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RAY STRUCTURE IN ROOT- AND STEM-WOOD OF *LARIX DECIDUA*: IMPLICATIONS FOR ROOT IDENTIFICATION AND FUNCTION

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SUMMARY

Differences in ray structure between root- and stem-wood of softwoods can cause confusion in identifying roots using keys based on stem-wood anatomy. Comparison of root- and stem-wood rays of *Larix decidua* showed root-wood had fewer ray tracheids, taller, wider but shorter ray parenchyma cells, and larger cross-field pits than stem-wood. The implications of these differences are considered in relation to the identification and function of roots.

Key words: *Larix decidua*, root-wood, root identification, ray structure.

INTRODUCTION

Keys to identification of softwood timber rely heavily on differences in ray structure: details such as types of cross-field pitting, presence or absence of ray tracheids, and numbers of epithelial cells around radial resin canals, have been used as guides to identification at genus and species levels (Phillips 1948; García Esteban *et al*. 2002; IAWA Committee 2004). There are, however, differences in ray structure between stem- and root-wood, which can cause confusion in identifying softwood roots using keys based on stem-wood anatomy.

Although quantitative differences between the wood structure of roots and stems have been described for some conifer species, these analyses have been mainly concerned with length and transverse dimensions of axial tracheids (Bannan 1965; Fayle 1968; Denne 1972). In dicotyledons wood rays have been reported to be wider in roots than in stems, both in cell number and cell diameter (De Bary 1884; Patel 1965; Metcalfe & Chalk 1983), but in softwoods little attention appears to have been paid to quantitative differences in ray structure. For that reason, this paper examines differences in wood ray structure between roots and stems of *Larix decidua* that may be crucial to identification of its roots; the implications of these differences for root function will also be considered.

MATERIAL AND METHODS

Sample material

Samples were taken from 10 roots of *Larix decidua* Mill. trees growing in several different locations within North Wales: 5 roots were selected to represent ‘juvenile’ root-wood (with 3 to 5 growth rings) and 5 larger roots to represent ‘mature’ root-wood

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(approximately 20 growth rings). To ensure correct identification, these roots were collected from wind-thrown trees. All the roots were laterals that had been growing horizontally or obliquely in the soil. Stem-wood was taken from 10 timber samples of *Larix decidua*, all grown in the UK: 5 samples were of juvenile wood (within about 3 to 8 rings from the pith) and 5 of mature wood (further from the pith).

Measurements and analysis

After soaking in water, hand sections were cut from transverse (TS), radial (RLS) and tangential (TLS) longitudinal surfaces and mounted unstained in water.

All measurements were taken from within the earlywood part of a growth ring, using an eye-piece micrometer scale. From RLS, numbers of layers of ray tracheids and ray parenchyma were counted, together with measurements of ray parenchyma cell length (in radial direction) and height (axially). Ray parenchyma cell height was measured by dividing the total height of the ray (excluding any ray tracheids) by the number of parenchyma layers. Cross-field pit number and diameter were also determined from RLS; pit diameter was measured radially across the pit border. Ray parenchyma cell width, and number of epithelium cells around radial resin ducts, were measured from TLS: ray parenchyma width was taken as the maximum width of the central cell of each ray. All the above parameters were counted or measured from a minimum of 15 rays from each root or stem sample, the only exceptions being ray parenchyma length (minimum of 10 cells from each sample) and number of epithelial cells around resin canals (aiming for 10 resin canals from each sample). Ray proportion was measured by point sampling from TLS, determining the percentage falling on ray cells in 550 points from each root- or stem-wood sample.

Data were entered into Excel 97 and analysed with the same programme. In a preliminary analysis, juvenile and mature wood samples were analysed separately, but since no significant differences ($P > 0.05$) were detected between juvenile and mature wood parameters in either root- or stem-wood, the data shown and discussed in this paper are combined values of juvenile and mature wood measurements.

RESULTS

Growth ring structure

The growth rings of root-wood had little or no latewood (Fig. 1) in contrast to the distinct latewood zone typical of stem-wood rings of *Larix decidua* (Fig. 5). Also, whilst stem-wood growth rings were usually clearly defined annual rings, those of root-wood were erratic or absent, making it difficult to distinguish annual from false rings.

Ray proportion

Though the percentage of rays appeared to be slightly higher in roots than in mature stem-wood (Table 1a) the difference was not statistically significant ($P > 0.1$).

Ray tracheids

The number of layers of ray tracheids (counted from RLS) was significantly less ($P < 0.001$) in root- than in stem-wood (Table 1b). Indeed, ray tracheids were absent

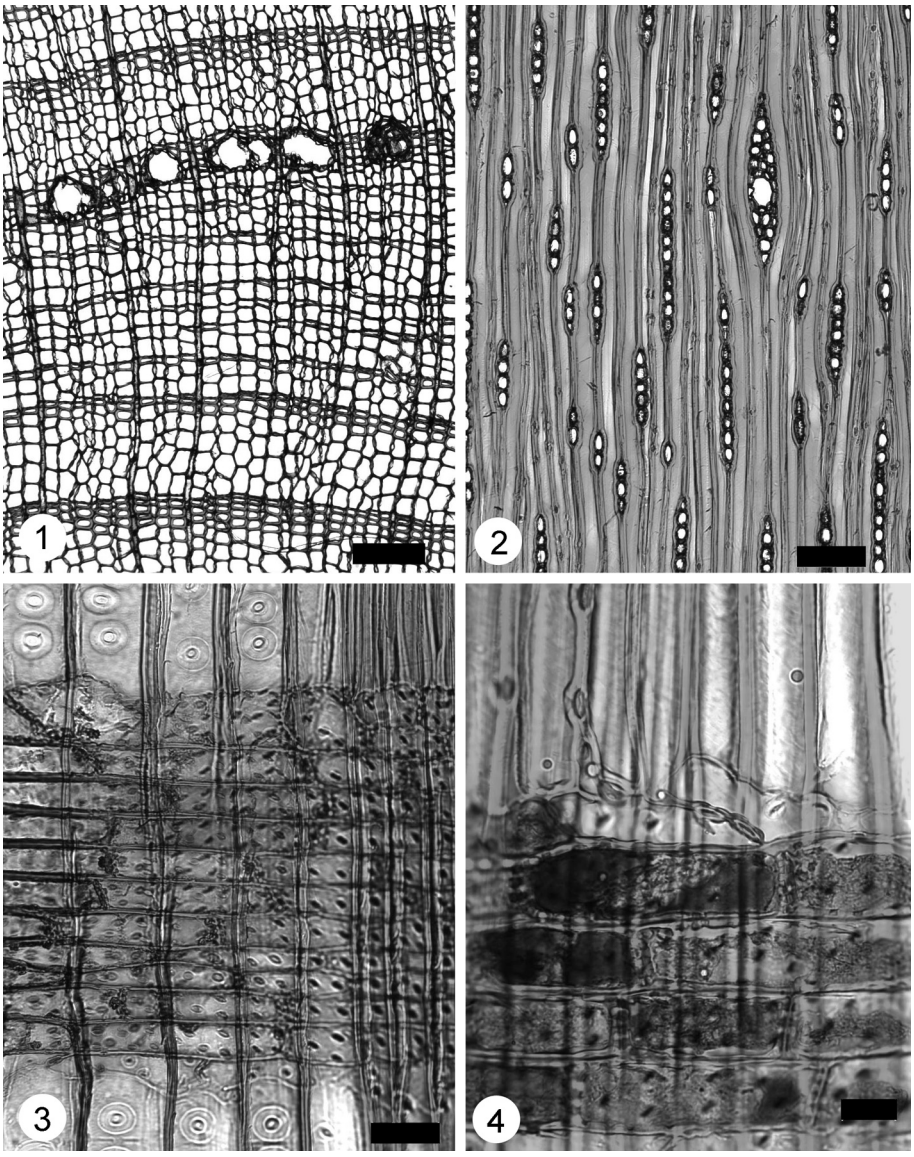
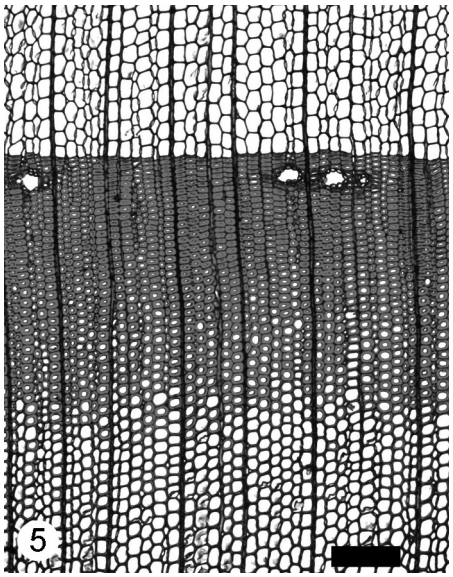


Figure 1. TS of root-wood of *Larix decidua* showing several indistinct growth rings and a tangential line of axial resin canals. — Figure 2. TLS of root-wood of *L. decidua* showing uniseriate rays of varying height (1–11 cells high) and one fusiform ray with a radial resin canal. — Figure 3. RLS of root-wood of *L. decidua* showing a ray 11 parenchyma cells high with a single ray tracheid row at the lower margin. The cross-field pits vary from piceoid to taxodioid. — Figure 4. RLS of root-wood of *L. decidua* showing a ray with distorted ray tracheids along the upper side. The ray tracheids are smooth-walled and have bordered pits. — Scale bar in 1 = 200 μm, in 2 = 100 μm, in 3 = 50 μm, in 4 = 20 μm.



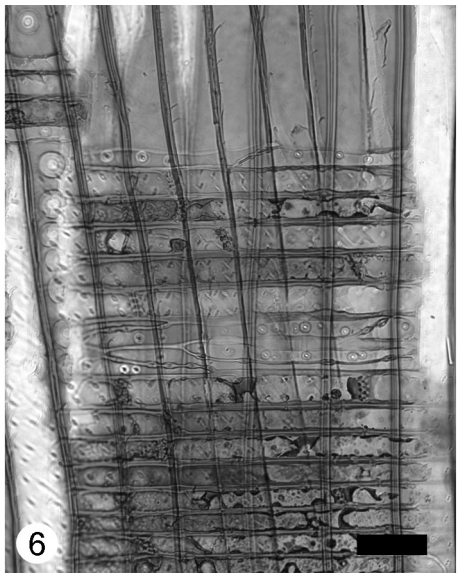


Figure 5. TS of stem-wood of *Larix decidua* showing clearly defined growth ring boundary with distinct latewood zone. — Figure 6. RLS of stem-wood of *L. decidua* showing several layers of elongated ray tracheids (along the upper margin and in the middle of the ray). The cross-field pits are piceoid. — Scale bar in 5 = 200 μm, in 6 = 50 μm.

Table 1. Comparison of wood ray proportion, cell numbers and cell dimensions between root- and stem-wood of *Larix decidua*. Data shown are means plus or minus standard error.

	Root-wood	Stem-wood	Level of significance
a) Ray proportion (as % area in TLS)	10.80 ± 0.65	9.64 ± 0.92	n.s.
b) Ray tracheids (number of layers in RLS)	0.34 ± 0.12	2.27 ± 0.09	***
c) Ray parenchyma (number of layers in RLS)	5.73 ± 0.32	7.46 ± 0.45	**
d) Ray parenchyma cell width in μm (from TLS)	19.08 ± 0.76	12.97 ± 0.69	***
e) Ray parenchyma cell height in μm (from RLS)	29.02 ± 1.33	19.63 ± 0.25	***
f) Ray parenchyma cell length in μm (from RLS)	94.92 ± 8.74	226.58 ± 12.41	***
g) Ray parenchyma cell volume in μm^3 (calculated from d × e × f)	$5.24 \times 10^4 \pm 0.53 \times 10^4$	$5.72 \times 10^4 \pm 0.29 \times 10^4$	n.s.
h) Cross-field pits, number	4.07 ± 0.19	3.19 ± 0.18	***
i) Cross field pits, radial diameter in μm	7.71 ± 0.46	4.36 ± 0.20	***
j) Radial resin canals, number of epithelial cells in TLS	9.35 ± 0.30	7.98 ± 0.34	***
k) Total height of parenchyma in ray in μm (calculated from c × e)	166	146	

n.s. denotes no significant difference at confidence level 0.1.
** denotes significant difference at confidence level 0.01.
*** denotes significant difference at confidence level 0.001.

from most rays in root-wood, and those that did occur were often irregular in shape, sometimes extending axially from the margin of the ray (Fig. 4). In contrast, stem-wood ray tracheids were relatively long and narrow, running horizontally along the top and bottom margins of each ray (Fig. 6).

Ray parenchyma

Number of layers — The number of layers of ray parenchyma (counted from RLS) was significantly less ($P<0.01$) in root- than in stem-wood (Table 1c).

Ray parenchyma cell dimensions — As seen in TLS, ray parenchyma cells were significantly wider ($P < 0.001$) in root- than in stem-wood (Table 1d). As seen in RLS, the ray parenchyma cells were significantly higher axially ($P < 0.001$) but shorter radially ($P < 0.001$) in root- than in stem-wood (Table 1e, f; Fig. 3, 4, 6). Root-wood ray parenchyma cells appeared to be brick-shaped, averaging 3.3 times longer radially than their axial height (Fig. 4), while stem-wood ray parenchyma cells averaged 11.5 times longer radially than their axial height (Fig. 6).

Ray parenchyma cell volume, calculated from the measured width, radial length and axial height, did not differ significantly between root- and stem-wood (Table 1g) ($P > 0.1$).

Cross-field pits

The cross-field pits in stem-wood were predominantly piceoid with cupressoid and taxodioid pits present occasionally. In contrast, those of root-wood were predominantly cupressoid or taxodioid, with few piceoid pits present. The number of pits per cross-field averaged more in root- than stem-wood (Table 1h) ($P < 0.001$). Root-wood cross-field pits were considerably wider than those of stem-wood (Table 1i) ($P < 0.001$).

Radial resin canal epithelium

As seen in TLS, the number of epithelial cells around the resin canals was variable, averaging more numerous in root- than in stem-wood (Table 1j) ($P < 0.001$). The number ranged from 7 to 17 around radial resin canals in root wood, compared with 5 to 11 around those in stem-wood.

DISCUSSION AND CONCLUSIONS

Implications for root identification

As shown by the above data, several parameters of ray structure that have previously been used as key features in softwood identification differ between root- and stem-wood. In the Forest Products Research (FPR) Softwood Key (Phillips 1948), the presence of ray tracheids is used to differentiate most genera of the Pinaceae from those of other families of Gymnosperms. But the present data from *Larix decidua* confirm the previous observations by Bannan (1941) that root-wood has far fewer ray tracheids than stem-wood, and that those which occurred in roots were often so misshapen as to be easily overlooked. According to Bartholin (1979) and Anagnost *et al.* (1994) *Larix* spp. can be distinguished from *Picea* spp. by the shape of the border on ray tracheid bordered pits: obviously this key feature would be difficult to apply in root-

wood where ray tracheids are rare or absent. The bordered pits of the few ray tracheids seen in root-wood were of the form described by Anagnost *et al*. (1994) as "*Larix*" or "intermediate" type (Fig. 4).

The FPR key to the identification of softwoods (Phillips 1948) indicated cross-field pitting to be predominantly piceoid, but with taxodioid occasionally present. In their table "Diagnostic characters in root anatomy of Gymnosperm trees", Cutler *et al*. (1987) recorded roots of *Larix* spp. as having exclusively piceoid pitting (along with *Picea* and *Pseudotsuga* spp.), distinguishing those genera from all the others listed. Whilst the present data for *L. decidua* agree that the cross-field pits of stem-wood were mainly piceoid, those of the root-wood were mostly of the cupressoid or taxodioid type, and this was consistent over the 10 samples of each examined. This confusion is compounded by other conflicting reports on cross-field pit type in timber of *Larix* spp.; thus Greguss (1955) indicated piceoid pitting, while Gale and Cutler (2000) and Schweingruber (1993) gave the whole range from piceoid through cupressoid to taxodioid for *Larix* spp.

Given the lack of ray tracheids and the tendency towards taxodioid pitting, the unwary might be tempted into identifying a *Larix* root as *Abies* or *Sequoia*, though the presence of radial resin canals in the *Larix* root (Fig. 2) should avoid that pitfall. In this study of *L. decidua*, the number of epithelial cells around the resin canals appeared to be greater, and with a wider range, in root- than in stem-wood. The range found in roots (7–17 cells) is slightly beyond the 7–12 cells given by Phillips (1948), though he did state that more epithelial cells may be present in traumatic canals. Clearly further investigations are needed to establish key features to distinguish reliably between genera in conifer roots.

Implications for root function

According to Metcalfe and Chalk (1983) dicotyledon root-wood tends to have a higher content of ray and axial parenchyma than stem-wood. In contrast, no axial parenchyma was detected in *Larix decidua* (apart from the axial resin canal epithelium), and there were fewer layers of ray parenchyma in root- than in stem-wood. The average ray proportion (Table 1a) and the calculated value of total parenchyma height per ray (Table 1k) was slightly greater in root- than in stem-wood, though these differences were not statistically significant.

The individual ray parenchyma cells were significantly ($P < 0.001$) higher, wider, and shorter in root- than in stem-wood. In spite of these widely different dimensions, the calculated ray parenchyma cell volumes (Table 1g) were remarkably similar in root- and stem-wood; it seems that the higher and wider dimensions of the root-wood parenchyma cells compensated for their shorter radial length compared with stem-wood parenchyma.

Root-wood also had much larger cross-field pits than stem-wood in *L. decidua*. It seems likely that these differences in ray parenchyma dimensions and pit size relate to differences in physiological function between root and stem. Ray parenchyma of roots provides a vital reservoir of storage reserves to support seasonal stem activity, and is also needed to retain the metabolic capacity to resist invasion by soil pathogens. The increased height and width of ray parenchyma enlarges the cross-field area, presumably

allowing larger pit membranes to increase rate of diffusion of metabolites into the sapstream. However, further research is needed to confirm these anatomical differences between root- and stem-wood in a wider range of conifer species.

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REFERENCES

Anagnost, S.E., R.W. Meyer & C. DeZeeuw. 1994. Confirmation and significance of Bartholin's method for the identification of the wood of *Picea* and *Larix*. IAWA J. 15: 171–184.

Bannan, M.W. 1941. Variability in wood structure in roots of native Ontario conifers. Bull. Torrey Bot. Club 68: 173–194.

Bannan, M.W. 1965. The length, tangential diameter, and length/width ratio of conifer tracheids. Canad. J. Bot. 43: 967–984.

Bartholin, T. 1979. The *Picea-Larix* problem. IAWA Bull. n.s. 1: 7–10.

Cutler, D.F., P.J. Rudall, P.E. Gasson & R.M.O. Gale. 1987. Root identification manual of trees and shrubs. Chapman and Hall, London.

De Bary, A. 1884. Comparative anatomy of the vegetative organs of the phanerogams and ferns. Clarendon Press, Oxford.

Denne, M.P. 1972. A comparison of root- and shoot-wood development in conifer seedlings. Ann. Bot. 36: 579–587.

Fayle, D.C.F. 1968. Radial growth in tree roots. Technical Report 9. Faculty of Forestry, University of Toronto.

Gale, R. & D. Cutler. 2000. Plants in Archaeology: Identification manual of vegetative plant materials used in Europe and the southern Mediterranean to c. 1500. Westbury Publishing & Royal Botanic Gardens, Kew.

García Esteban, L., P. de Palacios de Palacios, A. Guindeo Casasus, Ly. García Esteban, I. Lazaro Duran, L. Gonzalez-Fernandez, Y. Rodriguez Labrador, F. Fernandez Garcia, I. Bobadilla Maldonado & A. Comacho Atalya. 2002. Anatomia e identificacion de maderas de coniferas a nivel de especie / Anatomy and identification of conifers wood as a species. Fundacion Conde Del Valle De Salazar. Ediciones Mundi-Prensa.

Greguss, P. 1955. Identity of living gymnosperms on the basis of xylotomy. Akademiai Kiado, Budapest.

IAWA Committee. 2004. IAWA list of microscopic features for softwood identification (eds. H.G. Richter, D. Grosser, I. Heinz & P.E. Gasson). IAWA J. 25: 1–70.

Metcalfe, C.R. & L. Chalk. 1983. Anatomy of the dicotyledons. Vol. 2. Wood structure and conclusion of the general introduction. Ed. 2. Clarendon Press, Oxford.

Patel, R.N. 1965. A comparison of the anatomy of the secondary xylem in roots and stems. Holzforschung 19: 72–79.

Phillips, E.W.J. 1948. Identification of softwoods by their microscopic structure. D.S.I.R. Forest Products Research Bulletin No. 22.

Schweingruber, F.H. 1993. Morphological, anatomical and tree-ring analytical characteristics of trees frequently used in dendrochronology. Springer Series in Wood Science, Springer-Verlag, Berlin, Heidelberg.