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Ecological trends in the wood anatomy of Vaccinioideae (Ericaceae s.l.)

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Summary

The ecological wood anatomy of 128 vaccinioid wood samples (including 115 species, 35 genera), collected between 39° S and 60° N latitude and 10 m to 3400 m altitude is studied. Several wood anatomical features within the subfamily, viz. tangential vessel diameter, average length of tracheary elements, height of multiseriate rays, and presence of prismatic crystals are negatively correlated with increasing latitude, while vessel density and helical thickenings show a positive correlation with increasing latitude. Similar latitudinal trends are found within the genus *Vaccinium* (31 species studied). The correlation between various wood anatomical features and latitude is surprisingly high despite the fact that most tropical species grow in montane regions, which are rather similar to the temperate, non-tropical habitats as regards climatic conditions. Altitudinal trends, however, are weak. The impact of different life forms (shrubs, trees and lianas) and the amount of precipitation also plays a significant role in various continuous wood features. Furthermore, some of these anatomical features are correlated with each other. Part of the variation in vessel characters may be the result of functional adaptations to different climatic zones and environments, especially with respect to conductive efficiency and safety.

Key words: Altitude, Ecological and functional wood anatomy, Ericaceae, Latitude, Vaccinioideae, *Vaccinium*

Introduction

Functionally adaptive xylem evolution and the dominant role of macroclimatic adaptation have been documented repeatedly in the literature. A number of studies on the relations of wood anatomy to ecology are reported within species (e.g. Noshiro & Suzuki 1995; Noshiro & Baas 2000; Liu & Noshiro 2003), in genera (e.g. Baas 1973; van den Oever et al. 1981; Noshiro et al. 1995), and within families (e.g. Dickison & Phend 1985; Baas et al. 1988; Zhang et al. 1992; Noshiro & Baas 1998; Klaassen 1999). Similar studies have also been conducted for different regional floras (e.g. Baas et al. 1983; Carlquist & Hoekman 1985; Baas & Schweingruber 1987) and some general ecological trends suggested were reviewed (Baas 1982, 1986; Dickison 1989; Carlquist 1975, 2001). Most ecological trends conform to correlations established previously, but the degree of adaptation to ecological gradients may differ considerably among plant groups. For instance, in Rosaceae the percentage of anatomical variation explained by ecological factors was claimed to be relatively low (2–10%) (Zhang et al. 1992), while latitudinal and altitudinal trends are manifest within for instance *Symplocos* (van den Oever et al. 1981).

According to the most recent classification of Ericaceae, the subfamily Vaccinioideae consists of five tribes, viz. Andromedeae s.s., Gaultherieae, Lyonieae, Oxydendreae and Vaccinieae, comprising about 48 genera

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and more than 1325 species (KRON et al. 2002). Most Vaccinioideae are evergreen shrubs, including many epiphytes, whereas lianas and trees occur sporadically. The vast majority of taxa (about 32 genera and 1000 species, mainly belonging to Vaccinieae) are concentrated in the cool and moist montane areas of South America between 1500 m and 3000 m, although some species grow above 3000 m in páramo vegetation and others below 100 m in tropical lowland rainforest to mangroves (LUTEYN 2002). Most other members of Vaccinioideae grow in temperate to arctic regions of the northern hemisphere, in the montane regions of tropical Asia, and only a few species are restricted to southeast Africa and Madagascar. *Vaccinium*, the only genus that occurs in temperate regions as well as in the tropics of the Old and New World, is by far the largest genus of the subfamily including about 450 species. In addition to two recent studies of the systematic wood anatomy of Vaccinioideae (LENS et al. 2004, submitted), the wide ecological distribution of the study group raises interesting questions about the ecological impact on variation of secondary xylem.

Our previous wood anatomical studies on Vaccinioideae illustrate that several wood anatomical features, especially the arrangement and type of vessel-ray pitting, the width and height of multiseriate rays, the shape of the body ray cells in multiseriate rays, and the presence and location of prismatic crystals, largely support recent changes in phylogeny based on morphological and molecular data (KRON et al. 2002). This paper aims to investigate the impact of various ecological influences on secondary xylem within the subfamily. In order to do this, we have investigated 12 wood anatomical features of 128 wood specimens representing 115 species and 35 genera. These anatomical characters are evaluated according to rough ecological factors, both at the subfamily level and within the genus *Vaccinium* (31 species). Furthermore, correlations are investigated between most of the characters studied. This research also explores the impact of different life forms (shrubs, trees and lianas) on several continuous, wood anatomical features.

Material and methods

The material used is based on two previous studies on the systematic wood anatomy of the subfamily (LENS et al. 2004, submitted, see appendix). Wood specimens derived from juvenile stems were excluded, because of possible ontogenetic differences between juvenile and mature wood (NOSHIRO & SUZUKI 2001). However, mature wood could not always be easily defined within the study group. For example, a thin wood sample of less than 10 mm diameter with a relatively large amount of pith tissue was considered to be juvenile, while some wood samples with a diameter of 6 mm that showed a small amount of pith area together with several growth rings were regarded as mature. Also, we omitted all specimens for which no detailed ecological data were available, including altitude, latitude, the annual amount of precipitation and the presence or absence of frost. In addition, non-standardized sampling may have influenced quantitative data, but it is believed that this represents random sources of variation that cannot have influenced the general results substantially. As a result, 128 mature samples were used to trace major ecological trends in the wood of Vaccinioideae. With the aid of regression analyses, these trends are illustrated using the program Microsoft Excel version X (Macintosh). The sta-

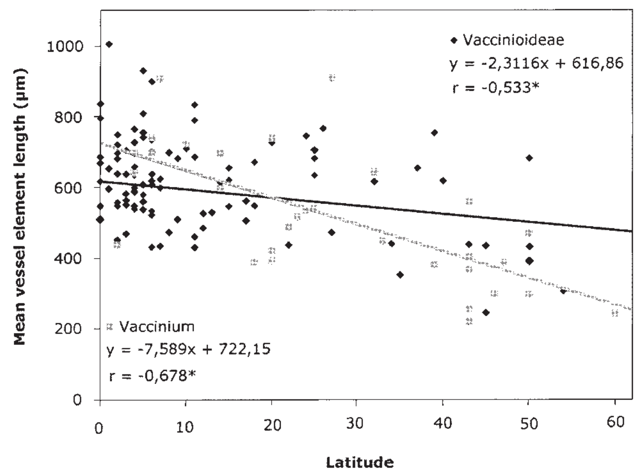

Fig. 1. Scatter plot of mean vessel element length and latitude for Vaccinioideae and *Vaccinium* with linear curve fitting. An asterisk means that the r-value is significant at the 0.5% significance level.

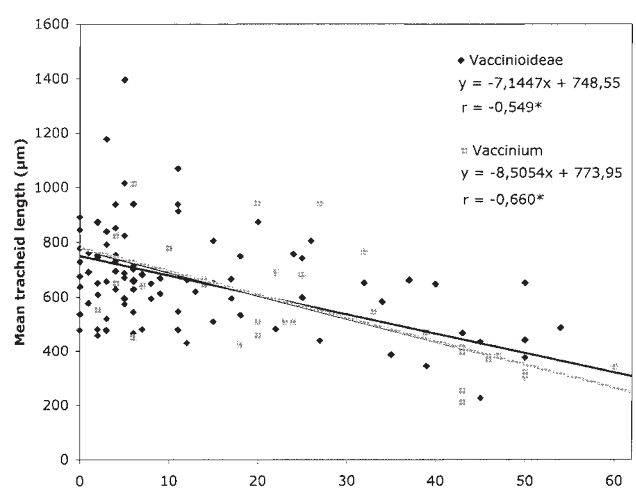

Fig. 2. Scatter plot of mean tracheid length and latitude for Vaccinioideae and *Vaccinium* with linear curve fitting. An asterisk means that the r-value is significant at the 0.5% significance level.

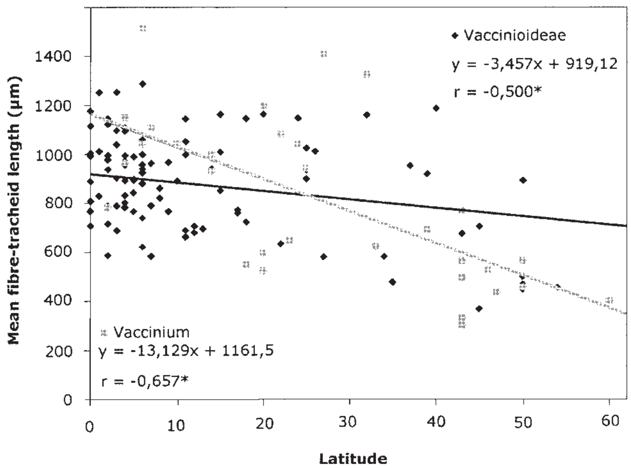

Fig. 3. Scatter plot of mean fibre-tracheid length and latitude for Vaccinioideae and *Vaccinium* with linear curve fitting. An asterisk means that the r-value is significant at the 0.5% significance level.

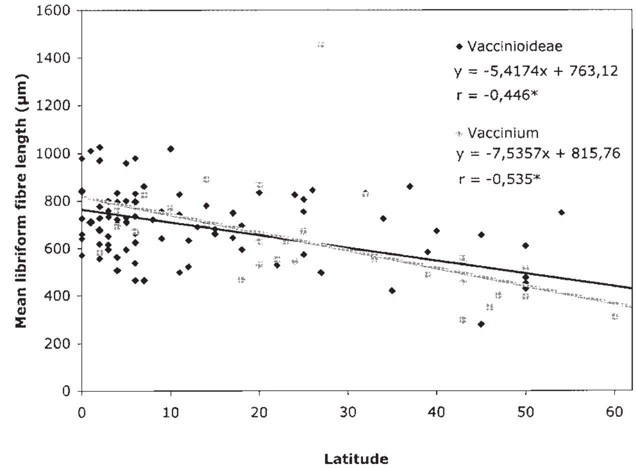

Fig. 4. Scatter plot of mean libriform fibre length and latitude for Vaccinioideae and *Vaccinium* with linear curve fitting. An asterisk means that the r-value is significant at the 0.5% significance level.

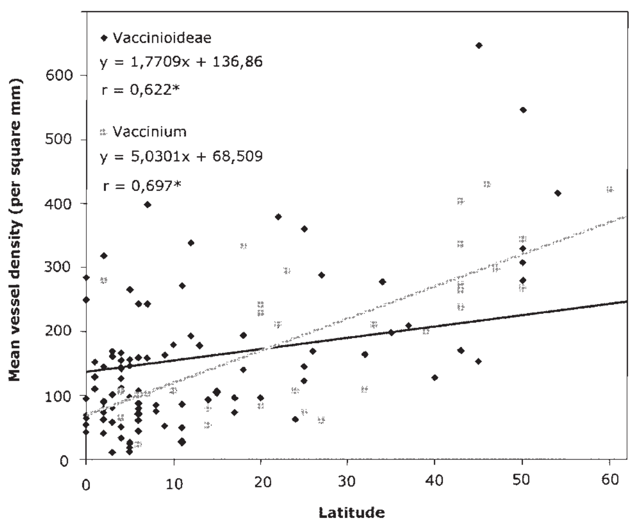

Fig. 5. Scatter plot of mean vessel density and latitude for Vaccinioideae and *Vaccinium* with linear curve fitting. An asterisk means that the r-value is significant at the 0.5% significance level.

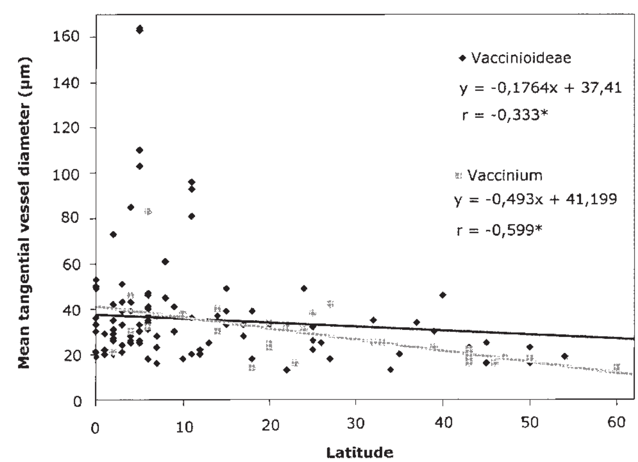

Fig. 6. Scatter plot of mean tangential vessel diameter and latitude for the vaccinioids studied with linear curve fitting. An asterisk means that the r-value is significant at the 0.5% significance level.

tistical significance of correlation coefficients and differences between mean values were analysed at the 0.5% significance level with the software package Statistics Calculator version 8.0.

The qualitative wood anatomical features analysed were as follows: presence of distinct growth rings, the occurrence of helical wall thickenings, and the presence of mineral inclusions. The quantitative characters included the tangential vessel diameter and vessel density, the percentage of scalariform perforation plates, the length of vessel elements, tracheids, fibre-tracheids and libriform fibres, and the height and width of multiseriate rays.

In order to discuss the influence of growth forms on wood anatomical features, we distinguished three groups within the species studied, viz. shrubs, trees and lianas. Shrubs are defined as multi-stemmed plants which are usually smaller than three metres, while trees are single-stemmed plants usually more than three metres high.

Because exact precipitation data for most species could not be found, the origins of the specimens studied were divided into three arbitrary categories, viz. (1) areas with an annual precipitation from 500 mm to 1000 mm, (2) from 1000 mm to 2500 mm, and (3) areas with more than 2500 mm annual precipitation.

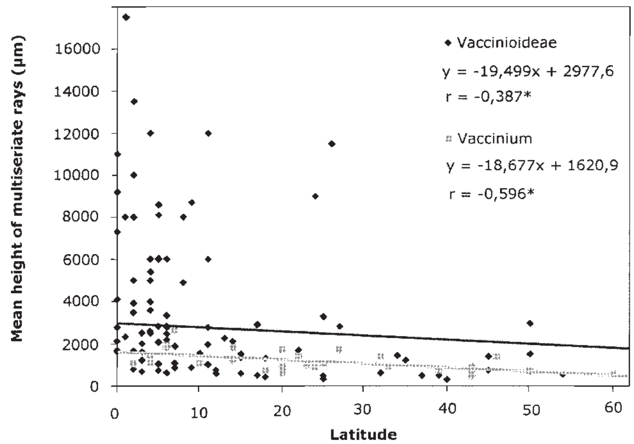

Fig. 7. Scatter plot of mean multiseriate ray height and latitude for Vaccinioideae and *Vaccinium* with linear curve fitting. An asterisk means that the r-value is significant at the 0.5% significance level.

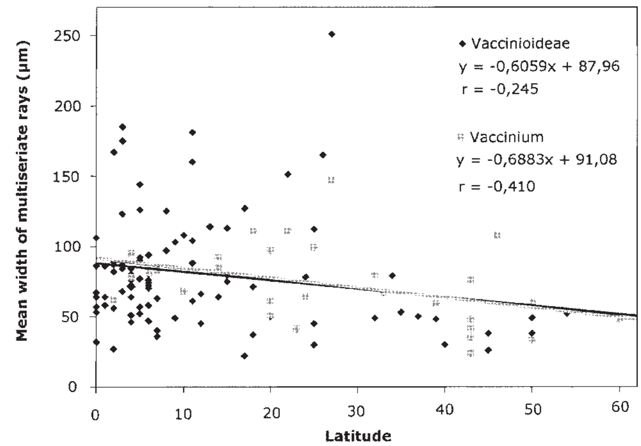

Fig. 8. Scatter plot of mean multiseriate ray width and latitude for Vaccinioideae and *Vaccinium* with linear curve fitting.

Table 1. Correlations of non-anatomical and wood anatomical characters of Vaccinioideae. LAT: latitude, SPP: percentage of scalariform perforation plates, VDIAM: mean tangential vessel diameter (µm), VDEN: mean vessel density (/mm^2), VEL: mean vessel element length (µm), TL: mean tracheid length (µm), FTL: mean fibre-tracheid length (µm), LFL: mean libriform fibre length (µm), MRH: mean multiseriate ray height (µm), MRW: mean multiseriate ray width (µm), ALT: altitude

	LAT	SPP	VDIAM	VDEN	VEL	TL	FTL	LFL	MRH	MRW	ALT
Latitude (n = 128)	–										
% scalariform perforation plates	0.127	–									
Mean vessel diameter	–0.333*	–0.543*	–								
Mean vessel density	0.622*	0.418*	–0.572*	–							
Mean vessel element length	–0.533*	–0.238	0.488*	–0.650*	–						
Mean tracheid length	–0.549*	–0.371*	0.697*	–0.723*	0.785*	–					
Mean fibre-tracheid length	–0.500*	–0.239	0.515*	–0.356*	0.859*	0.810*	–				
Mean libriform fibre length	–0.446*	–0.179	0.412*	–0.301*	0.804*	0.742*	0.779*	–			
Mean multiseriate ray height	–0.387*	–0.255	0.303*	–0.702*	0.466*	0.349*	0.299*	0.369*	–		
Mean multiseriate ray width	–0.245	–0.381*	0.317*	–0.651*	0.236	0.355*	0.214	0.238	0.299*	–	
Altitude (n = 108)	–0.630*	0.158	–0.033	–0.286*	0.206	0.039	0.156	0.063	0.106	0.007	–

Significance level: * = 0.5%

Table 2. Correlations of non-anatomical and wood anatomical characters of *Vaccinium*. LAT: latitude, SPP: percentage of scalariform perforation plates, VDIAM: mean tangential vessel diameter (µm), VDEN: mean vessel density (/mm^2), VEL: mean vessel element length (µm), TL: mean tracheid length (µm), FTL: mean fibre-tracheid length (µm), LFL: mean libriform fibre length (µm), MRH: mean multiseriate ray height (µm), MRW: mean multiseriate ray width (µm), ALT: altitude

	LAT	SPP	VDIAM	VDEN	VEL	TL	FTL	LFL	MRH	MRW	ALT
Latitude (n = 31)	–										
% scalariform perforation plates	0.263	–									
Mean vessel diameter	–0.599*	–0.515*	–								
Mean vessel density	0.697*	0.343	–0.779*	–							
Mean vessel element length	–0.678*	–0.254	0.702*	–0.855*	–						
Mean tracheid length	–0.660*	–0.411	0.798*	–0.823*	0.820*	–					
Mean fibre-tracheid length	–0.657*	–0.286	0.806*	–0.875*	0.894*	0.914*	–				
Mean libriform fibre length	–0.536*	–0.081	0.766*	–0.776*	0.895*	0.849*	0.848*	–			
Mean multiseriate ray height	–0.596*	–0.421	0.602*	–0.631*	0.797*	0.652*	0.749*	0.617*	–		
Mean multiseriate ray width	–0.410	–0.147	0.402	–0.460	0.585*	0.610*	0.631*	0.622*	0.604*	–	
Altitude (n = 22)	–0.623*	–0.126	0.322	–0.153	0.237	0.286	0.227	0.126	0.132	0.140	–

Significance level: * = 0.5%

Results

Within the subfamily, the average length of vessel elements, tracheids, fibre-tracheids and libriform fibres shows a negative correlation with increasing latitudinal ranges (r = –0.533, –0.549, –0.500 and –0.446, respectively, Figs. 1–4), while vessel density is positively correlated with latitude (r = 0.622, Fig. 5). These correlations are all statistically significant at the 0.5% level (Tab. 1). Vessel diameter illustrates a weaker, but still significant at 0.5%, negative trend (r = –0.333, Fig. 6). The frequency of scalariform perforations is not correlated with latitude (r = 0.127). There is also a minor increase of multiseriate ray frequency with increasing latitude (r = 0.073), and a slight decrease in multiseriate ray width (r = –0.245, Fig. 8). However, ray height is significantly correlated with latitude (r = –0.387, Fig. 7).

Within the genus *Vaccinium*, similar significant correlations with latitude are found (Figs. 1–8, Tab. 2). Relatively higher r-values are found for vessel diameter (r = –0.599) and height of multiseriate rays (r = –0.596) in *Vaccinium*, as compared to the overall subfamily.

Three qualitative wood features, viz. the presence of distinct growth rings, helical thickenings throughout vessel elements, tracheids or fibres, and the occurrence of prismatic crystals, show interesting latitudinal trends. Distinct growth rings are present in 44% of (sub)tropical, mostly montane species (n = 100), while this percentage increases to 86% in the temperate to boreal species (n = 28). Helical thickenings occur in tracheary elements from 17% of (sub)tropical species to 64% of temperate to boreal species. Prismatic crystals, on the other hand, are present in 47% of species growing in (sub)tropical regions, but only 14% of the species from temperate to boreal areas. In the genus *Vaccinium*, similar trends are found. Tropical *Vaccinium* species (n = 17) less frequently show distinct growth rings (41%) and helical hickenings (35%), and a slightly higher incidence of prismatic crystals (24%) than temperate to boreal *Vaccinium* species (n = 14), which have percentages of 93%, 64% and 14%, respectively.

There is a clearly positive correlation between vessel diameter and length of the tracheary elements, and a negative correlation with respect to vessel density (Tab. 1). In addition, the length of the different types of tracheary elements is clearly related to each other. The incidence of scalariform perforations is negatively correlated with tangential vessel diameter (r = –0.543), while a positive correlation is found for mean vessel density (r = 0.418). Moreover, mean vessel density is negatively correlated with tangential vessel diameter (r = –0.572), and with mean height and width of multiseriate rays (r = –0.702 and –0.651, respectively). Similar but usually stronger correlations are found within the genus *Vaccinium*. However, one may not compare the r-values of Vaccinioideae as a whole with *Vaccinium* because of difference in sampling between these two groups (128 vs. 31 samples, respectively; Tab. 1–2).

Based on altitudinal data within the subfamily, we only find a single wood anatomical feature that is significantly correlated with increasing altitude at the 0.5% significance level, i.e. vessel density (r = 0.286, Tab. 1). There is a slightly positive, but not significant correlation between vessel element length and altitude. A comparison of all species growing in the Andes region between 1500 m and 3500 m, representing 53% of the total number of species studied, illustrates that none of the wood features are correlated with altitude at the 0.5% significance level. Moreover, no significant altitudinal correlations are found in *Vaccinium* (Tab. 2).

According to the habit of the species studied, a considerable proportion of wood anatomical variation can be explained (Tab. 3). For example, the presence of scalariform perforations is more abundant in shrubs (71.9%) than in trees and lianas (56.9 and 14.5%, respectively). In addition, mean length of vessel elements, tracheids, fibre-tracheids and libriform fibres is higher in trees compared with shrubs, but only the difference of tracheid and fibre-tracheid length is significant at the 0.5% level. Except for a similar mean length of fibre-tracheids in trees and lianas, the highest values occur in lianas. Similar differences account for tangential diameter of vessels and mean width of multiseriate rays, while the opposite holds true for mean vessel density. Of these three features, especially differences between shrubs and lianas are statistically significant (Tab. 3). On the other hand, the lowest mean height of multiseriate rays is found in trees, while multiseriate rays are higher in shrubs and especially in lianas.

The correlations found between species from the three precipitation categories correspond with the correlations described above based on habit differences. Species growing in areas with an annual precipitation of 500 to 1000 mm show the narrowest vessel diameter, shortest tracheary elements, highest percentage of scalariform perforations and highest vessel density, although this tendency is not clear for the percentage of scalariform perforations and vessel diameter (Tab. 4). Species growing in regions with more than 2500 annual precipitation usually show a significant opposite trend, while species in the 1000 to 2500 mm precipitation zone represent intermediate values (except for fibre-tracheid length, multiseriate ray height and width).

Table 3. Mean values and standard deviation of selected continuous, wood anatomical features for shrubs (S, n = 105), trees (T, n = 13) and lianas (L, n = 10). The statistical significance (*P*) between the mean values at the 0.5% level is indicated for the three categories.

	Shrubs	Trees	Lianas	*P*
% scalariform perforation plates	71.9 ± 34.0	56.9 ± 43.5	14.5 ± 31.1	S–L
Vessel diameter (μm)	28.6 ± 11.1	39.1 ± 7.38	102 ± 36.1	S–L, T–L
Vessel density (/mm^2)	183 ± 118	102 ± 49.1	32.7 ± 16.6	S–L
Vessel element length (μm)	563 ± 153	641 ± 69.7	747 ± 110	S–L
Tracheid length (μm)	588 ± 164	763 ± 154	954 ± 187	S–T, S–L
Fibre-tracheid length (μm)	819 ± 235	1086 ± 157	1075 ± 77	S–T, S–L
Libriform fibre length (μm)	647 ± 176	762 ± 85.1	855 ± 117	S–L
Multiseriate ray height (μm)	2912 ± 3217	1100 ± 653	5663 ± 3422	T–L
Multiseriate ray width (μm)	74.4 ± 34.7	81.7 ± 52.2	110 ± 39.9	S–L

Table 4. Mean values and standard deviation of selected continuous, wood anatomical features for species growing in areas with a annual precipitation between 500 mm and 1000 mm (region A, n = 30), from 1000 mm to 2500 mm (region B, n = 15), and areas with more than 2500 mm (region C, n = 83). The statistical significance (*P*) between the mean values at the 0.5% level is indicated for the three categories.

	500–1000	1000–2500	>2500	*P*
% scalariform perforation plates	79 ± 29.1	66 ± 36.9	61 ± 40.1	/
Mean vessel diameter (μm)	26 ± 14.4	31 ± 8.4	40 ± 27.7	/
Mean vessel density (/mm^2)	260 ± 148	166 ± 81.2	128 ± 88.5	A–C
Mean vessel element length (μm)	481 ± 178	568 ± 132	626 ± 126	A–C
Mean tracheid length (μm)	486 ± 201	633 ± 171	689 ± 171	A–C
Mean fibre-tracheid length (μm)	713 ± 328	927 ± 247	906 ± 174	A–B, A–C
Mean libriform fibre length (μm)	583 ± 237	651 ± 153	710 ± 139	A–C
Mean multiseriate ray height (μm)	1143 ± 624	1000 ± 772	3900 ± 3566	A–C, B–C
Mean multiseriate ray width (μm)	62 ± 27.7	64 ± 29.9	86 ± 40.3	A–C

Discussion

Latitudinal trends

This paper illustrates that latitude, which can be considered as a rough indicator of macroclimatic conditions, plays a considerable role in wood anatomical variation within the subfamily Vaccinioideae (Tab. 1–2). Our results generally agree with latitudinal trends established in previous studies on wood anatomy (e.g. Baas 1973; van der Graaf & Baas, 1974; van den Oever et al. 1981; Noshiro & Baas 2000). The length of tracheary elements (i.e., vessel elements, tracheids, fibre-tracheids and libriform fibres), tangential vessel diameter, and height of multiseriate rays are all negatively correlated with increasing latitude, while distinct growth rings, vessel density and the occurrence of helical thickenings throughout tracheary elements show a positive correlation (Figs. 1–7). The higher incidence of prismatic crystals in tropical Vaccinioideae compared to temperate members has been found in various plant groups, such as Rosaceae (Zhang et al. 1992), Sapindaceae (Klaassen 1999), and other Ericaceae (Cox 1948; Greguss 1959; Lens et al. 2003), although it does not tend to be a general trend. Among these characters, presence (and location) of prismatic crystals and height of multiseriate rays provides clear phylogenetic signals within the subfamily (Lens et al. 2004, submitted). The distribution of prismatic crystals is mainly restricted to wood of the temperate Oxydendreae, some tropical *Lyonia* species (Lyonieae), and many tropical Vaccinieae. Furthermore, low multiseriate rays are observed in Oxydendreae, Lyonieae and Andromedeae s.s., relatively high rays are reported in Gaultherieae, and very high multiseriate rays are characteristic of most Vaccinieae (Lens et al. 2004, submitted). The conclusion published by Baas (1982) that axial parenchyma is more abundantly present in tropical wood than in wood from temperate zones, is not supported in Vaccinioideae. Nearly all vaccinioids studied show scanty paratracheal parenchyma. Nevertheless, banded marginal parenchyma is restricted to a few tropical Vaccinieae members (Lens et al. submitted).

Since the majority of tropical vaccinioid species grows at relatively high altitudes (above 1500 m), it could be expected that latitudinal trends in the wood of the subfamily are rather obscure because of the macroclimatic similarities between tropical, montane environments and cold, temperate to boreal regions. However, the above-mentioned latitudinal correlations are surprisingly manifest at the subfamily level and within the genus *Vaccinium*, probably because of positive interactions with habit data (see below).

When studying wood anatomy from an ecological point of view, it is not surprising that several continuous wood anatomical characters are correlated with each other. Indeed, the highest r-values, all significant at 0.5%, occur between length of various types of tracheary elements; correlations of tracheary element length with vessel density and vessel diameter, and the correlation between vessel density and vessel diameter are also relatively high. Furthermore, height of multiseriate rays is significantly correlated with all these wood features.

Based on recent phylogenetic studies in Ericaceae, Vaccinioideae have a North American origin. Indeed, North American representatives are found in every major evolutionary line within the subfamily, and major taxa with a southern distribution area (e.g. *Gaultheria* and Vaccinieae) have been derived independently from northern temperate taxa via dispersal (KRON & LUTEYN, in press, but see HEADS 2003). How long ago the first vaccinioids evolved is unclear, but they probably developed at the end of the Cretaceous, when a warmer climate prevailed and the latitudinal climatic gradient was gentle (CROWLEY & NORTH 1991). Therefore, the wood structure of early vaccinioids was probably only slightly influenced by climatic differences. At the end of the Eocene, the climate became cooler and more seasonal (WOLFE 1994). This climatic change also influenced the wood structure, since fossil wood illustrates that the number of shorter vessel elements and distinct growth rings has increased since the Cretaceous, indicating a shift to a more seasonal climate (WHEELER & BAAS 1991, 1993). In Vaccinioideae, this climatic change could have played an important role in the evolution of serveral northern taxa, for example, *Andromeda* (Andromedeae s.s.) and *Chamaedaphne* (Gaultherieae). Within Vaccinieae, the common ancestor of an Andean and Meso-American/Caribbean clade may have occurred across the Andean highlands and the mountains of Central America and the Antilles, suggesting that diversification within this clade occurred very late, namely during the last 20 million years when the Andes began to rise (KRON & LUTEYN, in press). The homogeneous wood structure of the Andean and Meso-American/Caribbean clade could support this idea (LENS et al., submitted).

Impact of frost

Latitudinal trends can partly be explained by the impact of frost on wood structure. This is certainly the case for vaccinioids that grow in temperate to boreal regions of the northern and southern hemisphere, where frost occurs at least during one month per year. Since cold and freezing temperatures result in temporary inactivity of the cambium, this may explain why 86% of temperate to boreal species have distinct growth rings, while this feature occurs in only 44% of tropical species examined. Nearly all other vaccinioid specimens studied show indistinct growth rings (LENS et al., 2004, submitted). The relatively high percentage of tropical species with distinct growth rings is probably due to the large number of representatives growing at high elevations, although only a fraction of the species in this study grows above 3000 m.

Another character that is clearly influenced by frost is vessel diameter. Mean vessel diameter of the 104 frost-free living species studied is significantly wider (39 μm ± 26) compared to the 24 species that grow in areas with at least one month of frost per year (20 μm ± 4). Likewise, nearly all frost susceptible species have a relative high vessel frequency (on average 300 mm^{-2}). The functional significance of narrow vessel diameter and high vessel frequency can largely be explained in terms of increased safety of sap flow as a reaction to freeze-thaw cycles. The explanation for this is the greater likelihood of freezing-induced cavitation in wider vessels, in which a much larger amount of water is present. This trade-off between conduit diameter and susceptibility to cavitation has been demonstrated by ZIMMERMANN & BROWN (1971), SPERRY & SULLIVAN (1992), SPERRY et al. (1994), and DAVIS et al. (1999). Moreover, the presence of narrow tracheids (and to a lesser extent fibre-tracheids with distinctly bordered pits) may also contribute to the safety of water transport in Ericaceae (WALLACE 1986; CARLQUIST 2001).

The impact of frost may also be illustrated by the type of vessel perforation plates. There is a tendency that species experiencing frost show (almost) exclusively scalariform perforations, which may negatively affect conductive efficiency and are suggested to catch air bubbles caused by freezing-induced cavitation (ZIMMERMANN 1983; ELLERBY & ENNOS 1998; SCHULTE 1999). Tropical lowland species, on the other hand, exhibit usually simple vessel perforations (e.g. CARLQUIST 1975, 2001; BAAS et al. 1983; BAAS 1986). This trend is also apparent in Vaccinioideae: species growing in areas with at least one month of frost per year show a significantly higher frequency of scalariform perforations (on average 84% ± 27) than species living in frost-free areas (on average 62% ± 39), and also the mean number of bars is somewhat higher in species experiencing frost compared to frost-free species (12 ± 6 versus 9 ± 7 bars per perforation plate). Moreover, the percentage of species with exclusively scalariform vessel perforations is significantly higher in areas with frost than in frost free regions (respectively 54% and 28%). Nevertheless, some counter examples can be listed. For example, simple perforations are generally present in *Vaccinium globulare* (100%) and *V. uliginosum* (85%), two species that experience at least 30 days of frost per year. Exclusively scalariform perforation plates occur also in several frost-free species, belonging for instance to *Agapetes*, *Agarista*, *Anthopterus*, *Ceratostema*, *Cavendishia*, *Demosthenesia*, *Gaultheria*, *Leucothoe*, *Lyonia*, *Pieris*, *Plutarchia*, *Sphyrospermum* and *Thibaudia*.

Altitudinal trends

In general, altitudinal trends are much less obvious than latitudinal trends, which is in agreement with previous studies (Van der Graaf & Baas 1974; van den Oever et al. 1981; Baas 1986; Carlquist 2001). At the subfamily level, only vessel density shows a statistically significant correlation with increasing altitude, while clear altitudinal correlations are lacking within *Vaccinium* (Tab. 1–2). A possible explanation for the weak altitudinal correlations could be the major differences between day and night temperatures in tropical mountains. A separate analysis of the Andean species, which usually grow above 1500 m, did not provide any higher correlations. This could also suggest that there might be a threshold altitude at 2000 m, as suggested by Noshiro & Baas (2000), indicating that the influence of altitude above 2000 m is more or less similar for all woody taxa.

Impact of habit and precipitation

The relationship between quantitative wood anatomical features and influences of habit is in general agreement with previous analyses within woody angiosperms (Baas & Schweingruber 1987; Carlquist 2001). Table 3 shows that shrubs are characterised by a high incidence of scalariform perforations, small vessel diameters, high vessel densities, short tracheary elements, and relatively narrow multiseriate rays. In lianas many wide vessel elements, a subsequently low vessel density, few scalariform perforation plates, and usually wide multiseriate rays occur. While shrubs and lianas show significant differences for these features, trees generally represent intermediate values. Nevertheless, the height of multiseriate rays demonstrates an aberrant correlation with habit types. We found that multiseriate rays are relatively low in trees, intermediate in shrubs, and high in lianas. A possible explanation for the low rays in trees could be due to the sampling and taxonomic impact: many tree species that were investigated belong to Oxydendreae and Lyonieae, two tribes that are characterised by low multiseriate rays (Lens et al., 2004). As documented by Carlquist (1989), wide vessels with simple perforation plates, broad rays, and an abundant presence of tracheids are common in lianas. Carlquist (1989) also mentioned that the length of tracheary elements in lianas does not differ greatly from that in woody, self-supporting plants, which is in agreement with our data (Tab. 3). Generally, trends in growth form correspond with latitudinal trends, which is not so surprising because most of the specimens of the study group living in temperate to boreal regions are shrubs, most vaccinioid trees grow in the subtropics, and lianas are restricted to tropical habitats.

The impact of precipitation on the wood structure of Vaccinioideae is similar compared to the habit effect. Species from environments with 500 to 1000 mm annual precipitation show a high percentage of scalariform perforation plates, a narrow vessel diameter and high vessel density, short tracheary elements, and relatively narrow and low multiseriate rays, while species growing in very wet environments (more than 2500 mm annual precipitation) have a higher percentage of simple perforations, wider and fewer vessels, longer tracheary elements, and broader and higher multiseriate rays. Except for the percentage of scalariform perforation plates and vessel diameter, these features are all significant at the 0.5% level (Tab. 4). Vaccinioids occurring in habitats with an annual precipitation from 1000 to 2500 mm show intermediate values, although the height and width of multiseriate rays is similar to the values observed in species growing in areas with 1000–2500 mm annual precipitation. Because the amount of precipitation is one of the major features that is used to define major climatic regions, these trends are very similar to the latitudinal trends described above. Indeed, all species from very wet regions (> 2500 mm) in this study are derived from the tropics, subtropical regions correspond well with areas with a annual precipitation of between 1000 and 2500 mm, and in temperate to boreal areas and in savannah regions the amount of precipitation lies usually between 500 and 1000 mm per year.

Conclusion

Although most tropical Vaccinioideae grow at relatively high altitudes, this study demonstrates that latitude shows a clear impact on several wood anatomical characters within the subfamily and within *Vaccinium*. Since differences in growth forms agree rather well with macroclimatic regions, the impact of habit supports the latitudinal trends, and may explain the relatively high latitudinal correlation values. The effect of altitude on wood structure of Vaccinioideae and *Vaccinium* is negligible.

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Appendix

Studied species, area of occurrence, collection identification number, specimen diameter

Agapetes flava (HOOK. F.) SLEUMER: Bhutan (Chukka), *A. Grierson & D. Long 3076* (E 19822403), 10 mm; *A. hosseana* DIELS: Thailand (Chiang Mai), *B. L. Burtt 958* (E 19672592), 7 mm; *A. mannii* HEMSL.: Myanmar, *F. Kingdon-Ward 19097* (E 19500046), 10 mm; *A. sikkimensis* AIRY SHAW: Bhutan (Phuntsholing), *I. Sinclair & D. Long 5778* (E 19842032), 12 mm; *A. variegata* G. DON: India (Meghalaya), *D. F. Chamberlain 106* (E 19751313), 9 mm; *Agarista duckei* (HUBER) JUDD: Venezuela (Amazonas), B. Maguire *et al.* 42692 (Tw 36848), 58 mm; *Agarista eucalyptoides* (CHAM. & SCHLTDL.) G. DON: Brazil, G. G. Hatschbach & J. C. Lindeman 20935 (Uw 20844), 70 mm; *Agauria salicifolia* OLIV.: Rwanda, G. Bouxin 877 (Tw 24171), mature; *Andromeda polifolia* L.: Belgium (BR), F. Lens, 4.5 mm; *Anthopterus wardii* BALL: Colombia (Nariño), *J. L. Luteyn & M. Lebrón-Luteyn 6865* (NY), 8 mm; *Cavendishia bracteata* (J. ST.-HIL.) HOEROLD: Bolivia (La Paz), *L. J. Dorr et al. 6890* (Lw), 12 mm; *C. compacta* A. C. SM.: Colombia, *van Rooden et al. 555* (Uw 25619), 15 mm; *C. callista* DONN. SM.: Surinam (Lely Mountains), *Lindeman & Stoffers 502* (Uw 21835), 11 mm; *C. lindauiana* HOEROLD: Colombia, *van Rooden et al. 630* (Uw 25642), 15 mm; *C. pubescens* (Kunth) HEMSL.: Venezuela, *L. Williams 10020* (Uw 35101), 43 mm; *C. urophylla* A. C. SM.: Colombia, *van Rooden et al. 371* (Uw 25568), 21 mm; *Ceratostema reginaldii* (SLEUMER) A. C. SM.: Ecuador (Loja), *L. J. Dorr & I. Valdespino 6562* (Lw), 15 mm; *Chamaedaphne calyculata* MOENCH: Germany, E. Smets, Botanical Garden of Bochum (Germany), 5 mm; *Craibiodendron stellatum* W. W. SM.: Thailand (Tunkamang), C. F. Van Beusekom & R. Geesink 4361 (L), 57 mm; *Demosthenesia spectabilis* (Rusby) A. C. SM.: Peru (Cuzco), *J. L. Luteyn 6452* (NY), 7 mm; *Dimorphanthera collinsii* SLEUMER var. *collinsii*: Indonesia (Irian), *Kalkman 4902* (Tw 23696), 60 mm; *D. cornuta* J. J. SM. var. *cornuta*: East New Guinea, *Vink 17084* (Kw 11639, Uw 18298), 51 mm; *D. dekockii* J. J. SM. var. *pubiflora* SLEUMER: East New Guinea, *Vink 17307* (Kw 11639, Uw 18316), 45 mm; *D. kempteriana* SCHLTR.: Indonesia (East Irian), *Vink 16888* (Tw 23733), 44 mm; *Diogenesia floribunda* (A. C. SM.) SLEUMER: Ecuador (Napo-Pastaza), *J. L. Luteyn & M. Lebrón-Luteyn 5675* (NY), 9 mm; *D. tetrandra* (A. C. SM.) SLEUMER: Colombia (Cauca), *J. L. Luteyn et al. 7388* (NY), 11 mm; *Diplycosia heterophylla* BLUME: Indonesia (Java, Gunong Pangrango), P. Woods 1046 (E 19680830), 9 mm; *Disterigma alaternoides* NIED.: Colombia (Cauca), *J. L. Luteyn et al. 7400* (NY), 11 mm; *D. cryptocalyx* A. C. SM.: Colombia (Huila), *J. L. Luteyn & M. Lebrón-Luteyn 7545* (NY), 7 mm; *Gaultheria anastomosans* (L.) H. B. K.: Colombia (Cauca), J. L. Luteyn, R. Callejas & J. J. Pipoly 10085, 27 mm; *Gaultheria buxifolia* WILLD. var. *buxifolia*: Venezuela (Trujillo), J. L. Luteyn, M. Lebrón-Luteyn, L. Ruiz- Terán & J. A. Dugarte 5195, 18 mm; *Gaultheria buxifolia* Willd. var. *ellasantha* (A. C. SM.) LUTEYN: Colombia (Antioquia), J. L. Luteyn & M. Lebrón-Luteyn 7079, 13 mm; *Gaultheria buxifolia* WILLD. var. *secunda* (J. REMY) LUTEYN: Peru (Cuzco), J. L. Luteyn & M. Lebrón-Luteyn 6376, 8 mm; *Gaultheria erecta* VENT.: Ecuador (Carchi), J. L. Luteyn & M. Lebrón-Luteyn 5739, 8 mm; *Gaultheria erecta* VENT.: Venezuela, Wagener (Kw 11654), 26 mm; *Gaultheria erecta* VENT.: Venezuela (Tachira), J. L. Luteyn, M. Lebrón-Luteyn & L. Ruiz- Terán 6020, 8 mm; *Gaultheria eriophylla* (PERSOON) BURTT. var. *mucronata* (J. REMY) LUTEYN: Peru (Cuzco), J. L. Luteyn & M. Lebrón-Luteyn 6375, 10 mm; *Gaultheria reticulata* H. B. K.: Ecuador (Azuay), J. L. Luteyn & E. Cotton 11158, 18 mm; *Gaultheria rigida* H. B. K.: Colombia, A. M. Cleef 2799 (Uw 20769), 9 mm; *Gaultheria shallon* PURSH: Belgium (BR), F. Lens, 6.5 mm; *Gaultheria strigosa* BENTH. var. *strigosa*: Colombia (Antioquia), J. L. Luteyn & M. Lebrón-Luteyn 7101, 10 mm; *Gaultheria strigosa* BENTH. var. *strigosa*: Ecuador (Azuay), J. L. Luteyn & M. Lebrón-Luteyn 5777, 12 mm; *Gaultheria tomentosa* H. B. K.: Peru (Amazonas, Chachapoyas), J. L. Luteyn & M. Lebrón-Luteyn 5569, 13 mm; *Gaylussacia baccata* C. KOCH: Belgium, *F. Lens* (BR), 7 mm; *G. decipiens* CHAM. var. *decipiens*: Brazil, *P. Clausen* 1840, 6 mm; *Leucothoe axillaris* D. DON: USA (Georgia), collector unknown (E 19881623), 13 mm; *Leucothoe grayana* MAXIM.: origin and collector unknown (E 19080096), 13 mm; *Lyonia ferruginea* NUTT.: USA (Florida), A. Curtis (Tw 53206), mature; *Lyonia heptamera* URB.: Dominican Republic, J. Pimentel & M. Mejia 993 (MADw 49103), 31 mm; *Lyonia jamaicensis* D. DON: Jamaica, World Colombian Exposition 14997 (MADw 3549), mature; *Lyonia lucida* C. KOCH: USA, C. D. Mell (MADw 2951), 22 mm; *Lyonia ovalifolia* (WALL.) DRUDE: Japan (Kumamoto), For. Exp. Stat. 2244 (Tw 17276), mature; *Lyonia squamulosa* M. MARTENS & GALEOTTI: Mexico, D. Breedlove 9683 (MADw 23903), 23 mm; *M. crassa* A. C. SM.: Colombia (Cauca), *J. L. Luteyn et al. 7378* (NY), 20 mm; *M. ericae* SLEUMER: Ecuador (Pichincha), *J. L. Luteyn & M. Lebrón-Luteyn 5639* (NY), 15 mm; *M. hirtiflora* (BENTH.) A. C. SM.: Colombia (Cauca), *J. L. Luteyn et al. 7386* (NY), 13 mm; *Macleania loeseneriana* HOEROLD: Ecuador (Carchi), *J. L. Luteyn & M. Lebrón-Luteyn 5726* (NY), 18 mm; *M. pentaptera* HOEROLD: Colombia (Valle), *J. L. Luteyn & M. Lebrón-Luteyn 6957* (NY), 19 mm; *M. rupestris* (Kunth) A. C. SM.: Venezuela, *L. Williams 10904* (Uw 35316), 18 mm; *Notopora cardonae* A. C. SM.: Venezuela (Bolívar), *J. L. Luteyn 9596* (NY), 10 mm; *N. schomburgkii* HOOK. F.: Venezuela, *Maas et al. 5808* (Uw 27397), 10 mm; *Orthaea fimbriata* LUTEYN: Ecuador (Morona-Santiago), *J. L. Luteyn & M. Lebrón-Luteyn 5794* (NY), 15 mm; *Oxydendrum arboreum* (L.) DC.: USA (Ohio), A. W. Green 245 (Tw 19787), mature; *Pernettya mucronata* (L. F.) A. SPRENG.: The Netherlands, A. M. W. Mennega (UN 835), 13 mm; *Pernettya mucronata* (L. F.) A. SPRENG. var. *angustifolia* (LINDL.) REICHE: Argentina (Rio Negro), P. Dezarbo 433 (BR), 8 mm; *Pernettya rigida* DC.: Chili (Juan Fernández Islands), Meyer 9490 (Uw 14995), 66 mm; *Pieris formosa* D. DON: India (Meghalaya), Birla Institute of Scientific Research (Tw 45532), mature; *Pieris japonica* (THUNB.) G. DON: Belgium (BR), F. Lens, 8 mm; *Plutarchia rigida* (BENTH.) A. C. SM.: Colombia (Cauca), *J. L. Luteyn 10108* (NY), 5 mm; *Polyclita turbinata* (KUNTZE) A. C. SM.: Bolivia (Cochabamba), *J. L. Luteyn* 15453 (NY), 10 mm; *Psammisia* sp.: Colombia, *van Rooden et al. 359* (Uw 25565), 30 mm; *P. ferruginea* A. C. SM.: Ecuador, *Maas et al. 3041* (Uw 23589), 20 mm; *P. graebneriana* HOEROLD: Colombia (Nariño), *J. L. Luteyn & M. Lebrón-Luteyn 6809* (NY), 10 mm; *P. guianensis* KLOTZSCH: Venezuela (Amazonas), *B. Maguire et al. 42397* (Tw 36530), 11 mm; *P*. cf. *ulbrichiana* HOEROLD: Ecuador (Pichincha), *J. L. Luteyn & M. Lebrón-Luteyn 6532* (NY), 12 mm; *Satyria* sp.; Colombia (Antioquia), *J. L. Luteyn et al. 7017* (NY), 16 mm; *S.* sp.: Brazil, *B. Maguire et al. 48650* (Uw 16976), 35 mm; *S.* sp.: Brazil, *B. Maguire et al. 46784* (Uw 17005), 22 mm; *S.* sp.: Colombia (Antioquia), *J. L. Luteyn & M. Lebrón-Luteyn 7177* (NY), 15 mm; *S. carnosiflora* LANJ.: Venezuela (Amazonas). *B. Maguire et al. 42061* (Tw 36580), 15 mm; *S. meiantha* DONN. SM.: Mexico, *D. Breedlove 9746* (MADw 23933), mature; *S. panurensis* (Meisn.) NIED.: Brazil, *B. Maguire et al. 48650* (MADw 20301), mature; *Siphonandra elliptica* KLOTZSCH: Peru (Cuzco), *J. L. Luteyn & M. Lebrón-Luteyn 6377* (NY), 14 mm; *Sphyrospermum* sp.: Ecuador (Pichincha), *G. Argent* (E 19762390), 11 mm; *S. buxifolium* POEPP. & ENDL.: Ecuador, *G. Argent* (E 19762390), 6 mm; *Symphysia racemosa* (VAHL) STEARN: Dominica, *Chambers 2555* (Uw 15385), 22 mm; *T. pendula* KLOTSCH: Venezuela (La Mucuy), Breteler 3476 (Uw 11013), 35 mm; *T. vegasana* A. C. SM.: Colombia (Boyacá), *J. L. Luteyn et al. 7590* (NY), 13 mm; *Thibaudia angustifolia* HOOK.: Peru (Amazonas), *J. L. Luteyn & M. Lebrón-Luteyn 5528* (NY), 13 mm; *T. floribunda* H. B. K.: Ecuador (Carchi), *J. L. Luteyn & M. Lebrón-Luteyn 5725*, 14 mm; *T. formosa* (KLOTZSCH) HOEROLD: Venezuela (Amazonas), *B. Maguire et al. 27673* (Tw 36552), 20 mm; *T. jahnii* S. F. BLAKE: Venezuela (Mérida), *J. L. Luteyn et al. 6185* (NY), 15 mm; *T. martiniana* A. C. SM.: Ecuador (Pichincha), *J. L. Luteyn & M. Lebrón-Luteyn 5654* (NY), 24 mm; *T. pachypoda* A. C. SM.: Colombia, *Cuatrecasas 19876* (Uw 25099), 11 mm; *T. parvifolia* HOEROLD: Colombia (Cauca), *J. L. Luteyn & M. Lebrón-Luteyn 6897* (NY), 14 mm; *T. rigidiflora* A. C. SM.: Colombia (Valle), *J. L. Luteyn & M. Lebrón-Luteyn 6985* (NY), 23 mm; *Vaccinium* sp.: USA (Hawaii), *W. Stern 2980* (Tw 24148), 33 mm; *V. angustifolium* BENTH.: Belgium, *F. Lens* (BR), 6 mm; *V. arboreum* MARSCHAL: USA (Texas), *H. Nogle 258* (Tw 18270), mature; *V. atrococcum* A.HELLER: USA (Maryland), collector unknown (Kw 11706), mature; *V. bancanum* MIQ.: Brunei, collector unknown, (Kw 74737), 67 mm; *V. barandanum* VIDAL var. *barandanum*: Philippines, *M. Jacobs 7249* (Uw 33743), 45 mm; *V. berberidifolium* (A. GRAY) SKOTTSB.: USA (Hawaii), *Stern & Herbst 496* (Uw 18579), 9 mm; *V. bracteatum* THUNB.: China (Guangdong), *Forest Research Institute 1623* (Tw 42071), mature; *V. calycinum* SM.: USA (Hawaii), *W. Stern 2950* (Tw 24121), 17 mm; *V. consanguineum* KLOTZSCH: Costa Rica (San José), *M. Wiemann 13* (Uw 30897), mature; *V. corymbodendron* DUN.: Colombia, *J. Cuatrecasas 20784* (Tw 20784), mature; *V. corymbosum* L.: Canada (Quebeq), *R. Dechamps* 5003 (Tw 33895), 8 mm; *V. cumingianum* VIDAL: Philippines, *M. Jacobs 7270* (Uw 33746), 36 mm; *V. exaristatum* KURZ: India (Assam, Lushai Hills), *N. E. Parry 45* (Kw 11747), 36 mm; *V. exul* BOLUS: South Africa, *J. Prior 464*, 23 mm; *V. floccosum* (L. O. WILLIAMS) WILBUR & LUTEYN: Panama (Chiriquí), *Maas et al. 4957* (Uw 26277), 33 mm; *V. floribundum* H. B. K.: Bolivia (Cumba de Sama), *J. R. De Sloover 399* (BR), 5 mm; *V. globulare* RYDB.: USA (Washington), *R. Dechamps 4460* (Tw 46335), 15 mm; *V. leschenaultii* WIGHT: India, collector unknown (Kw 70598), mature; *V. leucanthum* SCHLTDL.: Mexico (Puebla), *L. Lebacq 73* (Tw 24590), adult; *V. maderense* LINK: Spain (Madeira), *N. H. Mason* (Kw 11745), mature; *V. membranaceum* HOOK.: USA (Oregon), *R. Dechamps 4325* (Tw 46029), 9 mm; *V. meridionale* SW.: Venezuela, *L. Williams 10896* (Uw 35314), mature; *V. myrtillus* L.: Belgium (Luik), *R. Dechamps* (Tw 43142), 8 mm; *V. occidentale* A. GRAY: USA (Oregon), *R. Dechamps 4414* (Tw 46260), mature; *V. ovatum* PURSH: USA (Oregon), *R. Dechamps 4418* (Tw 46267), 23 mm; *V. parvifolium* SM.: USA (Oregon), *R. Dechamps 4310* (Tw 45996), 27 mm; *V. puberulum* C. F. W. MEISSN. var. *subcrenulatum* MAGUIRE, STEYERM. & LUTEYN: Guyana, *Maas et al. 5733* (Uw 27342), 13 mm; *V. scoparium* LEIBERG: USA (Oregon), *R. Dechamps 4383* (Tw 46187), 6 mm; *V. stanleyi* SCHWEINF.: Democratic Republic of Congo (Kivu), *P. Deuse 55* (BR), 9 mm; *V. uliginosum* L: Norway (Hordaland), *R. Dechamps 6033* (Tw 38581), 6 mm; *Zenobia pulverulenta* POLLARD: eastern USA, collector unknown (E 19721932), 10 mm.