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Distribution of Starch in Trunkwood of *Catalpa bungei* 'Jinsi': A Revelation on the Metabolic Process of Energy Storage Substances

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Abstract: Starch is stored in thin-walled tissue of wood for several years or even decades. Starch reserves vary by anatomical structure, growth ring, and tree species. The spatial distribution pattern of starch in *Catalpa bungei* 'Jinsi' wood is unclear. We sampled three *C. bungei* 'Jinsi' trees at the end of the growing season and cut discs from their trunks to stain starch granules in wood ray cells with iodine–potassium iodide. We studied starch content in the ray cells of the trunks' height position (stump, breast height, and crown base) from pith to bark in four directions (west, east, south, north) of the tree. There was a significant difference in starch content in three trunk height positions ($p < 0.01$), with stump (4.06 to 92.16%) > breast height (6.05 to 69.05%) > crown base (3.89 to 47.04%). There was a significant difference in starch content in different directions at the same height position. In the radial direction, the starch content of sapwood was much higher than that of heartwood, and the starch content showed an overall decreasing trend from bark to pith. The results indicated that starch distribution in tree trunks is uneven, which is related to energy metabolism processes, especially heartwood formation. This will contribute to further research on improving wood quality through the *C. bungei* 'Jinsi' tree breeding program.

Keywords: *Catalpa bungei* 'Jinsi'; xylem; ray cells; starch grains; metabolism

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1. Introduction

Starch, a common carbohydrate substance, is a product of photosynthesis in plant tissues [1]. Starch is widely distributed in plants and mainly exists in organs such as seeds, roots, stems, leaves, fruits, and pollen [2]. Synthetic starch is stored in the thin-walled tissue of wood. The distribution pattern of starch in wood can be divided into two types: trees that store starch only in thin-walled tissues are called thin-walled tissue storage tree species, while trees that store starch in thin-walled tissues and active fibers are called fiber storage species [3].

The starch content in wood can affect its physical and chemical properties. For example, wood with a higher starch content may be more prone to moisture absorption and mold growth, affecting its durability [4]. In some cases, it is necessary to reduce the starch content in wood to improve its performance or prevent mold growth. For example, rubber wood can be effectively reduced in starch content while maintaining its natural color through ultrasonic acidification and ultrasonic neutralization treatment [5]. Starch can be extracted from wood and used for various industrial purposes [6].

The distribution of starch in wood is an interesting and complex topic, and the distribution may be influenced by various factors, such as anatomical structure, growth ring, and tree species [7]. Some tree species (such as pine, birch, etc.) have a higher starch content, while others (such as oak, cherry, etc.) have a relatively lower starch content. In trunkwood, the starch content varies greatly [8,9]. Along a tree height gradient, the starch content in wood usually remains stable or increases [10]. However, Smith, et al. [11] showed the opposite trend of change. Cambou, et al. [12] also found that starch content appears to be quite high at the height of tree stumps. In the radial direction, starch tends to accumulate in the xylem of sapwood and decreases radially towards the pith [3,5]. Starch rarely appears in heartwood. Wood ray is considered to be the main storage thin-walled tissue in wood [3] and the most effective radial transport pathway [13]. Starch storage takes priority over growth, which is independent of growth conditions and may be a mechanism to ensure long-term survival [14].

In addition to providing carbon storage, starch is also a regulatory factor that controls plant growth, defense, and development processes [15,16]. When the demand for photosynthesis exceeds the supply, starch is broken down into glucose for physiological activities [1]. Starch granules can also regulate metabolic activities in plants, such as carbon metabolism and nitrogen metabolism [3]. Starch granules can serve as a medium for biosynthesis and decomposition, promoting the transformation and migration of metabolites in plants [17]. In addition, starch granules can also act as signaling molecules during storage, participating in signal transduction and regulation in plants [18]. Starch also plays an important role in the formation of heartwood. During heartwood formation, starch is consumed or converted into heartwood substances, such as pigments and tannins [8]. Therefore, the precise localization and quantification of starch is important as it is an important strategy reflecting tree metabolism [19]. However, this pattern varies widely between species. Some species may store starch in deeper layers of wood [20,21]. Guo, et al. [22] found that there is still a small amount of starch granules in the heartwood of the *Catalpa bungei* 'Jinsi' tree.

C. bungei 'Jinsi' is a cultivar of *C. bungei* with a relatively fast growth rate and strong soil fixation ability, which has received strong support and promotion from the government for cultivation [23]. The heartwood color is yellow, the sapwood color is light, and there are a golden zone and transition zone between the heartwood and sapwood of *C. bungei* 'Jinsi' [22]. Yellow heartwood is a typical feature of *C. bungei* 'Jinsi', which is completely different from other *C. bungei* cultivars. Guo, et al. [22] not only confirmed the difference in starch content between heartwood and sapwood, but also mentioned the asymmetric distribution of heartwood and sapwood caused by trunk eccentricity. However, they did not indicate whether this asymmetric distribution has an impact on starch content. There is little research on the chordwise distribution of starch in the cross section of tree trunks. Pasolon, et al. [24] hypothesized that starch content does not depend on trunk eccentricity. But Reghu and Patel [25] found that the starch content of the upper layer was lower than that of the lower layer of *Azadirachta indica*, *Mangifera indica*, and *Polyalthia longifolia* reaction wood. It should be noted that the starch content in any part of a tree is not constant. At one time, a specific tissue may be completely starch-free, while at another time, there may be a large amount of starch present, depending on the physiological activity of the tissue [11]. In the Northern Hemisphere, starch in broad-leaved deciduous trees accumulates at the end of the growing season, is depleted during winter dormancy and early spring growth, and is then replenished in the next growing season [21].

The objective of this study was to characterize starch distributions in the trunkwood of *Catalpa bungei* 'Jinsi' and to determine whether and to what extent starch distributions in the trunk are influenced by height positions, direction, and cambial age. If distributions can be more appropriately characterized and ultimately generalized, it may be possible

to understand the energy storage characteristics of trunkwood, evaluate the wood quality, and provide a scientific basis for breeding, wood processing, and utilization.

2. Materials and Methods

2.1. Materials

The *C. bungei* 'Jinsi' trees were collected from an even-aged (8-year-old) pure artificial forest (Luoyang Sifang Flower and Tree Planting Professional Cooperative, Luoyang, China) in the central part of the People's Republic of China, located at 36°41′ N, 140°41′ W at 60 m above sea level. The terrain here is flat, and the soil is fertile with an average organic matter content of 1.24% and an average pH value of 7.5. The regional climate is continental, cold in winter and hot in summer, warm in spring and cool in autumn, with an average annual temperature of 13.7 °C, an average total annual precipitation of 550 mm, and a long frost-free period (about 210 days).

Under the implementation of artificial afforestation measures, all golden silk catalpa trees in the artificial forest grow at the same time and experience similar growth conditions and ecological pressures. Their height and diameter are usually relatively uniform, forming a relatively neat canopy, and the lighting conditions in the canopy layer are relatively uniform.

Three trees with good growth status, straight trunk, and no pests and diseases were randomly selected from the artificial forest but at a long distance from the forest margin and avoiding roads (Table 1). After the trees were felled at the end of the growing season, 10 mm thick discs were cut at the stump (10 cm above the ground), breast height (1.30 m above the ground), and crown base (below the first living branch). Detailed information on wood discs is presented in Table 2. Each disc was divided into a 1 cm wide strip of wood from the pith to the bark in four directions (west, east, north, and south). The strips were placed in FAA (an equal part solution of formaldehyde, glacial acetic acid, and 70% ethanol) and brought back to the lab.

Table 1. Characteristics of sample trees.

Tree Number	Tree Diameter at Breast Height (cm)	Tree Height (m)	Crown Base Height (m)	Crown Width (m)
1	18.6	13.1	3.8	4.6
2	17.8	14.6	3.6	4.2
3	18.4	13.4	3.3	4.8

Table 2. Characteristics of sample discs (mean ± Std).

Position	Heartwood Diameter (cm)	Sapwood Width (mm)
Stump	14.1 ± 2.7	10 ± 2.6
Breast height	10.0 ± 1.8	10.7 ± 5.6
Crown base	10.0 ± 1.4	9.0 ± 2.8

2.2. Methods

A radial section of 15 μm was cut from the wood strip using a Leica RM2235 slicing machine (Leica Microsystems, Wetzlar, Germany) and it was stained with iodine–potassium iodide. The sections' photographs (resolution of 300 dpi, 84.667 μm/pixel) were obtained using an Mshot-MD50 (Micro-shot Technology, Guangzhou, China).

Under the same resolution, the number of pixels at 1 mm^2 square was quantified throughout the photographs [26]. When measuring pixels of a specific region in a photo, the actual area of that region can be converted. Starch coverage (A1) was manually out-

lined to determine its number of pixels using Adobe Photoshop software (Version 21.0, Adobe Systems Software Ireland Ltd., 4–6 Riverwalk, City West Business Campus, Saggart D24, Dublin, Ireland). Using the same method, the ray parenchyma area (A0) was also outlined [22]. The percentage of starch in the ray parenchyma area (PS) was calculated for each photograph by using Equation (1):

$$PS = (A1/A0) \times 100\% \quad (1)$$

where A1 and A0 are the pixel area of starch coverage and the total ray parenchyma area, respectively.

2.3. Data Analysis

Analysis of variance was used to examine the effects of height position, direction, heartwood/sapwood, and their interactions on the wood starch content. Multiple comparisons were used to compare the starch content between different parts of the trees. If the factor effects were significant with a margin of error of $p \leq 0.05$, comparisons were carried out using the Duncan test.

3. Results

The wood sections stained with iodine–potassium iodide clearly indicated that starch granules were mainly distributed within wood ray cells, although starch granules were also found in some axial parenchyma cells (Figure 1). Starch granules were abundant and block-shaped in sapwood ray cells. However, not all ray cells were filled with starch granules (Figure 1A–C). Starch granules in heartwood ray cells were rare, scattered sporadically, and some ray cells did not have starch granules, but residual starch lysate could be seen (Figure 1D–F).

From bark to pith, as cambial age changed, the starch content in ray cells gradually decreased overall (Figure 2A–H). The starch content degraded rapidly, gradually breaking down from the block-like starch accumulation. In the rings closest to the cambium (Figure 2A), starch granules in the ray parenchyma cells were most abundant and concentrated. The starch granules in the two adjacent inner rings (Figure 2B,C) decreased and dispersed, while the starch granules in the ray cells of the inner rings rapidly decreased and gradually decomposed. However, even in the rings closest to the pith (Figure 2H), sporadic starch granules still existed.

Trunk height position, direction, and heartwood/sapwood position significantly affected the starch content in *C. bungei* 'Jinsi' wood ray (Table 3). Interaction of trunk height position and heartwood/sapwood position also significantly affected starch the content ($p < 0.01$).

Starch content in the heartwood ray cells was significantly lower than in sapwood (Figure 3). The average starch content was lowest in the north at the breast height of the trunk, at only 18.4% (Figure 3A). The starch content of the heartwood ray in the three height positions of the trunk was lowest in the north and highest in the east, with significant differences between the two directions ($p < 0.05$). Regardless of the direction, the starch content of the heartwood ray at the stump was the highest, and there was a significant difference ($p < 0.05$) compared to the other two height positions.

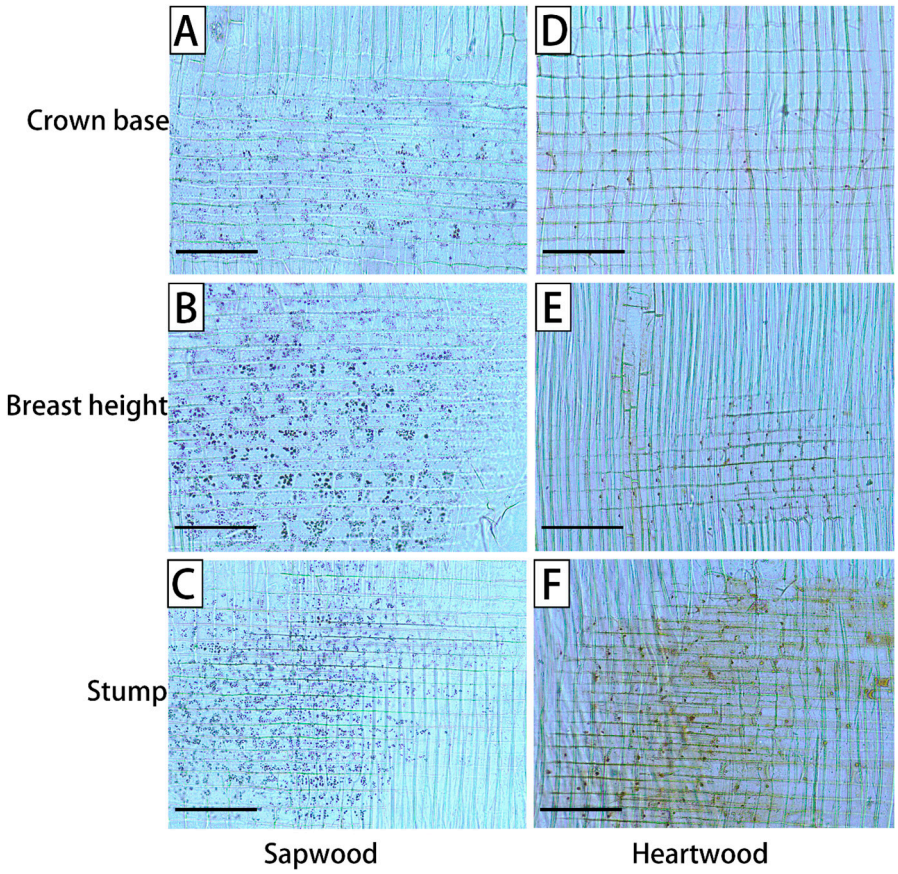

Figure 1. Starch morphology in radial sections of *Catalpa bungei* 'Jinsi' sapwood and heartwood. (**A**–**F**) show the starch grains in the sapwood of crown base, sapwood of breast height, sapwood of stump, heartwood of crown base, heartwood of breast height and heartwood of stump, respectively. Black bars = 100 um.

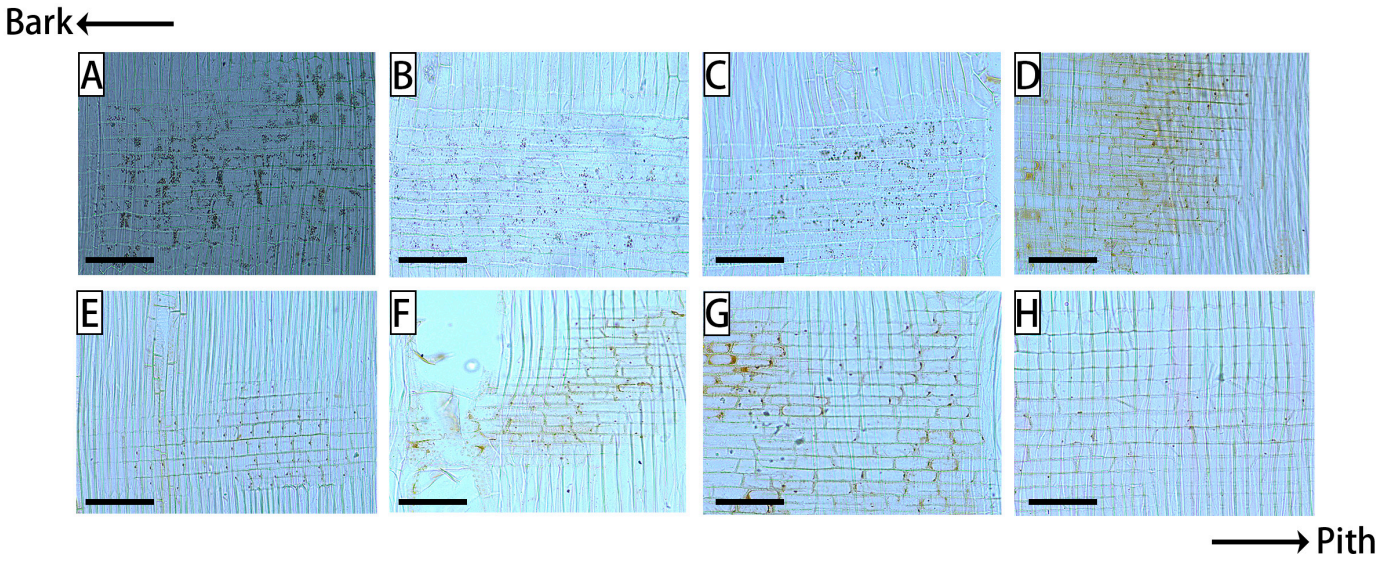

Figure 2. Starch morphology in radial sections of wood ray from the pith to the bark of *Catalpa bungei* 'Jinsi' sapwood and heartwood. (**A**–**H**) show the starch grains of the 8th, 7th, 6th, 5th, 4th, 3th, 2th and 1th growth rings, respectively. Black bars = 100 um.

Table 3. Analysis of variance for starch content of *Catalpa bungei* 'Jinsi' wood.

Factor	Degrees of Freedom	F Value	*p* Value
Height position	2	91.097	<0.01
Direction	3	5.147	0.02
Heartwood/sapwood	1	624.966	<0.01
Height position × Direction	2	25.388	0.100
Height position × Heartwood/sapwood	2	25.388	<0.01
Direction × Heartwood/sapwood	3	1.087	0.354

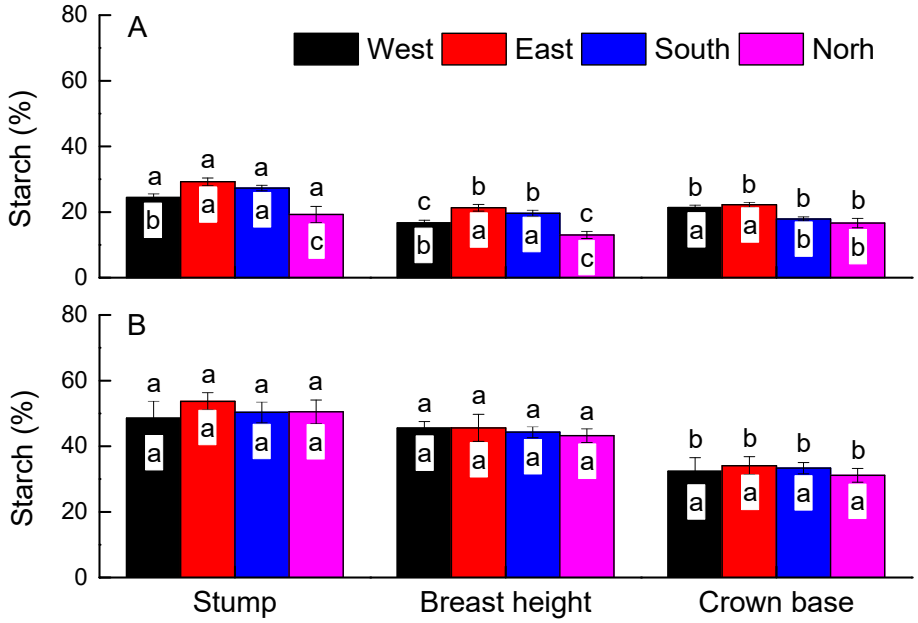

Figure 3. Starch content in radial sections of *Catalpa bungei* 'Jinsi' heartwood (**A**) and sapwood (**B**). Different lowercase letters above the bars indicate a significant difference among trunk height positions based on the Duncan test ($p < 0.05$). Different lowercase letters below the bars indicate a significant difference among trunk directions based on the Duncan test ($p < 0.05$).

As shown in Figure 3A, regardless of direction, the starch content in the sapwood ray cells was highest at the stump (average about 50%) and lowest at the crown base (average about 30%). There was a significant difference ($p < 0.05$) in the starch content between the sapwood ray cells at the crown base and at other height positions. Regardless of the part of the sapwood, the starch content was higher in the east than in the other three directions, but the difference was not significant.

Figure 4 showed the trend in starch content from pith to bark. In the first ring near the pith, the starch content in the wood ray was close to zero. As the cambial age increased, the starch content in the wood ray showed an overall increasing trend, but there was a decreasing trend in the sixth year compared to the previous year (Figure 4A,B,D). In the south direction of the trunk, the starch content from the pith to the bark also showed an overall increasing trend, but unlike the other three directions, the starch content in the south decreased slightly in the fifth ring (Figure 4C).

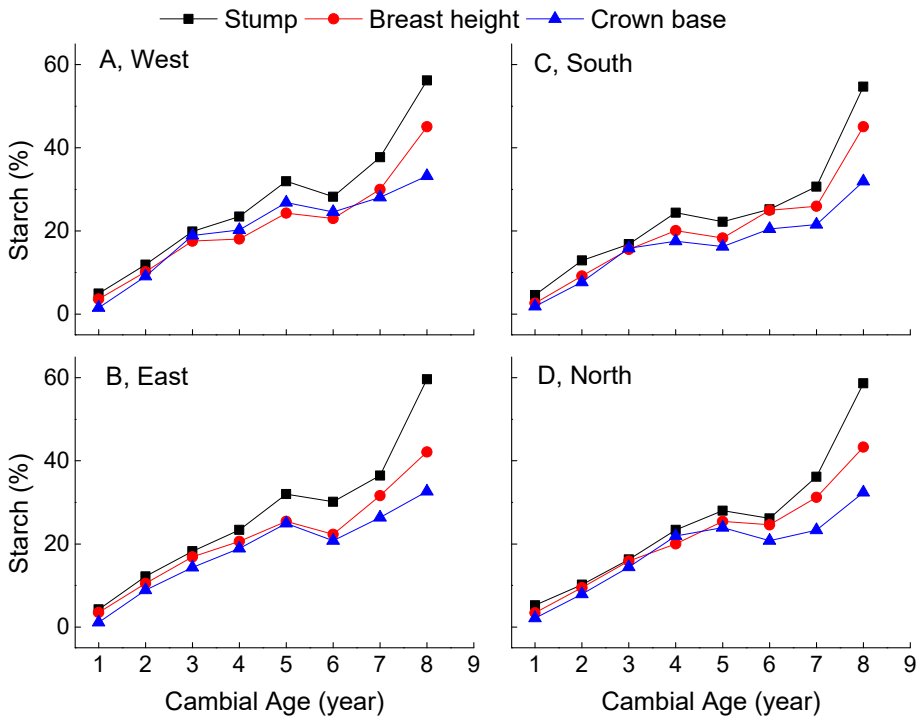

Figure 4. Radial variation of starch content in *Catalpa bungei* 'Jinsi' wood ray.

4. Discussion

This study attempts to link the observation of the ray structure in the xylem of *C. bungei* 'Jinsi' with the availability of its starch. Wood ray is the main storage tissue for starch (Figures 1 and 2). However, starch granules were also found in some axial parenchyma cells (Figure 1). In some species, e.g., *Dacryodes. microcarpa* and *Trattinnikia. Glaziovii* [3], live fibers also accumulate starch. No starch granules were found in the fibers, even in the sapwood fibers of *C. bungei* 'Jinsi'. It is speculated that there may not be active fibers in the secondary xylem of *C. bungei* 'Jinsi', even in the newly formed growth ring. Of course, this needs to be verified in the future. Therefore, according to Herrera-Ramírez, et al. [3], the *C. bungei* 'Jinsi' belongs to the parenchyma-storing species. The storage of starch only in the parenchyma tissue of *C. bungei* 'Jinsi' wood may limit the total storage capacity, but the cell walls of ray parenchyma cells and axial parenchyma cells have abundant and mostly single pits, which may facilitate the hydrolysis and reactivation of starch stored within the cells, while also making it easier and faster to export to adjacent cells.

Starch content was abundant in the ray cells of *C. bungei* 'Jinsi' sapwood, and the highest starch content was observed in the wood rays formed in the last year. This was similar to the wood-starch content distribution of the semi- deciduous/parenchyma-storing species (*Sacoglottis guianensis*) in the drying season, but different from its distribution in the wet season [3]. This indicates that the observed starch distribution in the wood of *C. bungei* 'Jinsi' is not constant, and it is necessary to study the seasonal dynamics of starch content in *C. bungei* 'Jinsi' in the future.

However, the high starch content in the sapwood may affect its wood processing and utilization performance [27]. *C. bungei* 'Jinsi' is a precious wood tree species, not only because of its beautiful patterns and colors, but also because of its water resistance, resistance to insect infestation, and good anti-corrosion performance [28]. However, these excellent properties are mainly due to the presence of starch-converted substances, such as fillers, in its heartwood, which have anti-corrosion and insect-proof effects [29]. Sapwood lacks these anti-corrosion and insect-proof substances, while its rich starch provides a source of nutrition for insect infestation, making it more susceptible to pests and decay [4].

Like most other angiosperms [30], the starch content in the *C. bungei* 'Jinsi' heartwood ray was much lower than the sapwood (Figure 3). The main reason was that some of the redundant starch in the parenchyma is converted into pigments, tannins, and other substances, which color the wood and play a role in resisting fungal decay [31,32]. Changes in starch content are important reference data for studying heartwood formation in *C. bungei* 'Jinsi'.

A small amount of starch was also found in some ray cells near the pith (Figure 4). Zhang et al. [33] found that starch still exists in the deep xylem of non-heartwood tree species, such as *Tilia amurensis* and *Betula platyphylla*. Piispanen and Saranpää [34] observed similar results in *Betula pendula*, a non-heartwood tree species. They even detected that the amount of starch near the pith appeared to be greater than that near the cambium at heights of 1 m and 6 m, suggesting that *Betula platyphylla* does not form heartwood. *C. bungei* 'Jinsi' is a typical heartwood tree species [22]. This challenges the traditional view that heartwood cannot store nutrients. Cui et al. [35] also found small amounts of starch granules in the heartwood of *Dalbergia odorifera*, a heartwood tree species. Dong et al. [36] studied 32 heartwood or non-heartwood tree species in temperate forests in China, and found varying degrees of starch granules in the heartwood of all tree species. Therefore, it cannot be reliably determined whether heartwood is formed solely based on the presence or absence of starch granules in the xylem.

In the radial direction, as the cambial age changed, the starch content in the ray cells generally decreased year by year from the pith to the bark (Figure 4). The sapwood ray cells contained a large number of starch granules, and the starch content in the heartwood forming wood ray cells began to degrade year by year. This trend is generally attributed to the fact that most of the starch stored in the aging rings is no longer usable [37] and has been degraded and converted into heartwood material. However, some people also believe that there is nutrient reflux in the radial direction of the tree trunk. According to the research results of Gérard and Bréda [38] and Michelot-Antalik et al. [39] on beech, trees transfer starch from the interior to the outermost layer of the trunk. Trees can use their deep-stored starch, which helps maintain the carbon–water balance in nutrient-limited conditions [40]. But so far, this assumption has never been mentioned in relation to the *C. bungei* 'Jinsi' tree.

It is interesting that our research found that the starch content of the *C. bungei* 'Jinsi' tree does not always increase from the pith to the bark. The starch content in the sixth ring (southbound in the fifth ring) showed a slight downward trend compared to the previous year (Figure 4). This is consistent with the research findings of Guo Ping et al. [22]. The number of annual rings in the sapwood of the *C. bungei* 'Jinsi' tree remains relatively stable within a range of two rings [41]. There is a transition zone between the heartwood and sapwood of the *C. bungei* 'Jinsi' tree [22,41]. The sixth annual ring of the Chinese parasol tree we studied was located in the transition zone between heartwood and sapwood. If there is radial nutrient reflux, the likelihood of starch content in the outer edge of the heartwood is much higher than that inside the heartwood, which can easily lead to lower starch content in ray cells at that location compared to the adjacent heartwood rings. Most importantly, some of the ray cells in the transition zone still have nuclei and are 'alive', responsible for converting starch into secondary metabolites [42,43]. Therefore, the changes in starch granules are most intense at the transition zone.

Along the trunk, the bottom wood ray had a higher starch content than at the top. However, Marler's study [44] showed that the axial difference in starch concentration at a height of 1 m in *Cycas microcnica* stems can be ignored. They think axial starch patterns in stems may not be limited by plant height. However, Woodruff and Meinzer [10] found that *Pseudotsuga menziesii* increased along a tree height gradient, and the starch content

in wood remained stable. The starch content of *Betula platyphylla* and *Tilia amurensis* decreased from root neck to breast height and then increased again [33], indicating that the trend of starch content variation along the trunk varied among tree species. Compared to heartwood, where starch content was generally very low, the maximum difference in wood ray starch content between the height positions of *C. bungei* 'Jinsi' occurred in sapwood. This is consistent with the results of *Eucalyptus obliqua* [11] and *Betula pendula* [34]. The difference in starch content of heartwood along the trunk may be related to the dynamics of heartwood formation at different heights [45]. The number of annual rings in the heartwood of the *C. bungei* 'Jinsi' tree decreased with an increasing trunk height, while the number of annual rings in the sapwood of the *C. bungei* 'Jinsi' tree remained relatively stable with an increasing trunk height [41]. Due to the influence of apical meristematic tissue, the cells of the upper sapwood of the tree trunk reached the boundary age later than those of the lower sapwood. Therefore, the programmed cell death and starch granule degradation processes of parenchyma cells in the upper part of the tree trunk also differ [45].

There were differences in starch content between the different directions of the *C. bungei* 'Jinsi' trunk, and both sapwood and heartwood had the highest starch content in the parenchyma cells of the eastward ray. This may be due to differences in light intensity, temperature, and moisture content in different directions of the trees. For the sunny direction (east and south for cold temperate regions of the Northern Hemisphere), photosynthesis was stronger, temperature is higher, and trees will eventually convert more carbon-containing compounds. On the contrary, the backlit side of the tree trunk had a lower temperature, which is not conducive to the synthesis and accumulation of starch [46]. The evaporation rate of water in different directions of the tree trunk varied, and the side exposed to light evaporated faster, which may have an effect on starch synthesis and transport. Compared to heartwood, sapwood is closer to bark and its starch content is more susceptible to external environmental influences. The difference in starch content in different directions of tree trunks is also related to tree species, as the crown shape of different tree species also varies greatly, which indirectly affects the environmental conditions in which branches in different directions are located. However, *C. bungei* 'Jinsi' is a narrow crown tree species, so differences in photosynthesis between orientations do not result in significant differences in sapwood starch content between directions.

This direction appears to affect starch degradation during the transition from sapwood to heartwood. Adequate light can promote heartwood formation, as light affects plant physiological activities and metabolic processes. Specifically, light affects plant photosynthesis, altering carbon and nitrogen metabolism within the plant, thus affecting the formation and development of heartwood [47]. In addition, light may indirectly affect heartwood formation by regulating the synthesis and distribution of plant hormones. For example, certain plant hormones, such as abscisic acid and jasmonic acid, have been shown to promote heartwood formation to some extent, and the synthesis and activity of these hormones may be affected by light [48]. This direction appears to affect starch degradation during the transition from sapwood to heartwood. Our study showed that the rapid degradation time of starch in the southern trunk lagged behind other directions by one year. Therefore, when studying the seasonal dynamics of starch, especially starch degradation during heartwood formation, it is necessary to consider not only cambial age and sampling period, but also the direction of tree growth.

5. Conclusions

The distribution of starch content in the trunkwood of *C. bungei* 'Jinsi' trees is uneven and is influenced by height positions, directions, and cambial age. Starch content increased from crown base to stump and from pith to bark, with the highest values in the

eastern direction, and it showed a turning point in the transition zone between heartwood and sapwood.

The uneven distribution of starch content in *C. bungei* 'Jinsi' trunkwood indicated that the starch conversion and consumption in ray cells is one of the key steps in heartwood formation, most intense at the position in the transition zone, but it is unreliable for determining whether heartwood is formed based on the presence of starch granules in the xylem. Based on the distribution of starch content in the trunk, scientific pruning, fertilization and other nurturing measures are taken to improve the quality of heartwood. Preservative treatment is required for the processing and utilization of sapwood with high starch content, especially for the lower position and east direction of trunkwood, to prevent biological hazards.

It should be noted that these conclusions were drawn from a limited number of sample trees and specific periods. In the future, it will be necessary to increase the number of sample trees to improve the reliability of research results. At the same time, the seasonal dynamics of starch content in *C. bungei* 'Jinsi' trees should be studied to verify whether there is radial nutrient reflux in the tree to utilize starch stored in the deep xylem.

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References

1. Moretti, M.M.d.S.; Costa, M.S.; Bai, Y.; Gilbert, R.G.; Rocha, T.d.S. Chapter 9—Structure of starch, focusing on those from underground plant organs. In *Starchy Crops Morphology, Extraction, Properties and Applications*; Pascoli Cereda, M., François Vilpoux, O., Eds.; Academic Press: Cambridge, MA, USA, 2023; pp. 217–244. [CrossRef]
2. Li, Z.; Wei, C. Morphology, structure, properties and applications of starch ghost: A review. *Int. J. Biol. Macromol.* **2020**, *163*, 2084–2096. [CrossRef]
3. Herrera-Ramírez, D.; Hartmann, H.; Römermann, C.; Trumbore, S.; Muhr, J.; Santos, L.M.; Brando, P.; Silvério, D.; Huang, J.; Kuhlmann, I.; et al. Anatomical distribution of starch in the stemwood influences carbon dynamics and suggests storage-growth trade-offs in some tropical trees. *J. Ecol.* **2023**, *111*, 2532–2548. [CrossRef]
4. Tanaka, Y.; Konno, N.; Suzuki, T.; Habu, N. Starch-degrading enzymes from the brown-rot fungus *Fomitopsis palustris*. *Protein Expres. Purif.* **2020**, *170*, 105609. [CrossRef] [PubMed]
5. Cherelli, S.G.; Bellasio, C.; Marcati, C.R.; Rodrigues dos Santos, T.P.; Rodrigues, S.A.; Leonel, M.; Ballarin, A.W. The corewood of 25-year-old *Hevea brasiliensis* from two rubber plantations has high starch content. *Eur. J. Wood Wood Prod.* **2023**, *81*, 847–855. [CrossRef]
6. Yamamoto, Y.; Yoshida, T.; Yanagidate, I.; Polnaya, F.; Siahaya, W.; Jong, F.; Pasolon, Y.; Miyazaki, A.; Hamanishi, T.; Hirao, K. Studies on growth characteristics and starch productivity of the sago palm (*Metroxylon sagu* Rottb.) folk varieties in Seram and Ambon Islands, Maluku, Indonesia. *Trop. Agric. Dev.* **2020**, *64*, 125–134. [CrossRef]
7. Herrera-Ramírez, D.; Sierra, C.A.; Römermann, C.; Muhr, J.; Trumbore, S.; Silvério, D.; Brando, P.M.; Hartmann, H. Starch and lipid storage strategies in tropical trees relate to growth and mortality. *N. Phytol.* **2021**, *230*, 139–154. [CrossRef] [PubMed]
8. Islam, M.A.; Begum, S.; Nakaba, S.; Funada, R. Distribution and pattern of availability of storage starch and cell death of ray parenchyma cells of a conifer tree (*Larix kaempferi*). *Res. J. Recent Sci.* **2012**, *1*, 28–37. [CrossRef]

9. Dietze, M.C.; Sala, A.; Carbone, M.S.; Czimczik, C.I.; Mantooth, J.A.; Richardson, A.D.; Vargas, R. Nonstructural carbon in woody plants. *Plant Biol.* **2013**, *65*, 667–687. [CrossRef]
10. Woodruff, D.; Meinzer, F. Water stress, shoot growth and storage of non-structural carbohydrates along a tree height gradient in a tall conifer. *Plant Cell Environ.* **2011**, *34*, 1920–1930. [CrossRef]
11. Smith, M.G.; Miller, R.E.; Arndt, S.K.; Kasel, S.; Bennett, L.T. Whole-tree distribution and temporal variation of non-structural carbohydrates in broadleaf evergreen trees. *Tree Physiol.* **2018**, *38*, 570–581. [CrossRef]
12. Cambou, A.; Thaler, P.; Clément-Vidal, A.; Barthès, B.; Charbonnier, F.; Van den Meersche, K.; María Elena, A.; Avelino, J.; Davrieux, F.; Labouisse, J.-P.; et al. Concurrent starch accumulation in stump and high fruit production in coffee (*Coffea arabica*). *Tree Physiol.* **2021**, *41*, 2308–2325. [CrossRef] [PubMed]
13. Lijuan, Y.; Lingyu, M.; Xiaomei, J.; Yonggang, Z.; Yupei, W.; Yuan, C.; Lihong, Y.; Juan, G. Positional differences in the micro- and ultra-structural variations of ray parenchyma cells during the transformation from sapwood to heartwood. *Front. Plant Sci.* **2024**, *15*, 1431818. [CrossRef]
14. Von Arx, G.; Arzac, A.; Fonti, P.; Frank, D.; Zweifel, R.; Rigling, A.; Galiano, L.; Gessler, A.; Olano, J.M. Responses of sapwood ray parenchyma and non-structural carbohydrates of *Pinus sylvestris* to drought and long-term irrigation. *Funct. Ecol.* **2017**, *31*, 1371–1382. [CrossRef]
15. Ingel, B.; Reyes, C.; Massonnet, M.; Boudreau, B.; Sun, Y.; Sun, Q.; McElrone, A.; Cantu, D.; Roper, C. *Xylella fastidiosa* causes transcriptional shifts that precede tylose formation and starch depletion in xylem. *Mol. Plant Pathol.* **2020**, *22*, 175–188. [CrossRef]
16. Pratt, R.B.; Tobin, M.; Jacobsen, A.; Traugh, C.; Guzman, M.; Hayes, C.; Toschi, H.; MacKinnon, E.; Percolla, M.; Clem, M.; et al. Starch storage capacity of sapwood is related to dehydration avoidance during drought. *Am. J. Bot.* **2020**, *108*, 91–101. [CrossRef] [PubMed]
17. Ma, M.; Xu, Z.; Li, P.; Sui, Z.; Corke, H. Removal of starch granule-associated proteins affects amyloglucosidase hydrolysis of rice starch granules. *Carbohyd. Polym.* **2020**, *247*, 116674. [CrossRef]
18. Sandmann, M.; Rading, M. Starch granules in algal cells play an inherent role to shape the popular SSC signal in flow cytometry. *BMC Res. Notes* **2024**, *17*, 327. [CrossRef] [PubMed]
19. Cho, Y.G.; Kang, K.K. Functional analysis of starch metabolism in plants. *Plants* **2020**, *9*, 1152. [CrossRef]
20. Furze, M.E.; Huggett, B.A.; Chamberlain, C.J.; Wieringa, M.M.; Aubrecht, D.M.; Carbone, M.S.; Walker, J.C.; Xu, X.; Czimczik, C.I.; Richardson, A.D. Seasonal fluctuation of nonstructural carbohydrates reveals the metabolic availability of stemwood reserves in temperate trees with contrasting wood anatomy. *Tree Physiol.* **2020**, *40*, 1355–1365. [CrossRef]
21. Zhang, H.; Wang, C.; Wang, X. Spatial variations in non-structural carbohydrates in stems of twelve temperate tree species. *Trees-Struct. Funct.* **2014**, *28*, 77–89. [CrossRef]
22. Guo, P.; Zhao, X.; Yang, Z.; Wang, Y.; Li, H.; Zhang, L. Water, starch, and nuclear behavior in ray parenchyma during heartwood formation of *Catalpa bungei* 'Jinsi'. *Heliyon* **2024**, *10*, e27231. [CrossRef] [PubMed]
23. Qiao, L.; Zhang, Q.; Li, J.; Guan, Z.; He, Q. Nutrient stoichiometry and tree development: Insights from a 5-year study on *Catalpa bungei* fertilization. *Forests* **2024**, *15*, 1836. [CrossRef]
24. Pasolon, Y.B.; Hayati, N.; Rembon, F.S.; Baka, L.R.; Cahyono, E. Prediction of distributed material based on disk measurements: An application on predicting sago starch of a tree trunk. Proceedings of International Conference on Mathematical, Computational and Statistical Sciences, Dubai, United Arab Emirates, 22–24 February 2015; pp. 466–469.
25. Reghu, C.P.; Patel, J.D. Distribution of starch and lipids in reaction wood of some angiosperm trees. *Nord. J. Bot.* **1984**, *4*, 357–363. [CrossRef]
26. Qi, Y.; Li, Z.; Zhang, Y.; Zheng, Y.; Zhang, X.; Duan, X.; Yang, F.; Zhang, W. Application of area analysis in mineral content analysis under microscope. *Adv. Geosci.* **2021**, *11*, 1400–1406. [CrossRef]
27. Karthäuser, J.; Treu, A.; Larnøy, E.; Militz, H.; Alfredsen, G. Resistance against fungal decay of Scots pine sapwood modified with phenol-formaldehyde resins with substitution of phenol by lignin pyrolysis products. *Holzforschung* **2024**, *78*, 231–243. [CrossRef]
28. Yang, J.; Wang, S.; Huang, Z.; Guo, P. The complete chloroplast genome sequence of *Catalpa bungei* (*Bignoniaceae*): A high-quality timber species from China. *Mitochondrial DNA B* **2020**, *5*, 3854–3855. [CrossRef] [PubMed]
29. You, J.; Jing, Z.; Tai, D.; He, W.; Zhang, H.; Hse, C.; Lee, d.; Samimoto, M. Studies on active antifungal substrates in natural durable species: III. Extraction, separation, purification and toxicity experiment of effective antifungal of heartwood of *Catalpa bungei*. *J. Nanjing For. Univ. (Nat. Sci. Ed.)* **1990**, *14*, 61–67.
30. Simpson, L.; Barton, A. Time dependence of starch levels in the sapwood of *Eucalyptus diversicolor* (Karri) as: Standing trees, stored saw-logs, ringbarked trees and trees felled without lopping. *Holzforschung* **1991**, *45*, 253–257. [CrossRef]
31. Galibina, N.; Nikerova, K.; Moshchenskaya, Y.L.; Ershova, M. Physiological, biochemical and molecular genetic aspects of heartwood formation mechanisms. *Trans. KarRC RAS* **2020**, *11*, 20–37. [CrossRef]
32. Yang, X.; Yu, X.; Liu, Y.; Shi, Z.; Li, L.; Xie, S.; Zhu, G.; Zhao, P. Comparative metabolomics analysis reveals the color variation between heartwood and sapwood of Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook. *Ind. Crop. Prod.* **2021**, *169*, 113656. [CrossRef]

33. Zhang, H.; Wang, C.; Wang, X.; Cheng, F. Spatial variation of non-structural carbohydrates in *Betula platyphylla* and *Tilia amurensis* stems. *Chin. J. Appl. Ecol.* **2013**, *24*, 3050–3056.
34. Piispanen, R.; Saranpää, P. Variation of non-structural carbohydrates in silver birch (*Betula pendula* Roth) wood. *Trees-Struct. Funct.* **2001**, *15*, 444–451. [CrossRef]
35. Cui, Z.; Hu, H.; Li, X.; Liu, X.; Zhang, Q.; Hong, Z.; Zhang, N.; Lin, W.; Xu, D. Physiological and biochemical mechanisms of drought regulating the size and color of heartwood in *Dalbergia odorifera*. *Tree Physiol.* **2025**, *45*, tpae157. [CrossRef] [PubMed]
36. Dong, H.-J.; Wang, X.-C.; Yuan, D.-Y.; Liu, D.; Liu, Y.-L.; Sang, Y.; Wang, X.-C. Radial distribution differences of non-structural carbohydrates in stems of tree species of different wood in a temperate forest. *Chin. J. Plant Ecol.* **2022**, *46*, 722–734. [CrossRef]
37. Millard, P.; Sommerkorn, M.; Grelet, G.A.J.T.N.p. Environmental change and carbon limitation in trees: A biochemical, ecophysiological and ecosystem appraisal. *New Phytol.* **2007**, *175*, 11–28. [CrossRef]
38. Gérard, B.; Bréda, N. Radial distribution of carbohydrate reserves in the trunk of declining European beech trees (*Fagus sylvatica* L.). *Ann. Forest Sci.* **2014**, *71*, 675–682. [CrossRef]
39. Michelot-Antalik, A.; Granda, E.; Fresneau, C.; Damesin, C. Evidence of a seasonal trade-off between growth and starch storage in declining beeches: Assessment through stem radial increment, non-structural carbohydrates and intra-ring δ13C. *Tree Physiol.* **2019**, *39*, 831–844. [CrossRef]
40. Richardson, A.; Carbone, M.; Czimczik, C.; Hollinger, D.; Murakami, P.; Schaberg, P.; Xu, X. Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees. *New Phytol.* **2012**, *197*, 850–861. [CrossRef]
41. Deng, L.; Ren, S.; Lv, J.; Wang, Y.; Ren, H.; Zhao, R. Growth characteristics and variation of heartwood and sapwood of *Catalpa bungei*. *China Wood Ind.* **2019**, *33*, 9–13. [CrossRef]
42. Burtin, P.; Jay-Allemand, C.; Charpentier, J.-P.; Janin, G. Natural wood colouring process in *Juglans* sp. (*J. nigra*, *J. regia* and hybrid *J. nigra* 23 × *J. regia*) depends on native phenolic compounds accumulated in the transition zone between sapwood and heartwood. *Trees-Struct. Funct.* **1998**, *12*, 258–264. [CrossRef]
43. Magel, E.A. Biochemistry and physiology of heartwood formation. *Exptl. Biol. Rev.* **2000**, 363–376.
44. Marler, T. Axial and radial spatial patterns of non-structural carbohydrates in *Cycas micronesica* stems. *Plants* **2018**, *7*, 49. [CrossRef] [PubMed]
45. Marcin, N.; Pazdrowski, W.; Szymański, M. Dynamics of heartwood formation and axial and radial distribution of sapwood and heartwood in stems of European larch (*Larix decidua* Mill.). *J. For. Sci.* **2008**, *54*, 409–417. [CrossRef]
46. Goodwin, P.; Campbell, L. Plant structure and function. In *The Scientific Basis of Modern Agriculture*, 2nd ed.; Campbell, K.O., Bowyer, J.W., Eds.; Oxford University Press: Oxford, UK, 1992; pp. 111–130.
47. Fu, Z.; Cui, Z. Effects of environmental factors and management measures on heartwood formation. *World For. Res.* **2024**, *37*, 43–48.
48. Li, G.; Zhang, M.; Chen, F.; Huang, C.; Dong, X.; Chen, L.; Lin, L. A review on artificially induced heartwood formation and its chemical composition in *Dalbergia odorifera*. *Mol. Plant Breed.* **2024**, 1–17.

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