

## COMPARATIVE WOOD ANATOMY OF PERENNIAL SHOOTS OF *POTENTILLA* (ROSACEAE)

A. Stepanova<sup>1,\*</sup>, E.S. Chavchavadze<sup>1</sup> and S. Jansen<sup>2</sup>

### SUMMARY

The wood anatomy of perennial shoots of 26 *Potentilla* species was studied using light and scanning electron microscopy. Secondary xylem of different growth forms was compared. The wood anatomy of perennial shoots of *Potentilla* species with growth forms intermediate between shrubs and herbs (except *P. biflora* and *P. palustris*) is similar to the wood anatomy of shrubs. Wood anatomy of herbaceous species is diverse, and some features have systematic significance. Parenchymatisation and the anatomical changes correlated with this process appear to be a general trend in the structure of secondary xylem in rhizomes of herbaceous *Potentilla*. This trend may also be common in rhizomes of other herbaceous plants, and further studies are required to investigate this.

**Key words:** *Potentilla* L., growth forms, herbaceous plants, perennial shoots, rhizomes, wood anatomy.

### INTRODUCTION

*Potentilla* L. is a relatively large genus (>300 species) in Rosaceae, including many herbs and few shrubs. The genus is broadly distributed in the northern hemisphere, covering a variety of habitats such as steppes, forests, mountains, and (sub)alpine areas. The latest worldwide monographic treatment of *Potentilla* was published in 1908 by Wolf. According to his classification *Potentilla* comprises 305 species arranged into 31 groups, which were interpreted as sections in later taxonomic treatments. Considerable support for Wolf's (1908) classification was found based on morphological characters (e.g. Golubev 1965; Zhitkov 1972; Panigrahi & Dixit 1985; Sojak 1987; Leht 1996), but recent studies using molecular evidence suggest that *Potentilla* is probably polyphyletic (Eriksson *et al.* 2003). The taxonomy of the genus is complex and most likely influenced by hybridisation and apomixis (Leht 1996; Kurtto & Eriksson 2003).

Most authors who investigated growth forms of *Potentilla* agree that the transformation from shrubs to herbs is a general evolutionary trend within the genus (Golubev 1965; Zhitkov 1972). Apart from perennial herbs and shrubs, *Potentilla* includes several species with growth forms that are intermediate between shrubs and perennial herbs. These intermediate growth forms show woody procumbent perennial stems or erect stems that are woody and perennial at the base only and are either underground

---

1) Komarov Botanical Institute RAS, Prof. Popov str. 2, St-Petersburg, 197376, Russia.

2) Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3DS, United Kingdom.

\*) Corresponding author [E-mail: stepanovabot@mail.ru].

or aboveground. The varying position of these perennial parts with regenerating buds frequently makes classification of such growth forms difficult. For example, *P. palustris* has been described as woody, semi-woody, and herbaceous.

The secondary xylem of herbaceous shoots often shows various characters that are rare in woody plants, for instance scalariform vessel pitting, very long vessel elements, raylessness, rays exclusively composed of erect cells, and the absence of fibres (Carlquist 1962; Shul'kina & Zykov 1980). Carlquist (1962, 2001b) explains the distribution of these characters based on his theory of paedomorphosis, suggesting that these unusual wood features can be considered as prolongations from the primary into the secondary xylem. This hypothesis was based on changes of vessel element length with age of stem. According to Carlquist (1962, 2001b) paedomorphosis is more closely associated with the growth form of particular plants rather than their systematic position and is common in herbaceous and herb-like plants, such as succulents, rosette trees and shrubs. However, there are relatively few studies of the anatomy of perennial shoots of herbs (e.g. Carlquist 1962, 1966, 1983, 2001a; Cumbie & Mertz 1962; Shul'kina & Zykov 1980; Carlquist & Eckhart 1984).

In a broad sense, all perennial underground shoots that do not develop into tubers, corms, stolons or bulbs can be defined as rhizomes, which are widespread among herbaceous angiosperms. Most wood anatomical information on rhizomes is based on transverse sections and can be found in literature from the end of the 19<sup>th</sup> and the first decades of the 20<sup>th</sup> century (Costantin 1883; Eames 1911; Jeffrey 1917; Radkevich 1926, 1928). Compared to annual aboveground shoots of herbs, rhizomes usually have more parenchyma cells and fewer fibres in their xylem. Broad rays composed of large unlignified cells, which are similar to parenchyma cells in the pith and cortex, are commonly present in rhizomes (Costantin 1883), although this is not always the case (Eames 1911; Jeffrey 1917). Moreover, tangential parenchyma bands are sometimes present in the rhizome wood (Radkevich 1926, 1928).

Little is known about the wood anatomy of rhizomes of *Potentilla*. Previous studies on the comparative wood anatomy of Rosaceae do not report in detail on the anatomy of *Potentilla*, and most studies include only brief descriptions of *P. fruticosa* and *P. caulescens* (e.g. Schweingruber 1990; Zhang 1992). The aim of this paper is to investigate wood anatomical features of perennial shoots of 20 herbaceous species of *Potentilla*. These features will be compared to perennial shoots of two shrubs and a few intermediate growth forms included in *Potentilla*. This paper is part of a project focussing on the evolutionary trends of the wood structure of perennial shoots in herbaceous plants.

## MATERIALS AND METHODS

Twenty-six species of *Potentilla* were investigated, including 2 shrubs (*P. fruticosa* and *P. salesowiana*), 20 species of perennial herbs, and 4 species that are intermediate forms between shrubs and herbs (*P. biflora*, *P. bifurca*, *P. palustris*, and *P. tridentata*). The herbaceous species represented various sections within the genus and 11 groups according to Wolf's (1908) classification, and the shrubs and species with intermediate growth forms belonged to five groups in Wolf's system. The material investigated represented

all the ecological areas *Potentilla* grows in and included all architectural models described for the genus. The sympodial and monopodial rosette models characterise all herbaceous species, while the two sympodial models with perennial shoots characterise shrubs and intermediate forms, except for *P. biflora* (Table 1). The latter species showed a monopodial rosette model similar to the majority of perennial herbs of *Potentilla*.

Table 1. List of *Potentilla* species investigated with reference to their systematic position following Wolf (1908), growth form, architectural model, their origin and collector if known. — GF: Growth form: S = shrub; H = perennial herb; I = growth form intermediate between shrub and herb. — AM: Architectural model: 1 = monopodial rosette, 2 = sympodial rosette, 3 = sympodial rosette-less. — Origin: LE = herbarium of the Komarov Botanical Institute RAS (Russia); LECB = herbarium of St-Petersburg State University (Russia). — Collector: ? = unknown.

Species (number of specimens studied)	Group (acc. to Wolf 1908)	GF	AM	Origin	Collector
<i>P. acaulis</i> L. (1)	Aureae	H	1	LECB	?
<i>P. alba</i> L. (2)	Fragariastra	H	1	LECB	?, Minjaev
<i>P. arguta</i> Pursh (1)	Rupestres	H	2	LE	?
<i>P. biflora</i> Willd. (1)	Biflorae	I	1	LE	V. Sapozhnikov
<i>P. bifurca</i> L. (3)	Bifurcae	I	3	LE	?
<i>P. brachypetala</i> Fischer <i>et</i> Mey. (1)	Crassinerviae	H	1	LECB	N. Desulavi
<i>P. crantzii</i> (Crantz) Becker (1)	Aureae	H	1	LE	A. Stepanova
<i>P. divina</i> Alb. (2)	Speciosae	H	1	LECB	N. Desulavi, I. Gladkov
<i>P. elatior</i> Willd. <i>ex</i> Schlecht. (3)	Eriocarpace	H	1	LE, LECB	U. Ivanenko, Petrova, S. Juzepchuk
<i>P. erecta</i> (L.) Hampe (1)	Tormentilla	H	1	LECB	?
<i>P. fruticosa</i> (L.) Rydb. (3)	Fruticosae	S	3	LE, LECB	A. Stepanova, N. Krylov
<i>P. haynaldiana</i> Jka (2)	Crassinerviae	H	1	LE	J. Dorfler
<i>P. lapponica</i> (F. Nyl.) Juz. (1)	Multifidae	H	1	LE	A. Stepanova
<i>P. micrantha</i> Ramon (1)	Fragariastra	H	1	LECB	V. Markovich
<i>P. palustris</i> Scop. (1)	Palustres	I	3	LECB	?
<i>P. raddeana</i> Juz. (1)	Persicae	H	1	LECB	S. Juzepchuk
<i>P. recta</i> L. (2)	Rectae	H	2	LECB, ?	M. Sokurova, ?
<i>P. reptans</i> L. (1)	Tormentilla	H	1	LECB	I. Borodin
<i>P. rupestris</i> L. (1)	Rupestres	H	2	LECB	V. Cinger
<i>P. ruprechtii</i> Boiss. (1)	Persicae	H	1	LECB	Forsh
<i>P. salesowiana</i> Steph. (2)	Palustres	S	3	LE	R. Kamelin, ?
<i>P. sericea</i> L. (2)	Multifidae	H	1	LECB	S. Juzepchuk, N. Krylov
<i>P. tanacetifolia</i> Willd. (1)	Tanacetifoliae	H	1	LECB	Abramova
<i>P. taurica</i> Willd. <i>ex</i> Schlecht. (1)	Rectae	H	2	LECB	S. Stuliva
<i>P. transcaspia</i> Th. Wolf (1)	Rectae	H	2	LECB	Zaleski
<i>P. tridentata</i> Ait. (1)	Tridentatae	I	3	LE	?

The specimens were collected from the herbarium of the St-Petersburg State University (LECB) and the herbarium of the Komarov Botanical Institute of the Russian Academy of Science (LE). Some samples were collected near St-Petersburg and in Cola Peninsula by the first author. Rhizomes were taken from mature plants more than three years old. One to three specimens were studied for each species. The wood samples were boiled in distilled water for softening and sectioned using a freezing microtome. Sections and macerations were prepared according to standard techniques (Jacenko-Hmelevskij 1954; Jansen *et al.* 1998). Light microscopic observations were carried out with an Olympus BX51 microscope and a ColorViewII digital camera (Soft Imaging System – Olympus GmbH). *Potentilla alba*, *P. divina*, *P. elatior*, *P. fruticosa*, *P. palustris* and *P. raddeana* were investigated by CLSM (Leica Microsystems Heidelberg GmbH). The following nine species were studied using scanning electron microscopy (SEM): *P. biflora*, *P. crantzii*, *P. elatior*, *P. haynaldiana*, *P. lapponica*, *P. rupestris*, *P. sericea*, *P. taurica*, and *P. tridentata*. Small blocks ( $\pm 3$  mm thick) were attached to stubs and coated with platinum using an EMITECH K550 sputter coater (Emitech Ltd., Ashford, U.K.). Observations were carried out with a Hitachi S-4700 field-emission SEM (Hitachi High Technologies Corp., Tokyo, Japan). Wood anatomical terms are used according to IAWA Committee (1989), but with minor changes. For example, the term “pseudo-scalariform pitting” was used according to Carlquist (2001b). We prefer to describe the tracheids in *Potentilla* as tracheids only, as it is difficult to conclude whether these are vasicentric or vascular tracheids.

## RESULTS

### Wood anatomy of perennial shoots from shrubs and intermediate forms of the genus *Potentilla*

*P. fruticosa* – Growth rings distinct, marked by one to four rows of radially flattened fibres, wider earlywood vessels, and marginal parenchyma (Fig. 1). Vessels numerous (from 655 to 966 per mm<sup>2</sup>), predominantly solitary and in oblique and tangential multiples, with an angular vessel outline. Mean vessel grouping index 1.5. Perforation plates simple, oblique to almost horizontal. Lateral wall pitting alternate, small to medium (4–10  $\mu$ m), round to angular, with narrow slit-like apertures; the pits between vessels and parenchyma cells slightly smaller than intervessel pits. Vessels narrow, mean tangential diameter of vessel lumina from 18 to 20  $\mu$ m. Mean vessel element length from 200 to 227  $\mu$ m; L/D ratio from 10 to 12. Imperforate tracheary elements thin- to thick-walled fibres with relatively narrow lumina (3–3.5  $\mu$ m) and simple or minutely bordered pits densely present in tangential and radial walls. Septate fibres rare. Axial parenchyma in strands of two lignified cells, scanty paratracheal, in marginal bands and diffuse. Rays numerous, 1-seriate (Fig. 2) to 3-seriate, composed of square cells and with slightly upright and slightly procumbent cells mixed throughout the ray.

*P. salesowiana* – Different from *P. fruticosa* by having slightly thinner fibre walls (1.2  $\mu$ m vs. 1.5  $\mu$ m in *P. fruticosa*).

*P. palustris* – Fibre walls slightly thinner than in *P. fruticosa*, growth rings (except the first) often very narrow, about two elements wide, and usually with indistinct

boundaries. Vessel elements with either simple or scalariform perforation plates. Scalariform perforations scarce, present in both wide and narrow vessels, usually with 2–5 bars (Fig. 3), and 1 or 2 branched bars. Intervessel pits minute (3–4  $\mu\text{m}$ ), sometimes coalescent. Rays almost exclusively uniseriate.

*P. bifurca* – Similar to *P. fruticosa* except for vessel outline, which is usually slightly angular to round, and fibres usually with distinctly bordered pits.

*P. tridentata* – Growth rings are faint to absent, vessel outline is usually slightly angular to round, fibres usually with distinctly bordered pits, and rays are exclusively uniseriate. Other characters similar to *P. fruticosa*.

*P. biflora* – Distinct from other species with an intermediate growth form. Growth rings, imperforate tracheary elements, narrow rays and axial parenchyma strands absent. Wood consists of vessel elements, fusiform parenchyma cells and broad rays. Vessels numerous and round in outline. Perforation plates simple and vessel wall pitting pseudo-scalariform (Fig. 4). Druses present in the broad ray cells.

### Wood anatomy of perennial shoots from perennial herbs of *Potentilla*

Growth rings distinct to faint or absent. The boundaries (continuous or interrupted) usually formed by differences in vessel diameter (Fig. 5), distribution of lignified cells, tangential bands of fusiform parenchyma cells (Fig. 6), and rarely by rows of radially flattened fibres or tracheids. Growth rings marked by continuous rows of radially flattened fibres and semi-ring porosity similar to *P. fruticosa* present in *P. arguta* (Fig. 7), *P. elatior* and *P. rupestris*. Growth rings usually absent if secondary xylem consists almost exclusively of vessel elements and parenchyma cells, as in *P. raddeana* (Fig. 8), *P. ruprechtii*, *P. taurica*, or if rare imperforate tracheary elements are included, as in *P. acaulis*, *P. reptans*, and one specimen of *P. sericea*.

Vessels numerous, mean number of vessels per  $\text{mm}^2$  from 225 in a specimen of *P. elatior* to 1,213 in *P. ruprechtii*. Earlywood vessels usually grouped in tangential, oblique or radial multiples, rarely in clusters. Latewood vessels mainly solitary. Mean vessel grouping index varying from 1 to 2. Vessel outline angular to oval and/or round. Round vessels are more common in samples that show a large number of parenchyma cells, while angular pores usually are more common in wood samples in which imperforate tracheary elements are abundantly present. Perforation plates exclusively simple, oblique (in very narrow vessel elements) to horizontal or almost horizontal (in relatively wide vessel elements). Lateral wall pitting alternate (*P. alba*, *P. micrantha*, *P. rupestris*) to pseudo-scalariform (*P. divina*, *P. raddeana*, *P. ruprechtii*, *P. sericea*) with a continuous range of intermediate forms (Fig. 9–13). If vessel pitting is alternate, intervessel pits are small to large in size (4–13  $\mu\text{m}$ ), round to angular with narrow, slit-like apertures; the pits between vessels and parenchyma cells are slightly smaller than the intervessel pits. If vessel pitting is pseudo-scalariform or intermediate, there are no differences between intervessel and vessel-parenchyma pits. Vessels narrow, mean tangential diameters of vessel lumina from 11  $\mu\text{m}$  in *P. ruprechtii* to 22  $\mu\text{m}$  in *P. brachypetala*. Mean vessel element length from 86  $\mu\text{m}$  in *P. acaulis* to 217  $\mu\text{m}$  in a specimen of *P. elatior*. The L/D ratio from 5.0 in *P. brachypetala* to 12.7 in *P. micrantha*.

Imperforate tracheary elements represented by fibres and tracheids. If fibres and tracheids are present in the same specimen, there can be two distinct categories, as in species of the Rectae and Fragariastra group, or, typical fibres, tracheids and intermediate forms, as in *P. arguta*, *P. erecta*, *P. reptans*, *P. rupestris* and *P. tanacetifolia* (Table 2). Fibres usually thin- to thick-walled with wide lumina (4–6  $\mu\text{m}$ ) and simple pits (sometimes minutely bordered). Mean fibre length from 200  $\mu\text{m}$  in *P. micrantha* to 350  $\mu\text{m}$  in a specimen of *P. elatior*; F/V ratio 1.4–2.1. Tracheids commonly very thick-walled, rarely thin- to thick-walled, with numerous distinctly bordered pits and narrow lumina (2–3  $\mu\text{m}$ ) (Fig. 14, 15). Mean tracheid length from 117  $\mu\text{m}$  in *P. acaulis* to 230  $\mu\text{m}$  in a specimen of *P. divina*; F/V ratio 1.3–1.7.

Axial parenchyma in strands of two cells or fusiform. Fusiform parenchyma cells with thin, un lignified walls present in most samples studied, except for *P. alba*, *P. arguta*, *P. divina*, *P. elatior*, *P. micrantha* and *P. rupestris*; they are arranged in one to several rows around broad rays and replace all other woody elements, excluding vessels and large rays. Tangential bands of fusiform parenchyma cells present in all species of the Rectae group investigated (*P. recta*, *P. taurica*, *P. transcaspia*). Height/width ratio of fusiform parenchyma cells can be similar to other xylem elements (fibres, tracheids, vessel elements), but commonly they are similar in size to fusiform cambium cells.

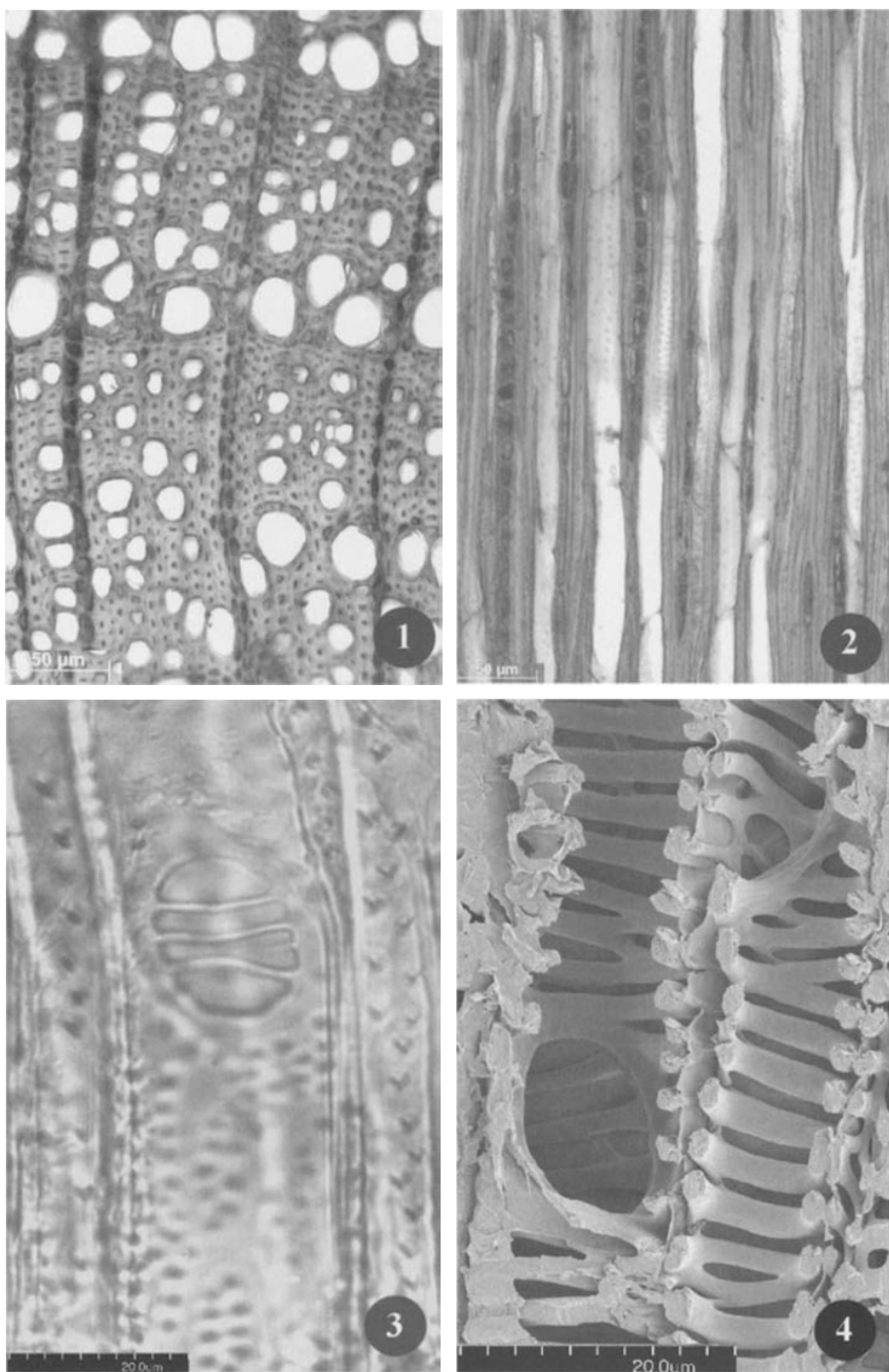
---

Figures 1–4. Perennial, aboveground shoots of shrubs and intermediate growth forms of *Potentilla*. – 1: *P. fruticosa*, LM, transverse section with distinct growth rings, solitary vessels, and thin- to thick-walled fibres with narrow lumina. – 2: *P. fruticosa*, LM, tangential longitudinal section showing 1–2-seriate rays. – 3: *P. palustris*, LM, tangential longitudinal section with a scalariform perforation plate and alternate vessel pitting. – 4: *P. biflora*, SEM, longitudinal section, pseudo-scalariform vessel pitting and simple perforation plates. — Scale bars for 1 & 2 = 50  $\mu\text{m}$ , for 3 & 4 = 20  $\mu\text{m}$ .

Figures 5–8. Transverse sections of rhizomes of herbaceous *Potentilla* species. – 5: *P. crantzii*, LM, growth ring marked by differences in vessel diameter. – 6: *P. recta*, LM, growth ring marked by tangential band of fusiform parenchyma cells. – 7: *P. arguta*, LM, growth ring marked by differences in fibre wall thickness and vessel diameter. – 8: *P. raddeana*, LM, growth rings absent. — All scale bars = 100  $\mu\text{m}$ .

Figures 9–13. Longitudinal sections showing pitting in tracheary elements in rhizomes of herbaceous *Potentilla* species. – 9: *P. rupestris*, SEM, detail of vessel pits. – 10: *P. elatior*, CLSM, alternate vessel pitting. – 11: *P. divina*, CLSM, pseudo-scalariform vessel pitting. – 12: *P. raddeana*, CLSM, pseudo-scalariform vessel pitting. – 13: *P. recta*, CLSM, vessel pitting intermediate. — Scale bars for 9 = 5  $\mu\text{m}$ , for 10–13 = 20  $\mu\text{m}$ .

Figures 14–17. Rhizomes of herbaceous *Potentilla* species. – 14: *P. haynaldiana*, SEM, longitudinal section showing wide vessel element with simple perforation plates on the left and narrow tracheids on the right. – 15: *P. brachypetala*, LM, transverse section showing numerous tracheids, which form most of the ground tissue elements. – 16: *P. alba*, LM, tangential longitudinal section with narrow rays (left and right) and a broad ray (centre) including druses. – 17: *P. recta*, LM, tangential longitudinal section with prismatic crystals in chambered parenchyma cells. — Scale bars for 14 & 17 = 50  $\mu\text{m}$ , for 15 = 100  $\mu\text{m}$ , for 16 = 200  $\mu\text{m}$ .



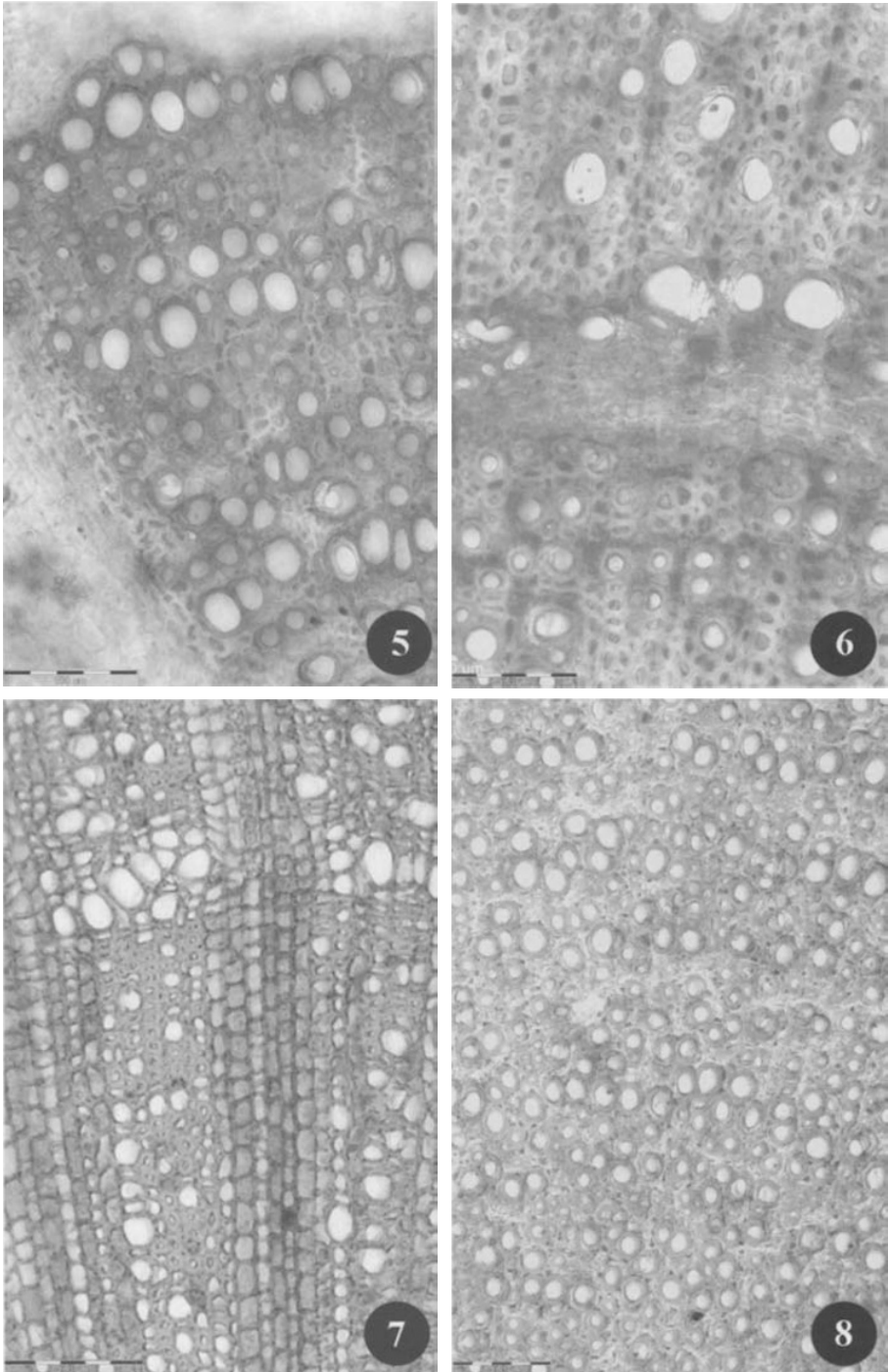


Figure 5–8. For legends, see page 410.



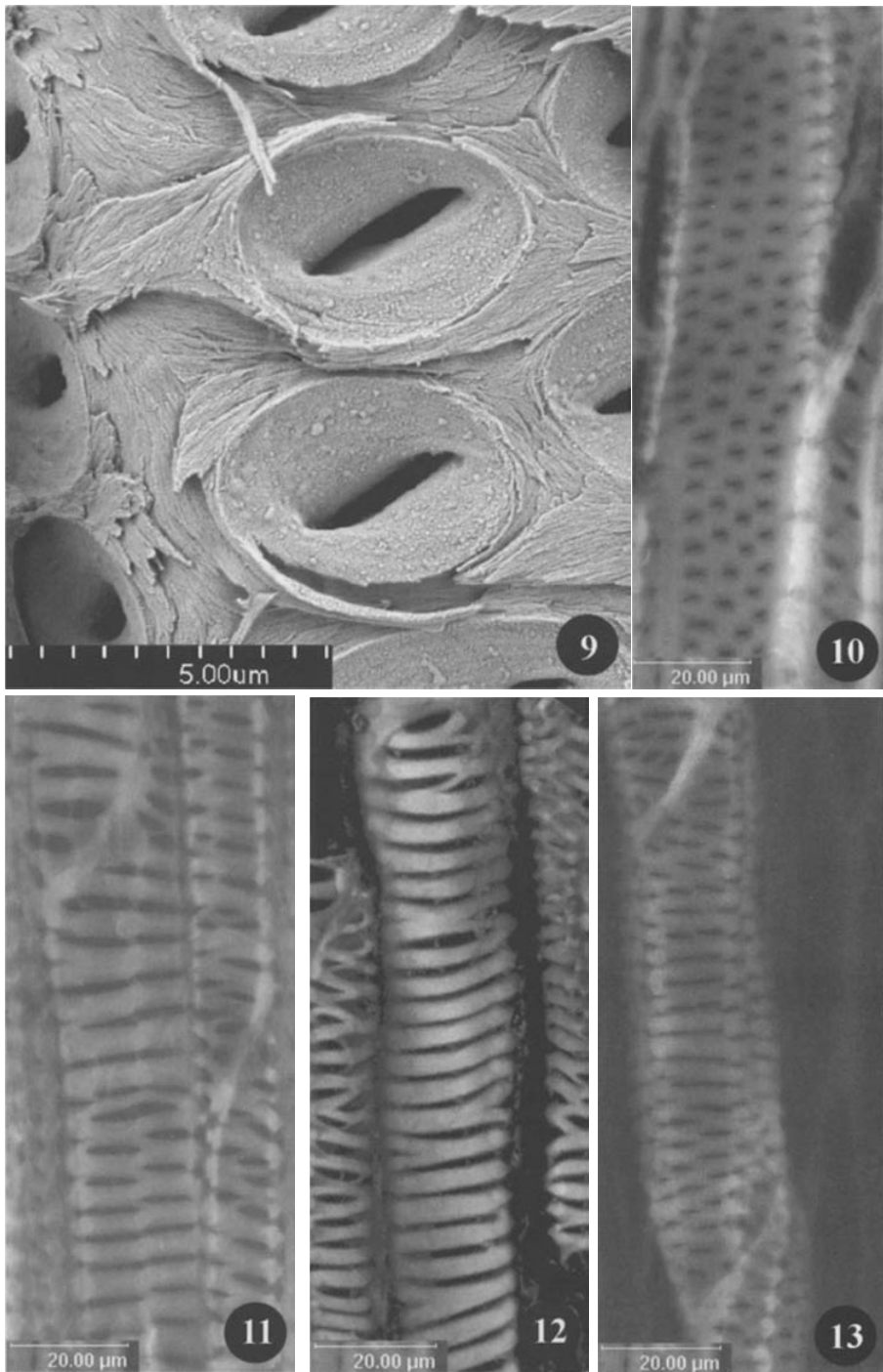


Figure 9–13. For legends, see page 410.

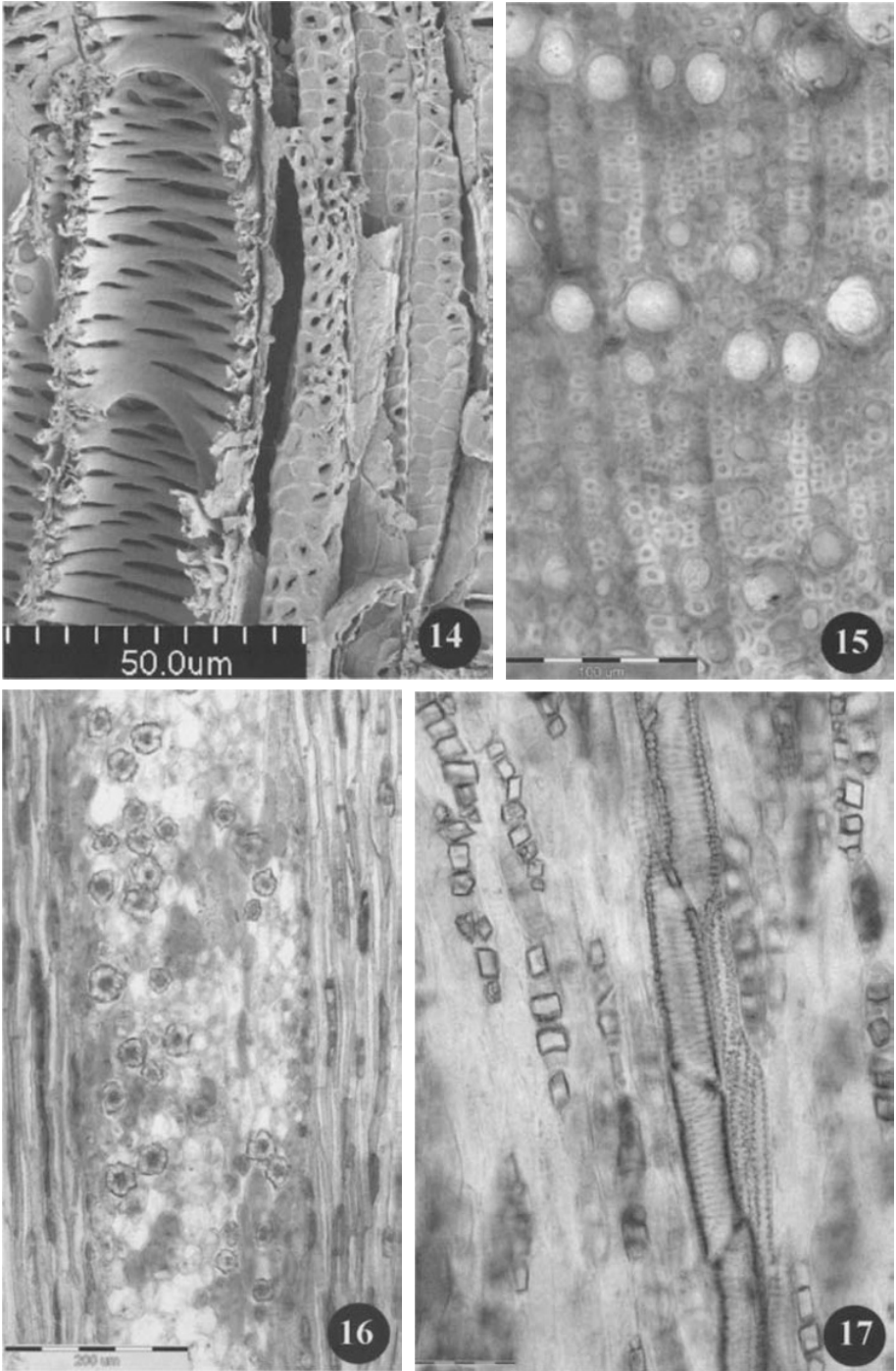


Figure 14–17. For legends, see page 410.

Parenchyma strands with lignified walls usually absent in wood with a high amount of fusiform parenchyma cells.

Rays of two distinct sizes (Fig. 16). Narrow rays generally uniseriate, composed of cells with lignified walls. Broad rays usually more than 10-seriate, composed of large, unligified cells. The form of the large ray cells usually square or slightly upright, with a low height/width ratio ( $< 2$ ). Aggregate rays observed in *P. rupestris* and *P. arguta* only. Narrow rays usually absent in species with abundant fusiform parenchyma cells.

Druses usually present in broad rays (Fig. 16) and in pith cells, sometimes abundant. The abundance of druses varies within a single species. In all species related to the Rectae group (*P. recta*, *P. taurica*, and *P. transcaspia*) chambered prismatic crystals present (Fig. 17).

## DISCUSSION

Rhizomes in *Potentilla* show a large wood anatomical variation in both qualitative and quantitative characters. Within *Potentilla*, it is clear that similarity of characters within the same group and within a single species shows that at least some features can be used for systematic purposes. However, the correlations of *Potentilla* wood anatomy with ecology are not obvious. Variation in vessel diameter in rhizomes of *Potentilla* does not correlate with humid or arid habitats as found in stem wood of many woody plants (*e.g.* Webber 1936; Baas *et al.* 2004).

It is difficult to determine whether the tracheids present in wood samples of *Potentilla* rhizomes containing both tracheids and libriform fibres (*P. alba*, *P. micrantha*, *P. recta*, *P. taurica*, *P. transcaspia*) are vasicentric or vascular. While most tracheids seem to be very similar to perforated elements (vessel elements), at least some have a vasicentric position. Within Rosaceae, vasicentric tracheids were observed in *Holodiscus*, *Prunus*, *Rosa*, and in few species in Prunoideae (Carlquist 1985; Carlquist & Hoekman 1985; Zhang 1992; Zhang & Baas 1992). These tracheids were mainly found in earlywood and were irregular in shape. Vascular tracheids integrating with narrow latewood vessel elements were observed within Rosaceae in *Lindleya* and *Sarcopoterium* (Zhang 1992).

The diversity of the rhizome wood structure is in general agreement with Wolf's (1908) system of the genus (Table 2). In many cases similar characters are found within one group and some interesting differences occur between various groups. The most distinct examples of qualitative features that are characteristic of particular groups include the composition of imperforate tracheary elements and the distribution of calcium-oxalate crystals. Fibres are mainly or exclusively present in *P. elatior*, which is a perennial herb, and in the two shrubs of *Potentilla* and in *P. palustris*. The latter species represents an intermediate growth form and is closely related to the shrub *P. salesowiana*. Tracheids are almost exclusively present in the herbaceous groups Aureae, Crassinerviae, Multifidae, Persicae, Speciosae, as well as in the monospecific group Biflorae. Moreover, species of the group Rectae and Fragariastra have both tracheids and fibres, which can easily be distinguished. The presence of chambered crystals appears to be characteristic of the Rectae group. This finding shows that mineral

Table 2. Summary of selected wood anatomical features of *Potentilla*. Imperforate tracheary element length could not be measured in *P. crantzii*, *P. raddeana*, *P. ruprechtii* and *P. reptans* as this cell type was rare in these species.

Group (following Wolf 1908)	Species	Growth rings <sup>1)</sup>	Density of vessels (per mm <sup>2</sup> )	Solitary vessel outline <sup>2)</sup>	Vessel member pits <sup>3)</sup>	Average tangential vessel diameter (µm)	Average vessel element length (µm)	L/D ratio of vessel elements	Average vessel wall thickness (µm)	Imperforate tracheary elements <sup>4)</sup>	Average length of imperforate tracheary elements (µm); * = data only for fibres	F/V ratio <sup>5)</sup>	Fusiform parenchyma cells <sup>6)</sup>	Broad rays <sup>7)</sup>	Narrow rays <sup>8)</sup>	Druses <sup>9)</sup>
<b>Shrubs</b>	Fruticoseae															
		<i>P. fruticosa</i> 1	2	745	1	1	20.5	199	9.8	1.5	1	323	1.6	0	2	0
		<i>P. fruticosa</i> 2	2	966	1	1	18.5	226	12.3	1.4	1	323	1.4	0	2	0
		<i>P. fruticosa</i> 3	2	655	1	1	18.1	226	12.5	1.6	1	355	1.6	0	2	0
Palustres	<i>P. salesowiana</i> 1	2	669	1	1	19.8	212	10.7	1.2	1	328	1.5	1	0	2	0
	<i>P. salesowiana</i> 2	2	759	1	1	16.8	194	11.5	1.2	1	271	1.4	1	0	2	0
<b>Intermediate growth forms</b>																
Biflorae	<i>P. biflora</i>	0	1336	3	4	11.2	105	9.3	2.6	3	143	1.4	3	1	0	1
	Bifurcae	<i>P. bifurca</i> 1	2	579	2	1	13.6	147	10.9	2	2	247	1.7	1	0	2
<i>P. bifurca</i> 2		2	600	2	1	15.6	163	10.5	1.7	2	226	1.4	1	0	2	0
<i>P. bifurca</i> 3		2	600	2	1	17.9	161	9	2.1	2	210	1.3	1	0	2	0
Palustres	<i>P. palustris</i>	2	545	1	1	20	176	8.8	1.1	1	278	1.6	1	0	2	0
	<i>P. tridentata</i>	0	497	2	1	16.7	177	10.6	3.1	2	291	1.6	1	0	2	0
<b>Herbaceous plants</b>																
Aureae	<i>P. acaulis</i>	0	775	2	2	12.2	85	6.7	3.3	3	117	1.4	1	1	1	1
	<i>P. crantzii</i>	1	998	2	3	16.3	136	8.4	3.1	3	-	-	2	1	0	1

Crassinerviae	<i>P. brachypetala</i>	1	549	3	3	22.1	111	5	3.6	3	177	1.6	1	1	1	1
	<i>P. haynaldiana</i> 1	1	640	3	3	19.2	115	6	3.4	3	170	1.5	1	1	1	1
	<i>P. haynaldiana</i> 2	1	518	3	3	17.7	127	7.2	2.9	3	180	1.4	1	1	1	1
Eriocarpace	<i>P. elatior</i> 1	2	299	1	2	20.7	170	8.2	2.1	1	268	1.6	0	1	2	1
	<i>P. elatior</i> 2	2	583	1	2	16.5	205	12.4	2.2	1	291	1.4	0	1	2	1
	<i>P. elatior</i> 3	2	225	1	2	19.2	216	11.3	2.5	1	350	1.6	0	1	2	1
Fragariastra	<i>P. alba</i> 1	1	991	1	1	14.1	160	11.3	2.1	2	246*	1.5	0	1	2	1
	<i>P. alba</i> 2	1	726	1	1	16.4	176	10.7	2.3	2	266*	1.5	0	1	2	1
	<i>P. micrantha</i>	1	834	1	1	11.3	144	12.8	1.9	2	200*	1.4	0	1	2	1
Multifidae	<i>P. lapponica</i>	1	679	3	3	14.1	148	10.5	3.2	3	207	1.4	1	0	1	0
	<i>P. sericea</i> 1	0	876	3	4	16.3	140	8.6	3.2	3	183	1.3	1	1	0	1
	<i>P. sericea</i> 2	1	716	3	4	13.9	102	7.3	2.9	3	158	1.5	1	1	0	1
Persicace	<i>P. raddeana</i>	0	919	3	4	16.6	115	7	3.5	3	—	—	2	1	0	1
	<i>P. ruprechtii</i>	0	1213	3	4	10.8	105	9.7	2.9	3	—	—	2	1	0	1
Rectae	<i>P. recta</i> 1	1	466	2	2	16.8	138	8.2	2.7	2	283*	2	0	1	1	1*
	<i>P. recta</i> 2	1	670	2	2	15.3	125	8.2	2.9	2	256*	2	0	1	1	1*
	<i>P. taurica</i>	0	759	3	3	16.3	126	7.7	3.2	2	199*	1.6	1	1	0	1*
	<i>P. transcaspia</i>	1	930	2	2	16.4	117	7.1	3.1	2	237*	2	0	1	1	1*
Rupestres	<i>P. arguta</i>	2	479	1	2	16.6	105	6.3	1.9	2	185	1.8	0	0	2*	0
	<i>P. rupestris</i>	2	621	1	1	16.3	136	8.4	1.9	2	215	1.6	0	0	2*	0
Speciosae	<i>P. divina</i> 1	1	709	3	4	14.8	136	9.2	2.5	3	213	1.6	0	1	1	1
	<i>P. divina</i> 2	1	858	3	4	12.5	138	11.1	2.8	3	230	1.7	0	1	1	1
Tanacetifoliae	<i>P. tanacetifolia</i>	1	439	2	2	13.7	107	7.8	3.0	2	206	1.9	1	1	1	1
Tormentilla	<i>P. erecta</i>	0	640	1	3	16.8	150	9	1.8	2	303	2	1	1	0	1
	<i>P. reptans</i>	0	858	2	3	18.2	124	6.8	3.2	2	—	—	2	1	0	1

1) Growth rings: 0 = absent; 1 = distinct to faint; 2 = distinct

2) Solitary vessel outline: 1 = angular; 2 = angular to round and/or oval; 3 = round and/or oval

3) Vessel member pits: 1 = exclusively alternate; 2 = alternate to intermediate; 3 = intermediate to pseudo-scalariform; 4 = exclusively pseudo-scalariform

4) Imperforate tracheary elements: 1 = mainly or exclusively fibres; 2 = fibres and tracheids 3 = mainly or exclusively tracheids

5) F/V ratio: average length of imperforate tracheary elements/average vessel element length

6) Fusiform parenchyma cells: 0 = absent or rare; 1 = abundant= 2 = replaces all elements, excluding vessels and large rays

7) Broad rays: 0 = absent; 1 = present

8) Narrow rays: 0 = absent; 1 = very rare, reduced to several cells; 2 = present; 2\* = aggregate rays are present

9) Druses: 0 = absent; 1 = present; 1\* = druses in chambered cells

inclusions may have good systematic significance for taxa including different growth forms. Noteworthy is that the distribution of druses is associated with the presence or absence of broad rays. If broad rays are absent, druses can be found in the pith cells of shrubs and most intermediate growth forms, or in large unligified cells, which are rarely present in aggregate rays within the herbaceous species of the Rupestres group. The largest variation in both qualitative and quantitative features is observed within the Tormentilla group, represented in this study by *P. erecta* and *P. reptans*. This may be explained by the nature of the perennial shoot in *P. erecta*, which is tuber-like.

The assumption that wood anatomy of rhizomes can reflect the phylogeny of a taxon finds support in agreement between our results and molecular data. Molecular phylogenies of *Potentilla* are poorly resolved and only based on a small number of species. Analyses based on sequences of the internal transcribed spacers (ITS) of nuclear ribosomal DNA and the *TRNL/F* region of chloroplast DNA placed *P. arguta*, *P. fruticosa*, *P. palustris*, *P. salesowiana*, and *P. tridentata* in a well-supported clade (Eriksson *et al.* 2003). This may suggest that *P. arguta* represents the most ancient group of herbaceous *Potentilla* species. Among all herbaceous species, *P. arguta* and *P. rupestris* are most similar in wood anatomy to the two shrubs within this genus (*viz.* *P. fruticosa*, *P. salesowiana*).

The wood anatomy of *Potentilla* species with intermediate growth forms (except for *P. palustris* and *P. biflora*) is similar to shrubs of *Potentilla*, although intermediate growth forms share features that are characteristic of herbaceous species. This means that the intermediate forms take an intermediate position in wood anatomy as well as in their general morphology. *Potentilla palustris* is the only species within *Potentilla* in which scalariform perforation plates are sometimes present. This feature might be explained by this species' distribution in swamps or other areas with high moisture availability. It supports general ecological trends of scalariform perforation plates, which have been preferentially retained in cool, mesic areas (Carlquist 1975, 2001b; Baas *et al.* 2004). Perennial shoots of *P. biflora* resemble rhizomes of herbaceous species that are most different from perennial shoots of shrubs. This similarity might be due to secondary woodiness in *P. biflora*. Characteristic features of secondary woodiness include pseudo-scalariform vessel pitting and the replacement of fibres by parenchyma cells (Carlquist 1962). In addition, the architectural model of *P. biflora* is similar to that of most herbaceous species. A high degree of parenchymatisation, however, can also be characteristic of cushion plants that have not necessarily evolved from herbaceous ancestors (Radkevich 1926; Mele 1968).

The variation found within *Potentilla* illustrates that individual characters or wood anatomical patterns cannot be used to distinguish herbaceous plants from woody ones. However, it is most likely that perennial shoots of different growth forms show different trends of wood specialisation, depending on functional and/or ecological adaptations of wood. Thus, the variation mainly reflects trends of specialisation and not separate, distinguishing characters *per se*.

The following wood anatomical trends appear to have evolved in perennial shoots of herbaceous *Potentilla* species during their specialisation towards herbaceousness: 1) the development of broad rays composed of large cells with unligified walls, 2) the

loss of distinct growth ring boundaries marked by rows of flattened elements, (3) the replacement of alternate by pseudo-scalariform vessel pitting, 4) the shift from an angular vessel outline to round and/or oval vessel outline, 5) a higher frequency of imperforate tracheary elements with relatively wide lumina and/or many pits, and 6) the replacement of imperforate tracheary elements, lignified cells of narrow rays, and lignified cells of axial parenchyma strands by fusiform parenchyma cells. These trends can be interpreted as functional adaptations of the perennial shoots, which in herbaceous plants are underground and therefore less subject to mechanical forces than perennial shoots of woody plants. Moreover, a high density of parenchyma cells in perennial shoots of herbaceous plants provides storage capacity. The occurrence of pseudo-scalariform pitting could be interpreted as a more efficient way to increase conductivity or lateral transport between vessels and neighbouring parenchyma cells compared to alternate pitting (Orians *et al.* 2004, 2005; Ellmore *et al.* 2006). Anatomical changes such as the replacement of imperforate tracheary elements, narrow rays, or strands of axial parenchyma by fusiform parenchyma cells represent only one process in perennial shoots of herbaceous plants. Some wood anatomical features appear to be correlated with each other, especially with respect to the frequency of fusiform parenchyma cells. These characters include the occurrence of narrow rays, axial parenchyma strands, growth rings and vessel pitting. Parenchymatisation affects changes of the vessel outline from angular to round or oval as parenchyma cells surrounding vessels exert less mechanical tension than lignified elements.

This investigation underlines that for wood anatomical observations it is necessary to pay close attention to the general morphology and growth form of plants, as well as to the morphology of the investigated shoot. For example, tangential parenchyma bands are only present in perennial shoots of *Potentilla* species with a sympodial rosette architectural model. It is also possible that rhizomes are closer in their wood anatomical structure to perennial aboveground shoots with very short internodes than to annual shoots of herbs, or perennial shoots of woody plants with distinct, long internodes. Some wood anatomical characters observed in perennial shoots of herbaceous *Potentilla* species are present in other plants with various growth forms: rosette trees and shrubs (Carlquist 1962), semi-shrubs (Radkevich 1926, 1928), and cushion-like plants (Mele 1968). Usually all these shoots do not have distinct internodes as they are rosette shoots. It can be supposed that evolutionary trends of characters such as pseudo-scalariform vessel pitting and abundance of unligified parenchyma are common in rosette shoots. These characters have been described in a wide range of families (*e.g.* Asteraceae, Cactaceae, Caryophyllaceae, Crassulaceae, Fabaceae, Lobeliaceae, Piperaceae, Rosaceae), which illustrates convergent evolution of the wood structure in rosette shoots (Carlquist 1962, 1966; Mele 1968; Gibson 1978). There are several similarities between the wood anatomy of rhizomes and perennial roots, likely due to similarity in the function of secondary xylem in these organs. Growth rings are less distinct and both axial and ray parenchyma are more abundant in roots of trees than in trunks and branches (Metcalf & Chalk 1983; Cutler *et al.* 1987). These characters are also reported for perennial roots of herbs (Dietz & Ullmann 1997; Dietz & Fattorini 2002).

## ACKNOWLEDGEMENTS

We thank Prof. R.V. Kamelin and Dr. A.A. Oskolski (Komarov Botanical Institute, St-Petersburg) for useful suggestions and discussions. We are grateful to Dr. P. Gasson (RBG, Kew) for reading over this manuscript. CLSM figures were made by the optical research group of the Institute of Developmental Biology, Moscow. A research visit by the first author to the Jodrell Laboratory (RBG, Kew) was financially supported by a travel grant from the Ministry of Science and Education of the Russian Federation.

## REFERENCES

- Baas, P., F.W. Ewers, S.D. Davis & E.A. Wheeler. 2004. Evolution of xylem physiology. In: A.R. Hemsley & I. Poole (eds.), *The evolution of plant physiology: 273–295*. Elsevier Academic Press, Amsterdam.
- Carlquist, S. 1962. A theory of pedomorphosis in dicotyledonous woods. *Phytomorphology* 12: 30–45.
- Carlquist, S. 1966. Wood anatomy of Compositae: a summary with comments on factors controlling wood evolution. *Aliso* 6: 25–44.
- Carlquist, S. 1975. Ecological strategies of xylem evolution. Univ. California Press, Berkeley.
- Carlquist, S. 1983. Wood anatomy of Calyceraceae and Valerianaceae, with comments on aberrant perforation plates in predominantly herbaceous groups of dicotyledons. *Aliso* 10: 413–425.
- Carlquist, S. 1985. Vascentric tracheids as a drought survival mechanism in the woody flora of southern California and similar regions; review of vascentric tracheids. *Aliso* 11: 37–68.
- Carlquist, S. 2001a. Wood anatomy of the endemic woody Asteraceae of St. Helena I: phyletic and ecological aspects. *Bot. J. Linn. Soc.* 137: 197–210.
- Carlquist, S. 2001b. Comparative wood anatomy. Systematic, ecological and evolutionary aspects of dicotyledon wood. Ed. 2. Springer-Verlag, Berlin, Heidelberg.
- Carlquist, S. & V.M. Eckhart. 1984. Wood anatomy of Hydrophyllaceae. II. Genera other than *Eriodictyon*, with comments on parenchyma bands containing vessels with large pits. *Aliso* 10: 527–546.
- Carlquist, S. & D.A. Hoekman. 1985. Ecological wood anatomy of the woody southern Californian flora. *IAWA Bull. n.s.* 6: 319–347.
- Costantin, J. 1883. Etude comparée des tiges aériennes et souterraines des dicotylédones. *Annls Sci. Nat. Bot.* 16: 5–176.
- Cumbie, B.G. & D. Mertz. 1962. Xylem anatomy of *Sophora* (Leguminosae) in relation to habit. *Amer. J. Bot.* 49: 33–40.
- 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.
- Dietz, H. & M. Fattorini. 2002. Comparative analysis of growth rings in perennial herbs grown in an alpine restoration experiment. *Ann. Bot.* 90: 663–668.
- Dietz, H. & I. Ullmann. 1997. Age-determination of dicotyledonous herbaceous perennials by means of annual rings: exception or rule? *Ann. Bot.* 80: 377–379.
- Eames, A.J. 1911. On the origin of the herbaceous type in the angiosperms. *Ann. Bot.* 25: 214–224.
- Ellmore, G.S., A.E. Zanne & C.M. Orians. 2006. Comparative sectoriality in temperate hardwoods: hydraulics and xylem anatomy. *Bot. J. Linn. Soc.* 150: 61–71.
- Eriksson, T., M.D. Hibbs, A.D. Yoder, C.F. Delwiche & M.J. Donoghue. 2003. The phylogeny of Rosoideae (Rosaceae) based on sequences of the internal transcribed spacers (ITS) of nuclear ribosomal DNA and the trnL/F region of chloroplast DNA. *Int. J. Plant Sci.* 164: 197–211.



- Gibson, A.C. 1978. Dimorphism of secondary xylem in two species of cacti. *Flora* 167: 403–408.
- Golubev, V.N. 1965. Ecological-biological peculiarities of herbaceous plants and plant associations in forest steppe. Nauka, Moscow [In Russian].
- IAWA Committee. 1989. IAWA list of microscopic features for hardwood identification. *IAWA Bull.* n.s. 10: 221–331.
- Jacenko-Hmelevskij, A.A. 1954. Research and methods of anatomical investigation of woody plants. Izd. AN SSSR, Moscow [In Russian].
- Jansen, S., P. Kitin, H. De Pauw, M. Idris, H. Beeckman & E. Smets. 1998. Preparation of wood specimens for transmitted light microscopy and scanning electron microscopy. *Belg. J. Bot.* 131: 41–49.
- Jeffrey, E.C. 1917. The anatomy of woody plants. The University of Chicago Press.
- Kurto, A. & T. Eriksson. 2003. Generic delimitation and nomenclatural adjustments in *Potentilla* (Rosaceae). *Ann. Bot. Fennici* 40: 135–141.
- Leht, M. 1996. Cladistic analysis of the data published in “Monographie der Gattung *Potentilla*” by T. Wolf. *Proc. Estonian Acad. Sci. Biol.* 45: 171–180.
- Mele, L.S. 1968. The paedomorphosis in secondary wood of few cushion-plants from East Pamir. *Izv. AN Tadžikskoj SSR* 2: 19–23 [In Russian].
- Metcalfe, C.R. & L. Chalk. 1983. Anatomy of the Dicotyledons: wood structure and conclusion of the general introduction. Volume 2. Clarendon Press, Oxford.
- Orians, C.M., B. Babst & A.E. Zanne. 2005. Vascular constraints and long-distance transport in dicots. In: N.M. Holbrook & M.A. Zwieniecki (eds.), *Vascular transport in plants*: 355–371. Elsevier Academic Press, Amsterdam.
- Orians, C.M., M.M. van Vuuren, N.L. Harris, B.A. Babst & G.S. Ellmore. 2004. Differential sectoriality in long-distance transport in temperate tree species: evidence from dye flow, <sup>15</sup>N transport, and vessel element pitting. *Trees* 18: 501–509.
- Panigrahi, G. & B.K. Dixit. 1985. Systematics of the genus *Potentilla* L. (Rosaceae Juss.), its infrageneric classification and evolutionary trends. *Bull. Bot. Surv. India.* 27: 177–196.
- Radkevich, O.N. 1926. Development of sclerenchyma in axial organs of helophytes from Middle Asia. *Bjull. Sredne-Aziatskogo Gos. Univ.* 14: 145–160 [In Russian].
- Radkevich, O.N. 1928. Relation of soft and hard tissues in herbaceous and semi-shrubby helophytes from Middle Asia. *Izv. Gl. Bot. sada AN SSSR* 27: 420–450 [In Russian].
- Schweingruber, F.H. 1990. Anatomy of European woods. WSL, Birmensdorf, Verlag Paul Haupt, Bern, Stuttgart.
- Shul’kina, T.V. & S.E. Zykov. 1980. The anatomical structure of the stem in the family Campanulaceae s.str. in relation to the evolution of life forms. *Bot. Zhurn.* 65: 627–639 [In Russian].
- Sojak, J. 1987. Notes on *Potentilla*. IV. Classification of Wolf’s group “*Potentilla trichocarpae*”. *Candella* 42: 491–500.
- Webber, I.E. 1936. The woods of sclerophyllous and desert shrubs of California. *Amer. J. Bot.* 23: 181–188.
- Wolf, T. 1908. Monographie der Gattung *Potentilla*. *Biblioteca Botanica* 71.
- Zhang, S.-Y. 1992. Wood anatomy of the Rosaceae. *Blumea* 37: 81–158.
- Zhang, S.-Y. & P. Baas. 1992. Wood anatomy of trees and shrubs from China. III. Rosaceae. *IAWA Bull.* n.s. 13: 21–91.
- Zhitkov, V.S. 1972. Morphobiological features of monocarp shoots of cinquefoils (genus *Potentilla* L.). *Doklady TSKhA* 180: 243–249 [In Russian].

advertisement

## **Bibliography of Systematic Wood Anatomy of Dicotyledons**

by **Mary Gregory**

Jodrell Laboratory, Royal Botanic Gardens, Kew, United Kingdom

**IAWA Journal Supplement 1**, 1994, 265 pp. – ISBN 90-71236-22-6

Price : EUR or USD 60.00 (for Members of IAWA EUR or USD 25.00)\*

This comprehensive bibliography of wood anatomical literature covers the years 1900 to late 1993. Over 2,400 full references are included, arranged by author and cross references by family. Annotations indicate the type of information included in each paper and the genera covered. It provides an indispensable source of information for plant anatomists, taxonomists, palaeobotanists, archaeologists, and forest botanists.

The bibliography is prepared from the index to anatomical literature at the Jodrell Laboratory and based on the Kew Library collection of 120,000 books and 3,000 periodicals, supplemented by an extensive reprint collection and the scanning of abstracting journals, notably Forestry Abstracts. Mary Gregory has worked in the Jodrell Laboratory for over thirty years, and during most of that time has been responsible for maintaining the index to anatomical literature, taking over the task from Dr. Metcalfe, who started this index in the 1930s.

## **Wood Anatomy of the Sapindaceae**

by **René Klaassen**

**IAWA Journal Supplement 2**, 1999, 214 pp., illus. – ISBN 90-71236-40-4

Price: EUR or USD 45.00 (paperback)\*

This book comprises a comprehensive wood anatomical study of the chiefly tropical, but nearly cosmopolitan woody family of the Sapindaceae: the soap-berry family famous for its fruit trees (lychee, rambutan) and several commercial timbers (*e.g.*, *Pometia*). Full descriptions of 104 genera are given, as well as a synoptical key for their microscopic identification.

The wider affinities of the Sapindaceae family and a phylogenetic classification of all genera and tribes is discussed in the light of the wood anatomical diversity patterns. Moreover, ecological adaptations in the wood of the Sapindaceae have been analysed. Ninety light and scanning electron micrographs illustrate this unique monograph, indispensable in libraries specialising in tropical botany, systematics, or forest products.

---

To be ordered from: IAWA Office  
c/o Nationaal Herbarium Nederland / Leiden branch  
PO Box 9514 – 2300 RA Leiden – The Netherlands  
Fax: +31 71 5273511 — E-mail: [eevn@euronet.nl](mailto:eevn@euronet.nl)

---

\*) Excluding handling and postage