

## ANATOMICAL CHARACTERISTICS AND ECOLOGICAL TRENDS IN THE XYLEM AND PHLOEM OF BRASSICACEAE AND RESEDACEAE

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### SUMMARY

The xylem and phloem of Brassicaceae (116 and 82 species respectively) and the xylem of Resedaceae (8 species) from arid, subtropical and temperate regions in Western Europe and North America is described and analysed, compared with taxonomic classifications, and assigned to their ecological range. The xylem of different life forms (herbaceous plants, dwarf shrubs and shrubs) of both families consists of libriform fibres and short, narrow vessels that are 20–50 µm in diameter and have alternate vested pits and simple perforations. The axial parenchyma is paratracheal and, in most species, the ray cells are exclusively upright or square. Very few Brassicaceae species have helical thickening on the vessel walls, and crystals in fibres. The xylem anatomy of Resedaceae is in general very similar to that of the Brassicaceae. Vested pits occur only in one species of Resedaceae.

Brassicaceae show clear ecological trends: annual rings are usually distinct, except in arid and subtropical lowland zones; semi-ring-porosity decreases from the alpine zone to the hill zone at lower altitude. Plants with numerous narrow vessels are mainly found in the alpine zone. Xylem without rays is mainly present in plants growing in the Alps, both at low and high altitudes. The reaction wood of the Brassicaceae consists primarily of thick-walled fibres, whereas that of the Resedaceae contains gelatinous fibres. The frequency of sclereids in Brassicaceae bark is an indicator of ecological differences: sclereids are rare in plants from the alpine zone and frequent in plants from all other ecotones.

**Key words:** Xylem, phloem, herbs, shrubs, transect, climatic zones, ecological trends, Western Europe.

### INTRODUCTION

The families Brassicaceae and Resedaceae belong to the order Brassicales. Both families are botanically characterised and their position in the phylogenetic system of angiosperms is explained by Judd *et al.* (2002). The Brassicaceae include 350 to 400 genera and 3000 to 4000 species (distributed worldwide), whereas the Resedaceae consist of only 6 genera and 70 species (northern hemisphere) (Sitte *et al.* 2002; Judd

*et al.* 2002). The presence of glycosinolates and myrosin cells is characteristic of both families, whereas vessels with vestured pits are typical of the Brassicaceae. Intra-family classifications are mainly based on fruit shape, and on the shape and position of the embryo. Most species are herbaceous. Until now, only one xylem feature has been used for defining the family Brassicaceae: vestured pits (Judd *et al.* 2002; Sitte *et al.* 2002). Although numerous molecular biological studies concentrate on *Arabidopsis thaliana*, a large intrafamily analysis does not exist (Koch *et al.* 2003) and studies on some genera contradict the morphological classification (Sitte *et al.* 2002).

No wood anatomical feature at all appears to be characteristic of the Resedaceae.

Anatomical differences of the xylem between most genera and species of the Brassicaceae are not very well known, whilst characteristics of the bark are virtually unknown. Hollendonner (1909), Betts (1918), Rollins (1939) and Messeri (1938) described the vegetative anatomy of a few herbaceous plants, and of the dwarf shrub *Schouwia schimperi*, from the arid zone Fezzan in northern Niger. Metcalfe and Chalk (1950) summarised the vegetative anatomy based on slides at the Royal Botanic Gardens at Kew and from the Commonwealth Forestry Institute in Oxford (mostly annual shoots) and from literature. Some recent studies concentrated on *Arabidopsis thaliana* (Konratieva-Melville & Vodolazsky 1982; Lev-Yadun 1994; Dolan & Roberts 1995; Busse & Evert 1999; Chengsong *et al.* 2000). Carlquist (1971) characterised eighteen “woody insular representatives” belonging to seven genera from Macaronesia, mainly deriving from subtropical dry sites on the Canary Islands (*Crambe*, *Descurainia*, *Lepidium*, *Matthiola*, *Parolina*, *Sinapidendron*, and a shrub from Mexico: *Stanleya pinnata*). Wood anatomical descriptions of dwarf shrubs exist for Russia (Benkova & Schweingruber 2004: *Alyssum obovatum*, *Brassica oleracea*, *Cheiranthus cheirii*), for the Sahara and Sahel zone (Neumann *et al.* 2001 see Table 1, species from the Sahara) and for Western Europe (Schweingruber 1990: *Biscutella frutescens*, *Brassica oleracea*, *Cheiranthus cheirii*, *Erysimum mutabile*, *Ptilotrichum spinosum*, *Sinapidendron* sp., *Vella spinosa*).

Carlquist (1998) analysed the Resedaceae xylem for seven species (*Caylusea hexagyna*, *Ochradenus baccatus*, *Oligomeris linifolia*, *Reseda alba*, *R. crystallina*, *R. lutea*, *R. luteola*).

Neumann *et al.* (2001) studied three shrubs from arid African areas (*Randonia africana*, *Ochradenus baccatus*, *Reseda villosa*), Fahn *et al.* (1986) recorded the wood anatomy of the desert shrub *Ochradenus baccatus*, and Schweingruber (1990) studied the dwarf shrub *Reseda suffruticosa* and the hemicryptophyte *Reseda luteola* from Central and Southern Europe. According to Metcalfe and Chalk (1950) and Carlquist (1998), no family-specific characteristics are found in the xylem of Resedaceae.

Metcalfe and Chalk (1950) came to the very general conclusion that “the xylem structure appears to be related to the mechanical and physiological requirements of different species rather than to their taxonomic relationships”, whilst Carlquist (1971) attempted to interpret several features of subtropical Brassicaceae ontogenetically, taxonomically and ecologically. The vague statements are understandable because only a small number of species was studied, and the material analysed consisted of roots, rhizomes and shoots of different life forms from various sites. Ecological interpretations have not been made for the Resedaceae.

On the basis of new material, collected along ecological gradients (Schweingruber & Dietz 2001; Schweingruber 2001), I aimed to determine the features of xylem and phloem in the root-shoot transition (root collar) that are typical of Brassicaceae and Resedaceae. The anatomical variation was also analysed in relation to the various ecosystems in which species of the two families occur.

#### MATERIAL

The xylem of phloem of 116 and 82 species of Brassicaceae, respectively, as well as eight xylem samples of Resedaceae were studied. The samples were from chamaephytes (perennial herbaceous plants and dwarf shrubs whose buds survive a few centimetres above the ground and are often protected by snow cover), hemicryptophytes (perennial herbaceous plants whose buds survive directly above the ground) and therophytes (annual, herbaceous plants). Transverse sections of the root collar, rhizomes or stem bases were taken from all species. The plants were identified and ecologically allocated on the bases of Tutin *et al.* (1964), Weber (1976, 1987), Ozenda (1983), Hohenester and Weiß (1993), Schönfelder and Schönfelder (1997), Bramwell and Bramwell (2001), Lauber and Wagner (1998), and Aeschmann *et al.* (2004). Some species occurring over a wide ecological range were assigned to the zone where they are most frequent, even if the analysed plant did not come from that zone. I collected mainly in the Western European alpine range. Smaller collections come from the Rocky Mountains, USA, the Canary Islands, the Iberian Peninsula and Northern Africa (details are given in Table 1). Photographs of each species can be seen in <http://www.wsl.ch/dendro/xylemdb/index.ph>. The analysed species belong to the vegetation zones shown in Table 2.

The following climatic parameters characterise the provenance of the samples. The climate is characterised by the following mean July temperatures (warmest monthly temperature) and annual precipitation (mm):

*Hill zones of the Alps* — Temperate climate (<http://www.meteoschweiz.ch/de/index.shtml>):

Swiss Central plateau (300–700 m), meteorological station Bern, 570 m a.s.l.: 16 °C, 1029 mm.

Swiss central Alps (300–900 m), meteorological station Sion, 483 m a.s.l.: 16.5 °C, 599 mm.

Swiss southern Alps (200–1000 m), meteorological station Locarno-Monti, 270 m a.s.l.: 20.5 °C, 1669 mm.

*Arid zone* — Central Sahara, meteorological station El Golea, 394 m a.s.l. 34 °C, 63 mm (Ozenda 1983).

*Subtropical, arid zone* — Canary Islands 0–700 m, meteorological station Fanabe, Tenerife, 100 m a.s.l.: 24 °C, 100 mm (Schönfelder & Schönfelder 1997).

*Mediterranean zone* — 0–300 m, meteorological station Marseille, 0 m a.s.l. 28.3 °C, 500 mm.

*Montane zones of the Alps and the Canary Islands* — The climatic values lay in between the hill and subalpine zone.

Table 1. Analysed species in relation to life forms. — Ch = chamaephytes, G = geophytes, H = hemicryptophytes, T = therophytes), site conditions, altitude and provenance (ARG = Argentina, CH = Switzerland, D = Germany, F = France, I = Italy, P = Portugal, SL = Slovenia, SP = Spain, USA = United States of America [CO = Colorado, WY = Wyoming]). \* = native in Eurasia.

Species	part of plant	life form	site	altitude (m)	Locality
<b>Brassicaceae – alpine and subalpine zone of Western Europe and the Rocky Mountains, USA</b>					
<i>Arabis alpina</i> L., <i>alpina</i> , s.l.	root collar	H	ruderal	3150	Gomergrat, CH
<i>Arabis caerulea</i> All.	root collar	H	snow bed	2751	Piz Arina, Engadin, CH
<i>Arabis ciliata</i> Clairv.	root collar	H	rock	1700	Clavadel, Davos, CH
<i>Arabis subcortaria</i> Gren.	root collar	H	wet meadow	2200	Oberalp-Pass, CH
<i>Braya humilis</i> (C.A. Mey.) B. L. Rob.	root collar	H	alpine meadow	3700	Cottonwood Pass, CO, USA
<i>Capsella bursa-pastoris</i> (L.) Medik.	root collar	T	ruderal	2050	Fliela-Pass, Davos, CH
<i>Cardamine resedifolia</i> L.	root collar	H	alpine meadow	2100	Septimer, CH
<i>Cardaminopsis halleri</i> (L.) Hayek	root collar	H	alpine meadow	2200	Simplon, CH
<i>Draba aizoides</i> L.	root collar	Ch	rock	2100	Simplon, CH
<i>Draba aurea</i> Vahl	root collar	H	alpine meadow	3000	Monte Vista, CO, USA
<i>Draba crassifolia</i> Graham	root collar	H	alpine meadow	3500	Monte Vista, CO, USA
<i>Draba dubia</i> Suter	root collar	Ch	rock	2200	Lenzerheide, CH
<i>Draba siliquosa</i> M. Bieb.	root collar	H	meadow	3150	Gomergrat, CH
<i>Draba streptocarpa</i> A. Gray	root collar	H	alpine meadow	3702	Cottonwood Pass, CO, USA
<i>Erysimum capitatum</i> Greene	root collar	H	alpine meadow	2000	Klamath Lake, WY, USA
<i>Erysimum nivale</i> Rydb.	root collar	H	Abies forest	3500	Summitville, CO, USA
<i>Erysimum scoparium</i> Wettst.	root collar	H	alpine meadow	2200	Teide, Tenerife
<i>Kernera saxatilis</i> (L.) Sweet	root collar	H	volcanic ash	2300	Strela-Pass, Davos, CH
<i>Lepidium perfoliatum</i> L.	root collar	H	rock	3300	Monte Vista, CO, USA
<i>Lesquerella alpina</i> Watson	root collar	H	alpine meadow	3701	Cottonwood Pass, CO, USA
<i>Sisymbrium loeselii</i> L.	root collar	H	alpine meadow	3000	Monte Vista, CO, USA
<i>Smelowskia calycina</i> Mey.	root collar	H	ruderal	3703	Cottonwood Pass, CO, USA
<i>Thlaspi rotundifolium</i> (L.) Gaudin	root collar	H	alpine meadow	2600	Cottonwood Pass, CO, USA
<i>Thlaspi sylvium</i> Gaudin	root collar	H	snow bed	3099	Flimsenstein, CH
<b>Brassicaceae – montane zone of Western Europe</b>					
<i>Arabis hirsuta</i> (L.) Scop.	root collar	H	field	351	Tavernelle, Toscana, I
<i>Arabis hirsuta</i> (L.) Scop.	root collar	H	ruderal	1400	Monstein, Davos, CH
<i>Arabis turrita</i> L.	root collar	H	rock	900	Masun, SL

<i>Cardaminopsis arenosa</i> (L.) Hayek	root collar	H				600	Ljubljana, SL
<i>Cardaminopsis halleri</i> (L.) Hayek	root collar	H				1300	Vál Strona, Lombardia, I
<i>Dentaria enneaphyllos</i> L.	rhizome	G		meadow		1000	Les Rangier, Jura, CH
<i>Dentaria pentaphylla</i> L.	rhizome	G		<i>Fagus</i> forest		600	Lopper, Hergiswil, CH
<i>Ericastrum nasturtifolium</i> (Poir.) O.E. Schulz	root collar	H		rock		800	Ausserberg, VS, CH
<i>Erysimum rhaeticum</i> (Hornem.) DC.	root collar	H		rock		700	Teglio, Veltlin, I
<i>Erysimum virgatum</i> Roth s.l. (Polatschek)	root collar	H		river bed		1100	Strada, Unterengadin, CH
<i>Sisymbrium austriacum</i> (Willd.) O.E. Schulz	root collar	H		rock		1400	Benasque, Pyrenees, SP
<i>Sisymbrium sophia</i> L.	root collar	T		ruderal		900	Ausserberg, VS, CH
<i>Sisymbrium strictissimum</i> L.	root collar	H		ruderal		1300	Ramosch, GR, CH
<b>Brassicaceae – hill zone of Western Europe and Rocky Mountain steppe, perennial</b>							
<i>Alliaria petiolata</i> Cavara & Grande	root collar	H		forest border		600	Oggio Tessin, CH
<i>Alyssum montanum</i> L.	root collar	H		field		700	Luberon, F
<i>Alyssum parviflorum</i> Bieberstein	root collar	H		steppe		2750	Monte Vista, CO, USA
<i>Arabis hirsuta</i> (L.) Scop.	root collar	H		field		500	Serres, F
<i>Arabis rosea</i> DC.	root collar	H		rock		800	Spoletto, Umbria, I
<i>Arabis turrita</i> L.	root collar	H		forest border		600	Spoletto, Umbria, I
<i>Aubrieta deltoidea</i> (L.) DC.	rhizome	H		garden		500	Birmensdorf, ZH, CH
<i>Barbarea vulgaris</i> R. Br.	root collar	H		field		350	Randersacker, D
<i>Barbarea vulgaris</i> R. Br.	root collar	H		field		1550	Davos-Dorf, CH
<i>Berteroa incana</i> (L.) DC.	root collar	H		ruderal		10	Rendburg, D
<i>Bunias orientalis</i> L.	root collar	H		ruderal		350	Heidnigsfeld, Würzburg, D
<i>Calepina irregularis</i> (Asso) Thell.	rhizome	H		ruderal		600	Niaux, Ariège, F
<i>Cardamine bulbifera</i> (L.) Crantz	rhizome	H		rock		700	Serpiano, Meride TI, CH
<i>Cardamine flexuosa</i> With.	root collar	H		ruderal		450	Birmensdorf, ZH, CH
<i>Cardamine pratensis</i> L.	root collar	H		bog		200	Ljubljana, SL
<i>Cheiranthus cheirii</i> L.	root collar	Ch		rock		800	Erschmatt, VS, CH
<i>Ericastrum gallicum</i> (Willd.) O.E. Schulz	root collar	H		ruderal		450	Birmensdorf, ZH, CH
<i>Erysimum asperum</i> DC.	root collar	H		steppe		2752	Monte Vista, CO, USA
<i>Erysimum ochroleucum</i> (Schleich.) DC.	rhizome	H		rock		300	Auttun, Burgund, F
<i>Iberis sempervirens</i> L.	rhizome	Ch		cultivated		500	Grünigen, ZH, CH
<i>Lepidium campestre</i> (L.) R. Br.	root collar	H		ruderal		500	Serres, F
<i>Lepidium draba</i> L.	root collar	H		ruderal		350	Randersacker, D
<i>Lunaria annua</i> L.	root collar	H		moist canyon		400	Veneto, I
<i>Nasturtium officinale</i> R. Br.	root collar	H		wet meadow		600	Oggio Tessin, CH
<i>Rorippa austriaca</i> Besser	root collar	H		ruderal		300	Randersacker, D
<i>Sisymbrium altissimum</i> L.	root collar	H		ruderal		2753	Monte Vista, CO, USA

Species	part of plant	life form	site	altitude (m)	Locality
<i>Symbrium andinum</i> Phil.	root collar	H	rock	2700	Passo del Inqua, ARG
<i>Symbrium officinale</i> (L.) Scop.	root collar	H	ruderal	600	Grosotto, Veltlin, I
<i>Turritis glabra</i> L.	root collar	H	ruderal	2754	Monte Vista, CO, USA
<b>Brassicaceae – hill and montane zone of Western Europe, annual</b>					
<i>Alyssum alyssoides</i> L.	root collar	T	field	300	Ht. Provence, F
<i>Arabidopsis thaliana</i> (L.) Heynh.	root collar	T	field	450	Birmensdorf, ZH, CH
<i>Capsella bursa-pastoris</i> (L.) Medik.	root collar	T	ruderal	2050	Fliela-Pass, Davos, CH
<i>Capsella bursa-pastoris</i> (L.) Medik.	root collar	T	field	451	Birmensdorf, ZH, CH
<i>Cardamine hirsuta</i> L.	root collar	T	ruderal	500	Birmensdorf, ZH, CH
<i>Clypeola jonthlaspi</i> L.	root collar	T	field	600	Sion, VS, CH
<i>Erophila verna</i> (L.) Bess.	root collar	T	ruderal	502	Birmensdorf, ZH, CH
<i>Eruca sativa</i> L.	root collar	T	field	400	Garifia, La Palma*
<i>Homungia petraea</i> (L.) Rehb.	root collar	T	field	450	Martigny, VS, CH
<i>Lepidium densiflorum</i> Schrad.	root collar	T	ruderal	600	Grosotto, Veltlin, I
<i>Sinapis arvensis</i> L.	root collar	T	ruderal	500	Birmensdorf, ZH, CH
<i>Sinapis arvensis</i> L.	root collar	T	field	500	San José, Gran Canaria*
<i>Symbrium sophia</i> L.	root collar	T	ruderal	2700	Passo del Inqua, ARG*
<i>Thlaspi arvense</i> L.	root collar	T	ruderal	500	Birmensdorf, ZH, CH
<i>Thlaspi arvense</i> L.	root collar	T	field	1550	Davos, CH
<i>Thlaspi perfoliatum</i> L.	root collar	T	field	500	Fully, VS, CH
*) major distribution in the European hill zone.					
<b>Brassicaceae – subtropical montane Macaronesia</b>					
<i>Descurainia bourgaeana</i> O. E. Schulz	stem	Ch	volcanic rock	2200	Canadas, Tenerife
<i>Descurainia millefolia</i> Webb & Berth.	stem	Ch	volcanic rock	600	Carbonara, Tenerife
<i>Descurainia preauxina</i> Webb	stem	Ch	volcanic rock	1000	Barr. Guaydeque, Gran Canaria
<i>Erucastrum varium</i> Webb ex Christ	root collar	H	ruderal	1100	Chio, Tenerife
<i>Erysimum bicolor</i> (Hornem.) DC.	root collar	Ch	volcanic rock	1200	Ayacate, Gran Canaria
<i>Erysimum mutabile</i> Wettst.	stem	Ch	volcanic rock	1800	Pico Ruivo, Madeira
<i>Erysimum scoparium</i> Webb	stem	Ch	volcanic rock	2000	Canadas, Tenerife
<i>Lobularia canariensis</i> (DC.) Borgen	stem	Ch	rock	500	El Paso, La Palma
<b>Brassicaceae – Mediterranean or Western Europe</b>					
<i>Biscutella cichoriifolia</i> Lois.	root collar	H	rock	300	Luberon, F
<i>Diplotaxis tenuifolia</i> (L.) DC.	root collar	H	field	400	Vesime, Piemont, I

<i>Isatis tinctoria</i> L.	root collar	H	field	300	Roussion, F
<i>Matthiola</i> sp.	root collar	H	littoral	11	Algarve, P
<i>Ptilotrichium spinosum</i> (L.) Boiss.	stem	Ch	rock		Andalusia, SP
<i>Vella spinosa</i> Boiss.	stem	Ch	rock		Andalusia, SP
<i>Vella spinosa</i> Boiss. subsp. <i>lucentina</i> Boiss.	stem	Ch	rock	200	Andalusia, SP
<b>Brassicaceae – subtropical lowland, Macaronesia</b>					
<i>Lobularia canariensis</i> (DC.) Borgen	stem	H	rock	500	El Paso, La Palma
<i>Lobularia maritima</i> (L.) Desv.	root collar	H	rock	500	El Paso, La Palma
<i>Matthiola parviflora</i> R. Br.	root collar	T	ruderal	50	El Medano, Tenerife
<i>Notoceras bicorne</i> Willk. & Lange	root collar	H	ruderal	250	Maspalomas, Gran Canaria
<i>Parolinia intermedia</i> Svent. & Bramwell	stem	Ch	volcanic rock	300	Chio, Tenerife
<i>Parolinia ornata</i> Webb	stem	Ch	volcanic rock	300	Maspalomas, Gran Canaria
<i>Sinapidendron angustifolia</i> Link	stem	Ch	volcanic rock	51	Ribeira Brava, Madeira
<i>Sinapidendron frutescens</i> Link	stem	Ch	volcanic rock	50	Ribeira Brava, Madeira
<i>Sinapis flexuosa</i> Poir.	root collar	T	ruderal	450	Chio, Tenerife
<i>Sisymbrium irio</i> L.	root collar	H	ruderal	350	Llodosjanos, La Palma
<b>Brassicaceae – arid, warm desert, Sahara</b>					
<i>Anastatica hierochuntima</i> L.	root collar	T	sand desert		Sahara, Algeria
<i>Diplotaxis harra</i> (Forssk.) Boiss.	root collar	H	sand desert		Sahara, Algeria
<i>Farssetia</i> sp.	root collar	Ch	sand desert		Sahara, Algeria
<i>Farssetia aegyptica</i> Turra	root collar	Ch	sand desert		Sahara, Algeria
<i>Malcolmia aegyptica</i> Spr.	root collar	Ch	sand desert		Sahara, Algeria
<i>Moricandia arvensis</i> DC.	root collar	H	sand desert		Sahara, Algeria
<i>Oudneya africana</i> R. Br.	root collar	Ch	sand desert		Sahara, Algeria
<i>Zilla spinosa</i> (L.) Prantl	root collar	Ch	sand desert		Sahara, Algeria
<b>Resedaceae – from all studied regions</b>					
<i>Ochradenus baccatus</i> Del.	stem	Ch	desert		Sahara, Algeria
<i>Randonia africana</i> Coss.	stem	Ch	desert		Sahara, Algeria
<i>Reseda lutea</i> L.	root collar	H	ruderal	700	Postoina, SL
<i>Reseda luteola</i> L.	root collar	H	riparian	500	ToImezzo, Friaul, I
<i>Reseda luteola</i> L.	root collar	H	ruderal	1600	Pico Descada, La Palma
<i>Reseda phyteuma</i> L.	root collar	H	dry meadow	300	Luberon, F
<i>Reseda scoparia</i> Brouss.	stem	Ch	ruderal	50	Los Cristianos, Tenerife
<i>Reseda suffruticosa</i> Loefl.	stem	Ch	field	900	Sierra Cazorla, SP
<i>Reseda villosa</i> Coss.	root collar	Ch	field	1000	Quarzazat, Morocco

*Subalpine zones* — Swiss northern prealps (1300–1900 m), meteorological station Pilatus, 2106 m a.s.l.: 8 °C, 1953 mm (<http://www.meteoschweiz.ch/de/index.shtml>). Swiss central and southern Alps (1600–2200 m), meteorological station Zermatt, 1638 m a.s.l.: 12 °C, 612 mm (<http://www.meteoschweiz.ch/de/index.shtml>). Colorado, USA (2400–3300 m) near lower timberline, meteorological station Buena Vista, 2400 m: 27.7 °C, 310 mm (<http://www.wrcc.dri.edu:80/cgi-bin/cliMAIN.pl?cobuen>). Colorado, USA (2400–3300 m) near upper timberline, meteorological station Wolf Creek pass, 11.8 °C, ? (<http://www.wrcc.dri.edu:80/cgi-bin/cliMAIN.pl?cobuen>). Tenerife, Canary Islands (1700–2200 m), meteorological station Las Mercedes, 24 °C, 900 mm (Schönfelder & Schönfelder 1997).

Table 2. Number of microscopically analysed species, studied from different vegetation zones.

Family: vegetation zone	Number of species studied		
	xylem transverse	longitudinal	phloem transverse
<b>Brassicaceae:</b>			
alpine/subalpine	24	12	20
montane	13	6	10
hill zone, perennial	29	20	25
hill zone, annual	16	6	13
Mediterranean	8	6	5
arid, warm	8	6	0
subtropical montane	8	7	6
subtropical lowlands	10	8	3
<b>total</b>	<b>116</b>	<b>71</b>	<b>82</b>
<b>Resedaceae:</b>			
<b>all regions studied</b>	<b>8</b>	<b>4</b>	<b>1</b>

## METHODS

Most samples were stored in 40% alcohol before being sectioned with a sliding microtome. The sections were stained with safranin (alcohol-preserved material) or astrablue/safranin (wet material), dehydrated with alcohol and xylene, and mounted in Canada balsam (Chaffey 2002). I used normal transmitted light and polarised light for the microscopic analysis (Olympus BX51). Digital photographs were taken with an Olympus 5005.

The anatomical descriptions were carried out on the basis of the IAWA list of microscopic features for hardwood identification (Wheeler *et al.* 1989). As this list is intended for tree and shrub wood, it had to be slightly modified. I added the following terms for the xylem classification:



- 2.1: Only one growth ring present. This feature was used for annual herbaceous plants and perennial specimens that did not show any annual growth ring delimitation.
- 4: The term “semi-ring-porous” was used in a very strict sense. When the average ratio of the vessel diameter between latewood and earlywood exceeded 1 : 3, I called it semi-ring-porous (Fig. 4).
- 5.1: The vessels cannot be distinguished from the ground tissue (fibres, fibre tracheids and/or parenchyma) in transverse section only (Fig. 5).
- 9.1: Vessels in short radial multiples (2–4 vessel elements).
- 40.1: Tangential diameter of vessels <20 µm (Fig. 4).
- 40.2: Tangential diameter of vessels: 20–50 µm.
- 50.1: Number of vessels per square millimetre in the earlywood: 100–200.
- 50.2: Number of vessels per square millimetre in the earlywood: 200–500.
- 70.1: Intra-annual tangential fibre bands (Fig. 6 & 14).
- 89.1: Very thin-walled marginal parenchyma; cells without secondary walls. The parenchyma appears dark under polarised light (no birefringence) (Fig. 7 & 8).
- 89.2: Ring shake. Rings break easily along the ring boundary (Fig. 9).
- 99.1: Incomplete formation of a xylem ring; perennial vascular bundles (Fig. 10 & 11).
- 100.1: Rays intergrading with fibre tissue (Fig. 12).

Vestured pits (feature 29; Fig. 1) were frequently observed, but the quality of the slides and the microscopic optics (objective lens ×1000), even with green filters, were not sufficient for the conclusive evaluation of all specimens.

In addition, I added some characteristics of the bark/phloem classification of the Brassicaceae to the IAWA list:

- B1: Groups of sieve tubes present (Fig. 13).
- B2: Groups of sieve tubes in tangential rows (Fig. 14).
- B3: Distinct ray dilations (Fig. 15), defined by Trockenbrodt 1990.
- B4: Sclereids present in the phloem (Fig. 16), defined by Trockenbrodt 1990.
- B5: Sclereids present in the cortex, defined by Trockenbrodt 1990.
- B6: Sclereids present in radial rows (Fig. 16).

## RESULTS

### Family characteristics of Brassicaceae xylem

All species contained fibres with reduced pit borders (<3 µm) with round to slit-like apertures on radial and tangential walls (libriform fibres). All transitions between pits with almost missing pit borders, e.g. *Draba* sp., and those with very distinct pit borders, e.g. *Berteroa incana*, were found. Unlignified walls without secondary cell walls, for example in alpine plants, had no or invisible pits.

In most species, fibre walls are fairly thin, but the family also contains species with extremely dense xylem consisting of very thick-walled fibres. The dwarf shrubs *Descurainia millefolia* and *D. preauxina* (Fig. 3) from the Canary Islands have extremely thick-walled and intensively lignified fibres. The specific weight in these species aver-

*(text continued on page 432)*

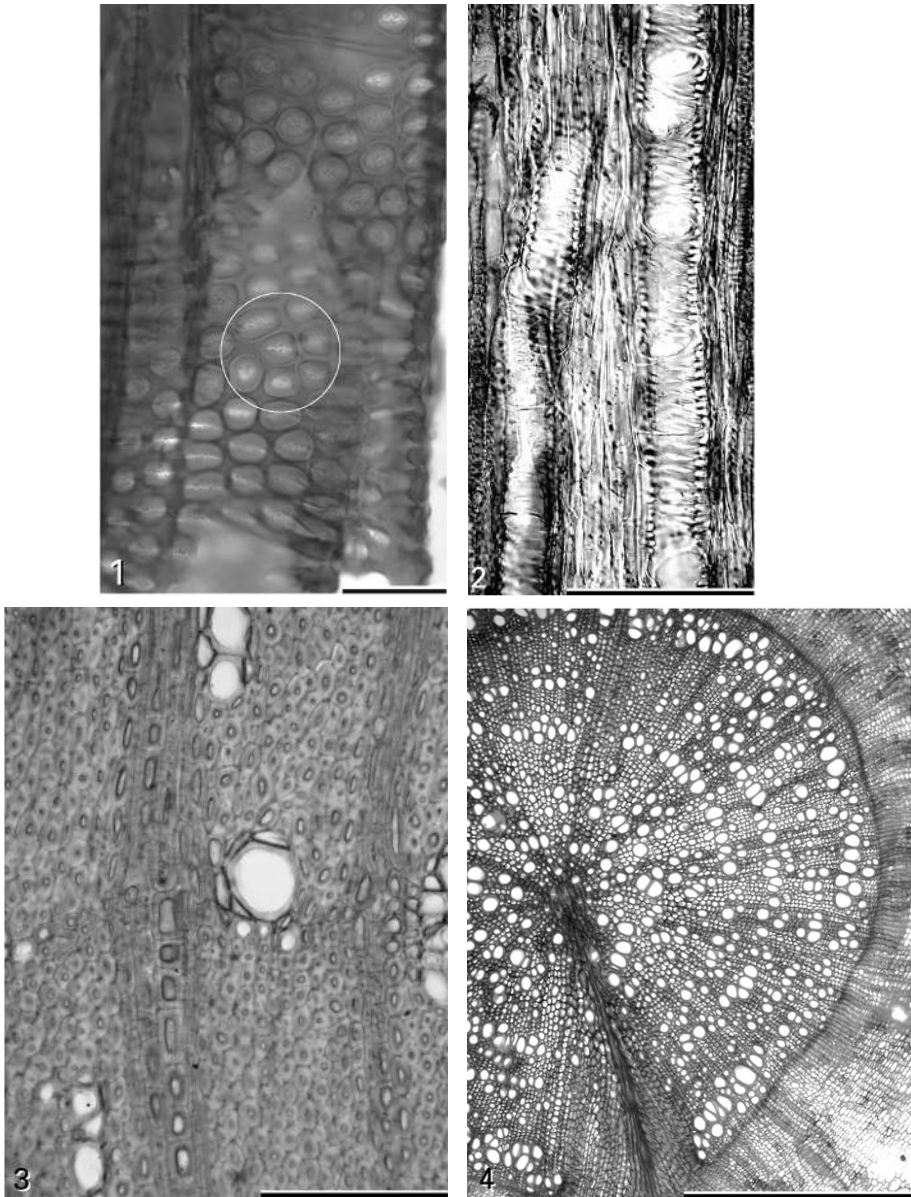


Fig. 1. Vestured inter-vessel pits in the xylem of the chamaephyte *Cheiranthus cheirii*, from a dry site in the Valais, Switzerland. — Fig. 2. Short vessel elements with small diameters and simple perforations and gash-like pit apertures. Chamaephyte *Cheiranthus cheirii*, from a dry site in the Valais, Switzerland. — Fig. 3. Scanty paratracheal parenchyma between very thick-walled fibres in the dwarf shrub *Descurainia preauxina*, from the montane zone of the Canary Islands. — Fig. 4. Semi-ring-porous xylem with a very large ray or a lateral shoot of a 5-cm-tall hemicytrophite, *Thlaspi rotundifolium*, from the alpine zone of the Swiss Alps. — Scale bar for 1 = 10  $\mu\text{m}$ , for 2 & 3 = 100  $\mu\text{m}$ , for 4 = 500  $\mu\text{m}$ .

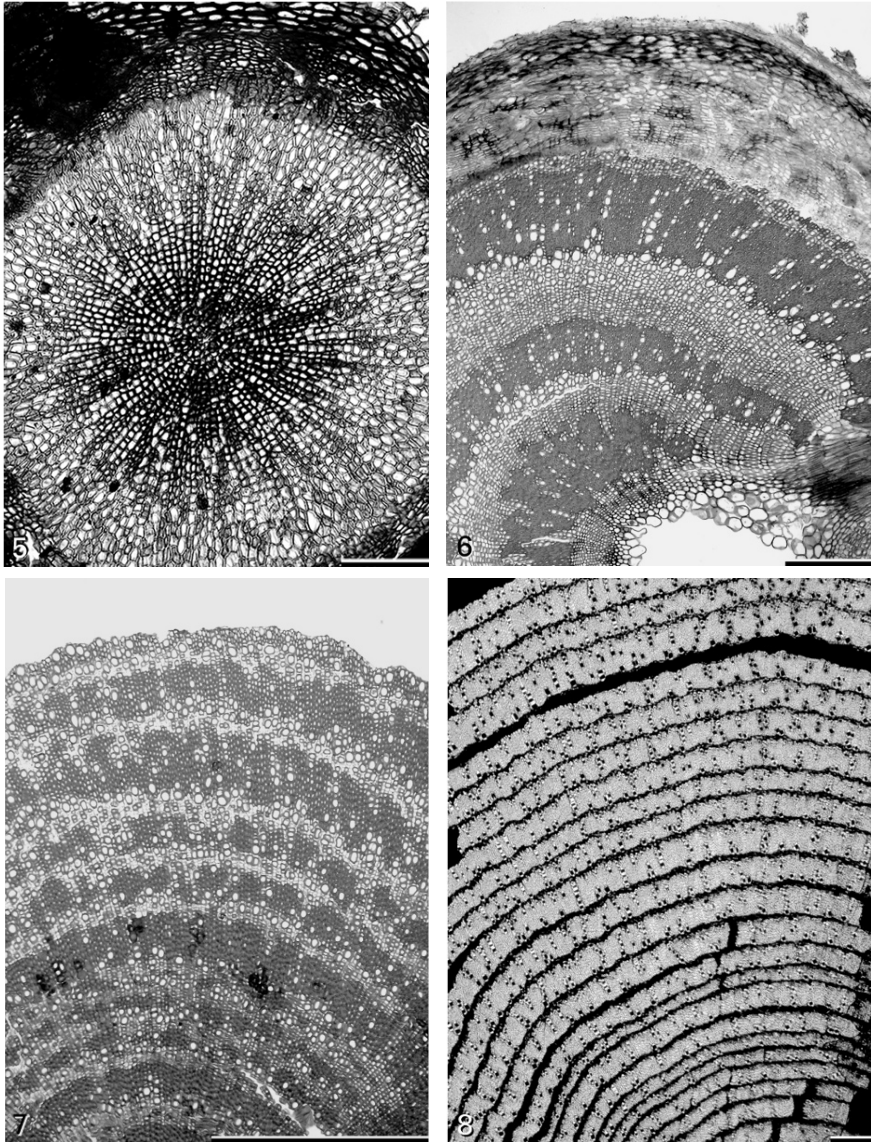


Fig. 5. Vessels, fibres and ray cells have almost the same diameter. Therefore it is difficult to distinguish them in the cross section. Root collar of a 6-cm-tall therophyte, *Erophila verna*. — Fig. 6. Intra-annual bands of thick-walled fibres in the root collar xylem of the cushion-shaped hemicyptophyte *Arabis ciliata* from the subalpine zone of the Swiss Alps. — Fig. 7. Thin-walled, hardly lignified marginal parenchyma in the xylem of a 5-cm-tall hemicyptophyte, *Arabis alpina*, growing in a snow bed in the alpine zone of the Swiss Alps. Locally, thin-walled parenchyma cells are also present between earlywood vessels and fibres. — Fig. 8. Thin-walled, marginal parenchyma in the very dense xylem of the dwarf shrub *Ptilotrichium spinosum*, growing on limestone rocks in the Mediterranean zone in the south of Spain. Polarised light. — Scale bar for 5 = 50  $\mu\text{m}$ , for 6–8 = 500  $\mu\text{m}$ .



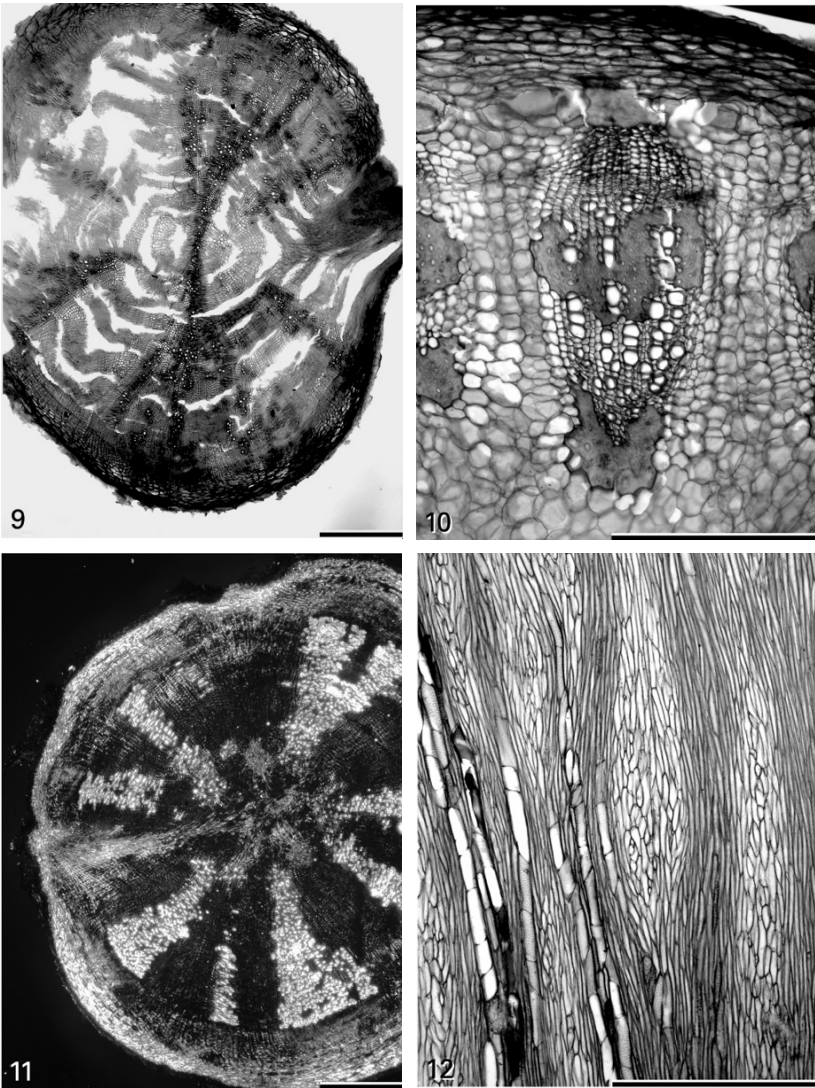


Fig. 9. Ring shake. Annual rings split between latewood and earlywood, because the marginal parenchyma walls are very thin. *Cardamine resedifolia*, a 5-cm-tall hemicryptophyte, growing on meadows in the subalpine zone of the Swiss Alps. — Fig. 10. Vascular bundle in a 3-year-old rhizome of the geophyte *Cardamine enneaphyllos*, growing in a mountain beech forest in the Jura. As secondary growth is reduced after the first year, the vascular bundles remain isolated. Some fibre zones are intensively sclerified. — Fig. 11. Radial vessel/fibre zones, similar to vascular bundles, in the stem of a 10-cm-tall hemicryptophyte, *Arabis alpina*, from a snow bed of the alpine zone in the Alps. Between the intensively lignified radial strips, very large, hardly lignified rays remain. The stem expansion is compensated by ray dilatation and insertion of secondary rays. Polarised light. — Fig. 12. Very large rays with thin-walled cells intergrade with the fibre tissue. The therophyte *Calepina irregularis* grows on limestone rocks in the French Pyrenees. — All scale bars = 500  $\mu\text{m}$ .

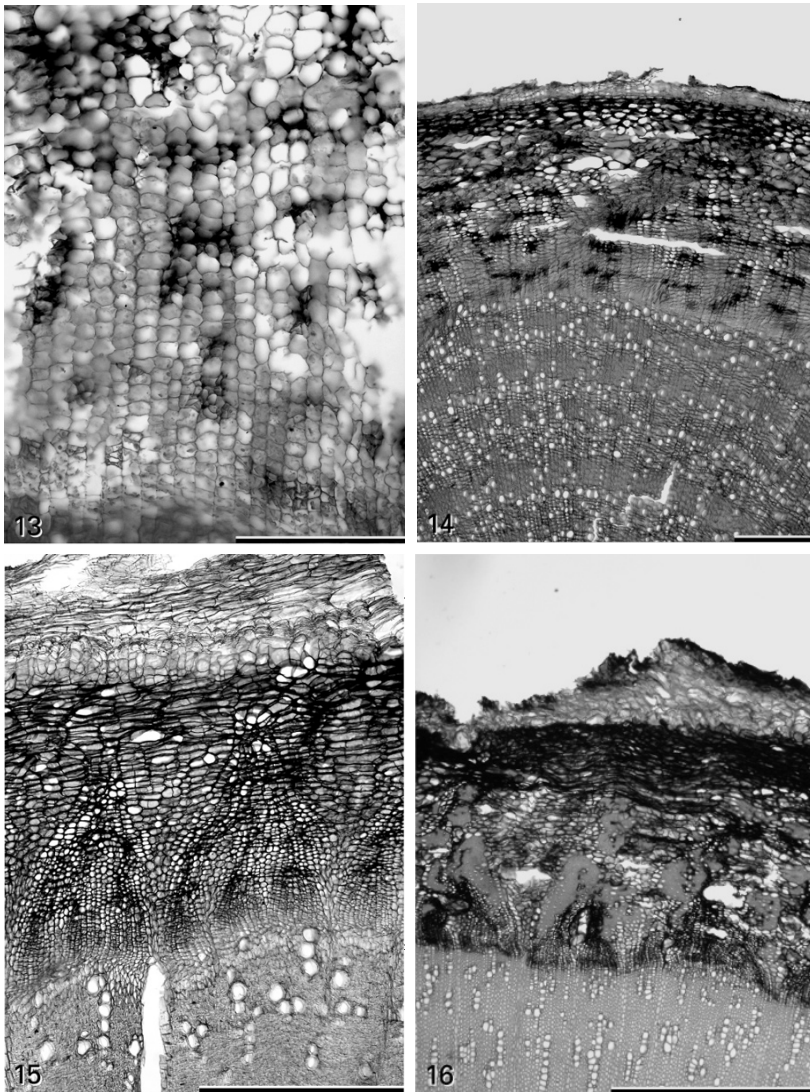


Fig. 13. Groups of sieve tubes in the phloem (dark cell group) of the hemicytrophite *Arabis subacoriacea*, growing on a rock of the subalpine zone in the Alps. The young sieve tubes near the cambium (below) are turgid; the older ones have partially collapsed and are encrusted with dark staining substances. — Fig. 14. Tangential sieve tube group arrangement in the phloem (dark cell groups) of a 10-cm-tall hemicytrophite, *Arabis alpina*, growing in a snow bed of the alpine zone in the Alps. The xylem has intra-annual tangential bands of thick-walled fibre tracheids. The radial arrangement of cells in the phloem is typical of the entire family. — Fig. 15. Ray dilatation and expansion of parenchyma cells in the bark of the chamaephyte *Lobularia canariensis*, growing in the subtropical montane zone of the Canary Islands. The phellogen (cork cambium) and the cork zone are distinct. — Fig. 16. Radial sclereid arrangement occurring in the phloem and primary bark of this 30 cm tall therophyte, *Sisymbrium andinum*, growing in the subalpine zone of Patagonia. The ray dilatation is very distinct. — All scale bars = 500  $\mu\text{m}$ .



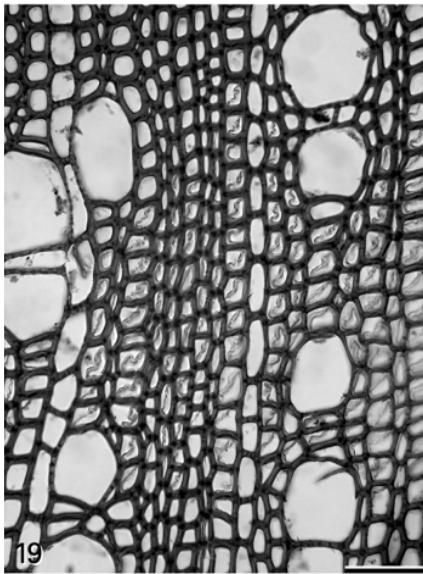
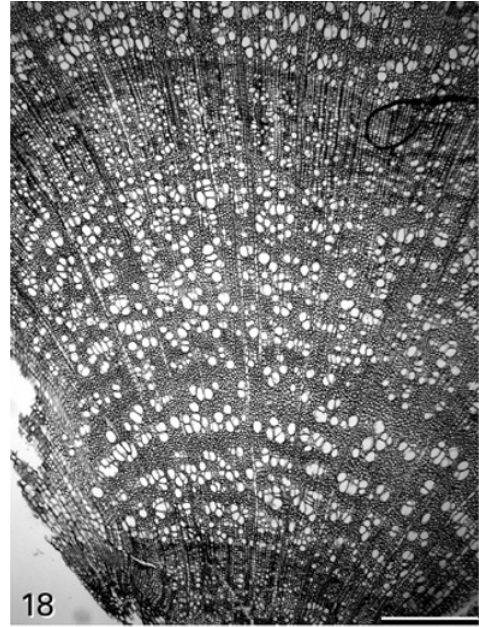
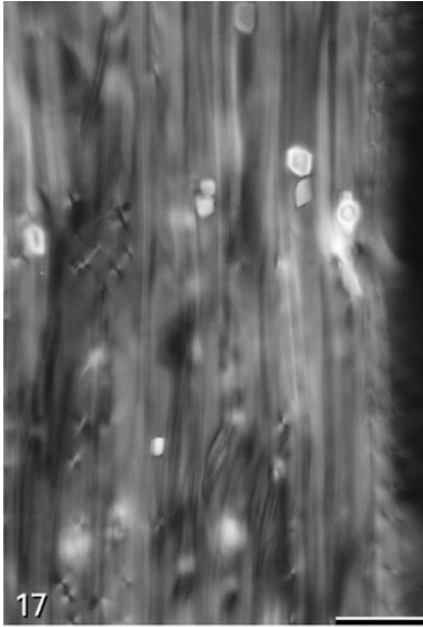


Fig. 17. Rhombic crystals in fibres of the shrub *Parolina ornata* from the montane zone of the Canary Islands. — Fig. 18. Intra-annual tangential bands of vessels in *Reseda luteola* xylem may indicate a taxonomic relationship to the Brassicaceae (Fig. 8). — Fig. 19. Gelatinous fibres in the xylem of the shrub *Reseda suffruticosa*. — Scale bars of 17 & 19 = 10  $\mu\text{m}$ , of 18 = 500  $\mu\text{m}$ .

ages 1.2 g/cm<sup>3</sup> (X-ray densitometric determination). The xylem of the dwarf shrubs *Vella spinosa* and *Ptilotrichium spinosum* is also very dense, but due to a marginal parenchymatous, thin-walled band, it is subject to ring shake (Fig. 8). Ring shake is also frequent in the genus *Draba* (Fig. 9).

The rays of most species have upright or square cells. Only the dwarf shrubs *Sinapidendron frutescens* and *Parolina ornata* from the Canary Islands, and the perennial her-

baceous plant *Sisymbrium altissimum* which has a woody base and grows at the lower timberline in Colorado, USA, have heterocellular rays with a few procumbent cells.

The following features are frequently observed and are associated with ecological or regional conditions. The apertures of the intervessel pits are often a bit gash-like (Fig. 2). Annual rings are often delimited by bands of thin-walled, marginal parenchyma (Fig. 7 & 8); and, in various species, ground tissue cells without secondary walls are often found in the centre of root collars. Both features appear very clearly under polarised light.

In some perennial species, the xylem ring is incomplete (feature 99.1); the vascular bundles retain their initial shape for one (*Barbarea vulgaris*, *Cardamine pratensis*) or many years (*Arabis alpina* - Fig. 11, *Cardamine resedifolia*, *Sisymbrium strictissimum*). In species with reduced secondary growth, the vascular bundles remain in an initial stage (*Cardamine bulbifera*, *Cardamine enneaphylos* - Fig. 10, *Nasturtium officinale*). The presence of very large, often hardly lignified rays is typical for these species.

Helical thickenings were found in the vessels of the dwarf shrubs *Descurainia millefolia* and *Vella spinosa* and in the herbaceous plant *Cheiranthus cheirii* with a woody base. Metcalfe and Chalk (1950) noted spiral thickening also in *Ptilotrichium spinosum*.

Prismatic crystals were only observed in the fibres of the shrub *Parolina ornata* (Fig. 17) and *P. intermedia*, from the montane zone of the Canary Islands, and in the rays of the herbaceous *Malcolmia aegyptica* that grows in the Sahara.

### **Family characteristics of Resedaceae xylem**

All perennial species analysed are diffuse- or semi-ring-porous (Fig. 18) and possess distinct rings. They have short vessel elements without spiral thickening but with simple perforations; vessels with diameters of 50–80 µm are mostly clustered, and the fibres have minutely bordered pits (3 µm). The axial parenchyma is scanty paratracheal. All perennial species contain rays (one to three cells wide) with upright or square cells. Rays are absent in the annual plant *Reseda phyteuma*. Vestured pits could only be detected in *Reseda suffruticosa* but they are at the border of optical resolution, even at a magnification of ×1000. The two desert shrubs *Randonia* and *Ochradenus* have very thick-walled fibres.

### **Ecological trends in the xylem characteristics of the Brassicaceae (Fig. 20)**

In contrast to a previous study on ecological trends in Western Europe (Baas & Schweingruber 1987) which was based exclusively on trees, shrubs and dwarf shrubs of the dicotyledonous flora, in the present study only the species belonging to one family were compared, including hemicryptophytes and therophytes.

Despite the small number of species analysed in some vegetation zones, for example the Mediterranean, arid and subtropical regions, ecological trends are clearly recognisable (Table 2).

*Life forms.* No shrubs or dwarf shrubs from this family occur in the alpine region. A few plants have a more or less woody base, e.g. *Draba aizoides* in the alpine zone and *Cheiranthus cheirii* in the hill zone.

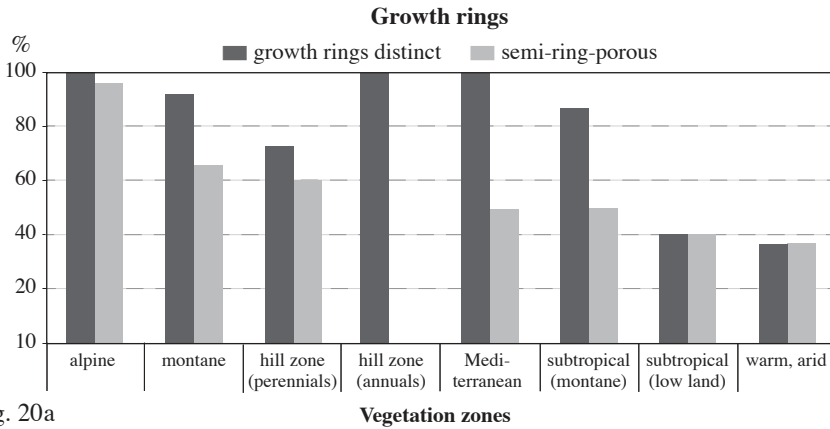


Fig. 20a

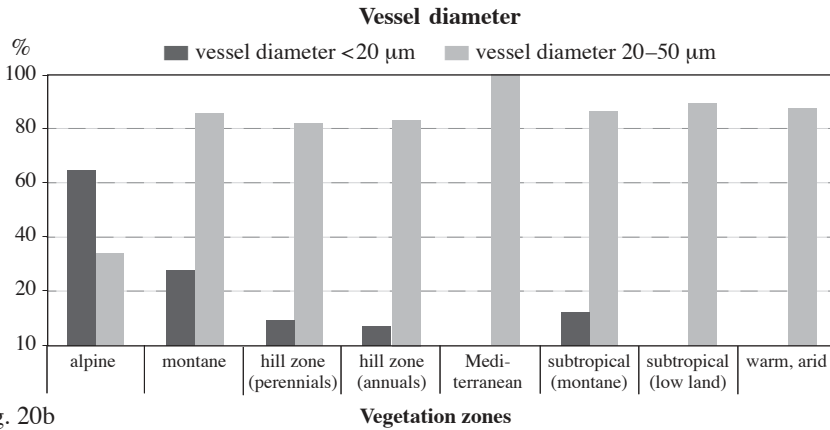


Fig. 20b

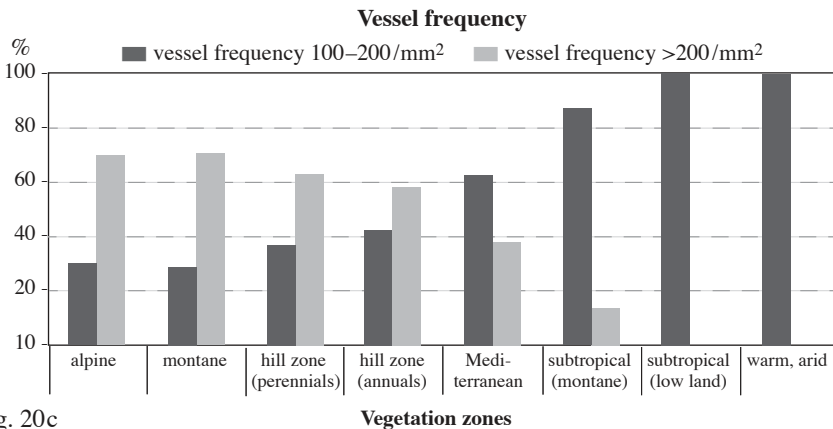


Fig. 20c



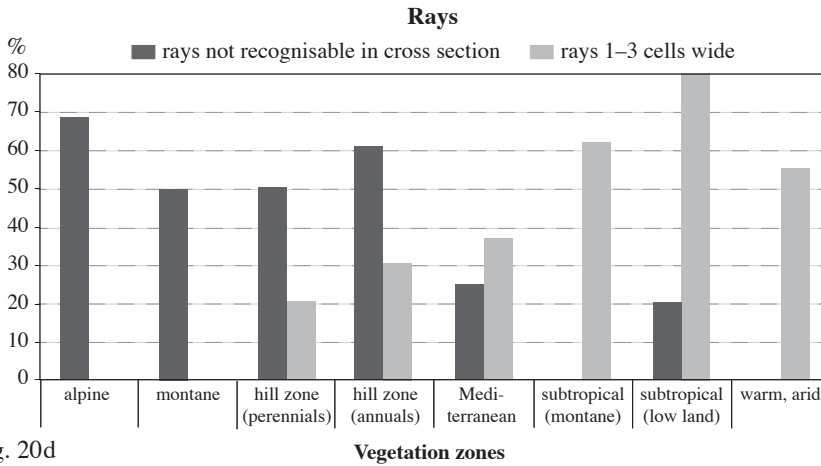


Fig. 20d

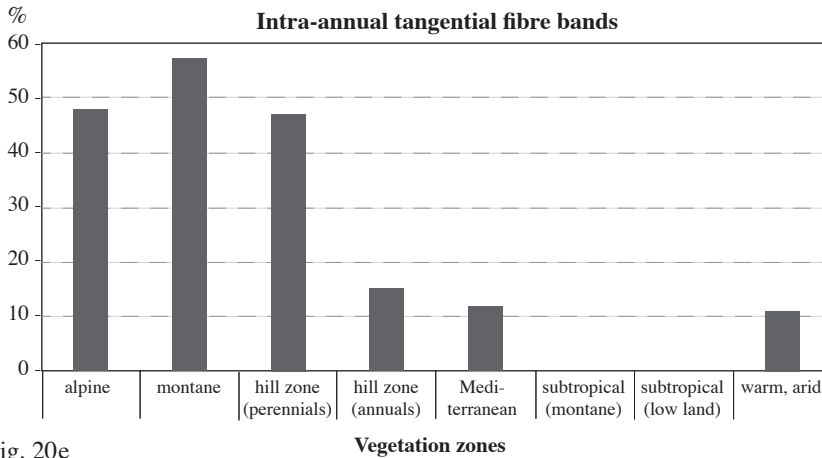


Fig. 20e

Fig. 20. Ecological trends in the xylem along climatic gradients from the alpine zone in the Alps to the arid zone in the Sahara. Each column expresses the percentage of the total number of analysed species per climatic zone, e.g. 100% of 24 analysed species from the alpine and sub-alpine zone have distinct ring boundaries and 96% of the 24 species are semi-ring-porous. The number of analysed species is indicated in Table 2. — a) Ring distinctness and semi-ring-porosity; b) Vessel diameter; c) Vessel frequency; d) Ray distinction and width; e) Intra-annual tangential bands of libriform fibres.

By contrast, dwarf shrubs and shrubs, e.g. *Parolina ornata* and *P. intermedia*, are common in the subtropical zone with few arid months (Bramwell & Bramwell 2001) and in the arid zone (Ozenda 1983).

*Age of plants with taproots and rhizomes.* The age of perennial herbaceous plants (hemicryptophytes) in alpine and subalpine zones averages ten years, with a maximum of forty-three years (*Draba aizoides*), whereas in the montane and the hill zone of the Alps, plants will average two and a half years' of age, with a maximum of four years.

*Ring distinctness* in the alpine, montane, Mediterranean and subtropical montane zone reaches almost 100%. This is less frequent in the hill zone of the Alps, the subtropical lowlands and the North African arid zone (Fig. 20a).

*Porosity.* All perennial herbaceous plants from the alpine and subalpine zones of the Alps are semi-ring-porous. The number of semi-ring-porous species decreases, and the number of species with diffuse vessels increases, towards all the lower-lying regions that were studied (Fig. 20a).

*Tangential vessel diameter.* The diameter of earlywood xylem vessels from alpine and subalpine zones is normally less than 20  $\mu\text{m}$  (Fig. 4). In all other regions, diameters of 20–50  $\mu\text{m}$  occur (Fig. 20b).

Vessels with diameters of 50–100  $\mu\text{m}$  were only observed in a few species in the hill zone of the Alps (*Alliaria officinalis* and *Lepidium draba* at ruderal sites, and *Rorippa austriaca* and *Sisymbrium austriacum* in dry places) and some species of the Sahara (*Malcolmia aegyptica*, *Moricandia arvensis* and *Zilla spinosa*).

*Vessel frequency.* Vessel frequency distinctly decreases from the alpine/subalpine zone towards warmer zones (Fig. 20c): the number of plants with many vessels (>200) is greater at high altitudes (approx. 70%) than in all other regions, and non-existent in the lower subtropical and the arid zone. The number of plants with a vessel frequency of 100–200  $\text{mm}^2$  increases from alpine and montane zones (30%) to subtropical and arid zones (100%) (Fig. 20c). Species with less than 100 vessels/ $\text{mm}^2$  have not been observed.

*Vessel arrangement.* Species with intra-annual, tangential rows of vessels are absent in the alpine and subalpine zones of the Alps, but are found in the higher-lying subtropical zone of Tenerife, for example in the dwarf shrub *Erysimum scoparium*. In all other regions, the frequency ranges from 12–70%. Species with radial rows are more frequent in subtropical and arid zones (60–86%) than in other regions (25–53%). Frequency is definitely high in annual plants from the alpine hill zone (84%).

*Intervessel pits with horizontal slit-like apertures* (Fig. 2). This feature is more frequent in small plants than in large plants (35% in alpine and subalpine zones, 29% in the montane zone, 13% in perennials of the alpine hill zone and 37% in the Mediterranean zone).

*Fibre wall thickness.* In the alpine region, many species (45–57%) have intra-annual tangential fibre bands (Fig. 20e).

*Rays.* The frequency of plants without rays, or rather of those in which rays are not visible in the transverse section, is high in the alpine region (average 58%) and low in all other regions (average 10%) (Fig. 20d). By contrast, the frequency of plants with rays consisting of one to three cells is wide in the Mediterranean, subtropical and arid zones (average 60%) and low in the alpine region (average 13%). Only a few plants in alpine and subalpine zones have large rays (Fig. 11), with indistinct borders towards the fibre tissue (Fig. 12); and some small plants have a few large rays embedded in a tissue that is otherwise free of rays.

*Axial parenchyma.* Very thin-walled marginal parenchyma is frequent, and can be found in most ecosystems, except in the arid zone. The presence of very thin-walled parenchyma cells between fibres and vessels (Fig. 7) is quite frequent in the alpine

(39%) and rare in the montane zone (14%) and in the hill zone (13%) of the Alps; it is absent in all other areas.

### ***Phloem and primary bark characteristics and ecological trends***

Phloem structure is simple. Rhombic crystals and crystal sand are present in all 82 species studied. The unligified parenchyma is arranged radially (Fig. 13). Sieve tubes and companion cells are mostly grouped in little clusters (Fig. 13). In 55% of the species examined, they are arranged in tangential rows (Fig. 14). Inactive sieve tubes collapse, and groups of collapsed cells appear as dark spots (Fig. 14). Parenchyma cells are mostly enlarged towards the primary bark, but the size of the sieve tubes remains constant. Ray dilatation takes place in most species, and it is very obvious in species with large xylem rays (Fig. 15). Sclereids are very frequent in the cortex and the phloem (Fig. 16). The presence of sclereids constitutes an ecological site indicator. Sclereids in the bark are much less frequent in the cortex of plants in the alpine zone. The frequency of sclereids in the alpine zone is 5% in the cortex and 0% in the phloem but 70% and 35%, respectively, in all other regions. The radial, tangential and dispersed arrangement around the stem greatly varies between the specimens examined. Whilst the stems are young (one to a maximum of forty-three years, *Draba aizoides*) and growth is slow, they expand very little and the cortex is preserved for a long time below the phellem (Fig. 14–16). The outer phellem remains for the total life period of slow growing hemicyptophytes and small chamaephytes. It gets replaced in fast growing shrubs as *Parolina* sp. by a second phellogen which is located in the cortex or even the phloem.

## DISCUSSION

Most previous observations on family characteristics in the xylem were confirmed. Due to the unsuitable staining method used in this study, the presence of myrosin cells could not be ascertained. As herbaceous life forms were examined here, the range of key features proposed by Wheeler *et al.* (1989) had to be extended. Of particular importance were differentiations of vessel size and frequency, the classification of intra-annual fibre bands and observations of the cell walls under polarised light.

The available plant material, which included annual and perennial large and small plants growing from the subtropical to the alpine zone, allowed some ecological considerations of Brassicaceae.

The anatomical differences between hemicyptophytes and therophytes can be explained for the hill zone of the Alps (Fig. 20). In annual plants intra-annual fibre bands are rare. Young, annual plants probably stabilise the body with collenchyma, while perennials require mechanical support.

A few features would appear to be characteristic of single species, but the available number of species studied is insufficient for further conclusions. Comparisons between the present wood anatomical study and molecular phylogenies are problematic because the anatomical variability in single species has not been considered and the species analysed in molecular studies are mostly not identical. Not more than 5 and 4 species

examined in this study were included in the analyses conducted by Koch *et al.* (2001) and Hall *et al.* (2002), respectively.

Some common features indicate a taxonomic relationship between Brassicaceae and Resedaceae. Common to both families are vessels with minute alternate pits and simple perforations, the absence of spiral thickenings, fibres with simple to minutely bordered pits, paratracheal parenchyma, rays with mostly square and upright cells, and the absence of crystals. The only distinct difference lies in the formation of the mechanical tissue: the Brassicaceae often contain intra-annual, thick-walled fibre bands, whereas the Resedaceae, at least *Reseda*, have gelatinous fibres (Fig. 19). Note, however, that Brassicaceae and Resedaceae are not considered as 'sister' families according to recent phylogenetic insights of the Brassicales (Judd *et al.* 2002).

### ***Ecological trends in the xylem characteristics of the Brassicaceae*** (Fig. 20)

In general, perennial herbaceous plants of alpine and subalpine zones attain a greater age than those of the lowlands (Diemer *et al.* 1992). A cold climate with a short vegetation period of one or two months reduces a plant's annual xylem production and prolongs its subterranean life span. Plants invest carbon, as a first priority, in the formation of permanent stems and roots, and much less in the production of annual leaves (Körner 2003). In addition, at high altitudes, rhizomes survive for a longer time-period than at lower altitudes. This statement is, however, only correct where it refers to the same species. Where a wide range of species is concerned, the above trend along altitudinal transects disappears, because each species has a different longevity (Schweingruber & Poschlod 2005). A long-lived species in the alpine zone is, for example, *Draba aizoides* (maximum forty-three annual rings) and an example of a short-lived plant is *Arabis alpina* (maximum five annual rings). Plants on dry sites also reach great ages (Fig. 8), because limited moisture reduces growth. The greatest ages can be expected for plants living on dry sites at very high altitudes.

Clearly defined seasons give rise to a distinct annual ring formation (Fig. 20a), which is easily visible under polarised light (Fig. 8). Most perennial plants of the alpine region, from the hill to the alpine zone, as well as plants in the Mediterranean and the subtropical montane zone, have distinct rings. Ring boundaries in subtropical lowlands and in the arid zone are often less distinct and some ring boundaries may correspond with a-periodic droughts (Fig. 20a). Semi-ring-porosity is less expressed in arid zones than in all other zones. These findings correspond with dendrochronological results which demonstrate a direct relationship between decreasing distinctness of ring boundaries and decreasing seasonality (Worbes 1994).

There is no heartwood formation (tylosis and phenolic deposits) at all in herbaceous plants at high altitudes. Phenolic deposits have sporadically been observed in plants of all other vegetation zones, but it is difficult to establish whether they belong to the heartwood or to defence barriers (barrier zones). Tyloses were absent from all plant material analysed. This can probably be attributed to the presence of exclusively small vessels (Bonsen 1991). The absence of distinct heartwood (Kaennel & Schweingruber 1995) allows the assumption that xylem tissues formed in previous years can be defined as water conducting sapwood.

In the family Brassicaceae vessel diameter corresponds to plant size. It is reduced in most small plants (<10 cm height) of alpine and subalpine zones (Fig. 20b). In general, small plants have narrow vessels, big plants wider vessels. Similar tendencies were seen for ash (*Fraxinus excelsior*); the wood of big trees with a large, photosynthetically active crown has very large vessels (>200  $\mu\text{m}$ ) in the earlywood, whereas small, suppressed individuals with few leaves have narrow vessels (<50  $\mu\text{m}$ ) (Schweingruber 2001). High water consumption demands an efficient transport system with wide vessels. By contrast, vessel frequency does not strictly correspond to plant size. In the montane and hill zone of the Alps, and in the Mediterranean area, most plants in all growth forms have a high vessel frequency. Plants in dry, tropical and arid zones have fewer and bigger vessels than those of temperate regions (Fig. 20c). Large vessels would appear to guarantee an intensive water supply (Körner 2003).

Vessel arrangement is related to plant size and ring width. Only large rings (>0.5 mm) have enough room for intra-annual growth rhythms. This is indicated by the frequent presence of intra-annual vessel/fibre bands and long radial multiples. Radial and tangential vessel arrangements would appear to be a family characteristic, but they are often suppressed by limiting growth factors. Vessel pits with horizontal gash-like apertures probably indicate a juvenile developmental stage. As it has mainly been observed in small plants, it may be interpreted as a primitive developmental stage (Zimmermann 1959) or as a relict of the primary xylem that contained vessels with scalariform inter-vessel pitting (Henes 1959).

Ray structure is very variable. The large number of plants with small or no rays, the indistinct delimitation between rays and fibres (Fig. 12) in general, and between rays and fibres with a structure similar to vascular bundles (Fig. 10 & 11), as well as the dominance of species with upright or square ray cells can be interpreted as juvenile features (Braun 1970). The development of a ray structure is probably not possible in young plants with small diameters. In some cases, large rays might be a true characteristic (Fig. 11), in others they represent lateral undeveloped shoots (Fig. 6).

Intra-annual thick-walled fibre bands occur predominantly in perennial plants of the Alps (Fig. 20e). As far as I know, there is no explanation for this regional dominance. In cases of eccentric occurrence of fibre bands in the stem they seem to be a response to mechanical stress (Fig. 9). This is comparable with phanerophytes which are not able to form tension wood (Höster & Liese 1966). They show mostly thick-walled fibres on the tension or the compression side of leaning stems.

The presence of marginal parenchyma, with normally thickened, lignified vessels and very thin-walled parenchyma, can be related to very short vegetation periods.

Ecological trends in the bark may only be recognised from the frequency of sclereids. In the growing conditions of the alpine zone, resources seem to be limited, hence cell-wall thickening in the bark has low priority.

### ***Comparison between ecological and geographical xylem trends in floras and in families***

The available material allows a comparison between the ecological trends of “woody” dicotyledons from the European flora (Baas & Schweingruber 1987) and a single family

from the same region. The comparison of a single predominantly herbaceous family (Brassicaceae) with trees and shrubs of a whole flora led to substantial differences.

Scalariform perforations are frequent in the flora of boreal and temperate areas, but they are absent in Brassicaceae from all climatic zones. Simple perforation plates are characteristic of the family, and are thus ecologically insignificant.

Spiral thickening in vessels is frequent in the European flora but very rare in the family. It only occurs in two dwarf shrubs of the Mediterranean and subtropical montane zone, and has in my opinion no ecological significance.

Ring-porous wood only occurs in the European flora of warm regions (temperate to subtropical), not in the boreal zone. The absence of this feature is also characteristic of the Brassicaceae. Semi-ring porosity in Brassicaceae seems to be related to vegetation zones (Fig. 20a).

A comparison of similar ecological units has shown that geographical trends do not seem to exist. At least, all the xylem structures from the United States fit perfectly into the European ecological groups.

#### ACKNOWLEDGEMENTS

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#### REFERENCES

- Aeschimann, D., K. Lauber, D.M. Moser & J.-P. Theurillat. 2004. Flora Alpina. Haupt, Bern, Stuttgart, Wien.
- Baas, P & F.H. Schweingruber. 1987. Ecological trends in the wood anatomy of trees, shrubs and climbers from Europe. IAWA Bull. s.n. 8: 245–274.
- Benkova, V.E. & F.H. Schweingruber. 2004. Anatomy of Russian woods. Haupt, Bern, Stuttgart, Wien.
- Betts, M.W. 1918. Notes on the autecology of certain plants on the peritotite belt, Nelson: Part I. Structure of some of the plants (No. 1). Trans. New Zealand Inst. 50: 230–243.
- Bonsen, K.J.M. 1991. Gefäßverschluss-Mechanismen in Laubbäumen. Vierteljahresschrift der naturforschenden Ges. Zürich 136: 13–50.
- Bramwell, D. & Z. Bramwell. 2001. Wild flowers of the Canary Islands. Ed. 2. Editorial Rueda SL, Madrid.
- Braun, H.J. 1970. Funktionelle Histologie der sekundären Sprossachse. I. Das Holz. Bornträger, Berlin, Stuttgart.
- Busse, J.S. & R.F. Evert. 1999. Vascular differentiation and transition in the seedling of *Arabidopsis thaliana* (Brassicaceae). Int. J. Plant Sci. 160: 241–251.
- Carlquist, S. 1971. Wood anatomy of Macronesian and other Brassicaceae. Aliso 7: 365–384.
- Carlquist, S. 1998. Wood anatomy of Resedaceae. Aliso 16: 127–135.
- Carlquist, S. 2001. Comparative wood anatomy. Ed. 3. Springer Series in Wood Science. Springer, Berlin, Heidelberg, New York.
- Chaffey, N.J. 2002. Wood microscopical techniques. In: N.J. Chaffey (ed.), Wood formation in trees: 17–40. Taylor & Francis, London, New York.

- Chengsong, Z., B.J. Johnson, B. Kositsup, & E.P. Beers. 2000. Exploiting secondary growth in *Arabidopsis*. Construction of xylem and bark cDNA libraries and cloning of three xylem endopeptidases. *Plant Physiol.* 123: 1185–1196.
- Diemer, M., Ch. Körner & S. Prock. 1992. Life spans in wild perennial herbaceous plants. A survey and attempts at a functional interpretation. *Oecologia* 89: 10–16.
- Dolan, L. & K. Roberts. 1995. Secondary thickening in roots of *Arabidopsis thaliana*. Anatomy and cell surfaces. *New Phytol.* 131: 121–128.
- Fahn, A., E. Werker & P. Baas. 1986. Wood anatomy and identification of trees and shrubs from Israel and adjacent regions. Israel Academy of Sciences. Jerusalem. 221 pp.
- Hall, J.C., K.J. Sytsma & H.H. Iltis. 2002. Phylogeny of Capparaceae and Brassicaceae based on chloroplast sequence data. *Amer. J. Bot.* 89: 1826–1842.
- Henes, E. 1959. Fossile Wandstrukturen untersucht, am Beispiel der Tracheidenwände paläozoischer Gefäßpflanzen. *Encyclopedia of Plant Anatomy*. Bornträger, Berlin-Nikolassee.
- Hohenester, A. & W. Weiß. 1993. Exkursionsflora für die Kanarischen Inseln. Ulmer, Stuttgart.
- Hollendonner, F. 1909. Über die Anatomie des Stengels von *Alyssum arduini*. *Bot. Kötzl.* 8: 26–40 (Hungarian with German summary).
- Höster, H.R. & W. Liese. 1966. Über das Vorkommen von Reaktionsgewebe in Wurzeln und Ästen der Dikotyledonen. *Holzforschung* 20: 80–90.
- Judd, W.S., Ch. S. Campbell, E. A. Kellogg, P.F. Stevens & M.J. Donoghue. 2002. *Plant systematics. A phylogenetic approach*. Ed. 2. Sinauer Ass., Sunderland, Massachusetts, USA.
- Kaennel, M. & F.H. Schweingruber. 1995. Multilingual glossary of dendrochronology. Haupt, Bern, Stuttgart, Vienna.
- Koch, M., B. Haubold & T. Mitchel-Olds. 2001. Molecular systematics of the Brassicaceae: Evidence from coding plastidic *MAT K* and nuclear *CHS* sequences. *Amer. J. Bot.* 88: 534–544.
- Koch, M., IA. Al-Shehbaz & K. Mummenhoff. 2003. Molecular systematics, evolution, and population biology in the mustard family (Brassicaceae). *Ann. Missouri Bot. Gard.* 90: 151–171.
- Konratieva-Melville, E.A. & L.E. Vodolazsky. 1982. Morphological and anatomical structure of *Arabidopsis thaliana* (Brassicaceae) in ontogenesis. *Bot. J.* 67: 1060–1069.
- Körner, Ch. 2003. *Alpine plant life*. Springer, Berlin, Heidelberg, New York.
- Lauber, K. & G. Wagner. 1998. *Flora Helvetica*. Haupt, Bern, Stuttgart.
- Lev-Yadun, S. 1994. Introduction of sclereid differentiation in the pith of *Arabidopsis thaliana* (L.), Heynh. *J. Exp. Bot.* 45: 1845–1949.
- Messeri, A. 1938. Studio anatomico-ecologico del legno secondario di alcune piante del Fezzan. *Nuovo Giorn. Bot. Ital.* 45: 267–356.
- Metcalfe, C.R. & L. Chalk. 1950. *Anatomy of the dicotyledons*. Clarendon Press, Oxford.
- Neumann, K., W. Schoch, P. Détienne & F.H. Schweingruber. 2001. Woods of the Sahara and the Sahel. An anatomical atlas. Haupt, Bern, Stuttgart, Wien.
- Ozenda, P. 1983. *Flore du Sahara*. Centre national de la recherche scientifique. Paris.
- Rollins, R.C. 1939. The cruciferous genus *Stanleya*. *Lloydia* 2: 109–127.
- Schönfelder, P. & I. Schönfelder. 1997. *Die Kosmos-Kanarenflora*. Franckh-Kosmos, Stuttgart.
- Schweingruber, F.H. 1990. *Anatomy of European woods*. Haupt, Bern, Stuttgart, Wien.
- Schweingruber, F.H. 2001. *Dendroökologische Holz Anatomie. Anatomische Grundlagen der Dendrochronologie*. Haupt, Bern, Stuttgart, Wien.
- Schweingruber, F.H. & H. Dietz. 2001. Annual rings in the xylem of dwarf shrubs and perennial dicotyledonous herbs. *Dendrochronologia* 19: 115–126.
- Schweingruber, F.H. & P. Poschlod. 2005. Growth rings in herbs and shrubs: life span, age determination and stem anatomy. *For. Snow Landsc. Res.* 79: 195–411.

- Sitte, P., E.W. Weiler, J.W. Kadereit, A. Bresinky & C. Körner. 2002. Strasburger Lehrbuch der Botanik. Ed. 35. Spektrum Akademischer Verlag, Heidelberg, Berlin.
- Trockenbrodt, M. 1990. Survey and discussion of the terminology used in bark anatomy. IAWA Bull. n.s. 11: 141–166.
- Tutin, T.G., V.H. Heywood, N.A. Burges, D.H. Valentine, S.M. Walters & D.A. Webb (eds.). 1964. Flora Europaea. Cambridge University Press, Cambridge.
- Weber, W.A. 1976. Rocky Mountains Flora. Ed. 5. Colorado Associated University Press, Boulder.
- Weber, W.A. 1987. Colorado Flora Western Slope. Colorado Associated University Press, Boulder.
- Wheeler, E.A., P. Baas & P. Gasson. 1989. IAWA list of microscopic features for hardwood identification. IAWA Bull. n.s. 10: 219–332.
- Worbes, M. 1994. Grundlagen und Anwendung der Jahrringforschung in den Tropen. Habilitationsschrift, Univ. Hamburg.
- Zimmermann, W. 1959. Die Phylogenie der Pflanzen. Fischer, Stuttgart.