

Evolutionary trends in secondary phloem anatomy of trees, shrubs and climbers from Africa (mainly Ivory Coast)

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SUMMARY

Trends were analysed in the occurrence of certain characteristics of secondary phloem in relation to the categories bark structure, habit and habitat of 463 woody plant species (belonging to 261 genera and 31 families) mainly from the Ivory Coast, Africa. Relationships were investigated between these three categories. Three types of bark structure were distinguished, mainly by differences in the arrangement of axial parenchyma and type of mechanical tissue.

Presumed primitive features of sieve tubes, axial parenchyma cells and cellular composition of phloem rays, become less prominent from climbers to trees and from rain forest to savannah. Presumed advanced types of axial parenchyma and mechanical tissue, often associated with primitive sieve tubes and companion cells (bark structural type *Datura*), were more frequently present in species from rain forest than from savannah. The same combination of types of secondary phloem from species from rain forest was more representative of climbers than of trees.

Secondary phloem of shrubs was often not intermediate between trees and climbers, especially in rain forest. Secondary phloem anatomy suggested that rain forest shrubs had evolved from trees by developing a more advanced axial parenchyma and mechanical tissue, and from climbers by developing more advanced sieve tubes and companion cells.

Key-words: Africa, bark trends, ecology, evolution, fibres, phloem anatomy, sieve tube, woody plants.

INTRODUCTION

The compound tissue outside the vascular cambium in a stem shows extensive variation in structure. In particular, the presence or absence of phloem fibres is of considerable taxonomic importance (Thorenaar 1926). In the secondary phloem, fibres are

Abbreviations: av.m.w.: average maximal width; Cl: climber; Dat.: bark structural type *Datura*; He: heterogeneous phloem ray; Ho: homogeneous phloem ray; numb.: number; Pop.: bark structural type *Populus*; PS: parenchyma strand; R: rain forest; S: savannah; Sh: shrub; ST: sieve-tube member; Til.: bark structural type *Tilia*; tot.: total; Tr: tree; 1–2-ser.: one-to-two-seriate phloem ray. For descriptions of several characters see Materials and Methods.

conspicuous elements because of their thick walls. One may distinguish true fibres (secondary phloem fibres as defined by Trockenbrodt 1990) that are differentiated directly from cambial derivatives, and fibre-sclereids that are differentiated by sclerosis of parenchyma cells. In non-collapsed secondary phloem (Trockenbrodt 1990), only true fibres may be present whereas fibre-sclereids, which will differentiate later in tissue life, are absent. However, the distinction between true fibres and fibre-sclereids is not always obvious and then both types are called fibres. In the secondary phloem of dicotyledons, fibre groups are usually surrounded by parenchyma, whereas in gymnosperms the concentric layers of phloem fibres are bounded by sieve cells (Moeller 1882). Chang (1951) used the distribution and arrangement of sclerotic elements for diagnosis and characterization of Rubiaceae. His investigations on North American softwood and hardwood barks (Chang 1954a,b) showed that these elements of the bark were useful for identification. Sometimes samples of woody species can be distinguished only by bark characteristics, for instance for *Entandrophragma* spp. (Parameswaran & Liese 1968). Characteristics of the secondary phloem, especially of sclerotic elements, are no less important than characteristics of secondary xylem (Parameswaran & Liese 1970). According to Esau (1979), a serviceable classification of secondary phloem based on the occurrence and distribution of sclerotic elements, is easily possible. Moeller reached the same conclusion in 1882. Holdheide (1951) gives some idea of the diversity of bark structures in tree species from central Europe; Thorenaar (1926), Parameswaran and Liese (1970) and Roth (1981) for the tropics.

Several classifications have been proposed of the secondary phloem, as well as of its component elements. Moeller (1882) classified secondary phloem as follows:

- (1) barks without sclerotic elements;
- (2) with only stone cells;
- (3) with only fibres;
- (4) with fibres and stone cells.

In types with sclerotic elements three variants were distinguished by their arrangement. Thorenaar (1926) distinguished five bark types, which partly corresponded with those of Moeller (1882), whereas Furuno (1990) defined ten bark types mainly based on arrangement of phloem fibres, fibre-sclereids and sclereids, as well as anatomical features of ray and axial parenchyma cells. Sieve elements were excluded because they frequently collapsed and could not be distinguished from axial parenchyma cells regardless of whether they were distributed in tangential bands or in groups.

One of the characteristics of phloem in dicotyledons (and conifers) is its regular renewal, i.e. with respect to transport of assimilates, and its usually short functional life (Zimmermann & Brown 1971). In hardwoods, non-collapsed secondary phloem usually only comprises the production of the previous year (Holdheide 1951). According to Huber (1939) manifestations of distinctive reactions to the climate of central Europe in hardwoods are a tangential arrangement of phloem elements of the same type, a non-collapsed phloem comprising only the production of one year, and a clear difference between early and late sieve tubes. In older trees, annual phloem production in terms of width and composition has adopted a form that corresponds to the essential. Holdheide (1951) noticed that hardwoods adapt flexibly to changing ecological conditions, but without losing their characteristic production pattern. According to him, this points to a long evolutionary process.

Hemenway (1913) and especially Zahur (1959) classified dicotyledonous sieve elements into three categories with different morphological specializations. Zahur (1959)

classified companion cells too into three categories, in order of presumed evolution. A well-established phylogenetic relation between fibres and conducting cells of secondary xylem was not observed between fibres and sieve-tube type. A correlation was only present between sieve-tube type and mechanical-tissue type when species were considered in which secondary partitioning of sieve-tube mother cells did not occur. However, when the author examined the axial system of secondary phloem from woody dicotyledons from the Ivory Coast, West Africa, a correlation was found between on the one hand an advanced companion-cell type (as long as the sieve-tube elements, but septated to form a strand of cells) and, less clearly, an advanced sieve-tube type (short; slightly oblique to transverse, simple sieve plates; diameter of the sieve tube smaller than diameter of axial parenchyma cell), and on the other a primitive axial-parenchyma type (not abundant; usually in tangential bands; some enlargement of the cells in the collapsed phloem and some variation in cell size) and a primitive mechanical-tissue type (true fibres, arranged in continuous or interrupted tangential bands). The reverse was present too (den Outer 1983). Roth (1981) observed that a regular arrangement of bark tissues was almost entirely associated with the occurrence of highly specialized sieve tubes. But her supposition that a regular arrangement of bark tissues in itself is more advanced than an irregular one is debatable and conflicts with Zahur's (1959) view.

The question arises as to whether there is a correlation between different secondary phloem characteristics or a combination of characteristics, and habitat or habit of the plant. The present paper demonstrates correlations between bark structural type, habit of the plant and habitat, as well as correlations between these categories and phloem characteristics. Only the well-developed inner (living) part of the secondary phloem of older trees, shrubs and climbers was considered. It comprises non-collapsed and collapsed secondary phloem (Troekbrodt 1990; conducting and non-conducting cf. Esau 1964, 1965). The basic structure can only be identified in this part of the secondary phloem, whereas the basic features are obscured in the outer (dead) part of the secondary phloem (rhytidome) (Esau 1979). Dilatation (Janssonius 1918; Reinders 1961) in the outer collapsed secondary phloem is not considered either. Furthermore, only the bark of hardwood species is dealt with. Bark structural types were used that were based mainly on the distribution of sclerotic elements, and the type and arrangement of axial parenchyma. Furthermore, presumed evolution (Zahur 1959) and correlations among the different types of secondary phloem characteristics were incorporated in the type distinctions.

MATERIALS AND METHODS

Bark samples from African trees, shrubs and climbers (all dicotyledons) were available from the collections of Versteegh and den Outer (Ivory Coast, 1969, 408 samples), Versteegh and Jansen (Liberia, 1969, 30 samples), den Outer and van Veenendaal (Madagascar, 1978, 14 samples) and Breteler (Cameroon, 1962, 11 samples). Samples from trees were collected from stems at breast height; the thickest part of the stems were taken from shrubs and climbers. The collected material was immediately fixed in formalin, acetic acid and ethanol, 1:1:12. The collection from the Ivory Coast, Liberia and Madagascar is housed at the Department of Plant Cytology and Morphology, that of Cameroon at the Department of Taxonomy, Agricultural University, both in Wageningen. All material studied is accompanied by herbarium vouchers, housed at the Department of Plant Taxonomy.

In total, 463 species of 261 genera of woody dicotyledons, belonging to 31 families were examined. These families (in brackets number of genera/total number of species investigated) were: Anacardiaceae (7/11), Annonaceae (15/25), Apocynaceae (21/29), Bixaceae (1/1), Bombacaceae (4/5), Caesalpiniaceae (20/26), Celastraceae (Hippocrateaceae included: 2/11), Combretaceae (5/16), Connaraceae (7/9), Dichapetalaceae (1/27), Ebenaceae (1/12), Euporbiaceae (30/45), Flacourtiaceae (7/8), Guttiferae or Clusiaceae (Hypericaceae included: 7/8), Loganiaceae (3/10), Meliaceae (7/12), Mimosaaceae (12/17), Monimiaceae (1/2), Moraceae (5/17), Ochnaceae (5/8), Papilionaceae (17/31), Pedaliaceae (1/1), Rhopalocarpaceae (1/3), Rubiaceae (32/57), Salvadoraceae (1/1), Sapindaceae (10/13), Sapotaceae (10/11), Sarcolaenaceae (3/4), Sterculiaceae (10/12), Tiliaceae (7/10), Verbenaceae (8/13). The examined species from the Ivory Coast and Liberia are listed in den Outer (1972), those of Dichapetalaceae in van Veenendaal & den Outer (1978). A list of all investigated species with their phloem characteristics is available on request from the author.

Anatomical features were studied in transverse, radial and tangential sections and macerations. All sections were embedded in Kaiser's gelatin-glycerin (Johansen 1940). Means and ranges of diameter and length of sieve-tube members, parenchyma strands and ray height were based on at least 25 measurements. Sieve tube, sieve area, companion cell, axial parenchyma and mechanical tissue were classified in line with Zahur (1959), ray type in line with Kribs (1935) as adapted by Zahur (1959) for rays of the secondary phloem, and bark types in line with den Outer & Fundter (1976) and den Outer (1977, 1983). The last three references indicate bark types with figures and letters (4mr, 2mr, s, etc.). In this paper, these types were arranged in three groups, the bark structural types. Each bark structural type is given as generic name (listed below). These generic names were based on earlier structural investigations of numerous, mainly European, bark samples (not published). The structural types were universally applicable, not only to bark samples from the Ivory Coast. So nearly any bark sample would fit one of the three structural bark types.

The following categories and phloem characteristics were distinguished:

Categories

- (1) Bark structural type (Fig. 4). Bark structural type *Tilia* (bst *Tilia*) is a combination of bark types 4u, 4mr, 4mi, and 3u, 3mr, 3mi; bark structural type *Populus* (bst *Populus*) a combination of bark types 2u, 2mr and 2mi; bark structural type *Datura* (bst *Datura*) a combination of s and g (den Outer & Fundter 1976; den Outer 1983).
- (2) Habit (habitus). Tree (Tr), shrub (Sh) and climber (liana; Cl), conform to the definition given by the IAWA Committee (1989).
- (3) Macroclimatic zone (habitat). Rain forest (R): a dense, high, evergreen forest with sufficient rainfall the year round; savannah (S): a xerophilous grassland containing isolated trees or small groups of trees or shrubs, and climbers in tropical and subtropical regions.

Phloem characteristics

- (1) Sieve-tube member length. This parameter plays a large role in the determination of the sieve-tube types I, II and III (cf. Zahur 1959; den Outer 1983). Lengths of sieve-tube members were measured.

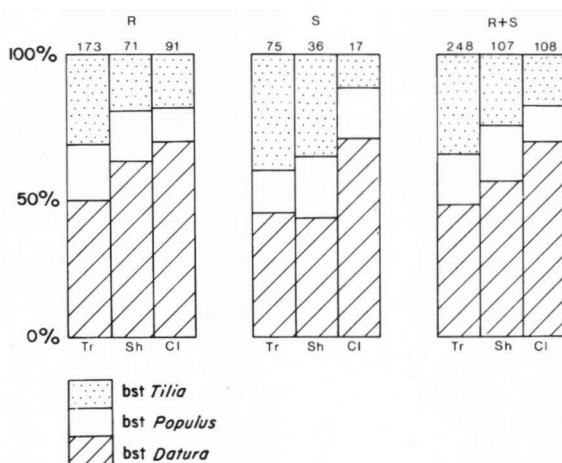


Fig. 1. Frequency distribution of bark structural types in relation to habit in different climatic zones. Total numbers of species indicated above the columns.

- (2) Axial parenchyma. Lengths of parenchyma strands, number of cells per strand, and strand length increase compared with sieve-tube member length, were measured.
- (3) Phloem-ray type. Heterogeneous rays (He) are a combination of HeI and II, homogeneous rays (Ho) a combination of HoI and II, and 1–2-seriate rays a combination of HeIII and HoIII (cf. Kribs 1935 and Zahur 1959, mentioned in den Outer 1983). Maximum ray width (in number of cells) and ray composition were determined.

Trends for the categories bark structural type, habit and habitat, and for phloem-ray characteristics, were analysed by calculating percentages of species possessing that specific character in each category. For other anatomical characteristics of the secondary phloem, measured values (lengths, number of cells, etc.) were given with the standard deviation in each category.

RESULTS

A. Relationships between categories bark structural type (bst), habitus and climatic zone (Figs 1–3, Table 7)

- (1) The percentage of bst *Datura* increases from trees through shrubs to climbers, especially in rain forest (Fig. 1). In savannah this percentage for shrubs is almost equal to that for trees. The percentage of bst *Populus* remains almost constant in the different habit categories.
- (2) Though the percentage of trees in all bst is higher than that of shrubs or climbers because trees had priority during the Ivory Coast collection trip, this percentage decreases from bst *Tilia* through bst *Populus* to bst *Datura*, especially in rain forest (Fig. 2a). This is allied to an increase in climber percentage especially in savannah (Fig. 2a and b).

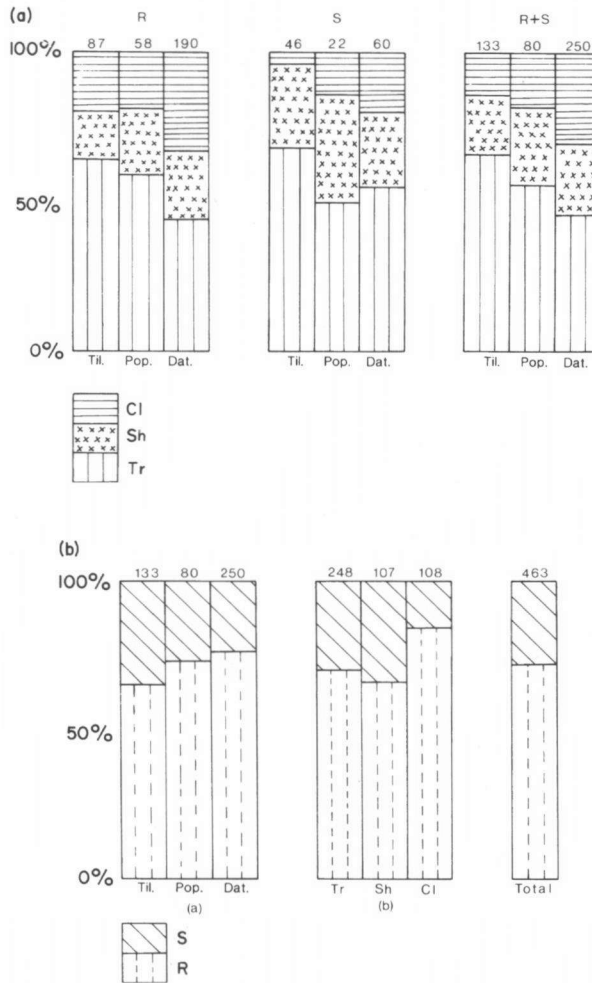


Fig. 2. (a) Frequency distribution of habit types in relation to bark structural types in different climatic zones. Total numbers of species indicated above the columns. (b) Frequency distribution of climatic zones in relation to bark structural types (a) and habit (b). Total numbers of species indicated above the columns.

- (3) In comparison with rain forest, in savannah the percentage of bst *Tilia* is increased at the expense of the percentage of bst *Datura*; the percentage of bst *Populus* remains constant (Fig. 3b).
- (4) In savannah, climbers are less numerous (Figs 2b and 3a); this means more bst *Tilia*.

B. Relationships between phloem characteristics and categories bark structural type, habitus and climatic zone

Sieve-tube member length (Tables 1–3).

- (1) The sieve-tube member length is always shortest in bst *Tilia*, except in shrubs from rain forest where it is shortest in bst *Populus* (Table 1). In trees, climbers and all habit categories together the sieve-tube member length then increases through bst *Datura* to bst *Populus* (Table 2).

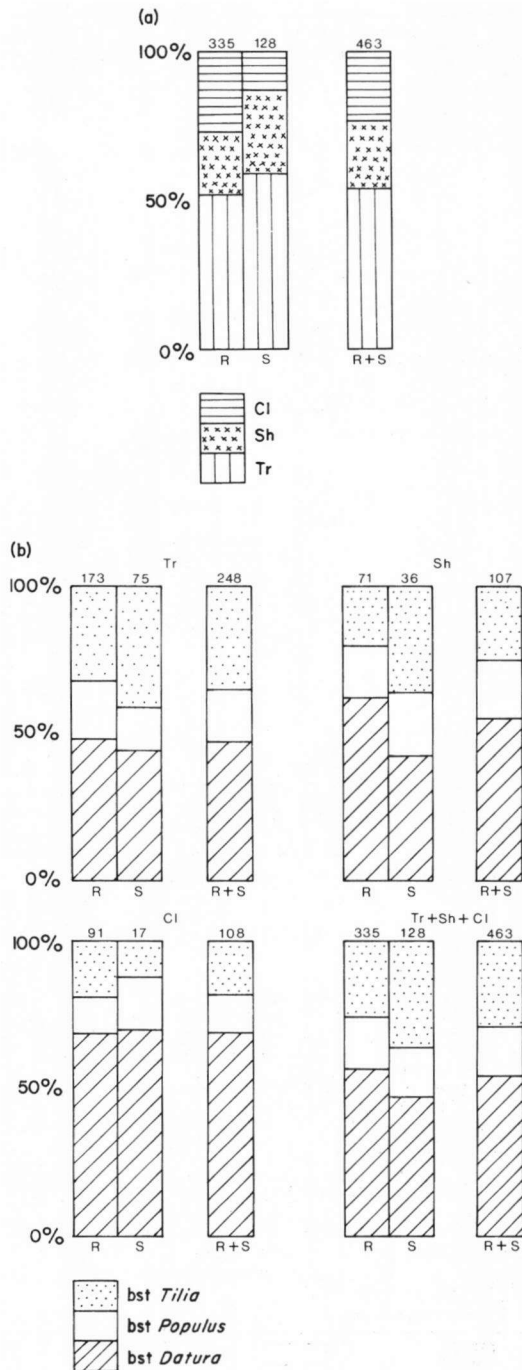


Fig. 3. (a) Frequency distribution of habit types in relation to climatic zones. Total numbers of species indicated above the columns. (b) Frequency distribution of bark structural types in relation to climatic zones for different habits. Total numbers of species indicated above the columns.

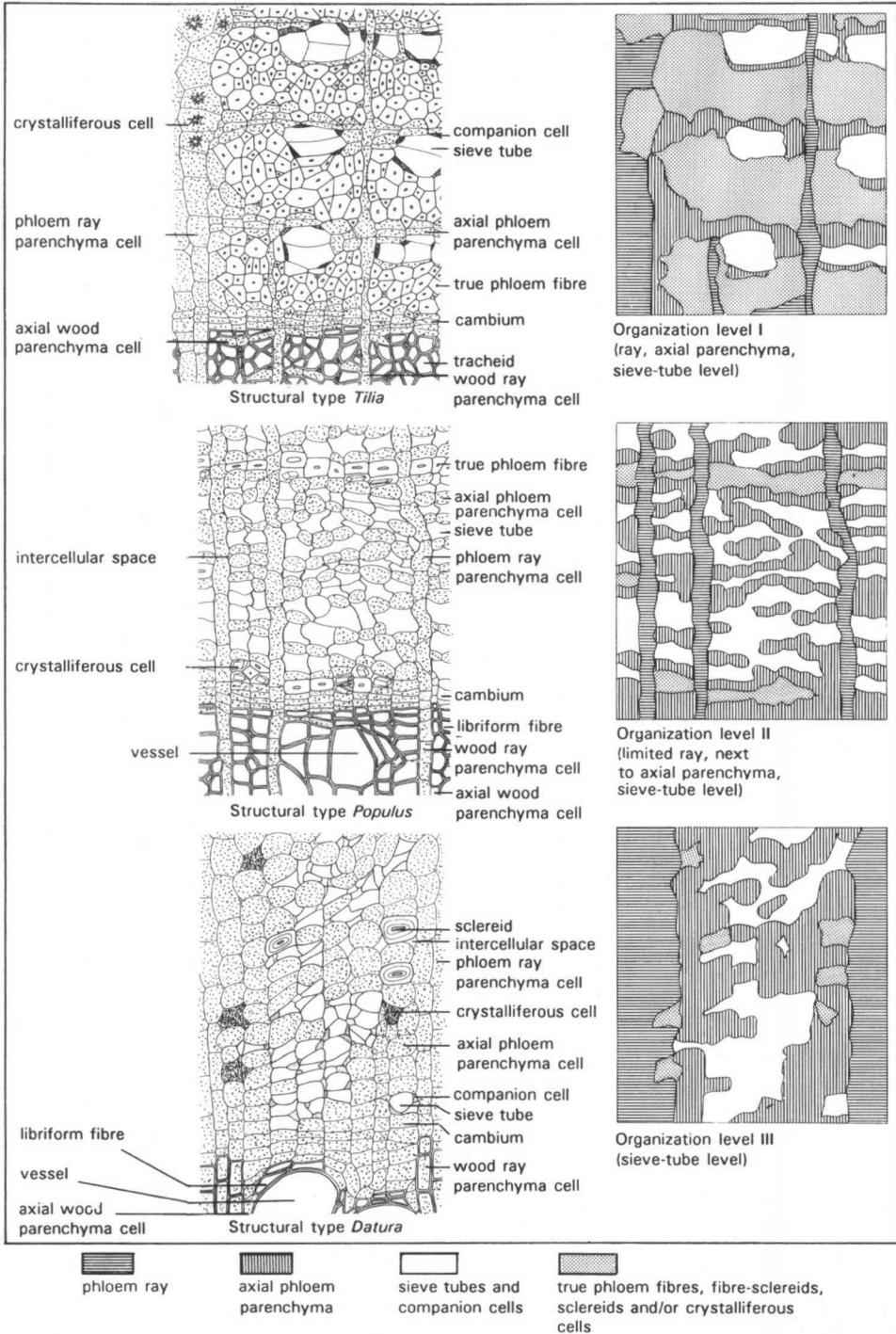


Fig. 4. Bark structural types and organization levels of angiosperm barks based on *Tilia platyphyllos* Scop., *Populus × canadensis* Moench 'Serotina' and *Datura arborea* L.

Table 1. Sieve-tube member (ST) length, parenchyma strand (PS) length, increase in PS length with respect to ST length, and number of cells per PS with standard deviation, in relation to bark structural types tabulated separately for trees, shrubs and climbers in rain forest and savannah

Bark structural type	Trees							
	Rain forest				Savannah			
	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS
<i>Tilia</i>	350 \pm 92	415 \pm 118	19	5.0 \pm 1.9	322 \pm 92	386 \pm 129	20	4.6 \pm 1.5
<i>Populus</i>	397 \pm 120	502 \pm 130	26	5.0 \pm 1.9	389 \pm 110	523 \pm 129	34	5.6 \pm 2.2
<i>Datura</i>	394 \pm 144	553 \pm 167	40	5.0 \pm 2.1	328 \pm 89	437 \pm 121	33	5.2 \pm 1.7
Bark structural type	Shrubs							
	Rain forest				Savannah			
	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS
<i>Tilia</i>	364 \pm 100	414 \pm 119	14	4.5 \pm 2.0	314 \pm 98	406 \pm 151	29	5.1 \pm 1.7
<i>Populus</i>	309 \pm 93	432 \pm 126	40	4.2 \pm 1.7	365 \pm 97	431 \pm 124	18	4.5 \pm 1.9
<i>Datura</i>	366 \pm 134	506 \pm 182	38	4.9 \pm 1.6	369 \pm 143	469 \pm 158	27	5.0 \pm 1.8
Bark structural type	Climbers							
	Rain forest				Savannah			
	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS
<i>Tilia</i>	354 \pm 102	399 \pm 112	13	5.2 \pm 1.6	298 \pm 38	313 \pm 38	5	4.0 \pm 0.0
<i>Populus</i>	476 \pm 118	588 \pm 108	24	6.3 \pm 1.3	407 \pm 98	438 \pm 116	8	4.0 \pm 0.0
<i>Datura</i>	405 \pm 131	515 \pm 70	27	5.4 \pm 2.5	451 \pm 139	525 \pm 67	16	5.4 \pm 2.1

- (2) In savannah the sieve-tube member length increases from trees through shrubs to climbers; in rain forest and both climatic zones together, from shrubs through trees to climbers (Table 3).
- (3) Sieve-tube member length increases from savannah to rain forest for trees, shrubs and all habit categories together, but decreases for climbers (Table 3).

Axial parenchyma: strand length (Tables 1–3).

- (1) The strand length is always shortest in bst *Tilia*. Strand length increases through bst *Populus* to bst *Datura*, except in climbers where it increases through bst *Datura* to bst *Populus* (Tables 1 and 2).

Table 2. Sieve-tube member (ST) length, parenchyma strand (PS) length, increase in PS length with respect to ST length, and number of cells per PS with standard deviation, in relation to bark structural types tabulated separately and jointly for trees, shrubs and climbers

Trees				
Bark structural type	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS
<i>Tilia</i>	340 \pm 93	405 \pm 123	19	4.9 \pm 1.8
<i>Populus</i>	395 \pm 118	507 \pm 156	28	5.1 \pm 2.0
<i>Datura</i>	375 \pm 135	499 \pm 160	33	5.1 \pm 2.0
Shrubs				
Bark structural type	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS
<i>Tilia</i>	340 \pm 103	410 \pm 135	21	4.8 \pm 1.5
<i>Populus</i>	330 \pm 98	431 \pm 124	31	4.3 \pm 1.8
<i>Datura</i>	367 \pm 136	496 \pm 176	35	5.0 \pm 2.2
Climbers				
Bark structural type	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS
<i>Tilia</i>	347 \pm 98	390 \pm 110	12	5.1 \pm 1.5
<i>Populus</i>	461 \pm 118	556 \pm 126	21	5.8 \pm 1.5
<i>Datura</i>	412 \pm 133	517 \pm 169	26	5.4 \pm 2.4
Trees + shrubs + climbers				
Bark structural type	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS
<i>Tilia</i>	341 \pm 96	403 \pm 124	18	4.9 \pm 1.7
<i>Populus</i>	389 \pm 120	496 \pm 149	28	5.0 \pm 1.9
<i>Datura</i>	384 \pm 136	513 \pm 167	34	5.1 \pm 2.0

- (2) In savannah the strand length increases from trees through shrubs to climbers; in rain forest and both climatic zones together from shrubs through trees to climbers (Table 3).
- (3) Strand length increases from savannah to rain forest (Table 3).

Table 3. Sieve-tube member (ST) length, parenchyma strand (PS) length, increase in PS length with respect to ST length, and number of cells per PS with standard deviation, in relation to habit tabulated separately and jointly for different climatic zones

Habit	Rain forest				Savannah				Rain forest + savannah			
	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS	Length ST (μm)	Length PS (μm)	Length increase PS/ST (%)	Number of cells per PS
Climbers	404 \pm 129	502 \pm 163	24	5.5 \pm 2.2	425 \pm 134	485 \pm 165	14	5.0 \pm 1.8	407 \pm 130	500 \pm 164	23	5.4 \pm 2.2
Shrubs	355 \pm 123	474 \pm 166	34	4.8 \pm 1.6	348 \pm 122	438 \pm 151	26	5.0 \pm 1.8	352 \pm 123	462 \pm 163	31	4.8 \pm 1.7
Trees	380 \pm 127	484 \pm 134	27	5.0 \pm 2.0	335 \pm 96	428 \pm 150	28	5.0 \pm 1.8	367 \pm 122	477 \pm 154	30	5.0 \pm 1.9
Total	381 \pm 128	487 \pm 160	28	5.1 \pm 2.0	351 \pm 113	439 \pm 153	25	5.0 \pm 1.8	373 \pm 125	479 \pm 160	28	5.1 \pm 2.2

Table 4. Phloem-ray characters in relation to habit, arranged separately and jointly for different climatic zones

Habit	Ho (in %)			He (in %)			1-2-Seriate (in %)			Av. m.w. (in cells)		
	R	S	R+S	R	S	R+S	R	S	R+S	R	S	R+S
Climbers	15	24	17	85	76	83	19	18	19	6.1	6.9	6.2
Shrubs	17	25	20	83	75	80	23	11	19	4.7	5.3	4.9
Trees	31	31	31	69	69	69	17	14	16	4.9	5.8	5.1

Table 5. Phloem-ray characters in relation to bark structural type, arranged separately and jointly for different climatic zones

Bark structural type	Ho (in %)			He (in %)			1-2-Seriate (in %)			Av. m.w. (in cells)		
	R	S	R+S	R	S	R+S	R	S	R+S	R	S	R+S
<i>Tilia</i>	38	43	40	62	57	60	24	12	20	5.6	5.8	5.7
<i>Populus</i>	24	27	25	76	73	75	19	14	18	4.9	4.6	4.8
<i>Datura</i>	17	17	17	83	83	83	17	15	17	5.1	6.3	5.3
Total	24	28	25	76	72	75	19	14	18	5.2	5.8	5.3

Axial parenchyma: number of cells per strand (Tables 1-3).

- (1) The number of cells per strand is lowest in bst *Tilia*, except in shrubs. The number however is almost independent of bst (Tables 1 and 2).
- (2) In rain forest and both climatic zones together the number of cells per strand increases from shrubs through trees to climbers; in savannah the number remains almost on the same level (Table 3).
- (3) The number of cells per strand increases in climbers from savannah to rain forest; for shrubs it decreases, while in trees it remains almost equal (Table 3).

Axial parenchyma: increase in strand length as a percentage of sieve-tube member length (Tables 1-3).

- (1) The percentage increases from bst *Tilia* through bst *Populus* to bst *Datura*; for trees in savannah and shrubs in rain forest, however, the parameter does not increase from bst *Populus* to bst *Datura*, but diminishes slightly (Tables 1 and 2).
- (2) In savannah the percentage increases from climbers through shrubs to trees; in rain forest and both climatic zones together, from climbers through trees to shrubs (Table 3).
- (3) The percentage increases from savannah to rain forest (Table 3).

Phloem rays: heterogeneous vs. homogeneous (Tables 4-6).

- (1) The percentage of heterogeneous rays increases from bst *Tilia* through bst *Populus* to bst *Datura* (Table 4); for climbers from both savannah and rain forest, and distantly also for shrubs from rain forest, this is less obvious (Tables 5 and 6).

Table 6. Phloem-ray characters in relation to bark structural types, arranged separately for habit and climatic zones

Climbers								
Bark structural type	Rain forest				Savannah			
	Ho (%)	He (%)	1-2-Ser. (%)	Av.m.w. (in cells)	Ho (%)	He (%)	1-2-Ser. (%)	Av.m.w. (in cells)
<i>Tilia</i>	24	76	29	5.0	50	50	0	7.5
<i>Populus</i>	27	73	18	6.7	0	100	33	3.3
<i>Datura</i>	11	89	16	6.2	25	75	17	7.8
Total	15	85	19	6.1	24	76	18	6.9

Shrubs								
Bark structural type	Rain forest				Savannah			
	Ho (%)	He (%)	1-2-Ser. (%)	Av.m.w. (in cells)	Ho (%)	He (%)	1-2-Ser. (%)	Av.m.w. (in cells)
	21	79	15	6.4	38	62	15	4.1
	23	77	15	4.8	25	75	0	4.6
	14	86	27	4.1	13	87	13	7.4
Total	17	83	23	4.7	25	75	11	5.3

Trees								
Bark structural type	Rain forest				Savannah			
	Ho (%)	He (%)	1-2-Ser. (%)	Av.m.w. (in cells)	Ho (%)	He (%)	1-2-Ser. (%)	Av.m.w. (in cells)
	46	54	12	5.6	45	55	11	6.8
	24	76	21	4.4	36	64	18	4.9
	23	77	12	4.7	15	85	15	5.2
Total	31	69	17	4.9	31	69	14	5.8

- (2) The percentage of heterogeneous rays increases from trees through shrubs to climbers (Table 4).
- (3) The percentage of heterogeneous rays increases from savannah to rain forest, except in trees where it is independent from climatic zones (Tables 4 and 6).

Phloem rays: 1-2-seriate (Tables 4-6).

- (1) The percentage of 1-2-seriate rays increases from bst *Tilia*, through bst *Populus* to bst *Datura* in savannah; it decreases however in rain forest and also when both climatic zones are considered as a whole (Table 5).
- (2) The percentage of 1-2-seriate rays slightly increases from trees through shrubs to climbers when both climatic zones are combined (Table 4).

- (3) In savannah the percentage of 1–2-seriate rays is lower than in rain forest, though the difference is slight for climbers (Tables 4 and 6).

Phloem rays: maximum width (Tables 4 and 6).

- (1) The maximum ray width in cells is lowest in bst *Populus* (Table 5), but this is caused only by trees from both climatic zones and by climbers from savannah (Table 6). For both climatic zones together the parameter increases through bst *Datura* to bst *Tilia* (Table 5).
- (2) The maximum ray width increases from shrubs through trees to climbers (Table 4).
- (3) In savannah the rays are wider than in rain forest (Table 4). This however does not hold for shrubs with bst *Tilia* and bst *Populus* or for climbers with bst *Populus* (Table 6).

DISCUSSION

Trends in bark structural categories

From the standpoint of the evolution of conducting cells, it is remarkable that gymnospermous sieve cell structure remains rather uniform (Taylor 1990). Likewise, the precise and complex physiological requirements of the angiospermous phloem have necessitated only a narrow range of structures and lines of development in this tissue, represented in the three sieve-tube types used here. The same phenomenon was found in the structures of secondary phloem as a whole, where large differences in habitat have brought about only a small number of bark types.

As for angiospermous secondary xylem (Braun 1970, 1984), several bark structural types (at different levels of organization) can be distinguished for secondary phloem in relation to the functions to be accomplished by the tissue. These functions include transport and storage of assimilation products as well as mechanical tasks and they depend on the number and type of constituent secondary phloem elements.

Bark structural type *Tilia* is composed of tangential layers of sieve tubes and companion cells surrounded by axial parenchyma and separated from one another by tangential layers of secondary phloem fibres or sclereids. This bark structural type usually possesses an advanced sieve-tube type accompanied by an advanced companion-cell type (Zahur 1959; den Outer 1983). Contact between sieve tubes and companion cells of the separate tangential layers is facilitated by axial parenchyma and phloem rays. In this type, sieve tubes and probably also axial parenchyma and rays (as connections between the tangential layers of sieve tubes) play an important role in the transport of assimilates: ray, axial parenchyma, sieve-tube organization level.

Bark structural type *Populus* is composed of a few radially narrow tangential layers of secondary phloem fibres or sclereids radially alternating with many almost tangential radially narrow layers of axial parenchyma and layers of sieve tubes. The sieve-tube type is intermediate between the previous advanced type and the primitive one of bark structural type *Datura*. The companion cells are as long as the sieve-tube members that they accompany. Here more direct contact is possible between the different tangential layers of sieve tubes and companion cells. The phloem rays are assumed to play a less important role in the transport function: limited ray, adjoining axial parenchyma and sieve-tube organization level.

Bark structural type *Datura* is composed of groups of sieve tubes and companion cells in a ground tissue of axial parenchyma. Sclereids or fibre-sclereids may be present. This bark structural type possesses a primitive sieve-tube type accompanied by a primitive companion-cell type. Here a sieve-tube network is present, branching in all directions. Sieve tubes are probably mainly responsible for transport: sieve-tube organization level.

Going from bark structural type *Tilia* through bark structural type *Populus* to bark structural type *Datura*, the following are achieved:

- (1) radially wide tangential layers of fibres produced by the vascular cambium changing into randomly scattered (fibre-)sclereids formed in the collapsed secondary phloem;
- (2) sieve tubes and companion cells arranged in tangential layers, transferring into a diffuse network of sieve tubes;
- (3) a small number of axial parenchyma changes into abundant axial parenchyma, forming the ground tissue;
- (4) the radial transport function of phloem rays as connections between the tangential layers or groups of sieve tubes and companion cells, presumably becoming less important.

A classification of bark types based on mechanical tissue as used by Moeller (1882), Thorenaar (1926) and Furuno (1990), coincides with the author's based on all elements of the secondary phloem. Bark structural type *Datura* is more frequently present in climbers than in trees (Fig. 1). So abundant parenchyma constitutes the ground tissue of the functioning secondary phloem in climbers. Since tropical lianas may support as much leaf biomass as big trees and their stems are narrower, the efficiency of the phloem for transport of assimilates must be much higher. Sieve-tube type in lianas is usually primitive (bark structural type *Datura*). This means very oblique, compound, sieve plates with small sieve pores. The sieve-tube members however are long and their diameter is large. In the secondary xylem of lianas, the vessels are also long and wide. Lianas have among the longest (up to 8 m or more) and widest (up to 500 μm) vessels in the plant kingdom (Ewers 1985). The wider sieve tubes probably remain conductive for a period longer than 1 year, as has been demonstrated for vessels of lianas (Ewers 1985). The total percentage of surface area occupied by sieve tubes, like those of vessels, as seen in transverse section is also much higher in climbing species than in non-climbing species. For vessels, these trends were found in climbers from tropical as well as from temperate areas (ter Welle 1985). Axial parenchyma cells are probably also involved in transport of assimilates, as well as companion cells which presumably act as intermediates in the transfer of assimilates from the sieve-tube members to (ray-) parenchyma cells and vice versa (Evert 1984).

The minor veins in mature leaves of most woody dicotyledonous plants have intermediate cells with numerous plasmodesmal fields (open woody type), symplastic transport as the main phloem-loading mechanism, as well as oligosaccharides and other complex sugars as the main phloem transport substances (Gamalei 1989). The open type is characteristic of tropical evergreen trees (woody plants), whereas a minor vein structure of the closed type without plasmodesmal contacts to the mesophyll is typical of temperate herbs. Constant rather vulnerable long-distance translocation with usually the same transport direction characteristic of evergreen trees (woody plants) seems to have limited the evolution of phloem structure in the minor veins (Gamalei 1989). In climbers, mainly present in rain forest, sieve tubes of secondary phloem are

also usually primitive. Dryness and lower temperatures have caused evolution of the closed-type structure, including three subtypes (A. J. E. van Bel, Utrecht: personal communication) with a perfection of the apoplastic mechanism of phloem loading. Plants have evolved in which less vulnerable short-distance transport is more important. This is associated with high transport mobility and changing source-sink systems. In tropical dry sites (savannah), shrubs have become more numerous at the expense of climbers and shrubs possess moderately advanced sieve tubes.

Sclerification of cells in rays is less common than it is in axial parenchyma, a feature probably associated with a longer maintenance of rays as paths of radial translocation of carbohydrates, as long as the bark remains alive (Esau 1979). Species with a distribution covering both rain forest and savannah indicate that specimens from the savannah tend to have more wood ray tissue (rays are higher, wider and more numerous; den Outer & van Veenendaal 1976). More phloem ray tissue is also present in savannah material if all species are considered together (Table 4), though phloem ray height and width (Table 4) and wood rays (ter Welle, 1985) are larger in climbers than in trees, and climbers are less numerous in savannah than in rain forest (Fig. 3a). Furthermore, phloem ray tissue appears to be more homogeneous (Tables 4 and 6) than in rain forest. Relations between the other categories and several phloem characteristics are discussed below.

Trends in habit categories

Most secondary phloem characteristics mentioned in Table 7 increase within the categories, from bark structural type *Tilia* to *Datura*, from tree to climber and from savannah to rain forest, so that advanced features become less prominent. For a number of 1-2-seriate phloem rays, however, an increase means a more advanced status. Phloem characteristics for shrubs were quite often not intermediate between those of trees and climbers. The arrows in Table 7 sometimes end in shrubs, but more often start in shrubs like the one for parenchyma strand length, especially for species from rain forest. So from phloem anatomy, one gets the impression that the phloem structure of shrubs in rain forest developed along different lines of specialization; from trees by developing a more advanced axial parenchyma and mechanical tissue, and from climbers by developing more advanced sieve tubes and companion cells.

Trends in habitat categories

Species from rain forest usually possess more primitive features than those from savannah; for climbers, however, this is uncertain. Baas and Schweingruber (1987) also concluded that for xylem characteristics there is a preferential selection for advanced features in dry warm regions. Apparently primitive features were eliminated in drier habitats like savannah. According to Gartner *et al.* (1989), differences in hydraulic conductivities of excised stem segments of vines as compared to trees seemed to relate to some aspect of differences in growth form itself, and not to differences in the habitat where the vines and trees grew. Shrubs have a preference for dry sites (Fig. 2b) and the arrows in Table 7 starting in shrubs indicate that shrubs possess many advanced phloem characteristics.

Trends in relation to phylogeny

Possible relationships seem to be absent or scarce between components of the categories used here on the one hand and a phylogenetic arrangement of families according to

Hutchinson (1973) or according to Takhtajan (1980) on the other. Only a weak trend for bark structural types is present. Going from primitive families towards more advanced ones, the percentage of species with bark structural type *Tilia* gradually shifts in favour of bark structural type *Datura*.

Guthrie (1989) demonstrated in a small geographical area that sets of closely and distantly taxonomically related tree species, with the same xylem anatomy share some common ecological characteristics. This suggests that xylem structure is a critical characteristic in the adaptation of trees to variation in the environment. This also goes for phloem structure; taxonomic implications hardly play any role in relationships between the different categories used in the author's investigation of secondary phloem.

Present analyses are based on percentages of species with certain properties. This implies that a proportion of the species does not obey the trend. In these species, a combination of phloem features may be applied to fulfil the demands that the tissue has to meet in different habits and habitats. Information on leaf anatomy, root system and microclimate was not used, partly because it was not available, although it certainly would have improved comprehension of the relationships between the categories distinguished here. Leaves constitute perhaps the most significant component of the hydrovascular system (Rury & Dickison 1984) and probably of the conducting secondary phloem as well. Evolutionary and biological interpretations of phloem anatomy within an ecological context are therefore not optimum in the absence of correlative structural data, particularly for leaves. Gamalei (1989) reported some correlations between the structure of intermediate cells in minor leaf veins (in relation to mechanisms of phloem loading and sugar transport) and the habit categories of trees and perennial herbs. Some correlations between bark structural types and habit as well as habitat categories have been demonstrated here.

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REFERENCES

- Baas, P. & Schweingruber, F.H. (1987): Ecological trends in wood anatomy of trees, shrubs and climbers from Europe. *IAWA Bull. n.s.* **8**: 245–274.
- Braun, H.J. (1970): Funktionelle Histologie der sekundären Sprossachse. I. Das Holz. *Handbuch der Pflanzenanatomie (Encyclopedia of Plant Anatomy)*. Borntraeger, Berlin, Stuttgart.
- Braun, H.J. (1984): The significance of the accessory tissues of the hydrosystem for osmotic water shifting as the second principle of water ascent, with some thoughts concerning the evolution of trees. *IAWA Bull. n.s.* **5**: 275–294.
- Chang, Y.P. (1951): *Anatomy of wood and bark in the Rubiaceae*. Dissertation, University of Michigan, Ann Arbor.
- Chang, Y.P. (1954a): Bark structure of North American conifers. *U.S. Dept. Agric., Tech. Bull. no.* **1095**: 1–86.
- Chang, Y.P. (1954b): Anatomy of common North American pulpwood barks. *TAPPI Monogr. Ser. no.* **14**: 1–249.
- den Outer, R.W. (1972): Tentative determination key to 600 trees, shrubs and climbers from the Ivory Coast, Africa, mainly based on characters of the living bark, besides the rhytidome and the leaf. I. Large trees. *Meded. Landb. hogesch. Wageningen* **72-18**: 1–73.
- den Outer, R.W. (1977): The secondary phloem of some Ochnaceae and the systematic position of *Lophira lanceolata* V. Tieghem ex Keay. *Blumea* **23**: 439–447.
- den Outer, R.W. (1983): Comparative study of the secondary phloem of some woody dicotyledons. *Acta Bot. Neerl.* **32**: 29–38.
- den Outer, R.W. & Fundter, J.M. (1976): The secondary phloem of some Combretaceae and the

- systematic position of *Strephonema pseudocola* A. Chev. *Acta Bot. Neerl.* 25: 481-493.
- den Outer, R.W. & van Veenendaal, W.L.H. (1976): Variation in wood anatomy of species with a distribution covering both rain forest and savanna areas of the Ivory Coast, West-Africa. *Leiden Bot. Ser.* 3: 182-195.
- Esau, K. (1964): Structure and development of the bark in dicotyledons. In: Zimmermann, M.H. (ed.): *Formation of Wood in Forest Trees.* 37-50. Academic Press, New York.
- Esau, K. (1965): *Plant Anatomy.* John Wiley & Sons, New York.
- Esau, K. (1979): Phloem. In: Metcalfe, C.R. and Chalk, L. (eds): *Anatomy of the Dicotyledons.* 181-189. Clarendon Press, Oxford.
- Evert, R.F. (1984): Comparative structure of phloem. In: White, R.A. and Dickison, W.C. (eds): *Contemporary Problems in Plant Anatomy.* 145-234. Academic Press, New York.
- Ewers, F.W. (1985): Xylem structure and water conduction in conifer trees, dicot trees, and lianas. *IAWA Bull. n.s.* 6: 309-317.
- Furuno, T. (1990): Bark structure of deciduous broad-leaved trees grown in the San'in region, Japan. *IAWA Bull. n.s.*, 11: 239-254.
- Gamalei, Y. (1989): Structure and function of leaf minor veins in trees and herbs. A taxonomic review. *Trees* 3: 96-110.
- Gartner, B.L., Mooney, H.A., Bullock, S.H., Whitbeck, J.L. & Brown, V.B. (1989): Stem hydraulic conductivities of vines vs. trees. *Am. J. Bot.* 76 (6, Suppl.): 35.
- Guthrie, R.L. (1989): Xylem structure and ecological dominance in forest community. *Am. J. Bot.* 76: 1216-1228.
- Hemenway, A.F. (1913): Studies on the phloem of the dicotyledons. *Bot. Gaz.* 55: 236-243.
- Holdheide, W. (1951): Anatomie mitteleuropäischer Gehölzrinden. In: Freund, H. (ed.): *Handbuch der Mikroskopie in der Technik, Band V, Teil 1.* 193-367. Umschau Verlag, Frankfurt am Main.
- Huber, B. (1939): Das Siebröhrensystem unserer Bäume und seine jahreszeitlichen Veränderungen. *Jb. wiss. Bot.* 88: 176-242.
- Hutchinson, J. (1973): *The Families of Flowering Plants, Arranged According to a New System Based on their Probable Phylogeny.* Clarendon Press, Oxford.
- IAWA Committee (1989): IAWA list of microscopic features for hardwood identification with an appendix on non-anatomical information: Wheeler, E.A., Baas, P. and Gasson, P.E. (eds). *IAWA Bull. n.s.* 10: 219-332.
- Janssonius, H.H. (1918): *De tangentielle groei van enige pharmaceutische basten.* Dissertation, University of Groningen. M. de Waal, Groningen.
- Johansen, D.A. (1940): *Plant Microtechnique.* McGraw-Hill Book Company Inc., New York.
- Kribs, D.A. (1935): Salient lines of structural specialization in wood rays of dicotyledons. *Bot. Gaz.* 96: 547-557.
- Moeller, J. (1882): *Anatomie der Baumrinden. Vergleichende Studien.* Springer Verlag, Berlin.
- Parameswaran, N. & Liese, W. (1968): Beitrag zur Rindenanatomie der Gattung *Entandrophragma*. *Flora, Abt. B.* 158: 22-40.
- Parameswaran, N. & Liese, W. (1970): Mikroskopie der Rinde tropischer Holzarten. In: Freund, H. (ed.): *Handbuch der Mikroskopie in der Technik, Band V, Teil 1.* 227-306. Umschau Verlag, Frankfurt am Main.
- Reinders, E. (1961). *Handleiding bij de Plantenanatomie.* Centraal Magazijn, Landbouwhogeschool, Wageningen.
- Roth, I. (1981): *Structural Patterns of Tropical Barks.* Gebr. Borntraeger, Stuttgart.
- Rury, P.M. & Dickison, W.C. (1984): Structural correlations among wood, leaves and plant habit. In: White, R.A. and Dickison, W.C. (eds): *Contemporary Problems in Plant Anatomy:* 495-540. Academic Press, New York.
- Takhtajan, A.L. (1980): Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev.* 46: 225-359.
- Taylor, E.L. (1990): Phloem evolution: an appraisal based on fossil record. In: Behnke, H.D. and Solund, R.D. (eds): *Sieve Elements. Comparative Structure, Induction and Development.* 285-297. Springer Verlag, Berlin.
- ter Welle, B.J.H. (1985): Differences in wood anatomy of lianas and trees. *IAWA Bull. n.s.* 6: 70.
- Thorenaar, A. (1926): *Onderzoek naar bruikbare kenmerken ter identificatie van bomen naar hun bast.* Dissertation, University of Wageningen, Veenman en Zonen, Wageningen.
- Trockenbrodt, M. (1990): Survey and discussion of the terminology used in bark anatomy. *IAWA Bull. n.s.* 11: 141-166.
- van Veenendaal, W.L.H. & den Outer, R.W. (1978): A provisional determination key to 54 continental African *Dichapetalum* species based on anatomical characters of the secondary xylem. *Meded. Landh. hogesch. Wageningen* 78-18: 1-23.
- Zahur, M.S. (1959): Comparative study of secondary phloem of 423 species of woody dicotyledons belonging to 85 families. *Cornell Univ. Agric. Exp. St. Mem.* 358: 1-160.
- Zimmermann, M.H. & Brown, C.L. (1971): *Trees: Structure and Function.* Springer Verlag, Berlin.