceolata* var. *Luotian*, (denoted as Luotian), was first discovered in Luotian County, Hubei Province in the mid-1970s (Hubei Institute of Forestry et al. 1977). Despite more than 100 years of cultivation history of Chinese-fir, the origin of this variety is unknown. The main morphological features of Luotian trees are narrow, pointed, tower-shaped crowns, thin branches, and older drooping branches that die naturally.

A fractal is a never-ending pattern, complex and self-similar across different scales. Trees are fractal organisms. The caulotaxis, (the arrangement of branches upon the stem), and root system architecture are important characteristics, and the morphology of the crown is relevant to physiological processes such as photosynthesis and respiration because light interception varies among the different crown layers (Noriyuki and Hiroshi 2003). Crown morphological structure directly determines the vitality and productivity of individual trees and forest ecosystems (Roloff 1991; In the 1970s, Halle and Olderman (1970) published the structural characteristics and index table of 23 tropical plant species. Since then, the number of studies on tree structural characteristics has increased rapidly. Oliver and Larson (1990) studied the shape characteristics and growth patterns of crowns, and concluded that crown characteristics were significantly correlated with tree growth and development. Zimmerman and Brown (1971) studied the inherent patterns and control factors of tree growth and shape, the variations in shape, and the correlation between growth factors and shape. Kramer and Kozlowski (1979) argued that the extent of branching, branch growth, and crown size were not only genetically controlled, but were also affected by the environment. Brünig (1976) noted that incident angle was the major

determining factor of crown structure. It not only reflects the light-use efficiency of trees, but also determines the activity and productivity of individual trees. Environmental factors play an important role in the formation of crown structure and consequently influence the adaptability of trees. Mäkinen and Colin (1998) investigated the vertical distribution of branch bending angles of Scots pine (*Pinus sylvestris* L.) in southern and central Finland and discovered that branch bending angle increased with increased depth of the upper crown, while it remained stable in the middle and lower crowns. Suzuki (2003) examined size structure of current-year shoots in mature crowns; the allocation of shoot biomass to foliage and wood was found to depend strongly on the age of the parent branch. Recently, Olivier et al. (2016) studied the response of sugar maple (*Acer saccharum* Marsh.) crown structure to competition in pure versus mixed stands, and Sharma et al. (2017b) modeled individual tree crowns of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.). At the same time, new methods have been used for tree crown delineation (Díaz-Varela et al. 2015; Miranda-Fuentes et al. 2015; Mongus and Žalik 2015; Strîmbu and Strîmbu 2015; Fang et al. 2016; Zhen et al. 2016; Panagiotidis et al. 2017; Paris et al. 2017). Such research helps in predicting tree crown growth and crown competition in stands and thus in determining the best time for thinning.

Studies on tree crown morphology and structure in China had a late start. Ye and Guan (1995) proposed the concept of the "three-state structure of trees", namely—morphology, mass, and dynamic architecture. Pei and Zheng (1990) and Zhu et al. (2000) studied the influence of different stand densities and marketing measures on crown morphology of *Populus* sp. Xiao et al. (2006) reported that the branch angle of Mongolian pine (*Pinus sylvestris* var. *mongolica* Litv.) had a direct impact on the absorption of internal forest light. A large branch angle was beneficial to the use of spatial resources by trees. Numerous research on crown structure, crown profile, branch dimension, crown dimension, and branch and leaf biomass of a variety of tree species has led to several basic prediction models (Liu and Guo 1996; Zhang and Xu 2001; Li 2004; Lei et al. 2007; Liao and Li 2007; Jiang 2012; Jiang et al. 2012; Wang et al. 2012; Dong et al. 2013). Few studies, however, have focused on the crown architecture of Chinese-fir. Jiang and Ye (1980) studied the crown morphological architecture and characteristics of the variety. Lin (2013) constructed models to calculate crown volume and surface area to analyze the architecture of young Chinese-fir. A mixed effects model for crown size was established for *C. lanceolata* (Fu and Sun 2013; Fu et al. 2013; Xu et al. 2015). Additionally, Wu (2014) analyzed structural characteristics such as crown morphology, size, and biomass,

and thereafter established corresponding prediction models. All these researches have improved the management of Chinese-fir plantations.

Compared with common Chinese-fir, the Luotian variety shows variation in crown morphology. The narrow, small crown, formed by natural drooping and exfoliation of lateral branches, is distinctly different from other *Cunninghamia* species (shown in supplementary materials 1 and 2). The variable morphological characteristics may result from the co-action of artificial cultivation and selection, and adaptation to a region's natural environment. During the 1970s and 1980s, the Forestry Institute of Hubei Province and Forest Bureau of Luotian County successively surveyed and studied the morphological characteristics of the Luotian variety, including branch size and crown shape, and also investigated side-branch exfoliation through observation (Hubei Institute of Forestry et al. 1977; Xiong 1984). The only plantation of the variety in the natural distribution range of Luotian exists in this study area. Through sample plot investigation, we selected Luotian and Lanceolata sample trees to study crown morphological structure, size, and biomass. The analysis of the spatial distribution and differences between the characteristics of Luotian and Lanceolata aimed at systematically and comprehensively characterizing morphological variations in crown structure and clarifying the relationship between variations in the characteristics and physiology of crown structure and its growth features.

Materials and methods

The study area is in Luotian County in northeastern Hubei province ($115°06'$–$115°46'$E and $30°35'$–$31°16'$N), at the southern foot of the Dabie Mountains. It is adjacent to Yingshan County in the east, Xishui County in the south, Tuanfeng and Macheng counties in the west, and Jinzhai County of Anhui province in the north. The area is mountainous, and the terrain inclines from northeast to southwest. Several mountain peaks are in the northern part, seven with elevations above 1000 m. The terrain of the central region is relatively open, with widely distributed hills having elevations above 200 m. The climate is northern subtropical monsoon, dry cold in winter and humid in summer, warm in spring, and cool in autumn. The average annual sunshine duration is 2047 h, the average annual radiant energy is 457.40 kJ m^{-2} and the average annual temperature is 16.4 °C. The maximum temperature is 41.6 °C, the minimum is $-$ 14.6 °C. There is an average annual frost-free period of 240 days, and the average annual precipitation is 1330 mm. Precipitation is concentrated in the months of May, June, and July, comprising 50% of the total annual precipitation. The study area is located at the junction of Hubei and Anhui provinces on the southwestern slope of the peak of the Dabie Mountains. The highest elevation is 1408.2 m. It is one of the main drainage divides of the Yangtze and Huai rivers and contains over 1600 species of plants, including 200 species that are nationally protected. Additionally, there are over 100 endangered species and 20,000 acres of virgin forest in this area, with forest coverage as high as 90%.

In the study area, a plantation of preserved *C. lanceolata* var. *Luotian* was selected (1–2-year-old clones, composite or seedling afforestation, density 2×2 –2×3 m, mixed with *C. lanceolata*). Twenty-six plots were established with an area of 120–200 m^2 for each plot, and a minimum of 30 trees per plot.

In each plot, diameter at breast height (DBH), height (H), height to the lowest live crown base (HCB), and crown size (CS, in east–south and north–west directions) for each tree was measured. The trees were counted, and average diameter and height were calculated. In accordance with the data, 26 Luotian and 9 Lanceolata sample trees with obvious morphological characteristics were measured. Age (A) was determined by counting the stump rings. Crown height ratio (CH/H) and height–diameter ratios (H/D) were calculated (Table 1).

After the sample trees were felled, a layered cutting method was used to separate the crown at 80-cm intervals. Each layer was assigned a number from the top to the base of the crown. For the Luotian variety, there were 3–4 layers, and for the Lanceolata trees, there were 5–7 layers. In each layer, 3–5 standard branches were chosen as samples and numbered. Height to the lowest live branch, branch length (BL), base diameter (BD), and projected width (horizontal direction) and height (vertical direction) of the lowest point of the sample branches were then measured. A positive value indicated that the projection point was above the branching point, and vice versa. Branch whorls and number of branches per whorl were recorded. Angles between the trunk and sample branches (CBA) were calculated based on the projected width, height and trigonometric functions. According to the number of branch whorls and associated branch number, the number of branches in each layer and in the whole crown were then calculated. The ages of the lowest live branches were determined by branch data analysis. Additionally, branches on 23-year-old sample trees (six and three for Luotian and Lanceolata, respectively) were analyzed to determine branch ages, length of secondary lateral branches, and the horizontal distance from the branch point to the trunk. Second- and third-order lateral branches were also counted.

The crown was divided into different layers according to depth into crown base. Assuming that the cross section of the crown was circular, the crown layer above the first

Table 1 Summary of data for *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata* sample trees

Tree	No. of sample trees	Mean age (year)	Mean height (m)	Mean diameter (cm)	Mean height to the lowest live branch (m)	Mean crown size (m)
Luotian	26	18.5 (15–23)	11.6 (9.5–15.3)	12.9 (10.0–17.8)	8.7 (6.9–12.1)	1.9 (1.6–2.1)
Lanceolata	9	19.9 (16–23)	10.3 (8.4–14.8)	13.1 (11.8–17.8)	3.8 (2.3–7.9)	4.6 (3.7–5.3)

Data in parentheses are minimums and maximums

sample branch was conical. The layers between two adjacent branches or between the last sample branch and the bottom live branches were cylindrical. The projected width of every sample branch was taken as the top or bottom radius (Rc) of the corresponding layer. The difference between depth into crown base of the first branch and its adjacent branch was taken as the height of a circular, truncated cone. The volume and surface area of the cone, or the circular, truncated cone, was used as the crown volume (CV_i) and the crown surface area (CSA_i) of each layer, thereby obtaining the total crown surface area (CSA) and the total crown volume (CV). The ratio of CSA to CV is termed the crown productivity.

After harvesting, the fresh mass of all live branches in each layer was weighed, the leaves removed and also weighed. The leaf and branch samples were numbered and weighed again after drying at 105 °C. Biomass of branches and leaves was used to calculate respective relative water moisture. The total biomass of branches and leaves was designated the standard branch biomass, and used to calculate the total biomass of each crown layer.

Regression analyses were carried out to determine the relationship between branch age and depth into crown base. The variables related to crown morphology were analyzed by descriptive statistics, significance levels between Luotian and Lanceolata samples, such as crown size and height were determined using SPSS 13.0 and SigmaPlot (v. 12), and the significance level was set at $p = 0.05$.

Results

Branch age structure

Lateral branch age structures of Luotian and Lanceolata samples differed remarkably (Table 2). The ages of the oldest live branches of Luotian and Lanceolata were 4–6 years and 8–11 years, respectively, significantly different at $p < 0.05$. The age of half of the oldest live branches of Luotian was 5 years, while that of Lanceolata was older than eight years. For Lanceolata sample trees, the older the tree ages, the older the branch ages were. Previous results indicated that the ages of the oldest live branches were 4–5 years and 5–6 years in 15-year-old and 20-year-old Luotian trees, respectively (Hubei Institute of Forestry et al. 1977). Our results are consistent with this finding. However, there was no significant difference in the age of the oldest live branches among sample trees of different ages ($p > 0.05$). The maximum age of the oldest live branches among all sample trees was 6 years, and the correlation with tree age was low ($R^2 = 0.2550$).

There is a linear relationship between age and depth into the crown base of 23-year-old Luotian and Lanceolata sample trees (Fig. 1a). Both showed a consistent increase in branch age and depth into the crown base, although the increase in the Luotian sample trees was greater. For the abundance of branch numbers for trees of different ages, 2-year-old branches had the highest percentage in both Luotian and Lanceolata sample trees (Fig. 1b). However, the peak value in the Luotian sample trees was 3.6% higher than that in Lanceolata. In the Luotian material, 88.3% of branch ages were concentrated in the 1–4 years range, and 5–6-year-old branches gradually aged, withered, and fell off. In the Lanceolata sample trees, 84.5% of the branch ages were in the range of 1–6 years, and although the number of branches in the lower crown decreased, the older branches were not all dead or did not naturally fall off.

### Number of branches and branching structure

Branching orders and ratios

Chinese-fir is a multi-order branching species, with four or more orders of branching, whereas the Luotian variety has two branching orders. The average number of branches/tree in 23-year-old Luotian sample trees was 66.9% less than in Lanceolata trees, in which the numbers of first- and second-order lateral branches were 14.2% and 20.4% lower, respectively (Table 3). If counting only the higher-order branches in Lanceolata trees, the number of branches in Luotian sample trees was 20% or less of that in Lanceolata. This simple branching pattern leads to the formation of the unique crown structure or tree architecture, directly affecting the use efficiency of light and water, as well as mechanical support and morphology (Xiao et al. 2006).

Table 2 Number of sample trees of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata* with the oldest live branches of different ages based on the growth rings at the base of the branches

Names of samples	Number of sample trees with the oldest live branches of different ages							
	4 year	5 year	6 year	7 year	8 year	9 year	10 year	11 year
Luotian	6 (15–21)	13 (15–23)	7 (16–23)	–	–	–	–	–
Lanceolata	–	–	–	–	2 (16–18)	3 (16–23)	2 (22–23)	1 (23)

Data in parentheses are the age ranges of the sample trees
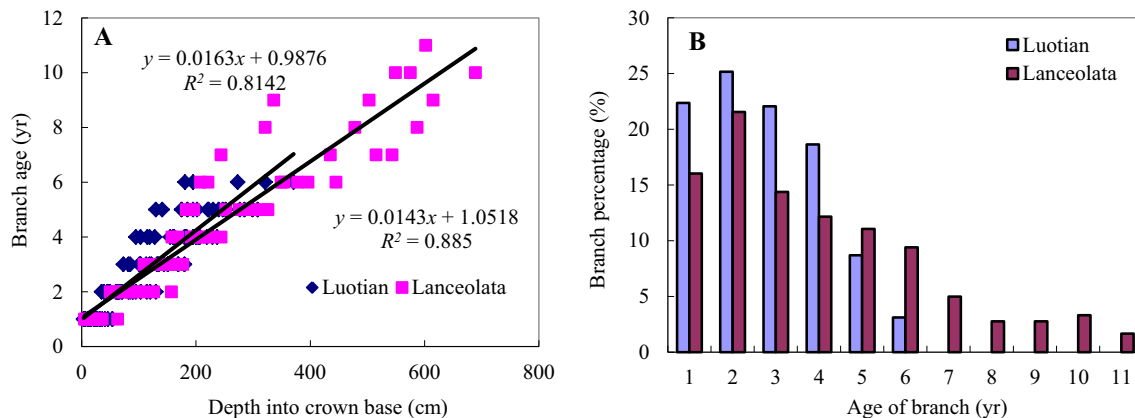
Fig. 1 Characterization of branches on *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. **a** Relationship between branch age and depth into crown; **b** percentage of branches of different ages

Table 3 Numbers of first- and second-order branches and their percentages in crowns of 23-year-old *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. Six and three 23-year-old sample trees were chosen for Luotian and Lanceolata, respectively

Names of trees	No. of sample trees	Branch orders	No. of first-order lateral branches	No. of second-order lateral branches	No. of third-order lateral branches	Total no. of branches	Total branching rate (%)	First-order branching rate (%)	Second-order branching rate (%)
Luotian	26	2	43	868	0	911	20.19	20.19	0
	28	2	64	1186	0	1250	18.53	18.53	0
	30	2	57	888	0	945	15.58	15.58	0
	31	2	51	892	0	943	17.49	17.49	0
	33	2	51	1015	0	1066	19.90	19.90	0
	35	2	53	995	0	1048	18.77	18.77	0
	Mean	2	53.17	974	0	1027.17	18.41	18.41	
	SD		7.00	120.35		125.64	1.70	1.70	
Lanceolata	29	5	80	1424	2684	4188	2.73	17.80	1.88
	32	4	55	1182	1606	2843	2.25	21.49	1.36
	34	4	51	1066	1163	2280	2.00	20.90	1.09
	Mean		62	1224	1817.6667	3103.6667	2.33	20.06	1.44
	SD		15.72	182.66	782.28	980.35	0.373	1.98	0.40

SD standard deviation

Only the total and first-order branching rates could be obtained for Luotian samples (Table 3). Compared to Lanceolata samples, the branching rate of the first-order lateral branches in Luotian samples was similar. Luotian branching was 8.2% lower than in Lanceolata trees. This difference was not obvious. Based on these results alone, it

is not possible to compare the branching and spatial use abilities of Luotian and Lanceolata sample trees. However, the results show changes in branching structure and crown architecture in Luotian sample trees and the effects of the changes on branching structure (Lu et al. 2011).

Number and distribution of lateral branches

The average number of first-order lateral branches and the total whorl number of first-order lateral branches in Luotian was, respectively, 12.9% ($p > 0.05$) and 32.2% ($p < 0.05$) lower than those in Lanceolata (Table 4). In contrast, the average first-order branch number of each whorl and the number of whorls at the average height of the crown in Luotian was 21.8% ($p < 0.01$) and 51.1% ($p < 0.01$) higher, respectively, than in Lanceolata. The average distance between the two adjacent whorls in Luotian was 15–18 cm, while the whorl distance was 24–26 cm in Lanceolata, suggesting that the Luotian variety had a thicker crown architecture (Lu et al. 2012). Compared to the Lanceolata trees, the number of first-order lateral branches, the number of whorls, and the density of branch whorls in Luotian did not differ significantly among ages ($p > 0.05$). Branching characteristics were similar, and the crown branching structure was almost the same. The results showed that, although the crown of Luotian was small, it had a higher density of first-order lateral branches, and thus enhanced light interception to better provide essential nutrition for growth. Additionally, as noted before, Luotian apparently has stronger apical dominance and hence faster growth.

In both Luotian and Lanceolata trees, the number of first-order lateral branches decreased with increasing depth into the crown base, and most were concentrated in the middle and upper layers of the crown (< 240 cm, Fig. 2a). The number of first-order branches in the three upper layers accounted for 90.3% and 58.0% of total first-order lateral branches in Luotian and Lanceolata, respectively. For Luotian and Lanceolata, crown depths of 80–160 cm had the most first-order lateral branches, accounting for 33.6% and 21.4% of the total, respectively. The vertical distribution of first-order branches in Lanceolata was similar to that in Chinese-fir of different ages in Fujian province (Wu 2014). The second layer of mature and over-mature trees had the greatest number of branches (21%), and the majority of branches were in the first three layers (56%). Due to natural abscission of old branches, the first-order lateral branches, 240–320 cm depth into the crown base of Luotian, made up less than 10% of the total first-order lateral branches, with a concentrated vertical distribution.

The distance between the branching point of each second-order lateral branch and the base of its first-order branch was segmented at 20-cm intervals. In both Luotian

Table 4 Number of first-order lateral branches and number of branch whorls in crowns of different-age trees of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*

Age of tree (year)	No. of first-order lateral branches			No. of branch whorls on the trunk			Average no. of first-order in each whorls			No. of branch whorls at average crown height			Average branch whorl distance (cm)		
	Luotian	Lanceolata	Ratio (%)	Luotian	Lanceolata	Ratio (%)	Luotian	Lanceolata	Ratio (%)	Luotian	Lanceolata	Ratio (%)	Luotian	Lanceolata	Ratio (%)
15	68.3			17.7			3.9			6.5			0.15		
16	62.3	66.0	94.4	18.2	26.0	70.0	3.4	2.5	134.9	6.2	4.2	147.4	0.16	0.24	67.9
17	58.3	78.5	74.3	18.0	26.5	67.9	3.2	3.0	109.4	5.9	4.1	143.9	0.17	0.24	69.5
18	53.0	65.0	81.5	17.4	25.0	69.6	3.0	2.6	117.2	6.7	3.9	170.8	0.15	0.26	58.5
20	67.3			17.7			3.8			6.0			0.17		
23	56.7	70.8	80.1	17.2	27.0	63.7	3.3	2.6	125.7	5.5	3.9	142.3	0.18	0.26	70.3
Means	61.0	70.1	87.1	17.7	26.1	67.8	3.4	2.7	121.8	6.1	4.0	151.1	0.16	0.25	66.5
SE	6.0919	6.1589		0.3688	0.8539		0.3243	0.1912		0.4218	0.1633		0.0115	0.0101	

SE standard error. Ratio: the number of Luotian to the number of Lanceolata in the same indexes
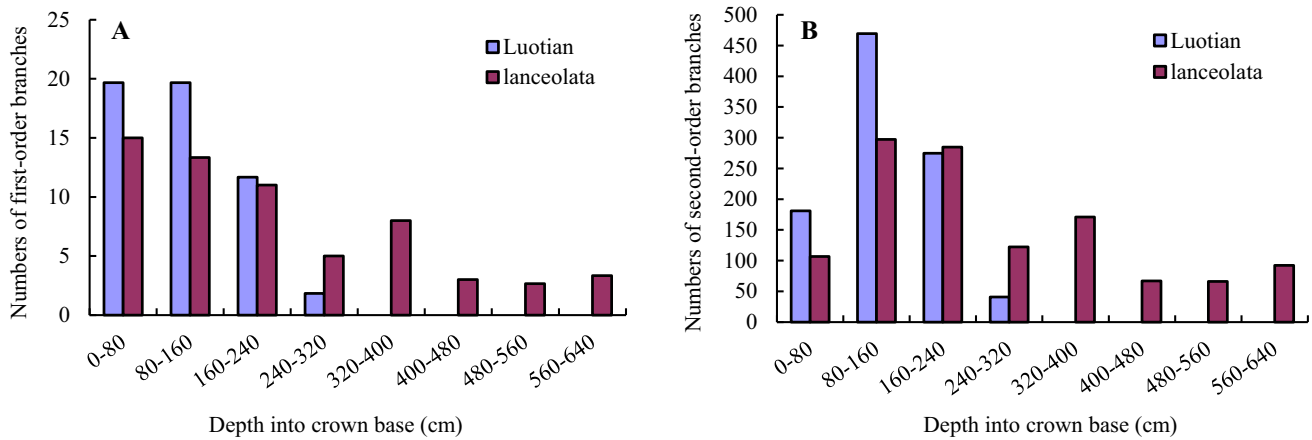
Fig. 2 Distribution of first-order (**a**) and second-order (**b**) branches in the different layers of the tree crowns of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. The tree crowns were stratified at 80-cm intervals along the trunks. Luotian has no third-order branches, the data only show the numbers of first- and second-order branches
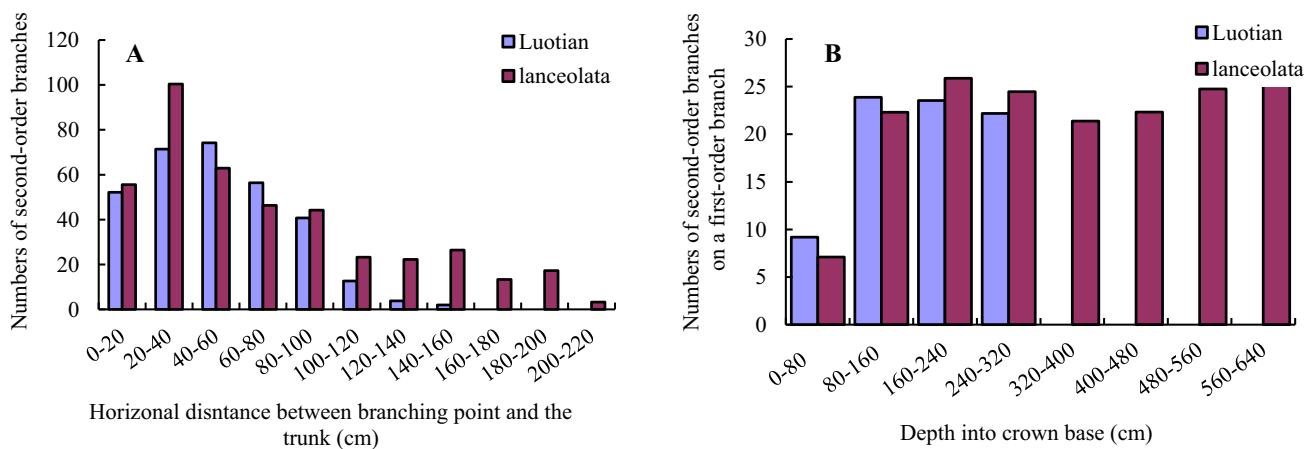

Fig. 3 Distribution of second-order branches on first-order branches (**a**) and the number of second-order branches on a first-order branch located in different crown layers (**b**) of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. In **b**, the tree crowns were stratified at 80-cm intervals along the trunks

and Lanceolata trees, most second-order lateral branches were within 100 cm. The average number of second-order lateral branches per tree were 294.9 and 309.5 for Luotian and Lanceolata, respectively, accounting for 94.2% and 73.7% of the total second-order lateral branches per tree, respectively (Fig. 3a). In Luotian, the horizontal distribution width was nearly half of that of Lanceolata, which is related to its small crown; thus, the results suggest that the crowns of the Luotian variety are denser.

The second-order lateral branches in Luotian and Lanceolata sample trees were mainly concentrated in two height levels, 80–160 cm and 160–240 cm, accounting for 77.1% and 48.2% of the total number of second-order lateral branches per tree, respectively. In Luotian, the second-order lateral branches were more concentrated. In the depth into the crown base of 80–160 cm, the proportion of second-order lateral branches was 48.6%, which was

57.9% higher than that in the same depth of Lanceolata and similar to that of 80–240 cm of Lanceolata (Fig. 2b). In the same crown layer, the average number of second-order lateral branches on first-order lateral branches were similar in Luotian and Lanceolata. Specifically, in the two depths into the crown base of < 80 and 80–160 cm, the numbers of second-order lateral branches in Luotian were 29.6% and 7.2% higher than those in Lanceolata, respectively. However, in the two depths into crown base of 160–240 and 240–320 cm, the number of second-order lateral branches in Luotian was lower than that in Lanceolata (Fig. 3b). The branch number and density of the upper crown in Luotian were greater than in Lanceolata, suggesting Luotian had enhanced light efficiency to maintain strong apical dominance and growth.
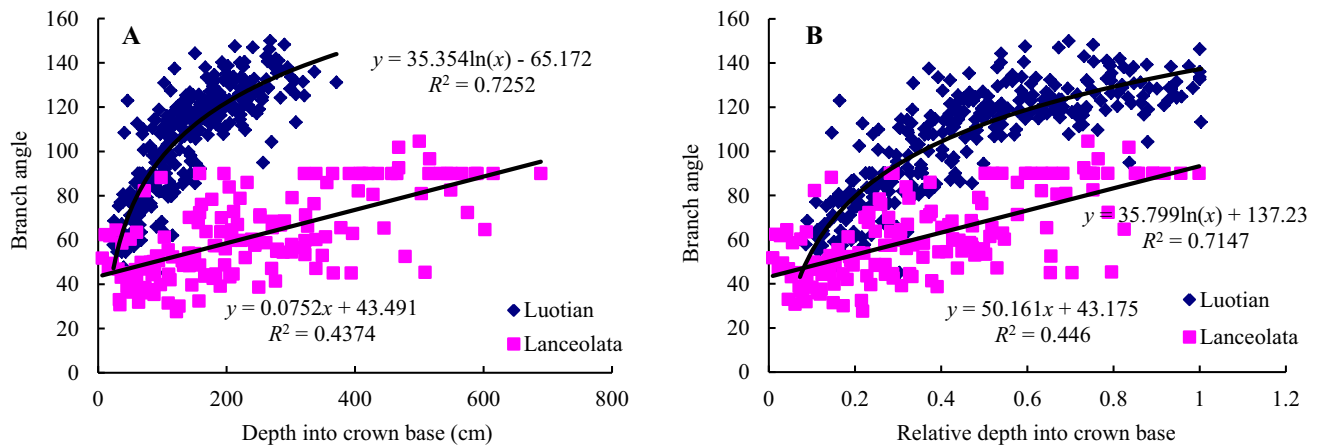
Fig. 4 Distribution of branches with different angles in the tree crowns (**a**) and relationship between branch angles and relative depth into crown (**b**) of *Cunninghamia lanceolata* var. *Luotian* and *C.* *lanceolata*. The relative height to the crown base was calculated as the height to the crown divided by the crown height

## Branch angle features

Branching angles

The branching angles of first-order lateral branches were calculated as mentioned above. The branching angles of Luotian and Lanceolata trees were in the range 45°–150° and 30°–105°, respectively. The average branching angle per tree in Luotian and Lanceolata was 108.8° (95.7°–117.3°, SE = 6.7185) and 66.6° (54.7°–82.0°, SE = 8.0953), respectively, and the difference between them was significant ($p < 0.05$). However, the difference among Luotian sample trees was not significant ($p > 0.05$); the largest variation was less than 20%. The variations in branching angles at different crown layers differed remarkably between Luotian and Lanceolata (Fig. 4a). In Luotian, the branching angle and depth into the crown base showed a logarithmic correlation (Fig. 4a, $R^2 = 0.7252$). The branching angles tended to increase proportionally with depth into the crown base. Within ∼ 1-m depth into crown base of Luotian, the branching angle sharply increased from 45° to ∼ 100°. This increasing trend became attenuated in the middle or lower part of the crown, as the branching angle gradually increased from 120° to a maximum of 150°. Meanwhile, the branching angle and depth into crown base in Lanceolata were linearly correlated (Fig. 4a, $R^2 = 0.4374$). The branching angle also tended to increase as depth into the crown base increased. However, the rate of increase was low, as the branching angle gradually increased from 40° at the crown apex to 90°–100° at the bottom of the crown. To minimize the effect of variations in crown height, we considered the relationship between branching angles and relative depth into crown base (i.e., the ratio of depth into crown base and total crown height of the sample) (Fig. 4b). Logarithmic ($R^2 = 0.7147$) and linear ($R^2 = 0.4460$) correlations were similarly identified in both Luotian and Lanceolata sample trees, and their trends were similar to those described above. In both functional relationships (Fig. 4), the branching angles and the range of variations in Luotian were significantly greater than those in Lanceolata at the same depth into crown base or relative depth into crown base, reflecting the variation trends and remarkable differences in the branching angles in both Luotian and Lanceolata.

Changes in branching angles at different depths in the crown base and distribution of lateral branches with different branching angles

As shown in Fig. 5a, the average branching angles increased as the depth into crown base increased. This increase was greater in the upper crown and stable at the lower crown. The trend in the variation of branching angle at different crown layers was greater in Luotian than that in Lanceolata. The average rate of increase in Luotian was 53.4°, a 13.4° increase for every layer. This was especially notable from < 80 to 80–160 cm and from 80–160 to 160–240 cm, where the branching angle increased by 25.7° and 21.0°, respectively, and then the rate of increase gradually declined, with the branching angle stabilizing at approximately 125°. The branching angle changes in Lanceolata were relatively small at increasing depth into crown base. The overall increase was 36.1°, with an average increase of 4.5° for every layer. The branching angle at the bottom of the crown stabilized at about 90°. At the same crown layer, the branching angle in Luotian was significantly larger than that in Lanceolata. The ratio ranged from 1.6 to 2.2, and the ratio increased proportionally with increases in the crown layer.
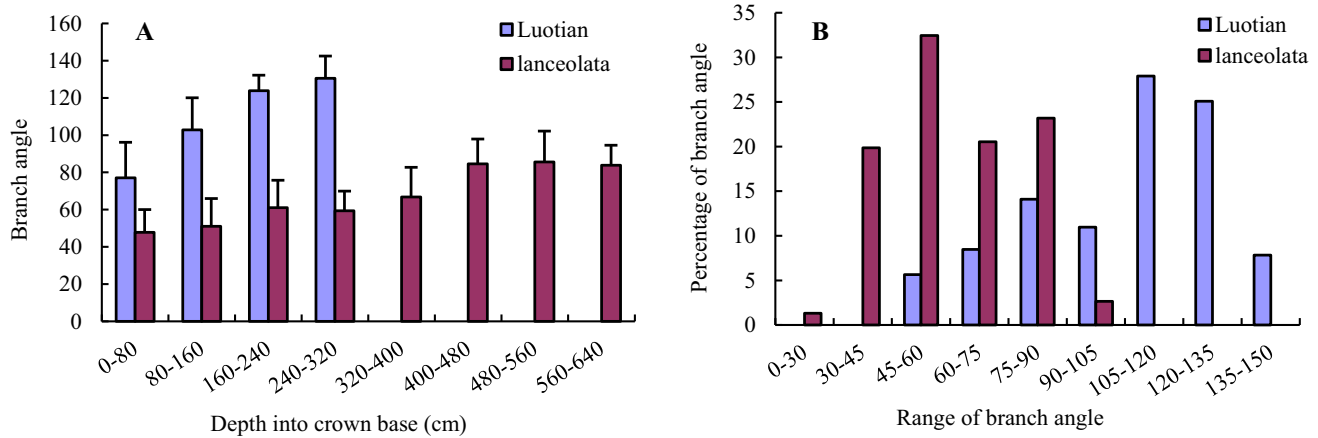
Fig. 5 Changes in average angles of first-order branches in relation to height to crown base (**a**) and distribution of first-order lateral branches with different branch angles (**b**) of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. In A, the tree crowns were stratified at 80-cm interval along the trunk, and the average angles were calculated as follows: the average angles of the branches located in the same crown layers in a sample tree; the average angles were then calculated according to the average angles in the same layers of all the sample trees

The branching angle was divided into nine levels with intervals of 15° (Fig. 5b). All lateral branch angles in the Luotian sample trees were greater than 45° and 53.0% of the branches were distributed in the two levels of 105°–120° and 120°–135°. However, all of the lateral branch angles in Lanceolata were smaller than 105° and 96.0% of the branching angles were in four consecutive levels (30°–90°). For Luotian, branching angles were classified into three levels: askew upward (≤ 75°), horizontal (75°–105°), askew downward (> 105°). The ratios of these three types of branch morphology and the number of lateral branches within each crown layer were calculated (Table 5). In Luotian, only 14.5% of the lateral branches were askew upward, and more than 60% were askew downward; in Lanceolata, 25% were classified as horizontal and no branches were askew downward. In Luotian, nearly half of the branches were askew upward at the < 80 cm layer, and only 5% were askew upward at the 80–160 cm layer. The percentage of branches which were askew downward rapidly increased from 13.8% at the < 80 cm layer to 54.2% at the 80–160 cm layer; all the branches located in the crown layers with depth into crown base of more than 160 cm were askew downward. The percentage of horizontal branches was slightly greater at the 80–160 cm layer, compared to that at the < 80 cm layer. However, no branches were horizontal at the 160–240 cm layer and below. In Lanceolata, the majority of branches in crown layers ranging from < 400 cm were diagonal. In some layers, the percentage of diagonal branches was even greater than 90%. However, at 400–480 cm and deeper crown levels, this percentage decreased by 20–30%. The percentage of horizontal branches gradually increased from 3.7% at the uppermost layer to 71.4% at the bottommost

layer, a 19-fold increase. As the depth into crown base decreased, the branches which were askew upward rapidly became horizontal and then to askew downward at the lower crown layers in Luotian. In Lanceolata, as the crown layer depth increased, the branches gradually changed from askew downward to horizontal.

Changes in base diameter and length along different depths into the crown base

The average base diameters of first-order lateral branches per tree in Luotian and Lanceolata sample trees were 1.3 ± 0.1 cm and 1.6 ± 0.4 cm, respectively, and the lengths of first-order branches were 75.8 ± 13.6 cm and 112.2 ± 29.0 cm, respectively. The base diameter and branch length both differed significantly between Luotian and Lanceolata sample trees ($p < 0.05$). However, there was no significant difference in average branch growth per tree among trees of different ages in Luotian ($p > 0.05$). In both Luotian and Lanceolata, branch diameters and branch lengths were correlated with depth into crown base according to a power function, with similar variations in trend. However, the branch diameters of Luotian showed more rapid increases in the upper crown layers, maximized at 60 cm into the crown base; further increases were minimal thereafter. As shown in Figs. 6 and 7, both base diameters and lengths of first-order branches increased as depth into crown base increased in both Luotian and Lanceolata. Branch growth in depth into crown base of < 80 and 80–160 cm in Luotian was greater. Compared to Lanceolata, in depth into crown base of < 80 and 80–160 cm, the branch base diameters in Luotian were 17.3% and 7.0% larger, respectively (Fig. 7a), and the

Table 5 Changes in the number of lateral branches with different morphologic features in *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. The first-order branches were classified according to their branching angles, i.e., angles between first-order branches and the vertical trunks): askew upward ($\leq 75°$), horizontal (75°–105°), and askew downward ($\geq 105°$)

Names of trees	Luotian			Lanceolata		
Branch morphology	Askew upward ($\leq 75°$)	Horizontal (75°–105°)	Askew downward ($\geq 105°$)	Askew upward ($\leq 75°$)	Horizontal (75°–105°)	Askew downward ($\geq 105°$)
Depth into crown base						
0–80						
n_{ij}/n_j	49.4	36.8	13.8	96.3	3.7	0
n_i/n	13.0	9.7	3.6	17.7	0.7	0
80–160						
n_i/n_j	4.2	41.5	54.2	93.9	6.1	0
n_i/n	1.5	14.8	19.4	21.1	1.4	0
160–240						
n_i/n_j	0	0	100.0	66.7	22.2	0
n_{ij}/n	0	0	27.3	12.2	4.1	0
240–320						
n_i/n_j	0	0	100.0	94.4	5.6	0
n_i/n	0	0	10.6	11.6	0.7	0
320–400						
n_i/n_j	0	0	0	68.4	31.6	0
n_i/n	0	0	0	8.8	4.1	0
400–480						
n_i/n_j	0	0	0	16.7	66.7	0
n_i/n	0	0	0	1.4	5.4	0
480–560						
n_i/n_j	0	0	0	33.3	66.7	0
n_i/n	0	0	0	2.0	4.1	0
560–640						
n_i/n_j	0	0	0	28.6	71.4	0
n_i/n	0	0	0	1.4	3.4	0
Total	14.5	24.5	60.9	76.2	23.8	0

n, total number of first-order lateral branches in the whole tree crown; n_j: number of first-order branches in the j crown layer; n_{ij}: number of branches with askew upward ($\leq 75°$), horizontal (75°–105°), askew downward ($\geq 105°$) branching patterns in the j crown layer

branch lengths were 25.4% and 15.6% greater, respectively (Fig. 7b). However, the differences diminished when depth into crown base increased to 160–240 cm, and the base diameters and lengths of first-order branches in Luotian were 15.6% and 2.4% smaller in depth into crown base of 240–320 cm, respectively (Fig. 7a). The total branch length of Luotian was smaller than that of Lanceolata. Compared to Lanceolata, the average branch base diameter per tree and the branch length in Luotian were 21.1% and 32.4% smaller, respectively (Fig. 7). The maximum branch base diameter and branch length in Luotian were only 59.5% and 57.9% of those in Lanceolata, respectively (Fig. 7).

Distribution of numbers of branches with different base diameters and lengths

Base diameters were categorized by 2-mm increments and lengths of branches by 20-cm increments. The maximum base diameter was 20–22 mm for Luotian and 38–40 mm for Lanceolata (Fig. 8a); maximum branch length was 220–240 cm and 320–340 cm, respectively (Fig. 8b). On both Luotian and Lanceolata, base diameters were clustered in the 10–16 mm range, making up 72.2% and 51.1% of the total number of branches, respectively. However, the 12–14 mm size in Luotian and the 10–12 mm level in Lanceolata had the greatest number of branches. There was an 8.1% difference in the maximum branch percentage between Luotian and Lanceolata (Fig. 8a). In both Luotian
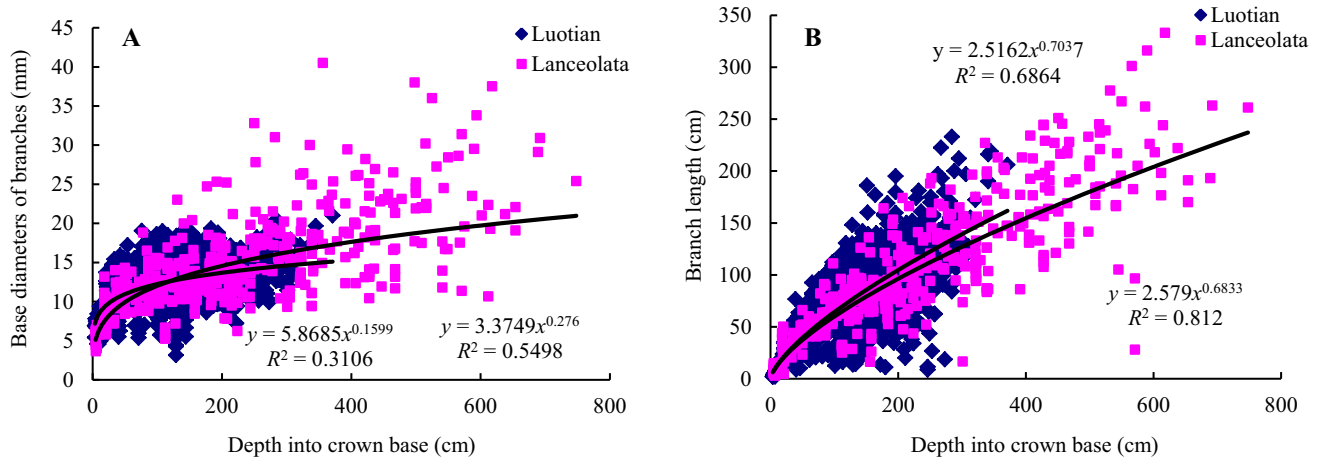
Fig. 6 Relationships between base diameter of branches (**a**) and branch length (**b**) and depth into crown base of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*
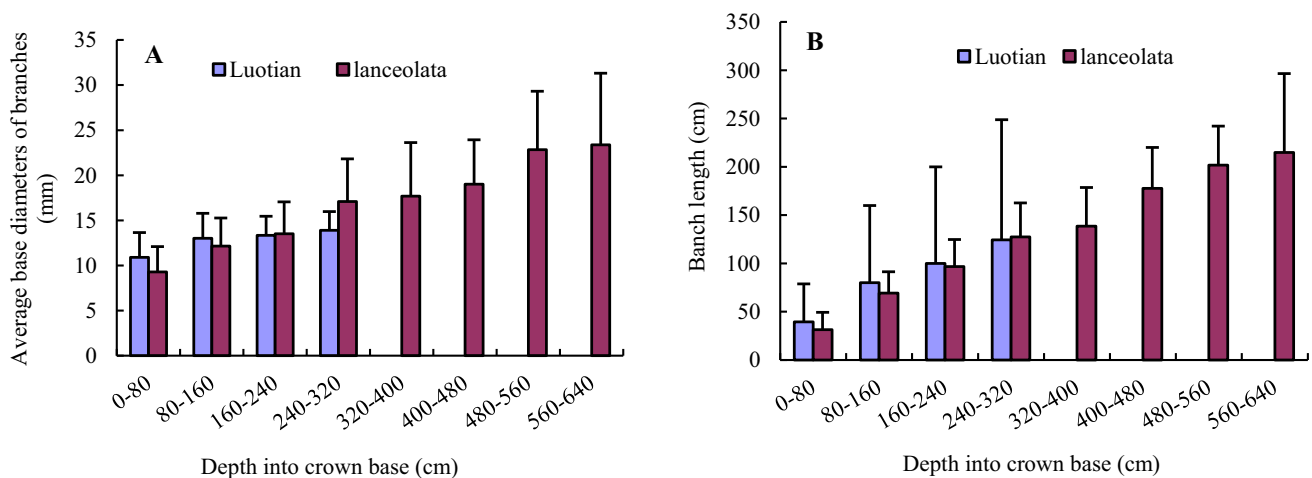
Fig. 7 Distribution of branch diameter (**a**) and branch length (**b**) in different layers of crowns of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. The crowns were stratified from the top at 80-cm intervals along the trunk. In **a**, the average diameter of branches in the same crown layer was calculated, and then the average diameters were dealt using statistical analysis. In **b**, the data was treated as in **a**

and Lanceolata, branch lengths were clustered in the range of 40–120 cm, and branches with lengths of 40–120 cm made up 65.4% and 51.4% of the total branches, respectively (Fig. 8b). Comparatively, the change in branch lengths and change in range of lengths in Luotian was small, which is related to the fast early growth and slow late growth of the lateral branches.

Changes in base diameters and lengths of lateral branches of different ages

There were significant logarithmic relationships between branch ages and base diameters and lengths of first-order lateral branches in 23-year-old trees of Luotian and Lanceolata (Fig. 9a, c). There was a significant power relationship between average annual growth of branch base

diameters and branch ages, but not between average annual growth of branch length and branch ages (Fig. 9b, d). Base diameters and lengths of first-order lateral branches increased with ages. The trends in the changes in base diameters and lengths were similar between Luotian and Lanceolata sample trees. The base diameters and lengths of 1-year-old first-order lateral branches of Luotian were 18.4% and 0.5% greater than those in Lanceolata, respectively. Changes in branch diameters and branch lengths in first-order lateral branches of 2-year-old in Luotian were 18.4% greater than those in Lanceolata, Branch lengths in Luotian were 3.1% less than those of Lanceolata. When branches were more than 2 years old, base diameters and lengths of first-order lateral branches in Luotian were also lower than those in Lanceolata. At branch 6 years, base diameters and lengths of first-order lateral branches in
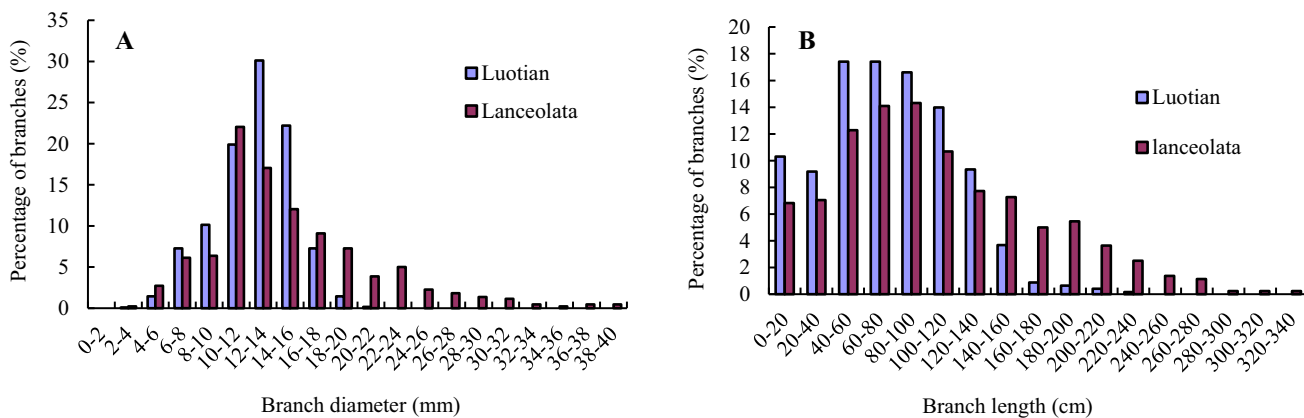
Fig. 8 Quantitative distribution of branches with different base diameters (**a**) and branch lengths (**b**) of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. Diameters were classified 2-mm intervals and branch length 20-cm intervals
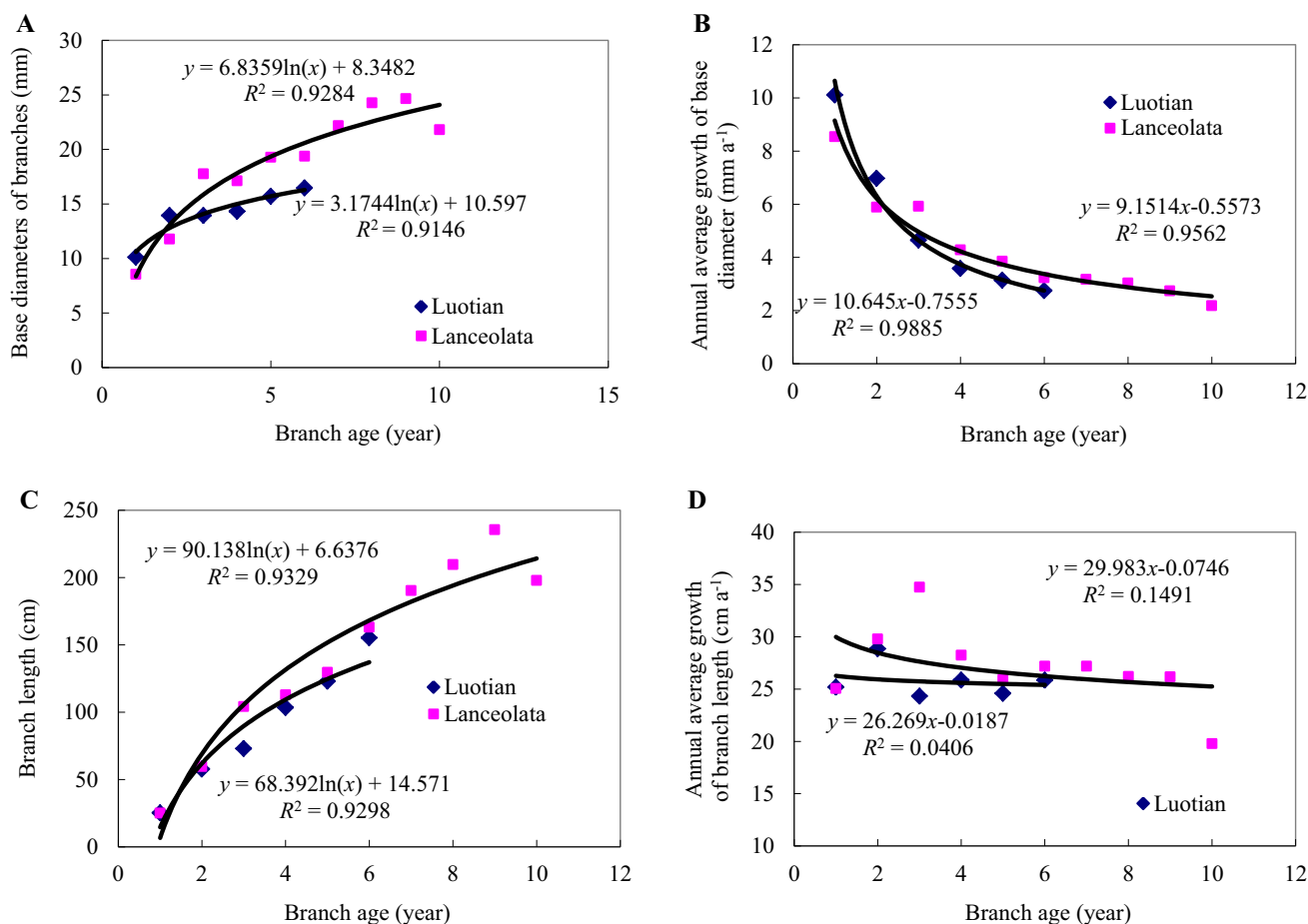
Fig. 9 Base diameters and length of first-order branches in relation to branch age of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. **a** base diameters; **b** mean annual growth of base diameters; **c** length of first-order branches; **d** mean annual growth in length

Luotian were 15.0% and 4.9% lower, respectively, than those for Lanceolata, and at 10 years, 28.0% and 37.9% lower, respectively, than those of first-order lateral branches. Average annual growth of base diameters and lengths of first-order lateral branches at 6 years in Luotian was close to the first-order lateral branches of 9 years in Lanceolata. The first-order lateral branches in 1 year in Luotian showed a rapid increase in base diameter and length, especially in base diameter. We speculate that the rapid growth of first-order branches in 1 year and their

weak lignification might result in a gradual increase in the lateral branch angle and drooping. Lateral branch drooping inhibits normal growth and the transport function of the phloem in related tissues below the lateral branch, ultimately resulting in the death of old branches.

Crown size

Absolute index

There were significant differences in height to the lowest live branch, crown height, size, height ratio, and diameter ratio between branches in Luotian and Lanceolata (Table 6, $p < 0.05$). The average height to the lowest live branch on Luotian was 128.3% greater than that on Lanceolata, while the average crown height and size for Luotian was 45.3% and 41.1% higher, respectively, than for Lanceolata. If the crowns of Luotian and Lanceolata are regarded as simple cone shapes, the projected areas of the two crowns were 2.8 m^2 and 16.3 m^2, respectively, and the longitudinal section areas were 2.7 m^2 and 35.4 m^2. The crowns of Luotian were significantly narrower and smaller, with the projected and longitudinal section area only 16.7% and 7.7% of Lanceolata crowns. There were no significant differences in crown size, height, or height ratio among sample trees of different ages ($p > 0.05$). The crown sizes were not significantly associated with tree age or growth.

Composite indexes

Crown surface areas per tree for Luotian and Lanceolata were 11.7–26.8 m^2 and 46.9–91.9 m^2, respectively. Crown sizes per tree in Luotian and Lanceolata were 3.8–10.0 m^3 and 44.2–67.7 m^3, respectively. Crown productivity per tree for Luotian and Lanceolata was 2.5–4.5 and 1.1–1.9 m^3, respectively. Average crown surface area and size for Luotian were 27.0% and 11.4% of that for Lanceolata, respectively (Table 6). However, average crown productivity of Luotian was 2.4 times that of Lanceolata. Though these differences between Luotian and Lanceolata were significant ($p < 0.05$), the differences

among Luotian sample trees at various ages were not ($p > 0.05$). Crown composite indexes help to better quantify variations in the characteristics of Luotian crown structures. Although the crown surface area and size per tree for Luotian were smaller, crown productivity was greater than in Lanceolata, indicating that Luotian crowns had higher photosynthetic capacity, providing more photosynthate for growth and development.

The average surface area and volume of different crown layers of Luotian and Lanceolata gradually increased as depth into the crown base increased (Fig. 10). For Luotian, the maximum values were for the bottom layers with depth into crown base of 240–320 cm, which constituted 37.1% of the total surface area and 41.7% of the total volume, but in the middle-bottom layers of the crown (480–560 cm) for Lanceolata, constituting 26.2% of the total surface area and 33.5% of the total volume. However, decreases in surface area and volume occurred near the bottom layer. The top crown layers of Luotian had the greatest increase in surface area and volume. At 80–160 cm into the crown base, the surface area and volume was 144.4% and 315.2% greater, respectively, than at < 80 cm deep. With a gradual decrease in branch growth, the increases in the middle to lower layers rapidly declined to 25–53%. In Lanceolata, the increases in surface areas and volumes in the upper crown layers were lower, and reached a maximum in the middle to lower layers. The increases in surface area and volume in the 400–480 cm layer were 107.3% and 164.5%, respectively, compared to those at 320–400 cm into the crown base. When compared within the same layer, the surface area and the volume in the middle to upper layers of the Luotian sample trees were greater than those of Lanceolata. The surface area of the first (depth into crown base of < 80 cm) and second (depth into crown base of 80–160 cm) crown layers was 92.6% and 173.6% greater, respectively, and the volume of the first and second layers was 36.8% and 44.9% greater, respectively. However, 240–320 cm into the crown base, the surface area and volume in Luotian were 18.1% and 37.8% lower, respectively, than in Lanceolata.

Table 6 Comparison of crown size and productivity *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*

Tree	No. of sample trees	Mean age (a)	Height to lowest live branch (m)	Crown height base (m)	Crown size (m)	Crown height ratio	Crown diameter ratio	Total surface area (m^2)	Total size (m^3)	Productivity
Luotian	26	18.6	8.7 ± 1.4	3.0 ± 0.5	1.9 ± 0.1	0.3 ± 0.0	14.82 ± 2.6	19.5 ± 4.2	5.9 ± 1.5	3.4 ± 0.6
Lanceolata	8	19.9	3.8 ± 1.8	6.5 ± 0.5	4.6 ± 0.6	0.65 ± 0.1	35.3 ± 5.4	72.7 ± 17.1	51.8 ± 8.0	1.4 ± 0.3
Ratio (%)			228.3	45.3	41.1	39.8	42.0	26.9	11.4	239.2
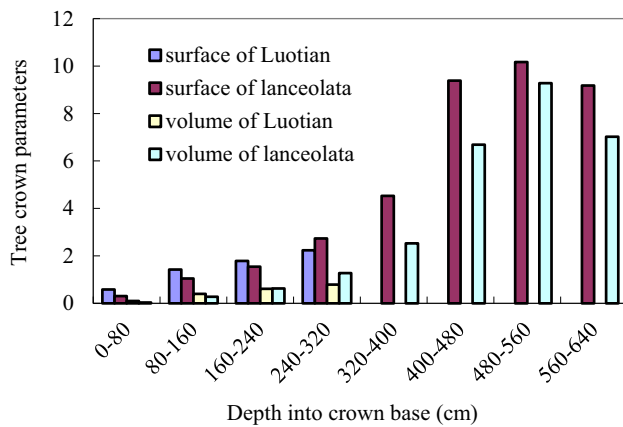
Fig. 10 Changes in average surface area and volume of different layers in the crowns of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. The crowns were stratified at 80-cm intervals along the trunk. The surface area is m², and volume is m³

Crown biomass

Changes in crown biomass

The dry crown biomass of Luotian sample trees was 2.6–7.4 kg, while for Lanceolata, it was 8.8–13.3 kg. The average crown, branch, and leaf biomass in Luotian was only 40.0%, 25.2%, and 54.1% of those in Lanceolata, all of which differed significantly from Lanceolata (Table 7, $p < 0.05$). The branch to leaf biomass ratio for Luotian and Lanceolata was 0.5:1 and 1.0:1, respectively. Leaf biomass constituted 65.3% and 51.5% of the total crown biomass in Luotian and Lanceolata, respectively, showing significantly difference ($p < 0.05$). Although the crown biomass in Luotian was lower, its leaf biomass was notably greater than that in Lanceolata, suggesting that Luotian has greater photosynthetic capacity.

Distribution of branch and leaf biomass in different crown layers

The branch biomass of both Luotian and Lanceolata increased with increased depth into the crown base

(Fig. 11a, b). Dry mass increased the most from the depth into crown base of < 80 cm to 80–160 cm. In Luotian, from the depth into crown base of < 80 to 80–160 cm, dry mass increased by 114.6% (Fig. 11a), and in Lanceolata, it increased by 286.0% (Fig. 11b). In Luotian, the dry mass of branches < 0–80 cm into the crown base was 10.5% greater than in Lanceolata (Fig. 11a, b). Similarly, the dry mass of branches at 80–160 cm into the crown base was 14.0% greater in Luotian than Lanceolata (Fig. 11a, b). In contrast, the dry mass of branches at 160–240 cm into crown base was 64.3% lower in Luotian than in Lanceolata (Fig. 11a, b). Similarly, at 240–320 cm into the crown base, the mass of branches in Luotian was 62.2% lower than in Lanceolata (Fig. 11a, b).

The greatest leaf biomass for both Luotian and Lanceolata sample trees was found at 80–160 cm into the crown base. In Luotian, the dry mass of leaves in the 80–160 cm layer increased by 84.6% and by 172.7% in Lanceolata compared to the < 80 cm layer (Fig. 11a, b). However, leaf biomass in Luotian gradually decreased as depth into to crown base successively increased, and the decrease varied from 1.7 to 5.2% (Fig. 11a). The leaf biomass increased to a maximum at 240–320 cm into the crown base of Lanceolata, with small-scale changes thereafter (Fig. 11b). The leaf biomass of the first three crown layers (i.e., < 80, 80–160, and 160–240 cm layers) in Luotian were 156.0%, 73.3%, and 18.4% greater, respectively, than in Lanceolata (Fig. 11a, b). However, the differences decreased layer by layer with increasing depth into the crown base until the 240–320 cm layer, where the leaf biomass in Luotian was 24.6% less than in Lanceolata (Fig. 11a, b).

The total biomass of branches and leaves for Luotian increased by 92.9% from the < 80 cm layer to the 80–160 cm layer (Fig. 11a). For the other crown layers, the total biomass ranged between 0.10 and 0.11 kg; the rate of change was less than 2.8% (Fig. 11a), indicating that growth and biomass increases of lateral branches had nearly stagnated in the lower layers with greater depth into crown base. In contrast, the total biomass of branches and leaves in Lanceolata increased as depth into the

Table 7 Biomass of branches, leaves, and branches + leaves in crowns of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*

Tree	Branch		Leaf		Total dry mass (kg)	FW/DW ratio (%)	Leaf dry mass ratio (%)
	Dry mass (kg)	Water moisture (%)	Dry mass (kg)	Water moisture (%)			
Luotian	1.29	56.88	2.91	55.01	4.21	44.46	69.25
Lanceolata	5.15	50.95	5.38	54.01	10.52	47.42	51.50
Ratio	25.16	111.63	54.13	101.84	39.97	93.75	134.46
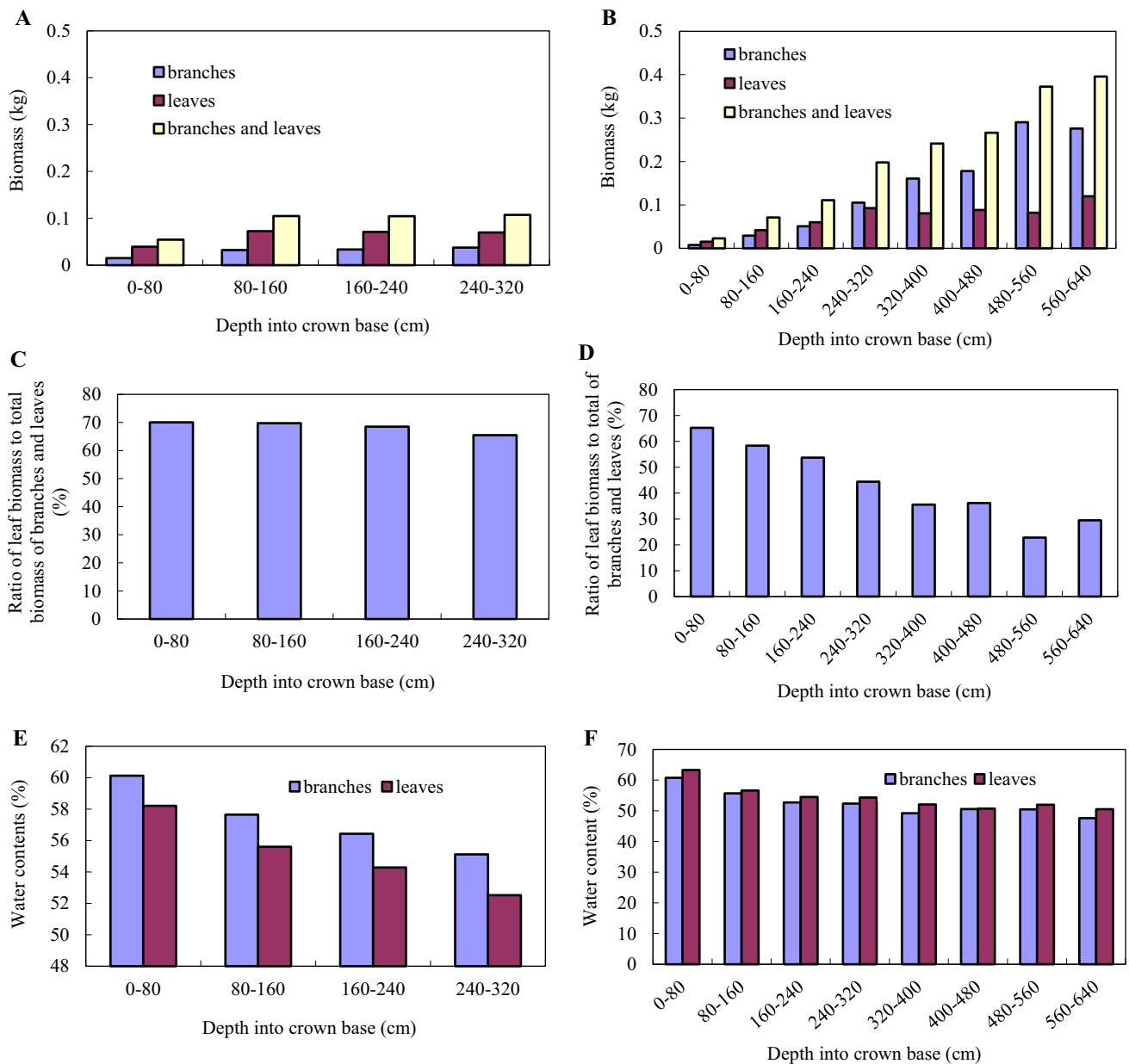
Fig. 11 Distribution of biomass and water content of leaves and branches in different crown layers of *Cunninghamia lanceolata* var. *Luotian* and *C. lanceolata*. Crowns were stratified at 80-cm intervals along the trunks. **a** and **b** biomass of leaves, branches, and leaves + branches of Luotian (**a**) and Lanceolata (**b**); **c** and **d** ratios of leaf biomass to total biomass of leaves and branches of Luotian (**c**) and Lanceolata (**d**); **e** and **f** water content of leaves and branches of Luotian (**e**) and Lanceolata (**f**)

crown base increased, but the amplitude of the increase gradually decreased (Fig. 11b). In Lanceolata, the greatest increase was found in the 80–160 cm layer (201.1%), while the smallest increase was found in the bottom crown layer (6.3%) (Fig. 11b). Compared with the same crown layers, the total biomass of branches and leaves was 137.1% and 47.5%, respectively, greater in the first two layers (i.e., < 80 and 80–160 cm) in Luotian than in Lanceolata (Fig. 11a, b). In contrast, the total biomass of branches and leaves was 5.8% and 45.8%, respectively,

and lower in the next two layers (i.e., 160–240 cm and 240–320 cm layer) in Luotian than in Lanceolata (Fig. 11a, b). Compared to Lanceolata, Luotian showed stronger apical dominance, as reflected by its greater branch and leaf biomass, resulting in enhanced photosynthetic capacity in the middle and upper crown layers. However, likely due to this strong apical dominance, growth of the lateral branches in the lower crown layers diminished rapidly, thus forming a crown with obvious structural features.

As shown in Fig. 11c, d, leaf biomass percentages ranged from 65.5% to 70.0% in Luotian and between 22.8% and 65.3% in Lanceolata, with both Luotian and Lanceolata showing that leaf biomass decreased as depth into the crown base increased. However, the leaf biomass percentage of Luotian only decreased slightly (Fig. 11c). There was a 4.5% decrease from the < 80 cm layer to the bottom layer, with an average decrease of 1.1% per layer. However, the leaf biomass percentage of Lanceolata showed a 44.4% decrease in the 240–320 cm layer (Fig. 11d), which gradually declined to 30.0% (with an average decrease of 5.3% per layer, a much larger decrease than that in Luotian). Within the same layer, the leaf biomass percentage of Luotian was greater than that of Lanceolata, with more increased amplitudes as depth into crown base increased (Fig. 11c, d). The densities of each layer in the first four crown layers (i.e., 0–80, 80–160, 160–240, and 240–320 cm) of Luotian were 4.8%, 11.4%, 14.8%, and 21.1% greater, respectively, than in Lanceolata (Fig. 11c, d). In the first three crown layers (i.e., 0–80, 80–160, and 160–240 cm), the leaf biomass percentage for Luotian was 20.4% higher than for Lanceolata, and the branch biomass was 38.7% lower (Fig. 11c, d). The apparently slower branch growth in Luotian may be a direct cause of its greater leaf biomass percentage. However, the higher leaf biomass may also be a compensating mechanism for Luotian to improve the photosynthetic capacity of its narrow crown.

The relative moisture in leaves and branches of Luotian was 55.1–60.1% and 52.5–58.2%, respectively, (Fig. 11e), and 47.6–60.7% and 50.5–63.3% for Lanceolata (Fig. 11f). The differences were small and decreased slightly as depth into crown base increased. However, in every crown layer, the relative branch moisture for Luotian was always higher than the relative leaf moisture by an average of 2.2% (Fig. 11e). Conversely, the relative leaf moisture was 1.8% higher than the relative branch moisture for Lanceolata (Fig. 11f).

Discussion

Canopy structure and tree morphology influence environmental conditions in a stand, tree growth, and most forest functions and services (Pretzsch 2014), while canopy structure and tree morphology are determined to some extent by the crowns of individual trees in a stand. Crown size thus influences the growth, carbon sequestration, shading, filtering of fine air particulates, and risk of windbreak for other trees (Pretzsch et al. 2015). Crown structure and size are closely related to branches, especially the number and length of first-order branches, and to tree crown height.

In general, age structure of tree branches is directly related to tree age and spatial competition. The maximum age of live branches is theoretically close to the tree age in the absence of competition. In this study, the oldest live branches on 15–23-year-old Luotian trees was 5–6 years. The oldest branch age was not much affected by tree age. Live branches that were 7 years old or more naturally died and broke off from the main trunk. In the same growth environment, the oldest branch ages in Lanceolata increased with tree ages. Few branches in the lower crown layers died, but they still remained on the trunk. This variation in the lateral branch age structure is unique to Luotian (supplementary material 3). This characteristic might be a key factor underlying the unique morphological structure of its crown. Through branch anatomical analysis, Xiong (1984) argued that nutrient supply in 3–5-year-old lateral branches was blocked by a concave under the center of the branch junction, resulting in the natural death of the lateral branches. However, the exact mechanism and physiological response are still unclear.

A crown feature of Luotian is that it only has two orders of branching, which is very different from other coniferous species that have multiple-order branching. Due to this relatively simple branching feature and the fact that its older branches naturally die and fall off, the total number of branches in Luotian was significantly lower, compared to Lanceolata. The average number of first-order lateral branches per tree in Luotian was 12.9% lower than in Lanceolata (Table 4). Meanwhile, the number of branches per whorl and the average number of branch whorls in the crown with average crown height in Luotian was 21.8% and 51.1%, respectively, greater than in Lanceolata (Table 4). Additionally, more than 90% of lateral branches in Luotian were concentrated in the middle and top parts of the crown and in the horizontal 1-m radius. Therefore, Luotian had a thicker crown. This characteristic may be related to the strong sprouting ability of the axillary buds of the main trunk in Luotian or to the simultaneous inhibition of the apical buds on the lateral branches (Xiong 1984). The dense crowns help to enhance the photosynthetic capacity of the crown.

The branching angles of Luotian and Lanceolata increased with increasing height of the crown base. The increase in branching angles is greater in the upper crown layers than in the middle and lower layers. This vertical distribution is in accordance with several studies (Zeide 1991; Deleuze et al. 1996; Baldwin and Peterson 1997; King 1998; Mäkinen and Colin 1998; Ishii et al. 2000; Gielen et al. 2002; Ruan 2003; Du et al. 2010; Beaulieu et al. 2011; Lintunen 2013; Yoshimura 2013; Wu 2014). However, branching angles and the range in vertical variation of the branching angles of Luotian were remarkably larger than those of Lanceolata; 71.8% of the branching

angles in Luotian were more than 90°, while 97.4% of the branching angles in Lanceolata were ≤ 90° (Fig. 5a). The larger branching angles reflected the branch drooping of Luotian. This feature is the most important and obvious characteristic of the crown structure of this variety. Xiao et al. (2006) showed that larger branching angles in *Pinus sylvestris* var. *mongolica* Litv. had a direct effect on the absorption and utilization of sunlight, improving the efficient use of spatial resources. While the photosynthetic rates in the leaves on 1–2-year-old branches were not very different in Luotian and Lanceolata, the photosynthetic rates in the leaves of more than 3-year-old branches in Luotian were obviously lower those in Lanceolata (Huang et al. 2013). The results suggest that larger branching angles may not improve the photosynthetic efficiency of Luotian: therefore, the photosynthetic characteristics of its crown have yet to be studied comprehensively and systematically.

For Luotian and Lanceolata, the base diameters and lengths of branches showed power function relationships with depth into crown base (Fig. 6) and logarithmic function relationships with branch ages (Fig. 9). The 1–2-year-old branch base diameters and lengths of branches in the middle and upper crown layers of the Luotian samples were all greater than those of Lanceolata. However, the growth of 3-year-old lateral branches was slower in Luotian. The base diameters and lengths of branches in the lowest crown layer were only 59.5% and 57.9%, respectively, of those of Lanceolata (Figs. 6, 7), consistent with the results of Xiong (1984) and Huang et al. (2013). The lengths of the branches directly determine the crown shape and size. Short branches and natural falling of old lateral branches characterize the crowns of the Luotian variety. The base diameters of the branches greatly impact the quality of the timber (Colin and Houllier 1991). In particular, the branch base diameters affect the size of scars on the trunks, and scar sizes affect the quality and value of the timber. Obviously, the narrow crowns of Luotian may enable an increase in stand density and timber yield, while small scar sizes enhance the quality and value of the timber and hence the potential for commercial use in plantations.

Several studies have shown that crown size reflects space utilization, tree growth and vitality (Daniels 1979; Esau 1982; Bechtold 2004; Brown et al. 2004; Xu et al. 2005; Wang et al. 2009). However, this is not the case for the Luotian variety. Considering the absolute index or composite index, the crown sizes of Luotian were significantly smaller than those of Lanceolata. Meanwhile, tree growth was very similar in Luotian and Lanceolata samples (Table 1). The narrow crowns of Luotian did not significantly affect main trunk growth. This may be related to its greater lateral branch density, greater branching angle, and strong apical dominance that improves light-use efficiency

and biomass accumulation. The crown surface area and crown productivity of Luotian are quite different from those reported for Fujian-fir (Wu 2014).

Niinemets (2010) examined forest trees with varying degrees of shade tolerance and concluded that, at the shoot scale, foliage inclination angle distribution and foliage spatial aggregation are the major determinants of light harvesting, while at the canopy scale, branching frequency, foliage distribution and biomass allocation to leaves modify light harvesting significantly, and the vertical distribution of crown and leaf biomass can reflect the spatial structure and productivity of stands (Maguire et al. 1999); therefore, biomass of leaves, branches, and crowns of Luotian were significantly less than those of Lanceolata (Fig. 11a, b). Although the crown biomass of Luotian was only 39.97% of Lanceolata, its leaf biomass was 69.25% of its crown biomass, and the number was 1.34 times that of Lanceolata (Table 7). Leaf biomass ratios at different crown layers in Luotian were greater than those in Lanceolata (Fig. 11c, d). Wu (2014) found that the ratio of leaf biomass to total crown biomass of trees in young stands of *C. lanceolata* was 53.0% and 32.5% in mature and over-mature stands. Our result is close to those of Wu (2014). Because of smaller crowns (Fig. 10), and more biomass allocation to leaves (Fig. 11c, d), *Cunninghamia lanceolata* var. *Luotian* should be planted at higher densities than *Cunninghamia lanceolata* in plantations, and higher light-use efficiency should occur in Luotian plantations.

A number of recent studies found that light availability and tree height affected crown architecture, biomass allocation and crown developmental patterns (Bongers and Sterck 1998; Claveau et al. 2002, 2005; Kawamura and Takeda 2002; Osada et al. 2004a, b), but branching features on Luotian are not related to light environment or tree height. As shown in supplementary materials 1 and 2, the Luotian variety has very narrow crowns in a good light environment. The branching feature is related to the woody characteristic at the point of branching. Xiong (1984) reported that in Luotian, secondary growth of the vascular cambium under junction with 3-year-old lateral branches was slow, which led to the formation of concave structures with soft tissues in the branch junctions, and the concave structures became deeper as trees grew. The experimental results might explain the drooping and falling of the old lateral branches and the entire development process, but does not clearly explain the mechanisms underlying the formation of the concave structure and the related physiological changes. In its natural habitat, Luotian usually grows on ridges of agricultural fields and the banks of ditches and small rivers. Due to high soil moisture or even water logging, axillary buds on the trunks grow fast; thus, dense branches occur on the trunks and grow faster in their

early stage. With great branching angles and high percentage of leaf biomass, Luotian exhibits enhanced transpiration through improved light, ventilation conditions, and leaf area to lose excess water. Due to the fast growth of 1–2-year-old live lateral branches in Luotian, weak lignification at the junctions of lateral branches does not support the fast-increasing mass of lateral branches; thus, branching angles continue to increase, resulting in the formation of the concave structures at the junctions of lateral branches. With the concave structures deepening, branch angles increase annually, and nutrient transport is inhibited more seriously. Growth of 4–5-year-old branches is slow and eventually stagnates. Meanwhile, 6–7-year-old branches die naturally and break off. The morphological variation in Luotian may result from the genetic differentiation under synergistic forces of human activities and the natural environment. This genetic differentiation possibly evolved gradually into stable and consistent genetic characteristics in the relatively isolated original habit, ultimately evolving into a unique geographical population or ecotype. Obviously, Luotian is a crop ideotype (Donald and Hamblin 1976; Cannell 1978; Martin et al. 2001). The interdependence and influence of these varietal characteristics need to be further studied. Their origin, mechanism of formation, physiological and biochemical reactions, and genetic control mechanisms have yet to be studied.

Crown condition is a function of soil, site and tree characteristics (Musio et al. 2007), and crown and leaf traits are thought to be predictors of subtropical sapling growth rates (Li et al. 2017). Some models for individual crown size and biomass distribution have been established for different tree species to predict changes in tree crowns (Tahvanainen and Forss 2008; Russell and Weiskittel 2011; Sharma et al. 2016, 2017a, b). Therefore, related models should be established for *Cunninghamia lanceolata* var. *Luotian* and used to predict changes in crown growth and distribution of crown biomass in order to manage effectively plantations composed of the variety, especially determining thinning time.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Baldwin J, Peterson KD (1997) Predicting the crown shape of loblolly pine trees. Can J For Res 27:102–107

Beaulieu E, Schneider R, Berninger F, Ung C-H, Swift DE (2011) Modeling jack pine branch characteristics in eastern Canada. For Ecol Manag 262:1748–1757

Bechtold WA (2004) Largest-crown-width prediction models for 53 species in the western United States. Western J Appl For 19(4):145–251

Bongers F, Sterck FJ (1998) Architecture and development of rainforest trees: responses to light variation. In: Newbery DM, Brown N, Prins HHT (eds) Dynamics of tropical communities. Blackwell Scientific, Oxford, pp 125–162

Brown PL, Doley D, Keenan RJ (2004) Stem and crown dimensions as predictors of thinning responses in a crowded tropical rainforest plantation of *Flindersia brayleyana* F. Muell. For Ecol Manag 196:379–392

Brünig EF (1976) Tree forms in relation to environment conditions: an ecological viewpoint. Tree Physiol Yield Improv 22:139–156

Cannell GR (1978) Improving per hectare forest productivity. In: Hollis CA, Squillace AE (eds) Proceedings of the 5th North American forest biology workshop, March 13–15. University of Florida, Gainesville, pp 120–148

Claveau Y, Messier C, Comeau PG, Coates KD (2002) Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. Can J For Res 32:458–468

Claveau Y, Messier C, Comeau PG (2005) Interacting influence of light and size on aboveground biomass distribution in sub-boreal conifer saplings with contrasting shade tolerance. Tree Physiol 25:373–384

Colin F, Houllier F (1991) Branchiness of Norway spruce in northeastern France: modelling vertical trends in maximum nodal branch size. Ann Sci For 48(6):679–693

Daniels RF (1979) Methods for modeling individual tree growth and stand development in seeded loblolly pine stands. Virginia Polytechnic Institute and State University, School of Forestry and Wildlife Resources, pp 2–19

Deleuze C, Colin F, Ribeyrolles L (1996) Modelling crown shape of *Picea abies*: spacing effects. Can J For Res 26:1957–1966

Díaz-Varela RA, de la Rosa R, León L, Zarco-Tejada PJ (2015) High-resolution airborne UAV imagery to assess olive tree crown parameters using 3D photo reconstruction: application in breeding trials. Remote Sens 7:4213–4232

Donald CM, Hamblin J (1976) The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Adv Agron 28:361–405

Dong LB, Liu ZG, Li FR, Jiang LC (2013) Primary branch size of *Pinus koraiensis* plantation: a prediction based on linear effect mixed effect model. Chin J Appl Ecol 24:2447–2456 (**in Chinese with English abstract**)

Du J, Fan ZX, Ye DY, Lu CT (2010) The predicting models of crown volume and LAI for *Phoebe zhennan* plantation. J Zhejiang For Sci Technol 30(4):37–41 (**in Chinese with English abstract**)

Esau K (1982) Anatomy of seed plants, 2nd edn (Lee CL, trans.). Shanghai Scientific and Technical Publishers, Shanghai, pp 241–242 (**in Chinese**)

Fang F, Im J, Lee J, Kim K (2016) An improved tree crown delineation method based on live crown ratios from airborne LiDAR data. Giosci Remote Sens 53(3):402–419

Fu LY, Sun H (2013) Individual crown diameter prediction for *Cunninghamia lanceolata* forests based on mixed effects models. Sci Silvae Sin 49(8):65–74 (**in Chinese with English abstract**)

Fu L, Sun H, Sharma RP, Lei Y, Zhang H, Tang S (2013) Nonlinear mixed-effects crown width models for individual trees of Chinese-fir (*Cunninghamia lanceolata*) in south-central China. For Ecol Manag 302:210–220

Gielen B, Calfapietra A, Claus A (2002) Crown architecture of *Populus* spp. is differentially modified by free-air CO_2 enrichment (POPFACE). New Phytol 153:91–99

Halle F, Olderman RAA (1970) Essai sur L'architecture et la Dynamique de Croissance des Arbres Tropicaux Masson, Paris

Huang GW, Hu XY, Zhang YD, Du CQ, Xu XY, Xu YZ (2013) Study on selection of superior of *Cunninghamia lanceolata* cv. Luotian. Hubei For Sci Technol 1:1–4 (**in Chinese with English abstract**)

Hubei Institute of Forestry, Huanggang Institute of Forestry, Luotian County Institute of Forestry (1977) A preliminary report on a fine type of Chinese-fir. Hubei For Sci Technol 1:15–19

Ishii H, Clement J, Shaw D (2000) Branch growth and crown form in old coastal Douglas-fir. For Ecol Manag 131(1/3):81–91

Jiang SL (2012) Research on canopy shape model of main coniferous tree species in Heilongjiang province. Doctoral dissertation. Northeast Forestry University, Harbin, pp 10–200

Jiang ZL, Ye JZ (1980) Preliminary study on crown morphology and structure of *Cunninghamia lanceolata*. J Nanjing For Ind Acad 4(1):46–52 (**Chinese with English abstract**)

Jiang LC, Zhang R, Li FR (2012) Modeling branch length and branch angle with linear mixed effects for Dahurian larch. Sci Silvae Sin 48(5):53–60 (**in Chinese with English abstract**)

Kawamura K, Takeda H (2002) Light environment and crown architecture of two temperate *Vaccinium* species: inherent growth rules versus degree of plasticity in light response. Can J Bot 80:1063–1077

King DA (1998) Relationship between crown architecture and branch orientation in rain forest trees. Ann Bot 82:1–7

Kramer PJ, Kozlowski TT (1979) Physiology of woody plants. Academic Press, London, pp 443–444

Lei XD, Zhang ZL, Chen XG (2007) Crown-width prediction models for several tree species including *Larix olgensis* in northeastern China. J Beijing For Univ 28(6):75–79 (**in Chinese with English abstract**)

Li FR (2004) Modeling crown profile of *Larix algensis* trees. Sci Silvae Sin 40(5):16–24 (**in Chinese with English abstract**)

Li Y, Kröber W, Bruelheide H, Härdtle W, von Oheimb G (2017) Crown and leaf traits as predictors of subtropical tree sapling growth rates. J Plant Ecol 10:136–145

Liao CX, Li FR (2007) The predicting models of crown surface area and crown volume for Mongolian pine plantation. Bull Bot Res 27(4):478–483

Lin YR (2013) Study on the canopy structure of young trees of Chinese-fir. Dissertation, Fujian Agriculture and Forestry University, Fuzhou (**in Chinese with English abstract**)

Lintunen A (2013) Crown architecture and its role in species interactions in mixed boreal forests. Dissertation. University of Helsinki. https://doi.org/10.14214/df.165

Liu ZG, Guo CL (1996) The prediction of canopy shape of *Larix gmelinii* plantation. J Northeast For Univ 24(6):14–20 (**in Chinese with English abstract**)

Lu KN, Zhang HQ, Liu M (2011) Study on plant architecture of *Cunninghamia lanceolata* based on measured data. For Res 24(1):132–136 (**in Chinese with English abstract**)

Lu KN, Zhang HQ, Liu M et al (2012) Design and implementation of individual tree growth visualization system of *Cunninghamia lanceolata*. For Res 25(2):207–211 (**in Chinese with English abstract**)

Maguire DA, Johnston SR, Cahill J (1999) Predicting branch diameters on second growth Douglas-fir from tree-level descriptors. Can J For Res 29:1829–1840

Mäkinen H, Colin F (1998) Predicting branch angle and branch diameter of Scots pine from usual tree measurements and stand structural information. Can J For Res 28(11):1686–1696

Martin TA, Johnsen KH, White TL (2001) Ideotype development in southern pines: rationale and strategies for overcoming scale-related obstacles. For Sci 47:21–28

Miranda-Fuentes A, Llorens J, Gamarra-Diezma JL, Gil-Ribes JA, Gil E (2015) Towards an optimized method of olive tree crown volume measurement. Sensors 15:3671–3687

Mongus D, Žalik B (2015) An efficient approach to 3D single tree-crown delineation in LiDAR data. ISPRS J Photogramm Remote Sens 108:219–233

Musio M, von Wilpert K, Augustin NH (2007) Crown condition as a function of soil, site and tree characteristics. Eur J For Res 126:91–100

Niinemets Ü (2010) A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecol Res 25:693–714

Noriyuki O, Hiroshi T (2003) Branch architecture, light interception and crown development in saplings of a plagiotropically branching tropical tree, *Polyalthia jenkinsii* (Annonaceae). Ann Bot 91:55–63

Oliver CD, Larson BC (1990) Forest stand dynamics. McGraw-Hill Pub Co., New York, pp 213–258

Olivier M-D, Robert S, Fournier RA (2016) Response of sugar maple (*Acer saccharum* Marsh.) tree crown structure to competition in pure versus mixed stands. For Ecol Manag 374:20–32

Osada N, Tateno R, Hyodo F, Takeda H (2004a) Changes in crown architecture with tree height in two deciduous tree species: developmental constraints or plastic response to the competition for light? For Ecol Manag 188:337–347

Osada N, Tateno R, Mori A, Takeda H (2004b) Changes in crown development patterns and current-year shoot structure with light environment and tree height in *Fagus crenata* (Fagaceae). Am J Bot 91:1981–1989

Panagiotidis D, Abdollahnejad Z, Surový P, Chiteculo V (2017) Determining tree height and crown diameter from high-resolution UAV imagery. Int J Remote Sens 38:2392–2410

Paris C, Kelbe D, van Aardt J, Bruzzone L (2017) A novel automatic method for the fusion of ALS and TLS LiDAR data for robust assessment of tree crown structure. IEEE Trans Geosci Remote Sens 55:3679–3693

Pei BH, Zheng SK (1990) Effects of forest density on light energy distribution and canopy structure of I—69 poplar. For Res 3(3):201–206 (**in Chinese with English abstract**)

Pretzsch H (2014) Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For Ecol Manag 327:251–264

Pretzsch H, Biber P, Uhl E, Dahlhausen J, Rötzer T, Caldentey J, Koike T, van Con T, Chavanne A, Seifert T, du Toit B, Farnden C, Pauleit S (2015) Crown size and growing space requirement of common tree species in urban centres, parks, and forests. Urban For Urban Green 14:466–479

Roloff A (1991) Crown structure and tree vitality. In: Longhurst JWS (ed) Acid deposition. Springer, Berlin, pp 193–213

Ruan ZC (2003) Genetic improvement of *Cunninghamia lanceolata*. Guangdong Science and Technology Press, Guangzhou, pp 25–27 **(in Chinese with English abstract)**

Russell MB, Weiskittel AR (2011) Maximum and largest crown width equations for 15 tree species in Maine. North J Appl For 28(2):84–91

Sharma RP, Vacek Z, Vacek S (2016) Individual tree crown width models for Norway spruce and European beech in Czech Republic. For Ecol Manag 366:208–220

Sharma RP, Bílek L, Vacek Z, Vacek S (2017a) Modelling crown width–diameter relationship for Scots pine in the central Europe. Trees 31:1875–1889

Sharma RP, Vacek Z, Vacek S, Podrázský V, Jansa V (2017b) Modelling individual tree depth into crown base of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.). PLoS ONE 12(10):e0186394. https://doi.org/10.1371/journal.pone.0186394

Strîmbu VF, Strîmbu BM (2015) A graph-based segmentation algorithm for tree crown cxtraction using airborne LiDAR data. ISPRS J Photogramm Remote Sens 104:30–43

Suzuki M (2003) Size structure of current-year shoots in mature crowns. Ann Bot 92:339–347

Tahvanainen T, Forss E (2008) Individual tree models for the - crown biomass distribution of Scots pine, Norway spruce and birch in Finland. For Ecol Manag 255:455–467

Wang ZJ, Li FY, Yan DF et al (2009) Study on crown width, crown length, and growth of different *Populus tomentosa* clones. J Henan Inst Sci Technol 37(4):14–18 **(in Chinese with English abstract)**

Wang XM, Lu J, Li FR (2012) Crown profile simulation of major broad-leaf species of natural secondary forest in north of China. J Nanjing For Univ 36(4):7–12 **(in Chinese with English abstract)**

Wu ZL (1984) *Cunninghamia lanceolata*. China Forestry Publishing House, Beijing, pp 202–203 **(in Chinese with English abstract)**

Wu MQ (2014) A study on crown structure of *Cunninghamia lanceolata* plantation in Fujian. Beijing Forestry University, Beijing, pp 5–30 **(in Chinese with English abstract)**

Xiao R, Li FR, Liu ZG (2006) Branching structure analysis of Mongolian plantation. Bull Bot Res 26(4):490–496

Xiong LD (1984) A preliminary study on the natural branch drooping and shedding characteristics of *Cunninghamia lanceolata* (Lamb.) Hk. *cv.* Luotian. Hubei For Sci Technol 2:8–12 **(in Chinese with English abstract)**

Xu CL, Zhang JL, Chen DL (2005) Study on the effect of the crown-fullness ratio on the growth of tree and the form of the tree-trunk. J Agric Univ Hebei 28(3):45–48 **(in Chinese with English abstract)**

Xu H, Sun Y, Wang X, Wang J, Fu Y (2015) Linear mixed-fffects models to describe individual tree crown width for China-fir in Fujian province, southeast China. PLoS ONE 10(4):e0122257. https://doi.org/10.1371/journal.pone.0122257

Ye WH, Guan WB (1995) A review and prospect of the studies on tree architecture: a brief comment on 3 statuses of tree architecture. World For Res 8(4):22–27 **(in Chinese with English abstract)**

Yoshimura K (2013) Irradiance and developmental stages of crown architecture affect shoot production in *Rhododendron reticulatum*. Am J Plant Sci 4:69–76

Zeide BP (1991) A method for estimation of fractal dimension of tree crowns. For Sci 37(5):1253–1265

Zhang SY, Xu H (2001) A preliminary study on the golden segmentation in the canopy. J Southwest For Univ 21(1):14–19 **(in Chinese with English abstract)**

Zhen Z, Quackenbush LJ, Zhang L (2016) Trends in automatic individual tree crown detection and delineation—evolution of LiDAR data. Remote Sens 8:333. https://doi.org/10.3390/rs8040333

Zheng WJ (1983) Chinese trees, vol 1. China Science and Technology Press, Beijing, pp 307–310 **(in Chinese)**

Zhu CQ, Lei JP, Liu XD, Cheng GZ, Li BD (2000) Crown structure of poplar trees in intensive and extensive management plantation. Sci Silvae Sin 36(2):60–68 **(in Chinese with English abstract)**

Zimmerman MH, Brown CL (1971) Tree-structure and function. Springer, Berlin, pp 203–238