A THREE-DIMENSIONAL COMPUTER MODEL OF THE TRACHEID CELL WALL AS A TOOL FOR INTERPRETATION OF WOOD CELL WALL ULTRASTRUCTURE

by

L.A. Donaldson

Forest Research, Rotorua, New Zealand

SUMMARY

Three-dimensional computer models were used to simulate transmission electron micrographs in order to determine the effects of changes in microfibril orientation and arrangement on the appearance of ultrastructural images based on thin sections. It is shown that the tangential fibrillar texture commonly associated with wood cell walls results not from individual microfibrils arranged in tangential lamellae but from overlapping of adjacent microfibrils irrespective of their arrangement. The tangential lamellae observed in transmission electron micrographs of wood cell walls do not necessarily reflect the underlying nanostructure of the wall. Tangential textures can occur irrespective of the arrangement of microfibrils in tangential, radial or random patterns as a direct result of the helical organisation of the cell wall. Comparison between model images and high resolution micrographs suggests that microfibrils are arranged randomly in weakly defined clusters, with perhaps varying amounts of tangential or radial organisation.

Key words: Cell wall models, ultrastructure, microfibril, macrofibril.

INTRODUCTION

Wood cell walls consist of microfibrils embedded in a lignin-hemicellulose matrix. The orientation of microfibrils varies in different parts of the cell wall forming different cell wall layers. Ultrathin sections examined with the transmission electron microscope (TEM) show that the cell wall in cross section typically has a texture consisting of tangential or sometimes radial or oblique lamellae, which varies in appearance among cell wall layers, reflecting the change in microfibril orientation. Field emission SEM images and TEM replica images showing longitudinal views of the secondary cell wall reveal linear and more or less parallel microfibrils (Abe et al. 1991, 1992; Kataoka et al. 1992; Awano et al. 2000). However, cross-sectional views indicate the presence of apparently curved, sinuous and tangled structures (Donaldson 1988, 1997; Donaldson & Singh 1998).

A number of conceptual models have been proposed for the wood cell wall which are basically divided into those with microfibrils arranged in either tangential lamellae (parallel to the lumen surface) (Kerr & Goring 1975) or radial lamellae (Sell &
Zimmermann 1993a, b). Because these models, at least in part, are mutually exclusive yet both seem to have convincing evidence, there is a need to enhance our interpretation of cell wall images at the resolution obtainable by transmission electron microscopy in order to understand how the textures in such images are produced. For example, typical ultrathin sections for transmission electron microscopy are about 60–80 nm thick. Microfibrils are about 3–4 nm in diameter (Kerr & Goring 1975; Ruel et al. 1978; Donaldson & Singh 1998). Therefore an ultrathin section must contain significant depth information because the section thickness is 20× greater than the diameter of the structures which make up the image. As an example a single microfibril passing through a 60 nm thick transverse section at an angle of 60° to the plane of the section (equivalent to a microfibril angle (MFA) of 30°) will appear as a strand 35 nm long. This depth information must contribute to image formation in electron micrographs but our understanding of how this occurs is limited.

A variety of techniques are available for providing high resolution spatial information on cell wall structure. These include ultrathin sectioning followed by positive or negative staining and transmission electron microscopy combined with a range of selective component removal procedures or selective stains, rapid-freeze deep-etching and conventional surface replication (Kataoka et al. 1992; Fujino & Itoh 1998; Duchesne & Daniel 1999). Field emission scanning electron microscopy (Abe et al. 1991, 1992; Sell & Zimmermann 1993a, b; Awano et al. 2000) and atomic force microscopy (Hanley & Gray 1994, 1999) have also been used to study cell wall nanostructure. These techniques all produce micrographs that must be interpreted based on knowledge of how the images were formed. An alternative approach is to use a known structure to try to predict observational data. This approach can potentially validate interpretations based on micrographs but has received little attention in the literature (Hanna 1971).

In order to enhance our interpretation of high resolution images of the wood cell wall, the present study attempts to use 3-dimensional computer models to produce an accurate simulation of the cell wall at the nanoscale. Modeling experiments allow the control of variables, such as microfibril orientation and arrangement, to predict or compare with observational data.

MATERIALS AND METHODS

Each computer model was generated using a series of identical 2-dimensional slices representing a cross-sectional view of the microfibrils. Slice images were generated from a Freelance Graphics™ drawing containing black rectangular microfibrils on a white background representing positively stained microfibrils. Each drawing was exported as a tiff image at a resolution of 1024 × 1024, and subjected to a gaussian filter to produce a softer, more realistic representation. A 3-dimensional model was then created by making 40 consecutively numbered copies of each image. The images were transferred to a Silicon Graphics Indy™ workstation and imported into Molecular Dynamics Image Space™ software, converting the series of tiff images into a volume file using appropriate x (1.7 Å) and z (60 Å) resolution with interpolation. Each model therefore represents a volume of 174 × 174 × 240 nm.
Models were then used to simulate transmission electron micrographs of ultrathin sections by varying the orientation and slice thickness ($z'$) used to generate a projection or projection sequence. Projection sequences were used to study the effect of changing microfibril angle (latitude), fibre orientation (longitude), and slice thickness. Figure 1A shows the assumed orientation of each image where each model represents an area of the left hand radial wall of a single tracheid. The normal secondary wall layers are ignored for simplicity. Results from six models, including ordered and random arrangements, radial lamellae, random and radially aligned clusters, and a representation of the Kerr-Goring model, are included. The 2-dimensional component of each model and a 3-dimensional perspective view are shown in Figure 2. Models are based on positively stained microfibrils of rectangular shape 3 nm in width in the radial direction and 4 nm in the tangential direction. The spacing between microfibrils varies with model type but is generally similar to the microfibril dimensions.

Fig. 1. A: Diagram showing the assumed orientation of model images with respect to latitude (microfibril angle – MFA), longitude (fibre tilt) and the cell wall. — B: Diagram showing how texture is generated from overlapping microfibrils passing through a sliced volume. Overlap is influenced by spacing between microfibrils (as shown), microfibril orientation and slice thickness. The greater the overlap the less contrast within the texture.
yielding a ratio of microfibril/matrix of less than 50%. In the absence of detailed quantitative data the dimensional aspects of the models are considered to be only approximations of reality and in some of the models, especially the two clustered models, features have been exaggerated to facilitate interpretation.

For each model the following projection series were created.

- Latitude (equivalent to microfibril orientation) was varied from 15 to 55° in 10 degree increments at 0° longitude (fibre tilt), and at standard slice thickness (80 units).
- Slice thickness (arbitrary units – each slice passes through the center of rotation) was varied in 10 unit increments from 40 to 130 at 15° latitude, 30° latitude, and 50° latitude. An appropriate range of slice thickness was found by trial and error (approximately equivalent to a section thickness range of 10–20 nm).
- Longitude (fibre tilt) was varied in 5° increments from 0° to 20°, at 30° latitude and standard slice thickness.
All projections were made using a ‘look-through’ method, which creates a transparent view of the volume assumed to be more or less analogous to that produced by electron scattering/absorption in a transmission electron microscope. A look-through projection represents the average voxel intensity along the line of sight.

Cell wall material was prepared for imaging in the transmission electron microscope for comparison with images generated from the models. Wood tracheids from *Pinus radiata* D. Don were embedded in Spurr’s resin, ultrathin sectioned with a diamond knife (approximately 70 nm thickness), and stained with 1% KMnO$_4$ in 1% sodium citrate (Donaldson 1992). Holocellulose was generated from a *Pinus radiata* D. Don growth ring boundary containing adjacent latewood and earlywood tracheids, by delignification in peracetic acid at 90° for 4 h, followed by extensive washing in water. Holocellulose was treated with 1% KMnO$_4$ for 1 hour at room temperature followed by further washing in water, dehydration in an acetone series, and embedding in Spurr’s resin. Ultrathin sections were stained with lead citrate prior to examination by transmission electron microscopy. Sections were examined with a Philips EM 300 or a Jeol 1200 EXII transmission electron microscope at 60 kV. The wood samples from which holocellulose was prepared were assessed for S$_2$ microfibril angle using the iodine method (Senft & Bendtsen 1985).

Digital images of wood ultrastructure were processed to enhance texture using the technique based on Fourier filtering described by Russ (1995).

The terms microfibril, macrofibril, and microfibril cluster are used as follows:

- **Microfibril** — The smallest component of the cell wall visualised by transmission electron microscopy occurring as a long fibril 3–4 nm in diameter and consisting of a group of cellulose molecules (protofibril) surrounded by a sheath of hemicellulose (Kerr & Goring 1975). The term ‘cellulose microfibril’ is avoided since the structures observed by electron microscopy are not necessarily composed of just cellulose.

- **Macrofibril** — A larger fibril component of the cell wall typically 30–100 nm in diameter as typically observed by field-emission scanning electron microscopy. Equivalent to a ‘fibril agglomeration’ (Sell & Zimmermann 1993a) or a ‘striped lamella’ (Kataoka et al. 1992).

- **Microfibril cluster** — Any grouping of microfibrils that can be distinguished including both lamellae and macrofibrils.

**RESULTS**

Although a large number of models were studied, only the most significant results are described in this report. A substantial amount of work was required to develop a realistic modeling procedure and to determine what variables were of significant interest using an iterative type process. Figure 2 shows a series of 3-dimensional projections for each model to show how the series of 2-dimensional images are rendered to give a structure with depth. A surface rendering technique with depth shading has

1) A voxel is the 3-dimensional equivalent of a pixel or digital picture element.
been used to produce these images. All other projections in this report were rendered using a look-through projection technique to give a representation of the average intensity along the line of sight. Table 1 provides a summary of the characteristics of each model, the textures generated and the similarity to actual electron micrographs.

The effect of microfibril orientation (latitude) is demonstrated in Figures 3–8 for each model where microfibril angle has been varied from 15 to 55°, the typical range of values found in radiata pine for example (Donaldson 1998). In model 1, increasing microfibril angle results in tangential blending of individual microfibrils (still visible at low angles) producing tangential lamellae of overlapping microfibrils with periodic variations in brightness along each lamella. In these images the periodic texture results in part from sectioning of microfibrils at the surface of the slice (the light gray areas within each lamella), and from overlap between adjacent microfibrils (the brightness range within the texture) (Fig. 1B). Although microfibrils are aligned in both tangential and radial directions, the tangential texture dominates except at very low microfibril angles. In comparison, model 2 (Fig. 4) also shows tangential blending of microfibrils with increasing microfibril angle but in this case the lack of alignment among microfibrils results in sinuous textures, similar in appearance to actual micrographs of wood cell walls (Fig. 10). Model 3 (Fig. 5) with its distinctive radial alignment, shows less tangential blending than the previous models at comparable slice thickness, due to the greater spacing between microfibrils in the tangential direction. However, a tangential texture is still developed at high latitudes (MFA > 30°). It is interesting to note that both tangential and radial textures are generated under these conditions but on notably different scales.

Table 1. Summary of cell wall models, the textures generated and their similarity to real electron micrographs.

<table>
<thead>
<tr>
<th>Model type</th>
<th>Description</th>
<th>Texture</th>
<th>Accuracy*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 / Ordered</td>
<td>Microfibrils aligned in both radial and tangential directions</td>
<td>Continuous, linear, tangential</td>
<td>1</td>
</tr>
<tr>
<td>2 / Random</td>
<td>Randomly arranged microfibrils</td>
<td>Discontinuous, sinuous, tangential</td>
<td>5</td>
</tr>
<tr>
<td>3 / Radial</td>
<td>Radially aligned microfibrils</td>
<td>Discontinuous, sinuous, radial and tangential</td>
<td>4</td>
</tr>
<tr>
<td>4 / Random cluster</td>
<td>Randomly arranged clusters of randomly arranged microfibrils</td>
<td>Discontinuous, sinuous, tangential</td>
<td>4</td>
</tr>
<tr>
<td>5 / Radial cluster</td>
<td>Radially aligned clusters of randomly arranged microfibrils</td>
<td>Discontinuous, sinuous, large scale radial and small scale tangential</td>
<td>3</td>
</tr>
<tr>
<td>6 / Kerr-Goring</td>
<td>Tangentially aligned clusters (lamellae) of microfibrils</td>
<td>Discontinuous, linear, tangential</td>
<td>2</td>
</tr>
</tbody>
</table>

*) Similarity to micrographs on a 1–5 scale where 5 is most similar to typical images.
Models 4 and 5 (Fig. 6 & 7) show similar results to model 2 for varying microfibril angle except that tangential blending results in distinctly discontinuous textures as a result of the clustered arrangement of microfibrils. The radial alignment of the clusters in model 5 is preserved and contributes to the texture at all orientations studied. Varying the microfibril orientation in model 6 representing the Kerr-Goring model (Fig. 8) also results in discontinuous lamellae but in this case they are linear because of the tangential alignment of individual microfibrils.

Increasing slice thickness has a similar effect to varying microfibril angle in all models and this effect is more pronounced at high microfibril angles resulting in an additive effect when both variables are changed simultaneously (Fig. 3–8). The ef-
fect of increasing slice thickness is to reduce resolution as expected. It is interesting to note that for model 3 (Fig. 5) increasing both microfibril angle and slice thickness results in a tangential texture, which partially obscures the underlying radial arrangement of the microfibrils.

Variation of longitude, equivalent to tilting the cell wall towards or away from the lumen with respect to the plane of the section, generates an oblique texture which rotates towards or away from the lumen (Fig. 9). This phenomenon is difficult to visualise but is apparently due to the combined effects of variation in latitude and longitude in these images. At very small microfibril angles (< 5°) radial textures can be generated with relatively small amounts of fibre tilt (10–20°) as shown in Figure 10.
DISCUSSION

The Kerr-Goring model of the wood cell wall (Kerr & Goring 1975) was based primarily on interpretation of transmission electron micrographs. This model states that microfibrils are arranged in short tangential lamellae embedded within a lignin-hemicellulose matrix. Microfibrils themselves consist of a cellulose core (protofibril) containing an unspecified number of cellulose molecules, coated with a thin hydrogen-bonded layer of hemicellulose. Since this model was published a number of modifications have been proposed, the most significant of which is the radially aligned model published by Sell and Zimmermann (1993a, b), based on observation of transverse fracture surfaces by field emission scanning electron microscopy, and by Larsen...
et al. (1995), based on scanning electron microscopy of decayed wood. The observation of mixed tangential and radial arrangements of macrofibrils (Zimmermann & Sell 1997) suggests that either the ultrastructure of tracheid cell walls is locally variable or that the evidence from high resolution images is subject to mixed interpretation. The nature of these macrofibrils has yet to be determined – comparable structures have not been described using transmission electron microscopy of ultrathin sections.

A major outcome of the present study has been to show that, for a cell wall constructed from microfibrils that are more or less parallel and linear, and arranged in a helix at some orientation to the fibre axis, tangentially aligned textures are generated.
entirely as a consequence of the helical arrangement, and irrespective of the actual alignment or lack of alignment of adjacent microfibrils. The greater the microfibril angle, the more pronounced is the tangential texture. Even radially aligned microfibrils can generate tangential textures under certain conditions, particularly at microfibril angles greater than 30°. A disordered arrangement of individual microfibrils in the model yields a more realistic representation than a highly ordered arrangement, with sinuous fibrillar textures being generated as a result of the offset between adjacent microfibrils within individual lamellae. It is thus more appropriate to describe the texture of electron micrographs as being predominantly tangential, radial or random rather than to say that the microfibrils are arranged in tangential or radial lamellae.

Fig. 7. A look-through projection series for model 5 (a disordered array consisting of microfibrils in a radially aligned, clustered arrangement) illustrating the effect of varying microfibril angle (left to right: 15°, 35°, 55°) and slice thickness (top to bottom: 40, 80, 130 units). Each projection is 174 × 174 nm planar area. The arrow indicates the direction of the lumen. Microfibrils are shown as positively stained structures.
Figure 11 illustrates the actual fibrillar texture in a small area of the S2 region of a tracheid where microfibrils are negatively contrasted by the positively stained lignin matrix. The texture is enhanced by a combination of Fourier filtering and edge detection (Russ 1995; Donaldson 1997) resulting in a discontinuous fibrillar texture showing sinuosity. Comparing this texture with Figures 4 and 8 we note that the actual texture is discontinuous as described by the Kerr-Goring model, not continuous as found with model 1 for example. This indicates that microfibrils are not uniformly distributed within the cell wall. The presence of a sinuous texture indicates a lack of alignment of individual microfibrils within each lamella, requiring some modification to the Kerr-Goring model. The whole concept of cell wall organisation is based around
Fig. 9. A look-through projection series for models 1–6 (top to bottom) illustrating the effect of varying fibre tilt in 5° increments from 0° to 20° (left to right) at 30° microfibril angle and standard slice thickness. Each projection is 174 × 174 nm planar area. The arrow indicates the direction of the lumen. Microfibrils are shown as positively stained structures.

details of microfibril clustering, as for example in the Kerr-Goring model, where microfibrils occur in short discontinuous linear lamellae (linear clusters). As a result of this modeling study, it seems likely that microfibrils are more disorganised than in the highly ordered Kerr-Goring model because modeling indicates that sinuous textures in micrographs result from a lack of alignment of microfibrils.
Fig. 10. A look-through projection series for model 2 illustrating the effect of varying latitude (top left to bottom right 0, 5, 10, 20, 30 and 40°) at 10° longitude and standard slice thickness. Note the presence of a radial texture artifact at low microfibril angles that becomes an oblique texture at MFA > 5°. Each projection is 174 × 174 nm planar area. The arrow indicates the direction of the lumen. Microfibrils are shown as positively stained structures.

The modeling approach offers useful insight into the proposed radial models of Sell and Zimmermann (1993b). Observations of a radial component to cell wall organisation are not new. The cell wall checking that commonly occurs in severe compression wood which reflects a degree of radial organisation in the cell wall, was described more than 100 years ago (Sanio 1873). Some forms of decay produce structures that have been interpreted as indicating an underlying radial organisation of the cell wall (Larson et al. 1995; Schwarze & Engels 1998).

A significant prediction from the radial model is that radial textures in transverse view may be more distinct at low microfibril angles and at thin section thickness. Radial textures have also been associated with variations in lignification especially in compression wood (Singh et al. 1998; Singh & Donaldson 1999; Singh & Daniel, in press). This does not necessarily imply an associated radial alignment of the microfibrils in this type of material. However, in Figure 12 we show an example of a radial microfibril texture in compression wood, particularly prominent in the highly lignified part of the secondary wall due to improved contrast. While compression wood may have increased microfibril angles compared to adjacent normal wood, this is known to be a highly variable feature (Harris 1977; Donaldson & Burdon 1995) and in a population of cells there is usually a wide distribution of angles (Donaldson 1998). The observation of radial microfibril textures in compression wood does not necessarily disagree
Fig. 11. Texture enhanced image of wood stained with KMnO₄ negatively contrasting the microfibril texture.

A: Original image.

B: Texture image extracted using a Fourier transform filter showing alternating lamellae of matrix and microfibrils of similar size. Note that the texture is discontinuous (dark irregular shapes) hinting at the presence of weakly defined clusters of microfibril lamellae.

C: A texture enhanced image created by combining A and B.

The arrow indicates the direction of the lumen. The scale bar represents 35 nm.
with the above conclusion in relation to microfibril angle and radial textures, although radial textures might be less frequently observed. This does not imply that compression wood is more or less likely to have a radially aligned nanostructure compared to normal wood.

Based on the results of modeling, a radial texture can be produced as an artifact as a result of increasing fibre tilt if sections are cut at an oblique angle rather than close to transverse. As shown in Figure 10 this effect is very sensitive to microfibril angle which must be less than 5° in order to produce a radial texture with only moderate fibre tilt. The oblique textures predicted as a result of increasing fibre tilt (Fig. 9) have been observed in real oblique sections by Yamanaka (1969) and the pattern can be used to measure microfibril angle on sections of known tilt (Fujita & Saiki 1990). Such patterns are also associated with the transition between wall layers where microfibrils undergo reorientation (Roland & Mosiniak 1983). It should be pointed out that even in a perfect transverse section, tracheids are not all parallel to each other resulting in oblique textures in those tracheids at significant angles to the plane of the section.

In order to investigate the occurrence of radial textures we briefly examined two holocellulose samples of known microfibril angle representing latewood (average MFA 13°) and earlywood (average MFA 27°) tracheids. Both random and radial textures (Fig. 12) were present in both samples with definite variations in texture among individual tracheids confirming that even at the nano level wood is an inherently variable material. A detailed quantitative study of these textures was considered beyond the scope of the present study. The examples of radial texture in Figure 12 could represent actual radial alignment or they could represent examples of the fibre tilt effect, although the latter explanation is considered much less likely due to the expected low frequency of tracheids with microfibril angles less than 5° (Donaldson 1998). In any case the effect of fibre tilt cannot account for the radial textures observed by scanning electron microscopy or atomic force microscopy because only the surface is visualised by these techniques.

Hanna (1971) used a simple modeling technique in an attempt to understand high resolution images of microfibrils in holocellulose. One of his conclusions was that vertical overlap between adjacent microfibrils in sections greater than 75 Å in thickness results in an increase in apparent microfibril diameter. In a transverse section, overlap is greatest in the S1 and S3 layers where microfibrils lie largely within the plane of the section. This effect can be investigated using the computer models. Since the microfibrils are of known diameter this can be compared to the diameter of microfibrils in projections of varying thickness. As an example, we can take the situ-

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Fig. 12. Examples of random and radial textures in wood and holocellulose. – A: Compression wood stained for lignin with KMnO₄ showing radial textures resulting from microfibrils. The scalebar represents 200 nm. – B: Holocellulose with positively stained microfibrils showing a random texture in the S2 region. The scalebar represents 100 nm. – C: Holocellulose with positively stained microfibrils showing a radial texture in the S2 region. The scale bar represents 100 nm.
ation of a 35° microfibril angle and the standard slice thickness. Because individual microfibrils in the model are fuzzy, the diameter is measured as the width at half maximum height from a plot of intensity variation across a single microfibril. This yields a width of 18 pixels (3 nm on the arbitrary scale) for the actual width and 18 pixels for the width in a slice at 35° suggesting that the effect is too small to measure under these conditions. Slice thickness is an important consideration but it is apparent that as slice thickness increases, microfibril diameter does not seem to change significantly by visual assessment (Fig. 3–8). Figure 13 shows a projection series of the random model at 60–90° latitude simulating for example the S₁ or S₃ layers of the cell wall. In this case an effect of microfibril overlap is apparent but this is offset by
the grayscale contrast between microfibrils, some of which are only partially within the sliced volume, allowing a reasonable judgement of what structures are overlapping. The effect of overlap on apparent microfibril diameter is thus not as great as might be expected.

Observational data describing ‘macrofibrils' (Abe et al. 1991, 1992; Sell & Zimmerman 1993a, b; Duchesne & Daniel 1999; Hanley & Gray 1994, 1999; Awano et al. 2000) supports the hypothesis of microfibril clustering. These reports describe fibrillar textures that are much larger than the 3–4 nm diameters observed by transmission electron microscopy. While such macrofibrils may be the result of the cutting or fracturing procedures used, there is no reason why macrofibrils cannot reflect the underlying microfibril based nanostructure. Figure 11 shows an enhanced image of the tangential textures typically described for wood. Using Fourier filtering it is possible to extract the periodic information from the original image as shown in Figure 11B (Russ 1995). This image reveals the presence of discontinuities or areas where the tangential texture is absent that form highly irregular boundaries across the field of view. These discontinuities are similar in size to typical macrofibrils and could thus represent the underlying nanostructure responsible for their formation as a result of fracturing or cutting procedures. While the clustered models examined here are likely to represent an exaggeration of the actual inhomogeneity there is a notable similarity between the randomly clustered model (Fig. 6) and the texture image in Figure 11B. There is increasing evidence that the cell wall is not as uniform as it was once thought (Singh et al. 1998; Singh & Daniel, in press).

Kataoka et al. (1992) have shown longitudinal views of microfibril clusters which they describe as ‘striped lamellae'. The models they proposed are similar to those described in this report with the addition of some twisting and entanglement of individual microfibrils within the clusters. Their ‘pressed pile' model requires some curvature of individual microfibrils as illustrated in their replica images. The woven texture described by these authors is similar to the texture shown in cross-sectional view in Figure 11B. Awano et al (2000) describe macrofibrils of varying size from 12 nm to 15 nm and thought to consist of bundles of smaller 5 nm fibrils and associated glucuronoxylans identified by immunogold staining. Some variation in the size and arrangement of macrofibrils among cell wall layers was noted by these authors. The ultrastructural origin of macrofibrils needs to be examined in detail by combining several microscopy methods on the same sample by, for example, attempting to thin section the surface produced by fracturing or cutting of unembedded wood.

CONCLUSIONS

Computer models of cell wall nanostructure can successfully simulate transmission electron micrographs and provide insight allowing more accurate interpretation of these images. The fibrillar texture in electron micrographs is produced by overlapping of adjacent microfibrils, resulting in sinuous structures due to the offset between adjacent microfibrils within individual lamellae. Tangential textures occur largely as a result of the helical arrangement of the cell wall, and do not necessarily reflect the
underlying arrangement of microfibrils. A tangential texture can occur even when microfibrils are radially aligned as either microfibril angle or slice thickness, are increased. The best agreement between model and observational data is for an arrangement where microfibrils occur in a random arrangement with varying amounts of tangential or radial alignment, and perhaps in weakly defined clusters.

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REFERENCES


Hanna, R.B. 1971. The interpretation of high resolution electron micrographs of the cellulose elementary fibril. J. Polymer Sci (C) 36: 409–413.