

Helical Orientation of the Microfibrils in Tracheids, Fibres and Vessels

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Abstract. The helical winding direction of microfibrils in the S2 wall layer in the tracheids, fibres and vessel members of over 250 woody species, both indigenous and exotic, growing in New Zealand has been determined. A Z helix was observed in all the tracheids, fibres and narrower vessel members. The orientation in the wider vessel members could not always be determined with any certainty.

The fine structure of the conifer tracheid wall is now well known to consist of a primary wall surrounding a three-layered secondary wall. In each of the secondary layers, the S1, S2 and S3, the helical winding angles of the microfibrils differ but usually follow an S – Z – S arrangement [Roelofsen 1959; Panshin, de Zeeuw 1970; Jane 1970]. A helix is defined as being either S or Z when the direction, as viewed from the outside of the cell, is the same as the centre stroke of the letter. A right-hand thread is therefore a Z helix and a lefthand thread an S helix. Less work has been reported on the fine structure of hardwood cells but fibres apparently have a similar structure to that of the conifer tracheid. Roelofsen [1959] notes that the same S – Z – S pattern is followed in the fibres of deciduous trees.

Compared with the gymnosperm tracheid wall, little is known about the fine structure of the vessel member wall [Preston 1974]. Evidence for a three layered secondary wall in vessel members of less specialised dicotyledons has come from the light microscope studies of Bailey and Vestal [1937] and Wardrop [1964]. The walls of the vessels of more specialised dicotyledons may appear more uniformly birefringent which Wardrop [1964] has suggested is due to small differences in the orientation of the microfibrils of the three layers. Transmission electron microscope studies by Harada [1962, 1965] have confirmed a three layered structure in some woods, but in the study of the vessel wall of some members of the Diptero-carpaceae, Yamanaka and Harada [1968] report a complex poly laminate wall structure. The orientation of the microfibrils in all the wall layers is also complicated in vessels with a high density of pits.

During the course of a long term investigation into the structure of New Zealand woods using scanning electron microscopy [Meylan, Butterfield 1978], we routinely examined the pits, lumens, and cut walls of fibres, tracheids and vessels of more than 200 indigenous species. We also examined the woods of many species exotic to New Zealand. A minimum of three, and often as many as ten wood samples, each from different trees of the same species, were examined during the survey and a total of more than 15,000 scanning electron micrographs taken.

Scanning electron microscopy enables the helical winding direction of the S2 layer to be determined quite easily and free from the ambiguity that may arise from the use of thin sections. We have used two methods of observation: (1) the direction of the pit apertures, and (2) cutting effects. First, in both tracheids and fibres, the pit apertures tend to follow the general direction of the S2 layer and provide a ready method of determining the direction of the helix, though not the exact angle of the microfibrils in this layer. Occasionally in some thick-walled cells, the pit apertures are aligned with the cell axis and no helix direction is apparent. In vessels, because of the apparently more complex wall structure in some woods, the direction of the pit apertures may not necessarily follow that of any particular layer. In our experience, however, while the alignment of pit apertures in wide vessels is variable, in narrow vessels the direction is always the same as that found in the fibres and tracheids of the same wood. Secondly, when a pair of adjacent cell walls is cut longitudinally, the surfaces on each wall may show a different texture depending on whether the cut is with or against the "grain" of the microfibrils [Exley et al. 1974]. This has proved to be a useful method for assessing the direction of the main wall layer when the direction of cutting is known and the microfibril angle is sufficiently large to produce a detectable effect. Compression wood or wall splits, if present, will also give a clear indication of the main helical direction of the S2 wall layer.

Our survey covered the woods of 23 gymnosperm species belonging to 9 genera from 7 families, and 233 angiosperm species belonging to 94 genera from 61 dicotyledonous families. In all of the fibres and tracheids that we examined in these woods, the helical orientation of the S2 microfibrils always wound in a Z direction. The orientation of the microfibrils in the S2 wall layer of vessels was not always so obvious, as mentioned above, but we have found that the main winding direction is nearly always the same as in the fibres. In those species where helical thickenings were observed [Butterfield, Meylan 1978] their orientation, although somewhat variable was predominantly in the S direction. Assuming that these thickenings follow the direction of the S3 microfibrils, then our observations are consistent with an S - Z - S arrangement for the S1, S2 and S3 layers in these vessel walls.

Early papers on the structure of the conifer cell wall state that both S and Z helices (presumably in the S2 wall) can be found in different tracheids even within the same sample [Preston 1934]. We have never observed this effect. Several recent texts, however [Panshin, de Zeeuw 1970; Jane 1970] report that the reversed configuration, i. e. Z - S - Z, can also be found. Roelofsen [1959] cites Wardrop

[1957], Wardrop and Dadswell [1957], and Frei et al. [1957] for evidence that the Z – S – Z sequence may be a normal feature for *Pinus radiata*. This has not been either our experience or that of Dr J. R. Barnett of the Forest Research Institute, Rotorua (personal communication). We have always found the S2 layer of this species to have a Z helix.

A Z helix for the orientation of the microfibrils in the S2 wall layer of tracheids, fibres and probably vessels appears, therefore, to be the normal arrangement. Our extensive survey found no exception to it. It would be interesting to learn from the data of other wood scientists if there are any known exceptions and to establish whether or not these follow any particular taxonomic or geographic pattern. Palaeobotanical information might also indicate whether or not this arrangement is a stable one.

It should be noted that care must be taken with microscope slides and photographic negatives to ensure that these are not inverted during examination since this will give a false orientation for all the features diagnostic in determining the microfibrillar orientation of the various wall layers.

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(Received March 14, 1977)

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