Cellulose (2022) 29:3153–3161
https://doi.org/10.1007/s10570-022-04485-x

ORIGINAL RESEARCH

Microfibril orientation of the secondary cell wall in parenchyma cells of *Phyllostachys edulis* culms

Caiping Lian · Jing Yuan · Junji Luo · Shuqing Zhang · Rong Liu · Hong Chen · Xuehua Wang · Mingxin Cao · Zhihui Wu · Benhua Fei

Received: 7 September 2021 / Accepted: 12 February 2022 / Published online: 3 March 2022

Abstract The secondary cell wall of bamboo parenchyma cells is microfibril-based. However, understanding of the microfibril orientation of secondary cell walls in bamboo parenchyma cells is lacking. This study characterized the microfibril orientation of the sub-layers of the secondary cell wall in the parenchyma cells by field-emission environmental scanning electron microscopy and the microfibril angle of the ground parenchyma cell wall with X-ray diffraction. The microfibril orientation of tight-loose alternating layers of the secondary cell wall was in the opposite direction along the longitudinal axis. Near the parenchyma cells' pit aperture, the microfibril orientation generally bypassed the pits and continued in a flow-like pattern. The mean microfibril angle of ground parenchyma cells was 63.3°. The average microfibril angle of adjacent sub-layers of the secondary cell wall was 60° and − 65° in ground parenchyma cells, and 54° and − 52° in vascular parenchyma cells. A structure model of microfibril orientation of parenchyma cell wall in moso bamboo was firstly constructed. The study provides insight into the anatomical structure of the parenchyma cell wall in the bamboo plant. Moreover, it provides a structural basis for further analysis of the mechanical properties of parenchyma cells.

Keywords Moso bamboo · Parenchyma cell wall · Sub-layers · Pit · Microfibril orientation · Microfibril angle

Introduction

Moso bamboo (*Phyllostachys edulis*) known for its high-speed growth and excellent mechanical performance (Jiang 2007; Wang et al. 2014), is economically the most important bamboo species globally in the bamboo industry (Liese and Köhl 2015). The anatomical structure of bamboo culm determines its properties (Liese 1998). All cells, including the parenchyma cells of internodes in bamboo culm, are strongly oriented axially. Parenchyma cells account for 52% of the total bamboo tissue and are the main contributors to the excellent flexibility of bamboo (Jiang 2007; Chen et al. 2020). The complex bamboo secondary cell wall structure is the critical determinant of bamboo's physical and mechanical performance. The cell wall is microfibril-based (Maleki et al. 2016). Chen et al. (2016) found that cellulose microfibril aggregates determine the mechanical

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10570-022-04485-x.

C. Lian · H. Chen · X. Wang · M. Cao · Z. Wu (✉)
Nanjing Forestry University, Nanjing 10037, China
e-mail: wzh550@sina.com

J. Yuan · J. Luo · S. Zhang · R. Liu · B. Fei (✉)
International Center for Bamboo and Rattan, Beijing 100102, China
e-mail: feibenhua@icbr.ac.cn

properties of the cell wall of fibers and parenchyma cells. Thus, it is necessary to fully characterize microfibril orientation and microfibril angle (MFA) for more efficient use of bamboo parenchyma cells.

Microfibrils are formed by elementary fibrils composed of a regular aggregation of cellulose molecular chains, and they are aggregated into different grades of fibrils, gradually forming the cell wall layers (Li 1983). The microfibril angle (MFA) is the angle between the cellulose fibrils and the cell's longitudinal axis in the secondary cell wall layer. The MFA in each layer determines the cell wall architecture and plant mechanical properties (Sultana and Rahman 2014). Recent studies of microfibrils in bamboo cell walls focused primarily on fibers. The microfibril orientation models of broad and narrow lamellae in fiber cell walls have been proposed successively (Preston and Singh 1950; Parameswaran and Liese 1976; Wai et al. 1985; Liu 2008; An 2013). Almost all studies focus on the average MFA for the microfibril orientation of bamboo parenchyma cells. Liese (1998) found that the fibrillar orientation of the parenchyma secondary cell wall has an ascending angle of 30° to 40° and forms a V-shape with the next lamella. An (2013) used SR-SAXS and postulate parenchyma cells with an MFA of 60°. Ahvenainen et al. (2017) demonstrated that parenchyma cells show a significantly lower degree of orientation with a maximum at larger angles (mean MFA 65°). Hu et al. (2017) showed that the average MFA of parenchyma cells is 36.59° in the odd-layer and 46.98° in the even-layer as measured by an LC-PolScope imaging system.

Microfibril orientation in parenchyma cells of bamboo has received less attention than that in the fibers. To our knowledge, only one research has studied the MFA in the secondary cell wall layers, which was indirectly calculated with an LC-PolScope imaging system (Hu et al. 2017). Therefore, since the microfibril orientation of parenchyma cell wall layers is rarely studied, the microfibril orientation model of the parenchyma cell wall is not yet available. In this study, the microfibril orientation of parenchyma (ground and vascular parenchyma cells (Lian et al. 2019)) secondary cell walls was directly observed using a field emission scanning electron microscope (FESEM). The microfibril angle was measured by ImageJ software based on the SEM images. The accuracy of the microfibril orientation measured by SEM was verified by X-ray diffraction (XRD) measurements of the average MFA of parenchyma cells. The in-depth study of microfibril orientation of secondary cell wall layers in parenchyma cells of moso bamboo provides insight into the anatomical structure of bamboo, which has theoretical and practical significance for the potentially high value-added bamboo utilization and bionic materials design.

Materials and methods

Samples preparation

4-year old mature culms of moso bamboo (average 15 cm diameter at breast height DBH, cut in 2018) were collected from the Taiping Experimental Base in Huangshan City, Anhui Province, China (118° 13′ E, 30° 3′ N). The section containing the bamboo internode just above the ground was considered to be the first section. Moso bamboo samples obtained from the center of the bamboo culm in the middle of the tenth section were prepared, as shown in Fig. 1.

Scanning electron microscopy (SEM)

The SEM method used is based on Lian et al. (2020). Hand-torn samples of longitudinal sections were

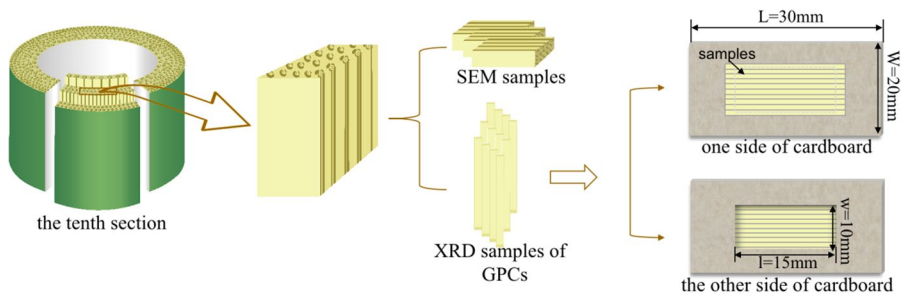

Fig. 1 Schematic illustrating sample preparation

observed by SEM, as it is relatively easy to observe microfibril orientation on cell wall surface after mechanical tearing. SEM samples were sputter-coated with 8 nm of gold (Bal-Tec, Herrenwyker, Germany) for 90 s, and then observed using FESEM (XL30 ESEM FEG; FEI Co., Hillsboro, OR, USA) at an accelerating voltage of 7–10 kV.

The distribution of ground and vascular parenchyma cells in the bamboo tissue is shown in Fig. 2b. The microfibril angles of 100 ground parenchyma cells (Fig. 2d) and vascular parenchyma cells (Fig. 2f) were measured using SEM images. The MFA of adjacent sub-layers of the secondary wall were obtained in each cell using ImageJ software (available at http://rsb.info.nih.gov/ij). The measurement schematic is shown in Fig. 2b.

X-ray diffraction (XRD)

Due to the small proportion of vascular parenchyma cells (VPCs) distributed in the vascular bundle, it is challenging to prepare VPCs XRD samples. Therefore, the XRD only measured the MFA of ground parenchyma cells (GPCs).

The XRD method is based on the approach adopted by Wang et al. (2010) and Cave (1997). Thin bamboo strips (1 mm × 2 mm × 20 mm, R × T × L) with only GPCs were glued on a rectangular opening in one side of the cardboard to prepare the XRD samples (Fig. 1). The chinks between the strips were eliminated by stacking multiple layers of bamboo strips. The X-ray patterns of the samples were collected using an X'Pert Pro-30X diffractometer (PHILIPS Ltd.) with a Cu Ka radiation ($\lambda = 0.1541$ nm), an operating voltage of 40 kV, a 40 mA current, and a 0.5° scanning step. The 2θ value of the scan was 22.4°. The incident beam radius was 240 mm. A full scan of the sample was made by rotating it through 360° about the X-axis. MFA measurement was performed in the symmetrical transmission mode. The scan intensity curve was processed by Origin17 software for Gaussian fitting, and the fitting equation (Eq. 1) was as follows,

$$y = a + b_1 \cdot \exp\left[\frac{-(x-\mu)^2}{2\sigma_1^2}\right] + b_2 \cdot \exp\left[\frac{-(x-\mu-180)^2}{2\sigma_2^2}\right] \quad (1)$$

where a is the baseline constant, b is the peak height of fitting, μ and $\mu + 180$ are the weighted average center, σ is the full width at half maximum (FWHM). The MFA was calculated using the 0.6 T method,

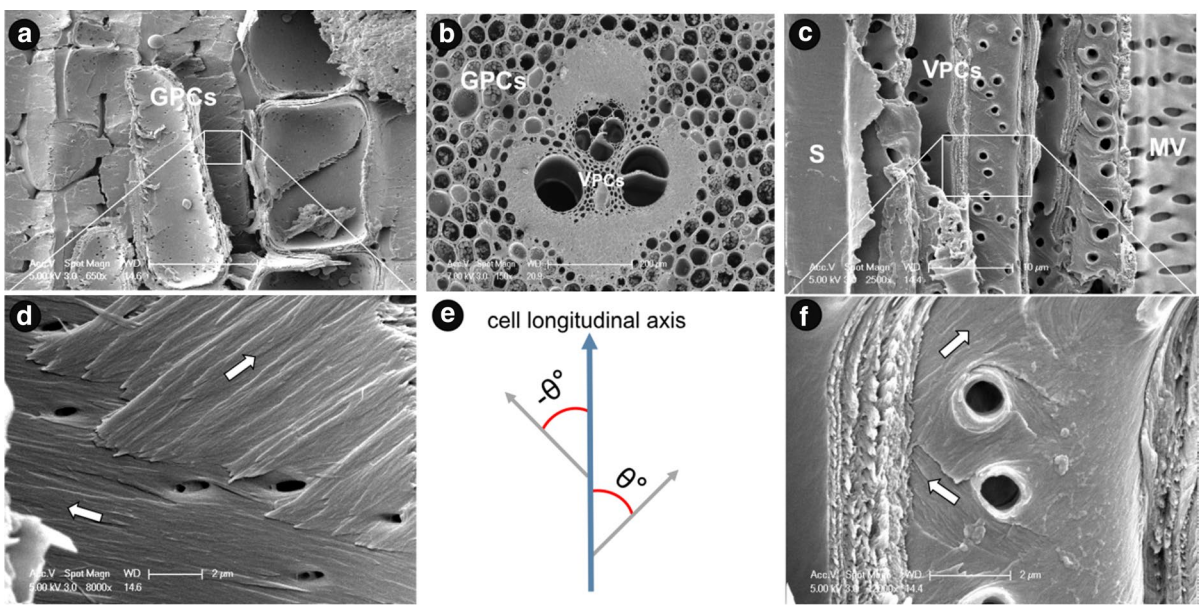

Fig. 2 Location of two kinds of parenchyma cells and schematic image of microfibril angle in parenchyma cells. **a** microfibril orientation of the secondary cell wall in GPCs. **b** the location of GPCs and VPCs. **c** microfibril orientation of the secondary cell wall in VPCs. **d** enlarged view of **a**. **e** the measurement schematic of MFA. **f** enlarged view of **c**

where T is equal to σ_1 plus σ_2, which were obtained by the fitting formula.

Results and discussion

Microfibril orientation (MO) of secondary cell walls in parenchyma cells

SEM images show that the microfibrils of adjacent sub-layers in the secondary cell wall of parenchyma cells are arranged in opposite directions along the vertical axis (Fig. 3a, i). Thus, if the MO of a sub-layer of the secondary cell wall is in a clockwise direction, the adjacent layer is arranged counter-clockwise (Fig. 3b). Moreover, the MO of adjacent lateral walls of parenchyma cells were in the same direction (Fig. 3c, d, k), allowing the microfibrils to be arranged helically in the secondary cell wall. A previous study proposed that the secondary cell walls of parenchyma cells exhibited tight-loosely alternating layers (Lian et al. 2020). SEM micrographs show that the MO of the tight (T) and the loose (L) layers are almost perpendicular (Fig. 3e, f), while the MO of the two tight layers are in the same direction. Furthermore, the MA on the inner cell wall closer to the cell lumen was disordered and reticular (Fig. 3g, l). The microfibrils on the primary cell wall were also in a disorderly network arrangement (Fig. 3h), consistent with a previous report (Chen et al. 2014). As with most plant cell walls, the primary cell wall in parenchyma cells of bamboo is between the middle lamella and secondary cell wall. Some parenchyma cells, such as short parenchyma cell (Fig. 3h′), only undergo primary cell wall thickening (Lian et al. 2020). The microfibrils on the adjacent cell wall layers of bamboo parenchyma cells are arranged approximately vertically, which may be because the microtubules depolymerized and repolymerized in opposite directions between the adjacent layers (Heath 1974; Green 1980; Li 1983).

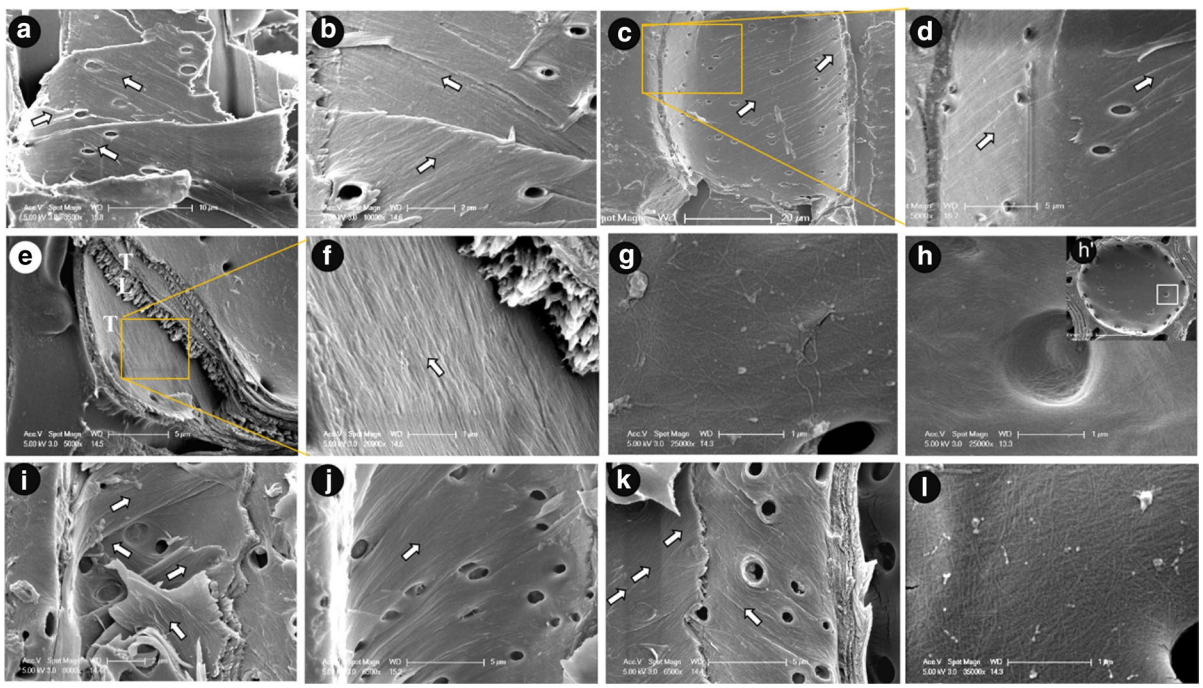

Fig. 3 Microfibril orientation of secondary cell walls in parenchyma cells. **a**–**h** MO of GPCs: **a** MO of three adjacent sub-layers in the secondary cell wall. **b** MO of adjacent sub-layers. **c** MO of lateral walls. **d** enlarged image of **c**. **e** tight-loose alternating layers. **f** enlarged view of **e**. **g** MO of the inner wall adjacent to cell lumen. **h** MO of the primary cell wall. **h′** only primary cell wall thickening of parenchyma cell. **i**–**l** MO of VPCs: **i** MO of multiple adjacent sub-layers. **j** MO of any sub-layer. **k** MA of lateral walls. **l** MO of the inner wall adjacent to cell lumen. Arrow, MO; *T* tight-layer, *L* loose-layer

It is well known that there are significant variations in the MO in the adjacent layers of the secondary cell wall of wood tracheid (Donaldson and Xu 2005) and bamboo fiber (Parameswaran and Liese 1976), which directly contributes to their higher stiffness. Therefore, we speculated that the approximate orientation of microfibers in the adjacent layers of secondary cell wall of bamboo parenchyma cells was the one reason for the low stiffness of parenchyma cells. Interestingly, the microfibril orientation of the inner cell wall and the primary cell wall is comprised of reticular structures. Our previous study (Lian et al. 2020) proposed tight-loose alternating layers for the secondary cell wall. So, we hypothesized that these structures make it easier for parenchyma cells to slip between layers under stress, resulting in the high ductility of parenchyma cells.

Microfibril orientation near the pit aperture

Analog to water flowing over an obstacle, the orientation of microfibrils near the pit aperture of GPCs and VPCs, generally bypassed the pits and continued in a flow-like pattern (Fig. 4a, b, d, e). Although MO deflected around the pit aperture, the main axis of microfibril orientation is maintained across the cell wall. Moreover, the MO of the secondary cell wall was similar to the long axis of the pit aperture (Fig. 4a, e, f). The result is similar to that given by Liu (2008). Figure 4c shows that the MO near the primary pit field presented a disordered network structure as the MO of the primary cell wall. Thus, it is concluded that the MO near the pit aperture was consistent with that on the cell wall.

Savidge (2014) proposed that the formation of bordered pits was associated with the bordered pit organelle (BPO). Moreover, the plasma membrane was involved in forming the cell wall (He et al. 2002; Yu 2008). Since BPO prevented the overgrowth of the plasma membrane, it facilitated the formation of pits. When the plasma membrane degenerated, it inhibited the cell wall formation at the pit aperture (Savidge 2014). Hence, degenerating of the plasma membrane inhibited the formation of microfibrils at the pit aperture. Additionally, the microfibril orientation may be controlled by microtubules or genetic factors of the cell wall. The orientation of microfibrils in the same sub-layer of the cell wall remains unaltered as long as the microtubules' orientation and the genetic factors of the cell wall remain unchanged. Therefore, the microfibrils on the same cell wall of parenchyma cells can bypass the pits and remain in the same direction (Fig. 4a, b, d, e).

Microfibril angle (MFA)

SEM—through the quantitative analysis of MFA SEM images, the results of MFA are shown in Fig. 5. As shown in table (Fig. 5), the MFA of the sub-layer of the secondary cell wall ranged from 35° to 80° in GPCs. On the longitudinal axis, the average MFA of each sub-layer of the secondary cell wall in GPCs arranged clockwise was 60°, while the mean MFA in the counterclockwise direction was 65°. In VPCs, the MFA of sub-layer of secondary cell wall ranged from 40° to 70°, and the average MFA was 54° and − 52°. From the boxplot (Fig. 5), the MFA of the secondary wall of GPCs mainly ranged between 50° and

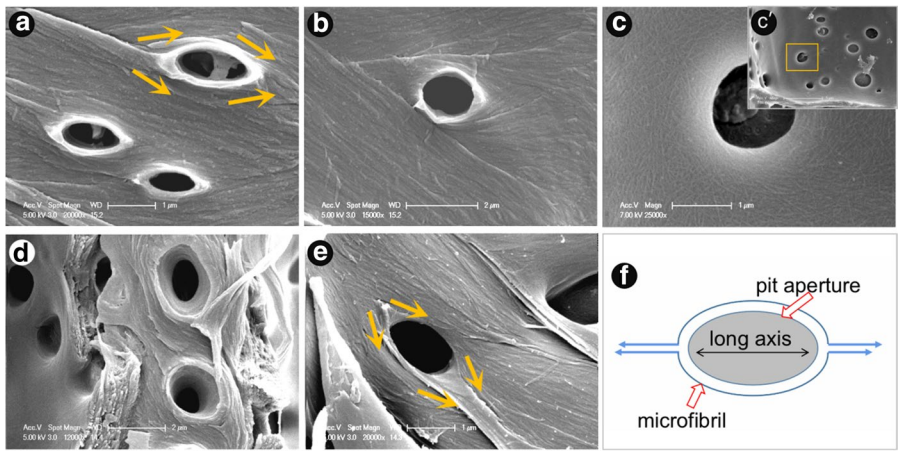

Fig. 4 Microfibrils orientation near the pit aperture. **a**, **b** that near the simple pit of GPCs. **c** that near the primary pit field of GPC, enlarge view of **c′**. **c′** only primary wall thickening of parenchyma cell with primary pit field. **d**, **e** that near the simple pit of VPCs. **f** the schematic of MO near pit aperture

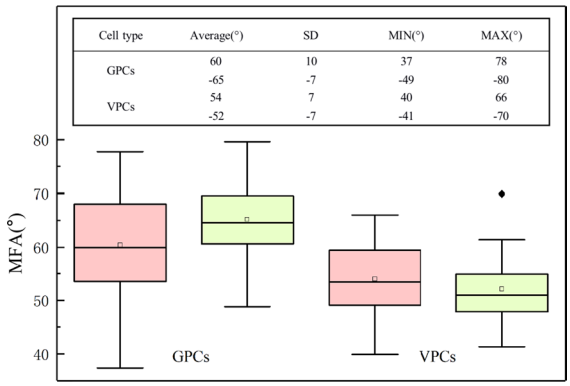

Fig. 5 The result of the MFA of the secondary cell wall in parenchyma cells and the boxplot of cellulose microfibril angle of sub-layer cell wall

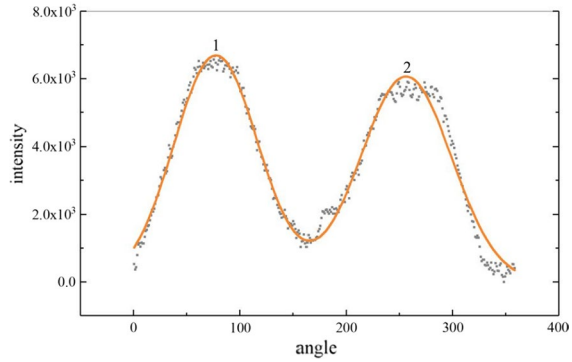

Fig. 6 The XRD fitting curve of MFA in GPCs; linear backgrounds were subtracted from raw data

70°, and that of VPCs mainly ranged from 45° to 60°. The MFA medians of the GPCs were greater than that of the VPCs. In general, analysis of the SEM images revealed that the MFA of the secondary wall of most GPCs was larger than that of most VPCs.

MFA greatly influences the physical and mechanical properties of the cell and even stem as a whole (Sultana and Rahman 2014); the small MFA can enhance the mechanical properties of bamboo (An 2013). Previous studies have shown that bamboo fiber cells have the characteristics of strong rigidity and high toughness (Wang et al. 2014). The MFA of parenchyma cells was larger than that of fibers, with an MFA of 0° to 15° (An 2013). However, some scholars proposed that bamboo parenchyma cells are highly elastic, ductile, and have relatively low mechanical properties (Chen and Fei 2018; Wang et al. 2020a, b; Chen et al. 2021), which may be due to their larger MFA compared to fibers (Wang et al. 2014). It has been proposed that the deformation capability of the layers with the larger MFA in the secondary cell wall is greater than that of the layers with the smaller MFA (Wang et al. 2020a, b). Sultana and Rahman (2014) proposed that the large MFA shows low stiffness and flexibility in the juvenile wood. So, compared with fibers, we speculated that parenchyma cells have great flexibility and lower stiffness. In addition, the MFA of the adjacent sub-layer secondary cell wall in fibers of bamboo is highly variable (Preston and Singh 1950; Parameswaran and Liese 1976; An 2013), while that in parenchyma cell is similar, which may also be one of the reasons for great flexible and ductility of parenchyma cells. In this study, the larger MFA of GPCs than VPCs indicated that GPCs are more flexible and ductile than VPCs. Moreover, cell morphology validate the results. Previous study showed that the larger the cell lumen of parenchyma cells, the greater the deformation and the better the ductility (Chen et al. 2020). The cell lumen of GPCs is significantly larger than that of VPCs (Lian et al. 2019), and the ductility of GPCs is better than that of VPCs. Moreover, two different MFAs of parenchyma cells also indicate two independent parenchyma cell structures in bamboo to meet different mechanical requirements.

XRD—X-ray diffraction (XRD) is a well-established method for determining the average MFA (Sarén and Sarimma 2006). The method is easy to perform, representative, reproducible, and does not require pretreatment of the samples (Wang et al. 2020a, b). In this study, the mean MFA of GPCs was calculated from the peak fitting of the intensity profile obtained by XRD using the 0.6 T method. Since gaussian fitting removes the noise of diffraction peak effectively, the above fitting formula was used to fit the angle-intensity data to a Gaussian curve shown in Fig. 6. MFA was determined from the intensity that has the strongest peak (Wang et al. 2020a, b).

Through fitting curve analysis, the FWHMs of intensity peaks at 1 and 2 have been used to calculate the parameter *T*. Figure 6 shows that the average MFA of GPCs was 63.3°. The calculation process of MFA was shown in the supplementary materials. The result was consistent to a certain extent with the SEM measurement of the mean MFA, which was 60° or 65°, and also consistent with that given by An (2013,

mean θ = 60°) and Ahvenainen et al. (2017, mean θ = 65°). So, the method of measuring MFA by SEM was practicable. The results suggested that SEM can measure the MFA of the sub-layer of the secondary cell wall. However, it is still challenging to obtain the MFA of the directional sub-layer of the secondary cell wall in parenchyma cells. Therefore, further research on the MFA of the parenchyma cell wall is required.

Model of parenchyma cell wall

Our previous study showed that the secondary cell wall of parenchyma cells in moso bamboo was tight-loose alternating layers and contained seven or five sub-layers (Lian et al. 2020). Based on the cross-sectional morphology characteristics of parenchyma cells (Fig. 7a), the structural parameters of the cell wall in GPCs (Fig. 7b), and the MO of the cell walls (Fig. 7c, d,e), a structure model of microfibril orientation of parenchyma cell wall of moso bamboo was constructed, as shown in Fig. 7f.

Conclusions

Microfibrils are the most important framework of cell walls, and their orientation influences the mechanical properties of cell walls, reflecting the patterns of cells morphogenesis. This study characterized the MO and MFA of the secondary cell walls in moso bamboo parenchyma cells. The relationship between MFA and mechanical properties was analyzed. SEM observation revealed that the microfibrils of adjacent sub-layers are arranged in opposite directions along the vertical axis in the secondary cell wall of parenchyma cells. The MO of adjacent lateral walls with the same direction suggested that the microfibril in the secondary cell wall have a spiral arrangement. Moreover, the MO of the cell wall closer to the cell lumen and on the primary cell wall were disordered and reticular. MO of the secondary cell wall was in the flow-like patterns bypassing the pit aperture, and its direction was the same as the long axis of the pit aperture. SEM quantification showed that the average MFA of the secondary wall of most ground parenchyma cells was larger than that of most vascular parenchyma cells. Additionally, XRD analysis revealed that the mean MFA (63.3°) measured by the 0.6 T method agrees to some extent with the SEM results (average MFA of either sub-layer is 65° or 60°). Thus, SEM was a viable method to measure the MFA of sub-layers of the secondary cell wall. Furthermore, an MA model of the parenchyma cell wall is proposed. These results increased our understanding of the microfibril orientation of the parenchyma secondary cell wall

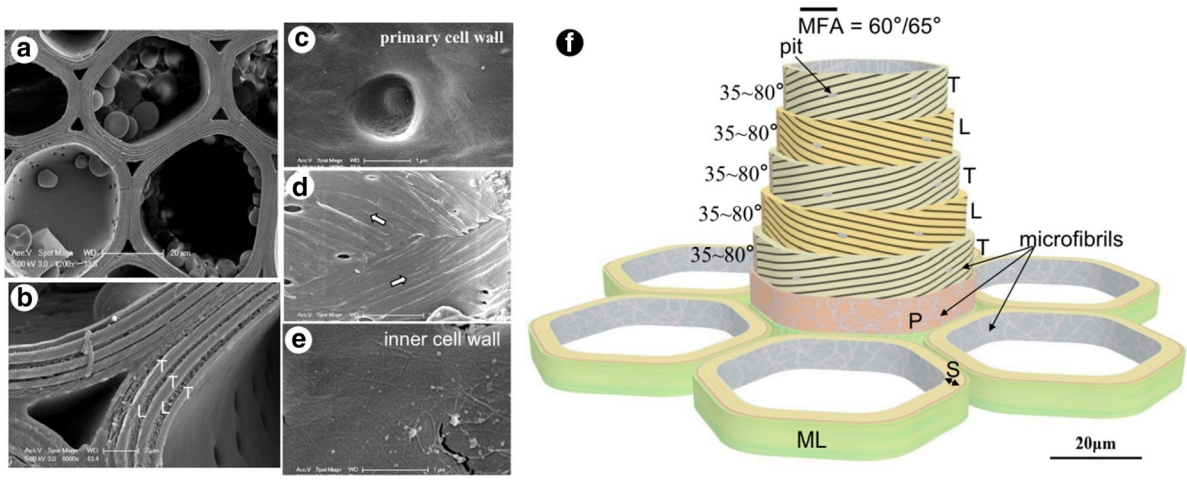

Fig. 7 The structure of parenchyma cells and the structure model of microfibril orientation of parenchyma cell wall. **a** the morphology of parenchyma cells in cross section. **b** the cell wall structure of parenchyma cells. **c** MA of the primary cell wall in parenchyma cell. **d** MA of the adjacent sub-layers in secondary cell wall of parenchyma cell. **e** MA of the inner cell wall in parenchyma cell. **f** the structure model of microfibril orientation of parenchyma cell wall. *ML* middle lamella, *P* primary cell wall, *S* secondary cell wall, *T* tight layer, *L* loose layer

suggesting that MFA had a larger effect on flexibility and ductility. Altogether, these results provide the theoretical and data basis for future improvements of bamboo production and utilization applied to the design of novel bionic nanostructure.

Acknowledgments The authors acknowledge the financial support from the National Natural Science Foundation (Grant No. 31770599) and 13th Five-Year the National key Research and Development Project (Grant No. 2018YFD0600304). We thank Miss. Xin Li from Nanjing Forestry University for helping the drawing of the structure model image.

Declarations

Funding National Natural Science Foundation of China,31770599,Benhua Fei,13th Five-Year the National key Research and Development Project,2018YFD0600304,Zhihui Wu

Conflict of interest The authors have not disclosed any competing interests.

References

Ahvenainen P, Dixon PG, Kallonen A, Suhonen H, Gibson LJ, Scedstöm K (2017) Spatially-localized bench-top X-ray scattering reveals tissue-specific microfibril orientation in Moso bamboo. Plant Methods 13:5. https://doi.org/10.1186/s13007-016-0155-1

An XJ (2013) Multi-scale tensile mechanical behavior and toughening mechanism for bamboo. Chinese Academy of Forestry Science, Beijing. https://doi.org/10.7666/d.Y2405267

Cave I (1997) Theory of X-ray measurement of mirofibril angle in wood. Wood Sci Technol 31:143–152. https://doi.org/10.1007/BF00702610

Chen M, Fei B (2018) In-situ Obeservation on the morphological behavior of bamboo under flexural stress with respect to its fiber-foam composite structure. BioResources 13:5472–5478. https://doi.org/10.15376/biores.13.3.5472-5478

Chen H, Tian G, Fei B (2014) Arrangement of cellulose microfibrils in primary cell wall of moso bamboo fiber studied with AFM. Scientia Silvae Sinicae 50(4):90–94. https://doi.org/10.11707/j.1001-7488.20140413

Chen H, Tian GL, Wu ZH, Fei BH (2016) Cellulose microfibril aggregates in cross-section of bamboo fiber and parenchyma cell wall with atomic force microscopy. Scientia Silvae Sinicae 52:99–105. https://doi.org/10.11707/j.1001-7488.20160212

Chen M, Ye L, Wang G, Ma X, Chen Q, Fang C, Fei B, Dai C (2020) In-situ investigation of deformation behaviors of moso bamboo cells pertaining to flexural ductility. Cellulose 27:9623–9635. https://doi.org/10.1007/s10570-020-03414-0

Chen H, Wu J, Shi J, Zhang W, Wang H (2021) Effect of alkali treatment on microstructure and thermal stability of parenchyma cell compared with bamboo fiber. Ind Crops Prod 164(1):113380. https://doi.org/10.1016/j.indcrop.2021.113380

Donaldson L, Xu P (2005) Microfibril orientation across the secondary cell wall of radiata pin tracheids. Trees 19:644–653. https://doi.org/10.1007/s00468-005-0428-1

Green PB (1980) Organogenesis—a biophysical view. Annu Rev Plant Physiol 31:51–82. https://doi.org/10.1146/annurev.pp.31.060180.000411

He XQ, Suzuki K, Kitamura S, Lin J, Cui K, Takao I (2002) Toward understanding the different function of two types of parenchyma cells in bamboo culms. Plant Cell Physiol 43(2):186–195. https://doi.org/10.1093/pcp/pcf027

Heath IB (1974) A unified hypothesis for the role of membrane bound enzyme complexes and microtubules in plant cell wall synthesis. J Theor Biol 48:445–449. https://doi.org/10.1016/s022-5193(74)80011-1

Hu K, Huang Y, Fei B, Yao C, Zhao C (2017) Investigation of the multilayered structure and microfibril angle of different types of bamboo cell walls at the micro/nano level using a LC-PolScope imaging. Cellulose. https://doi.org/10.1007/s10570-017-1447-y

Jiang ZH (2007) Bamboo and Rattan in the world. China Forestry Publishing House, Beijing

Li ZL (1983) The plant anatomy. Senior Education Press, Beijing

Lian C, Liu R, Cheng X, Zhang S, Luo J, Yang S, Liu X, Fei B (2019) Characterization of the pits in parenchyma cells of the moso bamboo [*Phyllostachys edulis* (Carr.) J. Houz.] culm. Holzforschung 73:629–636. https://doi.org/10.1515/hf-2018-0236

Lian C, Liu R, Zhang S, Yuan J, Luo J, Yang F, Fei B (2020) Ultrastructure of parenchyma cell wall in bamboo (*Phyllostachys edulis*) culms. Cellulose 27(13):7321–7329. https://doi.org/10.1007/s10570-020-03265-9

Liese W, Köhl M (2015) Bamboo, the Plant and its Uses. Springer, Geneva. https://doi.org/10.1007/978-3-319-14133-6

Liese W (1998) The anatomy of Bamboo Culms. Technical Report, Beijing/Eindhoven/New Delhi. https://doi.org/10.1163/9789004502468

Liu B (2008) Formation of cell wall in developmental culms of *Phyllostachys Pubescens*. Chin Acad For Sci Beijing. https://doi.org/10.7666/d.D602728

Maleki S, Modammadi K, Ji K (2016) Characterization of cellulose synthesis in plant cells. Sci World J. https://doi.org/10.1155/2016/8641373

Parameswaran N, Liese W (1976) On the fine structure of bamboo fibres. Wood Sci Technol 10(4):231–246. https://doi.org/10.1007/BF00350830

Preston RD, Singh K (1950) The fine structure of bamboo fibres. I. Optical properties and X-ray data. J Exp Bot 1(2):214. https://doi.org/10.1093/jxb/1.2.214

Sarén M, Serimaa R (2006) Determination of microfibril angle distribution by X-ray diffraction. Wood Sci Technol 40:445–460. https://doi.org/10.1007/s00226-005-0052-7

Savidge R (2014) Cell biology of bordered-pit formation in balsam-fir trees. Botany 7(92):495–511. https://doi.org/10.1139/cjb-2014-0030

Sultana R, Rahman M (2014) An overview of microfibril angle in fiber of tension wood. Eur J Biophys 2(2):7–12. https://doi.org/10.11648/j.ejb.20140202.11

Wai N, Nanko H, Murakami K (1985) A morphological study on the behavior of bamboo pulp fibers in the beating process. Wood Sci Technol 19(3):211–222. https://doi.org/10.1007/BF00392050

Wang X, Keplinger T, Gierlinger N, Ingo B (2014) Plant material features responsible for bamboo's excellent mechanical performance: acomparison of tensile properties of bamboo and spruce at the tissue, fibre and cell wall levels. Ann Bot 114:1627–1635. https://doi.org/10.1093/aob/mcu180

Wang C, Wang N, Liu S, Choo-Simth L, Zhang H, Zhi Z (2020a) Investigation of microfibril angle of flax fibers using X-ray diffraction and scanning electron microscopy. J Nat Fibers. https://doi.org/10.1080/15440478.2018.1546639

Wang D, Lian Y, Fu F (2020b) Fracture mechanisms of moso bamboo (*Phyllostachys pubescens*) under longitudinal tensile loading. Ind Crops Prod. https://doi.org/10.1016/j.indcrop.2020.112574

Wang X, Li Z, Ren H (2010) Variation of microfibril angle and density in moso bamboo (*Phyllostachys Pubescens*). J Trop For Sci 22(1): 88–96. https://www.jstor.org/stable/23616694

Yu F (2008) Studies on the differention and function of ground tissue in bamboo culms. Nanjing For Univ Nanjing. https://doi.org/10.7666/d.y1296027