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SOME FUNCTIONAL AND ADAPTIVE ASPECTS OF VESSEL MEMBER MORPHOLOGY

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Summary. The hypothesis of functionally adaptive diversification of wood structure in the course of evolution as advanced by Carlquist is critically tested for vessel member length and type of perforation plate. The functional significance of within-tree variation in vessel member morphology is discussed first, and a criticism of Philipson & Butterfield's theory for explaining classical length-on-age curves for fusiform initial length is given. At the genus and family level examples are cited which contradict the hypothesis that specialization of the perforation plate has a strong selective advantage for the occupation of more xeric environments or for high conductive rates. Other examples, however, seem to support this. The functional interpretation of correlations between vessel member length and ecological conditions is criticised. A comparison is made between whole woody floras or vegetation types with respect to the proportion of genera with scalariform perforation plates (Tables 1 and 2, Fig. 2). In tropical lowland rain forests the percentage of genera with scalariform plates is rather low. It strongly increases for tropical montane forests and for temperate to arctic floras. It is lowest in seasonally dry to arid regions. These trends support Carlquist's idea that scalariform plates are, in general, only successful for conditions which require low rates of water conduction. In addition, the role of temperature is stressed. The total evidence presented in this paper is discussed in terms of random '*patio ludens*' evolution which has to a considerable extent been canalized through selective pressures by environmental factors.

INTRODUCTION

Carlquist's recent book (1975) 'Ecological strategies in xylem evolution', induces the wood anatomist to view the structural diversity in the xylem of extant plants as the results of functionally adaptive evolutionary changes, brought about through selective pressures in the different ecosystems in which the taxa evolved. In this respect, Carlquist goes much further than Bailey (1944, 1953) who stressed the significance of vessels in the evolution of land plants, but did not interpret wood anatomical diversity and the major trends of xylem evolution in the Neo-Darwinistic sense, as Carlquist does.

The objective of this paper is to explore critically to which extent such an adaptive interpretation is applicable to vessel member morphology in woody dicotyledons, considered at different levels in the taxonomic hierarchy and for different woody floras. As such, it is partly an answer to Carlquist's provocative suggestions, many of which he admitted to be speculative, and to a certain extent it is also a follow up of previous studies (Baas, 1973; van der Graaff & Baas, 1974) exploring correlations between ecological factors and wood anatomy.

In his book, Carlquist has listed and/or deduced the functional and adaptive potentialities of many wood anatomical features in relation to moisture availability and transpiration rate, and to requirements for mechanical strength. For the vessel element and its evolution, the following of Carlquist's considerations are relevant: vessel member length was thought to be important with regard to conduction in that 1. great length reduces resistance to flow in woods with multiple (scalariform) perforations, 2. short vessel members would increase the total strength of a vessel in resistance to high negative pressures mainly occurring under xeric conditions. Moreover, vessel member length and fibre length are positively correlated and, consequently, a cambium with long fusiform initials may produce wood with longer fibres, possibly resulting in a stronger wood, making intrusive growth of fibres less important. Depending on the opportunities offered by the environment, one or more of the above aspects may result in a positive selective value for either long or short vessel members. As for the type of perforation, Carlquist (and several other authors e.g. Zimmermann & Brown, 1971) thought scalariform perforations to be functionally disadvantageous as compared to simple perforations because of the resistance to water conduction offered by the bars. However, for highly mesic conditions, wood with scalariform perforations might not be limiting for growth and evolutionary success, because of consistently low rates of water conduction. At the same time, some plants showing high conductive rates (e.g. the mangrove genera of the Rhizophoraceae) with scalariform perforations might benefit from strong bars to the perforation plate in order to assist the vessel against collapse, caused by excessively high negative pressures occurring at times of high transpiration. Carlquist went into very great detail in explaining the possibly positive selective value of numerous other minute variations of vessel and perforation plate morphology, but a full review of this would be out of place here. Most of his deductions on this level are, moreover, so purely hypothetical that a discussion without additional experimental data would be pointless.

Braun (1970) also approached wood anatomical diversity from a purely functional angle. In his mainly theoretical classification of the hydrosystem of wood, he emphasized the importance of vessel–fibre contacts and the lack thereof through paratracheal parenchyma, and of the nature of the fibre tissue (fibre-tracheids or libriform fibres). In his opinion the type of vessel perforation only plays a subsidiary role. From Braun's texts it is not clear to what extent the different organization stages and organization series of his hydrosystem should be given a phylogenetic interpretation. In my opinion, such an interpretation would anyway be most unfortunate and misleading as will immediately be apparent from Braun's choice of 5 genera belonging to the single family Fagaceae as typical examples for two different organization series and 2 different organization levels. Both Braun and Carlquist devoted attention to the correlations between the physical environment and the predominance of certain wood anatomical features. Both authors also devoted attention to vessel diameter. The obvious advantages and disadvantages of wide vessels: less resistance to water transport, increased risks of air bubbles are well known, and have also been experimentally demonstrated (Zimmermann & Brown, 1971, and literature cited therein). Therefore, I will refrain from elaborately discussing vessel diameter in this paper. Moreover, this character is known to be rather variable and of only restricted taxonomic significance.

It should be stressed that neither Carlquist nor Braun challenged the major phylogenetic trends for xylem evolution as established by the Bailey school, nor did they dispute the taxonomic value of the characters which they discussed in relation to function or adaptive advantage in the evolution of woody plants. From the onset of this paper, it should be stressed that the search for adaptive and functional correlations in wood anatomy is complementary to the purely phylogenetic and systematic approach. If, as Carlquist suggested, the structural diversification of secondary xylem has been mainly governed by selective pressures of the environment, including the internal environment created by growth form and habit of the plant itself, such a study will aid in the understanding of causes underlying present day diversity. If, on the other hand, the diversity of wood structure in extant plants arose through a process of random mutations, perhaps partly saltatory, without subsequent canalization through natural selection by the environment, as advocated by Van Steenis (1969, 1976) for the greater part of morphological diversity of plants in general, we must expect to fail in the establishment of straightforward correlations between wood structure and the ecology and physiology of the plants involved. According to van Steenis, evolution in the plant kingdom—as opposed to that in the animal kingdom—is to a great extent characterized by morphological changes which have no or little significance for the survival of the taxa involved. In other words, according to van Steenis, most characters of plants have a low survival level and there has been much scope for free form making or '*patio ludens*' in plant evolution. In this paper, I will discuss these two seemingly opposed views for vessel morphology in dicotyledons. The two views are basically only different in quantitative emphasis on selection of pre-adaptive or pre-disposed characters or, alternatively, on the possibility of non-adaptive diversification which poses no limiting factors for evolutionary success.

A discussion of such aspects of wood anatomical diversity should, ideally, take into account all aspects of wood structure as well as information on root structure, nodal and leaf anatomy, and tree architecture (cf. Huber, 1956). An analysis of all variables involved is, at this stage, obviously impossible for a broad representation of angiosperm woody taxa. I have therefore chosen to limit myself to two characters which are usually regarded to be the keys to the understanding of wood 'phylogeny': fusiform initial or vessel member length, and type of vessel perforation.

FUNCTIONAL ASPECTS OF VARIATION WITHIN A TREE

Each living tree is, under normal conditions, a perfect functioning unit, and we must assume that this also applies to the secondary xylem throughout the plant. Within the wood of the tree there are, however, well known variations in fusiform initial length and, in some cases, also in type of perforation plates. Whether these variations lend themselves to functional interpretation will be discussed below.

Carlquist has discussed the mechanical significance of the classical length-on-age curves for fusiform initials as first established by Sanio (1872) for *Pinus*. The rapid increase of tracheid length in conifers, and of fibres in hardwoods from the pith outwards was said to be functional in providing a better support for a stem which has to carry more weight as secondary growth continues. Only in deviating growth forms such as certain rosette trees, for which phylogenetically secondary woodiness was presumed, deviating curves showing a gradual decline of fusiform initial length from the pith outwards (and thus also of vessel member length) could be afforded and interpreted as release of mechanical strength, according to Carlquist (1962, 1975). Philipson *et al.* (1971) reviewed theories on the ontogenetic processes underlying the variation in cambial initial length. According to them, (see also Philipson & Butterfield, 1967) the proportionally high circumferential growth per unit of radial growth at the initial stages of secondary thickening would necessitate the cambial initials to elongate because anticlinal divisions per millimetre of radial growth would be insufficient to keep up with dilatation of the cambium. Mabberley (1974) used Philipson & Butterfield's plausible theory to challenge Carlquist's interpretation of the deviating curves in certain woody taxa of predominantly herbaceous groups as signs of juvenilism or 'paedomorphosis'. He drew attention to the fact that Carlquist's examples were characterized by a wide pith and that, consequently, deviating curves were to be expected. He substantiated his criticism with length-on-age curves in giant *Senecio*, in which he found a classical Sanio curve at the base of the stem where the pith is narrow, and a deviating curve in a higher position of the trunk where the pith is broad.

The theories of both Carlquist and Philipson *et al.* are highly speculative and each of them offers a more or less functional yet different interpretation of the major variation in fusiform initial length. Neither of the theories can be easily tested experimentally, but the comparative approach may give supporting or opposing evidence. In Araliaceae, a basically woody family, there are taxa of which the stems may have either a very broad or a normal (narrow) pith. Of 5 samples: 2 with a narrow pith (*Schefflera* and *Hederopsis*); 2 with a broad pith (*Harmsiopanax*, 2 x); and one with a pith of more or less intermediate diameter (*Tieghemopanax*) I plotted vessel member length as a function of the distance from the *centre* of the pith (Fig. 1). According to Philipson & Butterfield's theory as interpreted by Mabberley (1974), one would expect no or hardly any increase in vessel member length in the broad-pithed samples. However, the contrary is true: the two *Harmsiopanax* samples show a much stronger relative and absolute increase in vessel member length than the samples of *Schefflera* and *Hederopsis*. *Tieghemopanax* is more or less intermediate. These examples thus prove that Philipson & Butterfield's theory is at least not generally applicable, and one may even wish to use these factual data on Araliaceae to abandon it altogether. At the same time, the examples remove some grounds of Mabberley's criticism of the paedomorphosis theory advanced by Carlquist (1962). Carlquist's interpretation of mechanical functionality of classical

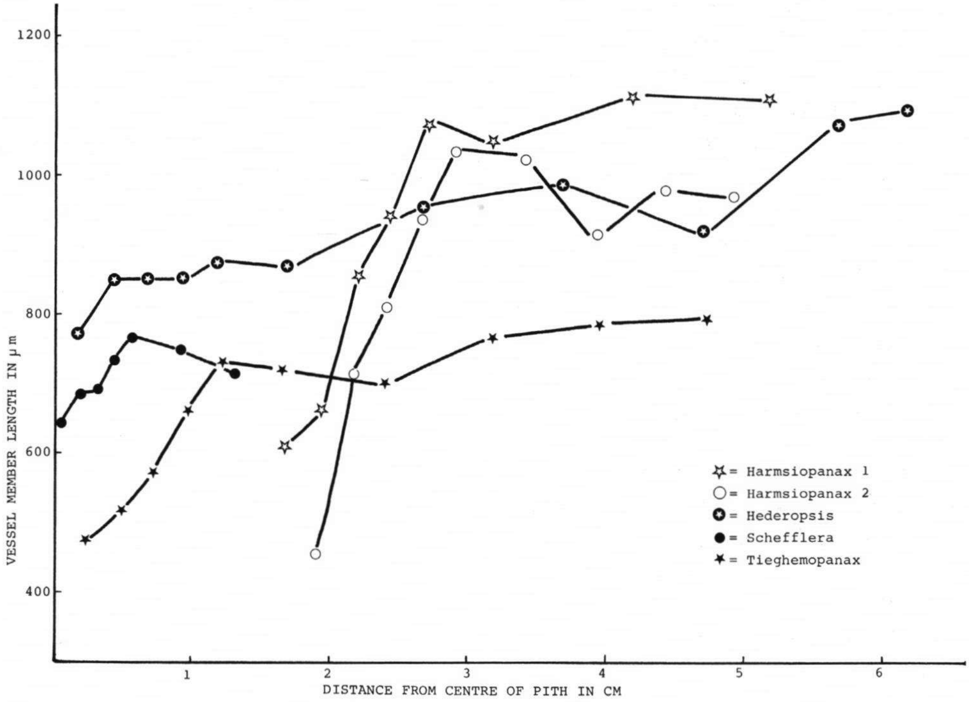

Fig. 1. Length-on-age curves for vessel members of some woods belonging to Araliaceae. The steep decline of vessel member length in the primary xylem observed for all species has not been plotted in the graphs. All points represent averages of 25 measurements.

Material studied: *Harmsiopanax* 1 and 2, *H. ingens* Philipson, Papua New Guinea, *Kalkman 4702* and *van Balgooy 736*; *Hederopsis maingayi* Clarke, Malaysia, *van Balgooy 2249*; *Schefflera* cf. *microphylla* Merr., Philippines, *Jacobs 7011*; *Tieghemopanax elegans* [= *Polyscias elegans* (C. Moore & F. Muell.) Harms], Australia, SFCw R 693/1.

length-on-age curves does not conflict with the above findings. Together with vessel member length, fibre length increases more strongly in the broad-pithed specimens, and this might be functionally significant in the initial stages of secondary growth of these thick stems with such a high proportion of weak pith tissue (cf. Carlquist's findings on fibre length in *Echium pinnata*, 1975: 186). It would, however, be far-fetched to quote the results on some Araliaceae as proof or strong support of the mechanical interpretation. Length-on-age curves may be different in different taxa, and any functional interpretation can be supported only by experimental testing.

Usually fusiform initial length and vessel member length have been found to be greater in root wood than in stem wood (Fayle, 1968; Süss & Müller–Stoll, 1973). Here, the mechanical interpretation of the implications for longer fibres is not applicable, since root wood is in several respects considerably weaker than stem wood. For conifers, Carlquist suggested the longer root wood tracheids to be functionally significant for decreased resistance to water transport. For vessel bearing dicotyledons such an interpretation of longer vessel members seems far-fetched and unlikely.

The type of perforation plate is usually constant in a given species and a given tree. There are, however, a number of taxa in which the wood vessels may have both simple and scalariform perforations. Within-tree-variation is mostly insufficiently known in these cases. However, the group of genera with predominantly simple perforations and a small proportion of scalariform plates in the narrow first-formed vessel elements or in the narrow late wood vessels in temperate species, form an exception to this rule. The reason why Solereder (1899, 1908) recorded scalariform perforations in more taxa than Metcalfe & Chalk is, for instance, due to the fact that Solereder's wood descriptions were often based on herbarium twigs, and those by Metcalfe & Chalk on mature wood. The restricted or more frequent occurrence of scalariform plates in the narrow late wood vessels of some temperate species is documented by, for instance, van der Graaff & Baas (1974). If it is true that scalariform plates decrease the conductivity of vessels, it is indeed not surprising to find vestiges of this primitive character in narrow late wood vessels. One may assume that the task of water conduction will be chiefly fulfilled by the simply perforated wider early wood vessels in those instances. However, whether such an interpretation is also applicable to first formed secondary xylem remains questionable.

Both vessel member length and type of perforation plate within a plant are governed by a complex of physiological and morphogenetic factors, amongst which phytohormones play an important role. The above discussed variations need not be interpreted in a functional way; they may be the result of varying distances from the sites of hormone production or of fluctuations of hormone concentration. The possibility that the resulting patterns of variation are functionally significant for the individual tree or shrub to fulfill its xylem functions of support and conduction with optimal efficiency remains purely hypothetical, however plausible or attractive such an interpretation may seem.

VARIATION WITHIN SPECIES

The variation within individual trees discussed above, often masks the differences that may exist between individuals of one species. Careful work on mainly coniferous woods or seedlings, however, has shown that the considerable variation which may be exhibited by one species must be partly attributed to a phenotypical component affected by such environmental factors as light, temperature, and moisture (Richardson, 1964; Kramer, 1964) partly to a genotypical component (Dinwoodie, 1963; de Zeeuw, 1965). Although the vessel characteristics discussed here have not been analysed to any great extent, there are no reasons to assume that infraspecific variability in vessel morphology is governed in a different way than e.g. tracheid length and diameter in conifers. In mature stem wood, the variation in vessel member length or number of bars per scalariform perforation may be very considerable within a species (cf. Baas, 1973; van der Graaff & Baas, 1974) and may amount to 50% of the maximum average value. Functional interpretations of this variability would be far-fetched and impossible in most cases where specimens from natural habitats are involved. For this descussion it is only relevant to realize the presence of a genetically controlled component of the vessel member characters concerned. If these characters do indeed have a strong adaptive significance, we might expect natural selection to have canalized this variability in the course of evolution so that, within genera, families and woody floras, correlations with ecological factors should be anticipated.

ADAPTIVE ASPECTS OF VARIATION WITHIN GENERA

The genus level is very suitable for an analysis of wood anatomical variation as related to the different ecologies of the species composing the genera involved. Within the scope of this paper, I have confined myself to a limited number of examples which, of course, bears the danger of drawing conclusions of restricted applicability.

Altitudinal and latitudinal trends for vessel member length have been demonstrated for a reasonable number of widely distributed genera (van der Graaff & Baas, 1974; Baas 1973) and, from recent studies by other authors, support is forthcoming or can be deduced (R. B. Miller, 1976, for *Juglans*; H. J. Miller, 1975, for arctic species of *Betula*, *Empetrum*, *Salix*, and several Ericaceae). With some confidence, one may claim that the trends for vessel member length to decrease with increasing altitude or latitude are generally applicable. The same probably applies to Carlquist's (1975 and several other recent papers) and Novruzova's (1968) suggestions that fusiform products, including vessel members, are shorter in xeric species than in more mesic species belonging to a certain genus or family. The two trends may be opposed in certain cases, e.g. in the case of tropical altitudinal differences where high montane species of the mossy forest may be growing under more mesic conditions than those of the lowland. In general, however, the different trends emphasizing either temperature or moisture availability should be regarded as complementary to one another. Interpreting these vessel member length trends in a functional or adaptive sense seems far-fetched and unfounded at this stage of our knowledge. Carlquist claims that short vessel members may have a mechanical advantage over long vessel members in resisting high negative pressures in certain xeric species but, to me, such an interpretation lacks any substantial basis and is certainly not applicable to latitudinal trends for vessel member length, which show that, e.g. in *Ilex* mesic temperate species have much shorter vessel members than tropical species (including a comparatively xeric species, *I. jenmanii* from savannas in South America). If one considers the positive correlation of vessel member length with fibre length, one may hypothesize that a mechanical advantage may ensue for the species with longer fusiform initials. This would make sense if the latitudinal and altitudinal trends for vessel member and fibre length were positively related with plant size. For *Ilex*, and probably for other genera as well, this is, however, not so. Shrubs or small trees in the understorey of the lowland forests have yet longer vessel members and fibres than some bigger trees from higher altitudes or latitudes. Moreover, the role of fibre length in mechanical properties of the wood remains to be elucidated in most cases. In conclusion, I find any adaptive explanation of the positive correlations between ecological factors and vessel member length unconvincing. I would favour indirect effects of these different ecologies on vessel element length through genetically fixed differences in morphogenetic processes controlled by, for instance, differences in phytohormone metabolism. Admittedly this suggestion also lacks any factual basis. However, indirect effects of the environment, mediated through such factors as auxins and photosynthates, have been advocated for control of tracheid diameter and cell wall thickness for conifers by Larson (1964).

As for perforation plate characteristics, the great majority of woody genera are constant with respect to this character. In cases where we deal with mixed simple and scalariform perforation plates or exclusively scalariform perforation plates, the number of bars or the percentage of scalariform perforations may, however, vary greatly within a genus. It has, however, been demonstrated that, if one considers a reasonably large sample of genera, no general trend relating this with ecological factors can be established (van der Graaff & Baas, 1974). Each genus has its own individual pattern. The very distinct latitudinal and altitudinal trends in *Ilex* escape any functional or adaptive explanation. Carlquist's view (1975) that temperate *Ilex* species might take advantage of a reduced number of bars in spring time when high transpiration rates would prevail is highly unlikely for the evergreen diffuse-porous *Ilex* species involved. Some other genera may serve as examples of seemingly non-adaptive variation. Most species of the genus *Escallonia* show exclusively scalariform perforations according to detailed studies by Stern (1974). *Escallonia millegrana* and *E. micrantha* form an exception, however, with most or at least some of the vessel perforations simple. Like most other *Escallonia* species, these species grow under mesic conditions (Sleumer, 1968), more mesic for instance than the closely related *E. pulvurulenta* which grows in exposed dry places and has exclusively scalariform perforations. In the genus *Ribes*, Stern *et al.* (1970) also found aberrant species with a large or small proportion of simple plates (*R. americanum* and *R. aureum*). These species again belong to the more mesic ones of the genus and have close relatives in dryer habitats with exclusively scalariform perforations (e.g. *R. cereum*). The tropical genus *Alangium* provides another interesting example. As noted by Metcalfe & Chalk (1950), one can distinguish two wood anatomically distinct groups within the genus. Group A with scalariform perforations and long vessel members, and group B with exclusively simple perforations and short vessel members. Ecological information from herbarium labels and from Bloembergen's revision (1939) of the genus reveals no ecological differences between the different species groups listed by Metcalfe & Chalk. It is, however, interesting to note that the species with scalariform perforations are included in one of Bloembergen's sections and that the simply perforated vessels belong to species of the three other sections recognized.

The above examples are strongly suggestive that, within the genera concerned, simple perforations arose irrelative to selective advantage. In other words, the variation in perforation plates below the genus level indicate a haphazard array of possibilities all of which are apparently not focussed at the survival or 'evolutionary success' of the species concerned.

The xylem of climbers is noted for its high rates of water conduction and several authors have hypothesized a functional 'acceleration' of vessel specialization for scandent or climbing species. Genera with both erect and scandent or climbing species are for instance *Ilex*, *Heisteria*, and *Quintinia*. The only climbing species in *Ilex* (Baas, 1973) shows a reduced number of widely spaced strong bars. *Heisteria scandens* from S. America is the only species of *Heisteria* known to have predominantly or exclusively simple perforations; all erect shrub or tree species have scalariform perforation plates. In *Quintinia*, the vessels have exclusively scalariform perforations, also in the climbing species *Q. epiphytica* from New Guinea. In both erect species and in *Q. epiphytica* the number of bars may be high, but in *Q. epiphytica* the bars are stronger and more widely spaced than in the arboreous species *Q. sieberi* studied for comparison. In these instances the wood anatomical deviations in the climbing species seem to confirm the hypothesized functional advantage for rapid water conduction.

ADAPTIVE ASPECTS OF VARIATION WITHIN FAMILIES

As within genera, one may expect the substantial wood anatomical variation within families to be clearly correlated with the different ecologies of the taxa constituting these families, if the hypothesis that selective pressure by the environment has played a decisive role in directing xylem evolution is a correct one. Carlquist (1975) quoted Violaceae and Ericaceae as examples where the varying type of perforation plate is related with ecology or habit of the genera involved: genera with mesic species were said to be characterized by scalariform perforation plates, xeric genera or lianas were quoted to have simple perforations. I have attempted to compare anatomical and ecological data in a number of other families in which both simple and scalariform perforations occur in order to obtain a more representative picture.

Metcalfe & Chalk (1950) listed perforation plate characteristics for a great number of Epacridaceae. A comparison with ecological notes on herbarium labels and in regional flora's of New Caledonia (Virot, 1975), Australia (Burbidge & Gray, 1970; Ewart, 1930), and New Zealand (Allan, 1961) indeed shows a mesic preference for the genera with scalariform plates and a xeric ecology for genera with exclusively or predominantly simple plates. A detailed revision of the wood anatomy of Epacridaceae backed by ample ecological data would be a necessary and interesting extension to this rather rough generalization.

Icacinaceae are wood anatomically better known (Bailey & Howard, 1941) and for the Malesian representatives Sleumer (1971) offered sufficient ecological information for comparison. For trees and shrubs it appears that genera with exclusively scalariform perforation plates, with mixed simple and scalariform plates, or with exclusively simple perforations all have a mesic ecology and that, in all three categories, the species may be shrubs or trees (up to 25–40 m tall) occurring in tropical forests of low to high altitude. So we can trace no differences in ecological preference or tolerance related to the different degrees of vessel perforation specialization. The climbing or scandent genera on the other hand all have exclusively simple perforations.

For Flacourtiaceae the detailed anatomical account by R. B. Miller (1975) lends itself well for comparison with ecological data of Sleumer (1954, and in preparation). In Malesia all representatives grow under rather mesic conditions, regardless of the type of perforation plate. Quite strikingly two genera with climbing or scandent habit viz. *Streptothamnus* from E. Australia and *Berberidopsis* from Chile are characterized by scalariform plates, albeit with widely spaced bars. In this family in which simple perforations have developed without any apparent ecological pressure, the occurrence of scalariform perforations in climbing representatives certainly negates the hypothesis of selective pressures leading to a functionally advantageous elimination of the scalariform perforation plate. The Dilleniaceae are a family with a diverse ecology, habit and also vessel member morphology (Hoogland, 1951; Dickison, 1967). The genera with scalariform perforations range in habit from woody herbs (*Acrotrema* growing in wet sites and *Pachynema* from extremely dry localities) to lofty trees or erect shrubs. These trees and shrubs may occupy a diversity of ecological niches. The genus *Dillenia* has, for instance, species in lowland rain forests as well as in savannas and monsoon forests with a pronounced dry period. Usually, the species which are subjected to seasonal drought are deciduous, but there are exceptions. The genera with predominantly simple plates consist largely of species with either scandent or climbing habit (*Tetracera*, *Doliocarpus*, *Davilla*) or are composed of xeric erect species (*Curatella*). Therefore only part of the wood anatomical diversity in Dilleniaceae is in line with the adaptive hypothesis by Carlquist, partly it is in conflict with it (*Dillenia* and the semi-herbaceous genera with scalariform plates).

OCCURRENCE OF GENERA WITH SCALARIFORM PERFORATION PLATES IN DIFFERENT VEGETATION TYPES AND GEOGRAPHICAL AREAS

In my paper on *Ilex* (1973) I have drawn attention to the differences between floras in the frequency of genera with scalariform perforations, as had Kanehira (1921) in comparing the anatomies of his wood collections from Japan, Formosa, and the Philippines, and as did Versteegh (1968) in considering the woods of Indonesian montane species. Carlquist (1975) elaborated on this theme and discussed the occurrence of taxa with scalariform perforation plates in Southern California, Hawaii, South Africa, and in upland and lowland tropics. Kanehira's and my own analyses were based on wood anatomical data obtained from a limited number of woody representatives (in my case using data of Greguss, 1959, and Janssonius, 1906–1936). On reconsideration I find this approach too rough, because regional wood anatomical surveys are usually based on incomplete, quite possibly not representative sampling. Moreover, for large regions with widely varying habitats (Europe, Java), the method does not allow considerations on ecological wood anatomy. Carlquist (1975) listed the figures I presented in a table (p. 146), thereby in a way giving them undue weight.

In the present approach, I have analysed floristic accounts of specific vegetation types or of regional floras, and have collected the wood anatomical data from the literature, chiefly from Metcalfe & Chalk (1950).

Of course this procedure has the risk of mistakes, because data from the literature may be inaccurate, taxa may have changed names and the species listed in the floristic works may be anatomically fully unknown. However, at this stage of our anatomical knowledge, I think it is possible to extrapolate confidently in cases where characters such as type of perforation plates are concerned. If, for instance, species of *Dillenia* or *Betula* are recorded which have not been described anatomically, one may yet be reasonably confident that these species will have exclusively scalariform perforations because all species of these genera studied so far share this character. This becomes more problematical in some genera of e.g. Araliaceae, Ericaceae, and Epacridaceae which still await a thorough updating of wood anatomical information, and in which scalariform perforations are rare, abundant, or absent in different species within a genus. This has been one of the reasons why I have separately analysed the percentages of genera with mixed simple and scalariform perforations. For the reasons outlined above the figure on genera with mixed types of perforation plates is less reliable than that on genera with exclusively scalariform perforation plates. In the former category, I have mostly left out genera with very rare vestigial bars such as frequently occur in e.g. Lauraceae; for this approach these are certainly irrelevant. In addition to this, I have also analysed some regional wood anatomical surveys for comparison. The new approach brings about some important changes in the percentages for Java and Europe as listed by me (1973) and Carlquist (1975). Greguss' wood anatomical survey (1959) of 155 genera (including some exotics) includes 21 genera (13.5%) with exclusively scalariform perforations; 3 genera (2%) with almost exclusively scalariform perforations; 13 genera (8.4%) with mixed simple and scalariform plates in varying frequencies and 8 genera with very rare multiple perforations. In Table 2 two percentages are given: 16 for perforations exclusively scalariform or almost so; 8 for perforations mixed simple and scalariform. For Java, the percentages are: 12 and 2 respectively. These figures convey more information than the total percentage 23 and 13 for Europe and Java respectively given in the previous publications.

In Tables 1 and 2, and Fig. 2, the results of the floristic analyses are summarized. The genera with exclusively scalariform plates are listed in the appendix, together with the total number of woody genera included in each analysis. The data are confined to trees and shrubs (including dwarf forms) belonging to the dicotyledons. They may be compared with Chalk's overall analysis of perforation plate characteristics in woody

TABLE 1. Occurrence of genera with scalariform perforation plates or with both simple and scalariform plates in the tropics. See also appendix

Vegetation type and locality or geographical region	Total number of woody erect genera	Percentage of genera with scalariform perforations	Percentage of genera with scalariform and simple perforations
LOWLAND RAIN FORESTS			
Mixed Dipterocarp forest Brunei	215	8	5
Peat swamp forests Sarawak and Brunei	134	5	9
Virgin forest near Sandakan	110	6	7
Jengka forest reserve, Malaya	135	6	7
New Guinea, Momi-Ransiki. Trees over 35 cm diam.	87	1	8
Malawi evergreen lowland forest (550—915 m)	30	3	3
Amazonas rain forest	40	0	3
North Suriname rain forest			
Upper and middle storey	99	5	4
Lower storey	26	8	0
Undergrowth	28	7	11

Table 1 (*continued*)

MONTANE VEGETATIONS (mostly forests)			
Mt Wilhelm, New Guinea (trees and shrubs respectively)			
Cloud forest (3100—3350 m)	30 & 20	33 & 20	7 & 10
Lower sub-alpine forest (3410—3590 m)	23 & 24	30 & 33	9 & 8
Upper sub-alpine forest (3590—3900 m)	11 & 20	27 & 30	9 & 10
Mt Pulog, Philippines (1200—2500 m)	100	17	3
Ibid., above 2200 m	44	27	7
Mt Tabayoc, Philippines, above 2200 m	47	31	5
Flores and Timor (600—2200 m)	209	15	7
Tjibodas, Java (1300—2500 m)	139	18	5
Malawi submontane forest (1370—2290 m)	60	15	7
Ibid., montane forest (1675—2590 m)	36	22	5
Colombia, above 1800 m	55	20	8
SAVANNAS AND MONSOON FORESTS			
Sumbawa and Timor	120	1	4
Arnhem land, Australia	140	2	3
Savannas North Surinam	98	5	3
REGIONAL FLORAS WITH DIVERSE VEGETATION TYPES			
Java (Janssonius' material for wood anat. study)	372	12	2
Philippines (Reyes' material for wood anat. study)	160	8	0
Ivory Coast	308	4	3

dicotyledons (in Metcalfe & Chalk 1950: xliv). In a sample of about 1800 woods he recorded exclusively scalariform perforation plates in 206 species. The resulting 11% may be assumed to be a good approximation of what would follow if the analysis had been carried out on a generic basis. From the tables and appended lists of taxa some striking patterns result, partly confirming my previous statements (1973) and those by Carlquist (1975), partly new and unexpected.

The tropical lowland rain forests invariably show a rather low percentage of representatives with scalariform plates. Going from the lowland forest to the cooler mountain forest the percentage of primitive woods invariably increases. The same applies if we move from the tropical lowland regions to higher latitudes with extremely high percentages in some cool temperate to arctic floras. To the other extreme we have a decrease in arid regions such as the Sahara, where not a single representative of the 76 woody genera listed by Ozenda (1958) has scalariform perforations. The seasonally dry flora's of the monsoon forests and savannas of Arnhem land, Timor, and Sumbawa, also have very low percentages; in the Surinam Savanna's it does not differ markedly from that of the rain forests.

Before further discussing the implications of the percentages listed in Tables 1 and 2, it should be emphasized that these percentages are derived from floras or samples thereof, highly varying in number of woody representatives. The tropical lowland forests are highly diverse, and each inventory contains a high number of woody genera (see appendix), even if these inventories were made in comparatively small areas. For the tropical montane to subalpine forests, the woody flora becomes poorer but the percentages are still based on sufficiently large numbers to be meaningful. The same applies to temperate floras for sufficiently large regions. In the arctic regions the flora is notably poor in woody species, and percentages for the floras on Greenland, Falkland, Iceland, etc. are based on a very small number of genera indeed. This means that the occurrence of one extra genus with scalariform perforations in those regions would shift the figure in Table 2 considerably (by 4 to 20%!). This is one of the reasons why, comparatively, many arctic and cool temperate floras have been analysed, so that the overall results would have some statistical significance.

The percentages listed in Tables 1 and 2 are of course primarily the result of the distribution patterns of dicotyledonous families and genera characterized by scalariform or, alternatively, by simple perforation plates in their woods. The high percentages for arctic regions are caused mainly by the predominance of Ericaceae (including Vacciniaceae) in their woody floras. The great majority of families with exclusively simply perforated vessels have not reached the arctic floras. The same applies to high montane tropical floras which do not have representatives of families such as e.g. Dipterocarpaceae, which dominate the lowland forests in some parts of Malesia. The phytogeographical history resulting from dispersal and geological events is primarily responsible for the present day distribution, and ecological preference or better tolerance constitutes only one of the factors determining the geographical range of families and genera. Considering this, it is all the more striking that the results mentioned above run parallel in such different floral regions as the different continents and the Northern and Southern Hemisphere. An exception to this is presented by the Hawaiian flora, for which the very low percentage of genera with scalariform perforations (3%) has been discussed by Carlquist (1975) in terms of phytogeographical factors, when he mentioned that many families with primitive xylem have not reached Pacific volcanic islands.

The overall results, however, invite a discussion centered around the ecological correlations following from the latitudinal and altitudinal trends, and from the mesic—xeric trends apparent from Tables 1 and 2, and summarized in Fig. 2. The fact that the scalariform perforation is more primitive than the simple perforation cannot simply be used to state that our figures indicate that tropical montane temperate to arctic floras, have retained a high number of primitive taxa. On the contrary, most of these floras have re-established themselves relatively recently in the present interglacial period. The trends following from Table 1 and 2 seem to support Carlquist's claims that, in general, woody plants with exclusively scalariform perforations are restricted to regions with relatively low rates of water conduction. This fits in with data from the tropics. According to Coster (1937) who measured transpiration in a number of Javanese plants, transpiration is usually less intensive in montane trees and shrubs as compared to lowland trees. For deciduous monsoon forests he reported a still lower annual transpiration but, if calculated for the wet season only, monsoon forest trees transpire more intensively than evergreen montane or lowland species. In the extremely arid environment of the desert high transpiration rates are well documented for a number of species (e.g. Stocker, 1956: 474), although some categories of desert plants have a strongly reduced transpiration and hence a low rate of water conduction. One may assume that, at higher latitudes, transpiration and thus water conduction is less intensive although I have been unable to find sufficient information in the literature to substantiate this.

A more detailed consideration of the lists of genera with scalariform perforations (see appendix) is interesting for a more refined evaluation of the percentages listed in Tables 1 and 2. Most genera listed for the Malesian lowland forests belong to the second or third storey of the forest. The only genus with truely emergent species is *Dillenia*. Other genera with large-sized trees are e.g. *Schima* and *Altingia*. This explains the very low percentage for the Momi-Ransiki (New Guinea) inventory. Here, only trees with a bole over 35 cm in diameter were listed, so that many species from the lower storeys of the forests were omitted. This further confirms Carlquist's suggestions that trees with scalariform perforation plates require a mesic environment. However, for the very detailed inventory of the Surinam rain forest, there are no great differences in the proportion of genera with scalariform plates for the different storeys. The percentages for Amazonas and Malawi lowland rain forests are of course not very reliable because they are both based on incomplete lists of the most common, probably large-sized, tree species. The consistently high percentage of genera with scalariform perforations in tropical montane forests is not influenced by exposure of the crown; for instance, for

TABLE 2. Occurrence of genera with scalariform perforation plates or with both simple and scalariform perforations in subtropical to arctic regions. See also appendix

Country, region, or vegetation type	Total number of woody erect genera	Percentage of genera with scalariform perforations	Percentage of genera with scalariform and simple perforations
Sahara desert (partly tropical)	76	0	0
New Zealand	91	13	8
Japan	250	22	7
Mt Fuji, Japan			
Prairie region (up to 1000 m)	90	29	0
Deciduous broad leaved region (870—1700 m)	33	40	8
Salix-Alnus region (above 2500 m)	11	36	8
Europe (Greguss' material for wood anat. study)	155	16	8
Holland	46	22	9
Norway and Sweden	47	30	11
Iceland	11	23	46
Greenland	15	53	27
Spitsbergen (Svalbard)	5	40	40
Alaska	32	47	9
Falkland	9	33	11
Auckland's and Campbell's islands	5	40	0

Mt. Wilhelm (New Guinea) the percentages for tree and shrub species are about the same, and several of the taxa involved also occur in open vegetation. With increasing altitude, the percentages generally increase, which accounts for the relatively low percentages for Flores and Timor, Java, and Mt Pulog (Merrill & Meritt's data), which are also based to a considerable extent on taxa below 2000 m alt. The savannas and monsoon forests with seasonal drought show very low percentages for Sumbawa and Timor, and Arnhem land. These percentages are directly comparable with the figures for the lowland and montane rain forests of the Malesian area; the difference between the monsoon forests and the wet montane and submontane forests of Timor are especially significant since they are based on comprehensive lists and cannot have been influenced by phytogeographical factors. The only representative with scalariform perforations in the seasonally dry woodland is a deciduous *Dillenia* species, so that we can even claim a more or less mesic ecology for this species at times of most intensive transpiration. The figures for the Surinam savannas is not completely in line with this; the percentage of genera with scalariform perforations is only very slightly lower than for the rain forests. Perhaps this is due to the fact that, in certain Surinam savannas, the water table remains high in the dry season. The genera listed in the appendix have species in savanna bushes or forests, very rarely in the open savanna. Moreover, most of the species belonging to such genera as *Ilex* and *Symplocos* occur in the rain forest. The wood anatomy of *Ilex jenmanii* of the dry Surinam savannas is not different from that of the rain forest species *Ilex guianensis* (Baas, 1973) with respect to vessel member length or number of bars per perforation.

The woody vegetation of the desert with its dwarf shrubs, often belonging to predominantly herbaceous families, is of course not quite comparable with that of the tropical forests. Yet, it is significant that in the extremely dry habitat of the Sahara none of the 76 woody genera has scalariform perforations. The subarctic regions of the Northern and Southern Hemisphere are also characterized by stunted dwarf shrubs, yet the percentage of representatives with scalariform plates is very high and concerns genera or species which mainly grow in the wetter environments. For Greenland the genera with mixed simple and scalariform perforations have a very high percentage of scalariform plates (H. J. Miller, 1975). The percentages for regional tropical, subtropical, or temperate floras are based on genera from a diversity of vegetation types and growth habits. The values for Europe (as based on Greguss, 1959) and New Zealand are comparatively low due to significant xeric components in the regional floras; most taxa with scalariform perforation plates listed in the appendix grow in mesic sites. The flora of Japan also covers a very wide latitudinal and ecological range, but the xeric component of this flora is smaller which may account for the higher percentage of genera with scalariform perforations than in the European and New Zealand flora. The percentages for Java and the Philippines as based on wood anatomical surveys can be accounted for if one considers the important montane forest as well as monsoon and lowland rain forest components. The low figure for Ivory Coast can be accounted for

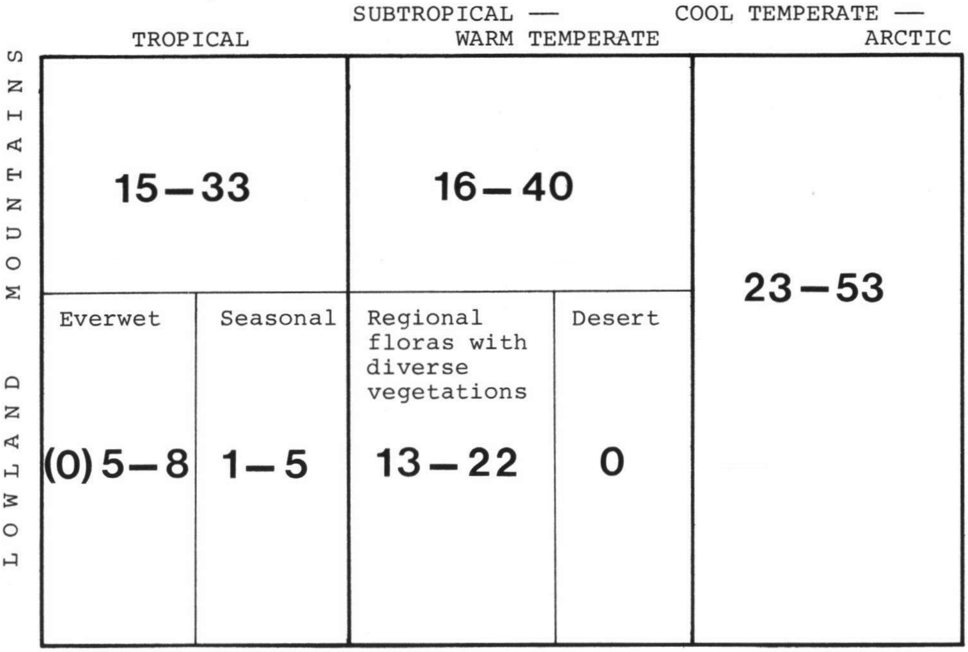

Fig. 2. Diagram illustrating the percentages of genera with exclusively scalariform perforation plates in different latitudinal, altitudinal and climatic zones or regions.

by the numerous genera growing in the savanna. Most genera listed in the appendix for Ivory Coast are represented by rain forest species.

Carlquist strongly emphasized moisture availability when interpreting the proportion of taxa with scalariform perforation plates in different floras. My results confirm this, but I think that temperature should receive equal emphasis. Plants of tropical high montane or temperate to arctic localities are not growing in a more mesic environment than plants of tropical lowland rain forests, yet the differences in frequency of taxa with scalariform plates are considerable. One may, however, assume that the low temperatures will considerably reduce transpiration rate and water uptake from the soil so that the rate of water conduction in the xylem will also be low. Average vessel member lengths for whole woody floras or vegetation types are insufficiently known to discuss this character on a similar basis as type of perforation plate.

GENERAL DISCUSSION

In the previous chapters two different approaches of functional or adaptive aspects of vessel member morphology have led to conflicting results. Based on analysis of variation at the genus and family level, examples were cited which do not support Carlquist's suggestion that wood anatomical diversity is governed by selective pressures of the external environment or such factors as growth habit. Other examples, including those discussed by Carlquist himself, however, support his claim that the primitive type of vessel member with scalariform perforation plates is only efficient in erect woody plants of mesic environments. The analysis of different vegetation types and regional floras supports this suggestion much more convincingly, and also points to an important role of the factor temperature.

The examples cited, which are not compatible with this hypothesis, may be regarded as mere exceptions to the rule, or they may invite to look for functional advantages of the retention of scalariform plates in these specific cases. Carlquist, for instance, did this when he hypothesized a function of the scalariform perforation plate in the prevention of collapse under high negative pressures for vessels of mangrove Rhizophoraceae. In my opinion, such interpretations are purely academic and it is perhaps appropriate to quote Bateson's wise statement (1894: 79) on adaptive interpretations, that 'on this class of speculation the only limitations are those of the ingenuity of the author'! On the other hand, to dismiss the conflicting examples as mere exceptions to the rule would be unjustified in view of their number and also in view of the fact that the trends in percentages for woody vegetations still show a number of taxa with scalariform perforations in environments 'where they should not occur' according to the hypothesis. In my opinion, the exceptions at the genus and family level are in fact highly significant because, at these levels, adaptive or selective pressures should be most clearly traceable. The absence of indications of any effect of selection in these cases reveals the true nature of xylem evolution as a random process leading to wood anatomical diversity which is not necessarily advantageous or disadvantageous for efficient water transport or for mechanical requirements. In terms of van Steenis' (1976) theory they exemplify the *patio ludens* of xylem evolution. It is impossible at this stage to estimate the relative importance which selective pressures or *patio ludens* diversification have played in the origin of wood anatomical diversity as we know it in extant plants. The trends for whole vegetations and regional floras, however, suggest that selection pressure by the physical environment may have been considerable.

For vessel member length diversity, consistent ecological trends have only been established for genera and some families. As discussed before, I cannot accept·all Carlquist's diverse functional interpretations emphasizing either advantages for water conduction or resistance to high negative pressures. I wonder whether different growth rates and growth patterns in xeric or cool conditions do not affect fusiform initial length. To certain extents growth dynamics probably also have become genetically fixed in evolution, so that one may hypothesize that vessel member length trends are thus the result of secondary effects. This offers a parallel with wood anatomical diversity within single trees which may be the result of growth rate and hormone production in different sites. The latter suggestions are admittedly equally academic as those by

Carlquist on the function of minute details of wood structure, but I find it essential that the basic problem of wood anatomical diverstiy be approached from as many angles as possible.

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APPENDIX

Total numbers of dicotyledonous genera and names of genera with (presumably) exclusively scalariform perforations used in the analyses of floras and vegetation types.

Mixed Dipterocarp forest Brunei (Ashton, 1964): 215 genera. *Adinandra* (Theac.), *Aromadendron* (Magn.), *Dillenia* (Dill.), *Eurya* (Theac.), *Gordonia* (Theac.), *Hydnocarpus* (Flac.), *Ilex* (Aq.), *Ochanostachys* (Olac.), *Platea* (Icac.), *Polyosma* (Escal.), *Rinorea* (Viol.), *Saurauia* (Act.), *Schima* (Theac.), *Scorodocarpus* (Olac.), *Strombosia* (Olac.), *Symplocos* (Sympl.), *Ternstroemia* (Theac.), *Turpinia* (Staph.).

Peat swamp forests Sarawak and Brunei (Anderson, 1963): 134 genera.
Aromadendron (Magn.), *Ctenolophon* (Cten.), *Dillenia* (Dill.), *Ilex* (Aq.), *Platea* (Icac.), *Ploiarium* (Theac.), *Ternstroemia* (Theac.).

Virgin forest near Sandakan (Nicholson, 1965): 110 genera. *Alangium* (Al.), *Dillenia* (Dill.), *Ilex* (Aq.), *Hydnocarpus* (Flac.), *Ochanostachys* (Olac.), *Symplocos* (Sympl.), *Talauma* (Magn.).

Jengka forest reserve, Malaya (Poore, 1968): 135 genera. *Alangium* (Al.), *Ctenolophon* (Cten.), *Dillenia* (Dill.), *Mastixia* (Corn.), *Ochanostachys* (Olac.), *Strombosia* (Olac.), *Symplocos* (Sympl.), *Turpinia* (Staph.).

New Guinea, Momi-Ransiki, trees over 35 cm in diam. (Kostermans & Tideman, 1948): 87 genera.
Dillenia (Dill.), cited as *Wormia*.

Malawi evergreen lowland forest (Chapman & White, 1970): 30 genera.
Rawsonia (Flac.).

Amazonas rain forest (Weber, 1969): 40 genera.
None with exclusively scalariform perforation plates.

North Surinam rain forest (Schulz, 1960).
Upper and middle storey: 99 genera. *Dendrobangia* (Icac.), *Goupia* (Goup.), *Poraqueiba* (Icac.), *Sacoglottis* (Hum.), *Styrax* (Styr.).
Lower storey: 26 genera. *Leonia* (Viol.), *Paypayrola* (Viol.).
Undergrowth: 28 genera. *Heisteria* (Olac.), *Rinorea* (Viol.).

Mt Wilhelm, New Guinea (Wade & McVean, 1969).

Cloud forest, 3100–3350 m.

Trees: 30 genera including 2 vesselless genera *Bubbia* and *Drimys* (Wint.).

Ascarina (Chlor.), *Daphniphyllum* (Daphin.), *Eurya* (Theac.), *Kibara* (Monim.), *Polyosma* (Escal.), *Quintinia* (Escal.), *Saurauia* (Act.), *Sphenostemon* (Sphen), *Symplocos* (Sympl.).

Shrubs: 20 genera including vesselless genus *Drimys*: (Wint.)

Eurya (Theac.), *Polyosma* (Escal.), *Saurauia* (Act.), *Symplocos* (Sympl.).

Lower sub-alpine forest, 3400–3590 m.

Trees: 23 genera including vesselless genus *Drimys* (Wint.). *Daphniphyllum* (Daphn.), *Eurya* (Theac.), *Polyosma* (Escal.), *Quintinia* (Escal.), *Rhododendron* (Eric.), *Saurauia* (Act.), *Symplocos* (Sympl.).

Shrubs: 24 genera including vesselless genus *Drimys* (Wint.). *Daphniphyllum* (Daphn.), *Gaultheria* (Eric.), *Polyosma* (Escal.), *Rhododendron* (Eric.), *Saurauia* (Act.), *Symplocos* (Sympl.), *Trochocarpa* (Epacr.).

Upper sub-alpine forest, 3590–3900 m.

Trees: 11 genera including vesselless genus *Drimys* (Wint.). *Quintinia* (Escal.), *Rhododendron* (Eric.), *Symplocos* (Sympl.). Shrubs: 20 genera including vesselless genus *Drimys* (Wint.). *Eurya* (Theac.), *Gaultheria* (Eric.), *Polyosma* (Escal.), *Quintinia* (Escal.), *Rhododendron* (Eric.), *Symplocos* (Sympl.).

Mt Pulog, Philippines, 1200–2500 m (Merrill & Merritt, 1909): 100 genera, including vesselless genus *Drimys* (Wint.).

Adinandra (Theac.), *Chloranthus* (Chlor.), *Clethra* (Clethr.), *Daphniphyllum* (Daphn.), *Deutzia* (Hydr.), *Eurya* (Theac.), *Hydrangea* (Hydr.), *Ilex* (Aq.), *Itea* (Escal.), *Perrottetia* (Cel.), *Polyosma* (Escal.), *Rhododendron* (Eric.), *Saurauia* (Act.), *Symplocos* (Sympl.), *Talauma* (Magn.), *Turpinia* (Staph.), *Viburnum* (Capr.).

Mt Pulog, Philippines, above 2200 m (Jacobs, 1972): 44 genera, including vesselless genus *Drimys* (Wint.).

Adinandra (Theac.), *Camellia* (Theac.), *Clethra* (Clethr.), *Daphniphyllum* (Daphn.), *Eurya* (Theac.), *Gordonia* (Theac.), *Ilex* (Aq.), *Rhododendron* (Eric.), *Saurauia* (Act.), *Symplocos* (Sympl.), *Ternstroemia* (Theac.), *Viburnum* (Capr.).

Mt Tabayoc, Philippines, above 2200 m (Jacobs, 1972): 47 genera. including vesselless genus *Drimys* (Wint.).

As above for Mt Pulog plus *Chloranthus* (Chlor.), *Deutzia* (Hydr.), *Gaultheria* (Eric.), *Polyosma* (Escal.), and *Turpinia* (Staph.); minus *Gordonia* and *Ternstroemia* (Theac.).

Flores and Timor, rather wet evergreen rain forest, *c.* 600–2200 m alt. (van Steenis, private communication): 209 genera of trees and shrubs.

Adinandra (Theac.), *Alangium* (Al.), *Apodytes* (Icac.), *Camellia* (Theac.), *Chloranthus* (Chlor.), *Clethra* (Clethr.), *Daphniphyllum* (Daphn.), *Dichapetalum* (Dich.), *Distylium* (Ham.), *Eurya* (Theac.), *Gaultheria* (Er.), *Gordonia* (Theac.), *Ilex* (Aq.), *Itea* (Escal.), *Laplacea* (Theac.), *Manglietia* (Magn.), *Mastixia* (Corn.), *Meliosma* (Sab.), *Michelia* (Magn.), *Myrica* (Myr.), *Perrottetia* (Cel.), *Platea* (Icac.), *Polyosma* (Escal.), *Rhododendron* (Eric.), *Rinoria* (Viol.), *Saurauia* (Act.), *Symplocos* (Sympl.), *Talauma* (Magn.), *Ternstroemia* (Theac.), *Turpinia* (Staph.), *Viburnum* (Capr.), *Weinmannia* (Cun.).

Tjibodas, Java, 1300–2500 m (Koorders, 1918–1923): 139 genera.

Alangium (Al.), *Altingia* (Ham.), *Apodytes* (Icac.), *Daphniphyllum* (Daphn.), *Dichroa* (Hydr.), *Eurya* (Theac.), *Gaultheria* (Eric.), *Hydrangea* (Hydr.), *Ilex* (Aq.), *Itea* (Escal.), *Laplacea* (Theac.), *Mastixia* (Corn.), *Michelia* (Magn.), *Myrica* (Myr.), *Nyssa* (Nyss.), *Platea* (Icac.), *Polyosma* (Escal.), *Rhododendron* (Eric.), *Saurauia* (Act.), *Schima* (Theac.), *Symplocos* (Sympl.), *Talauma* (Magn.), *Turpinia* (Staph.), *Viburnum* (Capr.), *Weinmannia* (Cun.).

Malawi submontane forest, 1370–2290 m (Chapman & White, 1970): 60 genera.

Afrocrania (Corn.), *Aphloia* (Flac.), *Apodytes* (Icac.), *Ficalhoa* (Eric.), *Ilex* (Aq.), *Rawsonia* (Flac.), *Strombosia* (Olac.), *Ternstroemia* (Theac.), *Xymalos* (Flac.).

Malawi montane forest, 1675–2590 m (Chapman & White, 1970): 36 genera.

Afrocrania (Corn.), *Aphloia* (Flac.), *Apodytes* (Icac.), *Cussonia* (Aral.), *Ilex* (Aq.), *Myrica* (Myr.), *Rawsonia* (Flac.), *Xymalos* (Flac.).

Colombia, above 1800 m (Weber, 1969): 55 genera, including vesselless genus *Drimys* (Wint.).

Clethra (Clethr.), *Escallonia* (Escal.), *Freziera* (Theac.), *Hedyosmum* (Chlor.), *Ilex* (Aq.), *Myrica* (Myr.), *Saurauia* (Act.), *Siparuna* (Monim.), *Turpinia* (Staph.), *Viburnum* (Capr.), *Weinmannia* (Cunon.).

Sumbawa and Timor (Meijer Drees, 1951; van Steenis, private communication): 120 genera in seasonal forest and savannas.
Dillenia (Dill.).

Arnhem land (Specht & Mountford, 1958): 140 genera in seasonal forest and savannas, excluding mangrove representatives.
Dillenia (Dill.), *Elaeodendron* (Cel.), *Hibbertia* (Dill.).

Savannas N. Surinam (Van Donselaar, 1965): 98 genera.
Humiria (Hum.), *Ilex* (Aq.), *Lacistema* (Lac.), *Ternstroemia* (Theac.), *Symplocos* (Sympl.).

Java (Janssonius, 1906–1936): wood anatomical survey of 372 genera.
Adinandra (Theac.), *Alangium* (Al.), *Altingia* (Ham.), *Apodytes* (Icac.), *Bruguiera* (Rhiz.), *Camellia* (Theac.), *Caryospermum* (Cel., = *Perrottetia*), *Daphniphyllum* (Daphn.), *Dillenia* (Dill.), *Distylium* (Ham.), *Eurya* (Theac.), *Gordonia* (Theac.), *Hydrangea* (Hydr.), *Itea* (Escal.), *Kibara* (Monim.), *Magnolia* (Magn.), *Manglietia* (Magn.), *Mastixia* (Corn.), *Meliosma* (Sab.), *Laplacea* (Theac.), *Michelia* (Magn.), *Myrica* (Myr.), *Myristica* p.p. (Myrist.), *Nyssa* (Nyss.), *Platea* (Icac.), *Polyosma* (Escal.), *Putranjiva* (Euph.), *Pyrenaria* (Theac.), *Rhizophora* (Rhiz.), *Ryparosa* (Flac.), *Saurauia* (Act.), *Schima* (Theac.), *Strombosia* (Olac.), *Styrax* (Styr.), *Symplocos* (Sympl.), *Talauma* (Magn.), *Taraktogenos* (Flac.), *Ternstroemia* (Theac.), *Turpinia* (Staph.), *Viburnum* (Capr.), *Weinmannia* (Cun.).

Philippines (Reyes, 1938): wood anatomical survey of 160 timber producing genera. Note that Reyes recorded several genera to have scalariform perforations, which are now known to possess mixed simple and scalariform perforations (marked with an asterisk). Likewise Reyes probably recorded exclusively simple perforations for some genera with mixed simple and scalariform perforations.
Alangium (Al.), *Bruguiera* (Rhiz.), *Ceriops* (Rhiz.), *Ctenolophon* (Cten.), *Dillenia* (Dill.), *Knema** (Myrist.), *Michelia* (Magn.), *Myristica** (Myrist.), *Rhizophora* (Rhiz.), *Strombosia* (Olac.), *Talauma* (Magn.).

Ivory Coast (Guillaumet, 1967): list of 308 woody genera from rain forests, deciduous forests and savannas.
Coula (Olac.), *Cussonia* (Aral.), *Dichapetalum* (Dich.), *Heisteria* (Olac.), *Microdesmis* (Euph.), *Octoknema* (Oct.), *Rhizophora* (Rhiz.), *Rinorea* (Viol.), *Saccoglottis* (Hum.), *Soyauxia* (Passifl.), *Strombosia* (Olac.).

Sahara (Ozenda, 1958): flora contains 76 woody genera.
No genera with scalariform perforations.

New Zealand (Allan, 1961): flora contains 91 dicotyledonous woody genera, including vesselless genus *Pseudowintera* (Wint.).
Ackama (Cun.), *Ascarina* (Chlor.), *Carpodetus* (Escal.), *Corokia* (Corn.), *Dracophyllum* (Epacr.), *Epacris* (Epacr.), *Griselinia* (Corn.), *Hedycarya* (Monim.), *Laurelia* (Monim.), *Pennantia* (Icac.), *Quintinia* (Escal.), *Weinmannia* (Cun.).

Japan (Ohwi, 1965): flora contains 250 dicotyledonous woody genera including 2 vesselless genera *Trochodendron* (Troch.), and *Sarcandra* (Chlor.).
Abelia (Capr.), *Alnus* (Bet.), *Andromeda* (Eric.), *Aucuba* (Corn.), *Betula* (Bet.), *Buxus* (Bux.), *Camellia* (Theac.), *Cassiope* (Eric.), *Cercidiphyllum* (Cerc.), *Chloranthus* (Chlor.), *Clethra* (Clethr.), *Cleyera* (Theac.), *Cornus* (Corn.), *Corylopsis* (Cor.), *Corylus* (Cor.), *Daphniphyllum* (Daphn.), *Deutzia* (Hydr.), *Disanthus* (Ham.), *Distylium* (Ham.), *Empetrum* (Emp.), *Euptelea* (Eupt.), *Eurya* (Theac.), *Euscaphis* (Staph.), *Hamamelis* (Ham.), *Helwingia* (Helw.), *Hydrangea* (Hydr.), *Ilex* (Aq.), *Illicium* (Ill.), *Itea* (Escal.), *Kandelia* (Rhiz.), *Ledum* (Eric.), *Loiseleuria* (Eric.), *Loropetalum* (Ham.), *Lyonia* (Eric.), *Menziesia* (Eric.), *Michelia* (Magn.), *Myrica* (Myr.), *Pachysandra* (Bux.), *Philadelphus* (Hydr.), *Phyllodoce* (Eric.), *Platycrater* (Hydr.), *Pterostyrax* (Styr.), *Rhododendron* (Eric.), *Ribes* (Gross.), *Schizandra* (Schiz.), *Securinega* (Euph.), *Stachyurus* (Stach.), *Staphylea* (Staph.), *Stewartia* (Theac.), *Styrax* (Styr.), *Symplocos* (Sympl.), *Ternstroemia* (Theac.), *Thea* (Theac.), *Turpinia* (Staph.), *Viburnum* (Capr.), *Weigelia* (Capr.).

Japan, Mt Fuji (Hayata, 1911).
Prairie region up to 1000 m; forest patches along streams: 90 genera.
Abelia (Capr.), *Alangium* (Al.), *Alnus* (Bet.), *Aucuba* (Corn.), *Buxus* (Bux.), *Chloranthus* (Chlor.), *Clethra* (Clethr.), *Corylus* (Cor.), *Cornus* (Corn.), *Deutzia* (Hydr.), *Diervilla* (Capr.), *Eurya* (Theac.), *Euscaphis* (Staph.), *Hamamelis* (Ham.), *Hydrangea* (Hydr.), *Ilex* (Aq.), *Illicium* (Ill.), *Rhododendron* (Eric.), *Ribes*

(Gross.), *Schizandra* (Schiz.), *Securinega* (Euph.), *Stachyurus* (Stach.), *Styrax* (Styr.), *Symplocos* (Sympl.), *Thea* (Theac.), *Viburnum* (Capr.).

Deciduous broad-leaved region, 870–1700 m: 33 genera in forests.

Andromeda (Eric.), *Cornus* (Corn.), *Corylus* (Cor.), *Diervilla* (Capr.), *Gaultheria* (Eric.), *Hydrangea* (Hydr.), *Ilex* (Aq.), *Menziesia* (Eric.), *Rhododendron* (Eric.), *Ribes* (Gross.), *Styrax* (Styr.), *Symplocos* (Sympl.).

Salix-Alnus region, above 2500 m: 11 genera from shrubbery. *Alnus* (Bet.), *Betula* (Bet.), *Rhododendron* (Eric.), *Menziesia* (Eric.).

Europe (Greguss, 1959): wood anatomical survey of 155 genera, including some cultivated exotics (marked with asterisk).

Alnus (Bet.), *Andromeda* (Eric.), *Arctous* (Eric.), *Betula* (Bet.), *Buxus* (Bux.), *Cercidyphyllum** (Cerc.), *Cornus* (Corn.), *Hamamelis* (Ham.), *Empetrum* (Emp.), *Ilex* (Aq.), *Linnaea* (Capr.), *Liquidambar* (Ham.), *Liriodendron** (Magn.), *Loiseleuria* (Eric.), *Myrica* (Myr.), *Myrtus* (Myrt.), *Parrotia** (Ham.), *Philadelphus* (Capr.), *Rhododendron* (Eric.), *Rhodothamnus* (Eric.), *Ribes* (Gross.), *Staphylea* (Staph.), *Viburnum* (Capr.), *Weigelia** (Capr.).

Netherlands (Heukels & Van Ooststroom, 1975): flora contains 46 dicotyledonous woody genera.

Alnus (Bet.), *Andromeda* (Eric.), *Betula* (Bet.), *Cornus* (Corn.), *Corylus* (Cor.), *Empetrum* (Emp.), *Ilex* (Aq.), *Myrica* (Myr.), *Ribes* (Gross.), *Viburnum* (Capr.).

Norway and Sweden (Lid, 1963): flora contains 47 woody dicotyledonous genera.

Alnus (Bet.), *Andromeda* (Eric.), *Betula* (Bet.), *Cornus* (Corn.), *Corylus* (Cor.), *Empetrum* (Emp.), *Ilex* (Aq.), *Ledum* (Eric.), *Loiseleuria* (Eric.), *Myrica* (Myr.), *Phyllodoce* (Eric.), *Rhododendron* (Eric.), *Ribes* (Gross.), *Viburnum* (Capr.).

Iceland and the Faeroes (Ostenfeld & Gröntved, 1934): flora contains 11 woody dicotyledonous genera.

Betula (Bet.), *Empetrum* (Emp.), *Loiseleuria* (Eric.).

Greenland (Böcher, Holmen & Jakobsen, 1968): flora contains 15 woody genera.

Alnus (Bet.), *Andromeda* (Eric.), *Betula* (Bet.), *Empetrum* (Emp.), *Ledum* (Eric.), *Loiseleuria* (Eric.), *Phyllodoce* (Eric.), *Rhododendron* (Eric.).

Spitsbergen (Rønning, 1964): flora (at 75° Northern latitude) contains 5 woody genera.

Betula (Bet.), *Empetrum* (Emp.).

Alaska (Anderson, 1959): flora contains 32 woody genera.

Alnus (Bet.), *Andromeda* (Eric.), *Betula* (Bet.), *Cassiope* (Eric.), *Empetrum* (Emp.), *Gaultheria* (Eric.), *Kalmia* (Eric.), *Ledum* (Eric.), *Loiseleuria* (Eric.), *Menziesia* (Eric.), *Myrica* (Myr.), *Phyllodoce* (Eric.), *Rhododendron* (Eric.), *Ribes* (Gross.), *Viburnum* (Capr.).

Falkland Islands (Moore, 1968): flora contains 9 woody genera.

Empetrum (Emp.), *Gaultheria* (Eric.), *Pernettya* (Eric.).

Auckland's and Campbell's Island (Hooker, 1847): list contains 5 woody genera.

Dracophyllum (Epacr.), *Richea* (Epacr.).

REFERENCES

ALLAN, H. H. 1961. Flora of New Zealand.

ANDERSON, J. A. R. 1963. The flora of the peat swamp forests of Sarawak and Brunei, including a catalogue of all recorded species of flowering plants, ferns, and fern allies. Gdns' Bull., Singapore 20: 131–228.

ANDERSON, J. P. 1959. Flora of Alaska and adjacent parts of Canada.

ASHTON, P. S. 1964. Ecological studies in the mixed Dipterocarp forests of Brunei state. Oxf. Univ. Mem. 25.

BAAS, P. 1973. The wood anatomical range in *Ilex* (Aquifoliaceae) and its ecological and phylogenetic significance. Blumea 21: 193–258.

BAILEY, I. W. 1944. The development of vessels in angiosperms and its significance in morphological research. Am. J. Bot. 31: 421–428.

BAILEY, I. W. 1953. Evolution of tracheary tissue of land plants. Am. J. Bot. 40: 4–8.

BAILEY, I. W. & R. A. HOWARD. 1941. The comparative morphology of the Icacinaceae II. vessels. J. Arnold Arbor. 22: 171–187.

BATESON, W. 1894. Materials for the study of variation, treated with special regard to discontinuity in the origin of species.

BLOEMBERGEN, S. 1939. A revision of the genus *Alangium*. Bull. Jard. bot. Buitenz., Ser. III, 16: 139–235.

BÖCHER, T. W., K. HOLMAN & K. JAKOBSEN. 1968. The flora of Greenland.

BRAUN, H. J. 1970. Funktionelle Histologie der sekundären Sprossachse I. In: Handb. Pfl. Anat. 9(1). Das Holz.

BURBIDGE, N. T. & M. GRAY. 1970. Flora of the A.C.T.

CARLQUIST, S. 1962. A theory of paedomorphosis in dicotyledonous woods. Phytomorphology 12: 30–45.

CARLQUIST, S. 1975. Ecological strategies of xylem evolution.

CHAPMAN, J. D. & F. WHITE. 1970. The evergreen forests of Malawi.

COSTER, C. 1937. De verdamping van verschillende vegetatievormen op Java. Tectona 30: 1–124.

DICKISON, W. C. 1967. Comparative morphological studies in Dilleniaceae I. Wood anatomy, J. Arnold Arbor. 48: 1–23.

DINWOODIE, J. M. 1963. Variation in tracheid length in *Picea sitchensis* Carr. Forest Prod. special Report 16, D.S.I.R.

DONSELAAR, J. VAN. 1965. An ecological and phytogeographic study of Northern Surinam savannas. Wentia 14: 1–163.

EWART, A. J. 1930. Flora of Victoria.

FAYLE, D. C. F. 1968. Radial growth in tree roots. Fac. For. Toronto techn. Report 9.

GRAAFF, N. A. VAN DER & P. BAAS. 1974. Wood anatomical variation in relation to latitude and altitude. Blumea 22: 101–121.

GREGUSS, P. 1959. Holzanatomie der Europäischen Laubhölzer und Sträucher.

GUILLAUMET, J. L. 1967. Recherches sur la végetation et la flore de la région du bas-Cavally (Côte d'Ivoire). Mém. O.R.S.T.O.M. 20.

HAYATA, B. 1911. The vegetation of Mt. Fuji.

HEUKELS, H. & S. J. VAN OOSTSTROOM. 1975. Flora van Nederland.

HOOGLAND, R. D. 1951. Dilleniaceae. Fl. Mal. I, 4(1): 141–174.

HOOKER, J. D. 1847. The botany of the antarctic voyage I. Botany of Lord Auckland's group and Campbell's Island.

HUBER, B. 1956. Die Gefässleitung. *In*: W. Ruhland (ed.), Handb. Pfl. Physiol.: 541–582.

JACOBS, M. 1972. The plant world of Luzon's highest mountains. Rijksherbarium, Leiden, 32 pp.

JANSSONIUS, H. H. 1906–1936. Mikrographie des Holzes der auf Java vorkommenden Baumarten I–VI.

KANEHIRA, R. 1921. Anatomical characters and identification of Formosan woods, with critical remarks from the climatic point of view.

KOORDERS, S. H. 1918–1923. Flora von Tjibodas I–III.

KOSTERMANS, A. & P. TIDEMAN. 1948. Bosonderzoek kolonisatie object Momi-Ransiki Nieuw Guinea. Dienst Boswezen Indonesië, afd. Bosplanologie.

KRAMER, P. J. 1964. The role of water in wood formation. *In*: M. H. Zimmermann (ed.), The formation of wood in forest trees: 519–532.

LARSON, P. R. 1964. Some indirect effects of environment on wood formation. *In*: M. H. Zimmermann (ed.), The formation of wood in forest trees: 345–366.

LID, L. 1963. Norsk og Svensk Flora.

MABBERLEY, D. J. 1974. Pachycauly, vessel-elements, islands and the evolution of arborescence in 'herbaceous' families. New Phytol. 73: 977–984.

MERRILL, E. D. & M. L. MERRITT. 1909. The flora of Mount Pulog. Philipp. J. Sci., C (Bot.) 5: 287–403.

METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons.

MEIJER DREES, E. 1951. Distribution, ecology and silvicultural possibilities of the trees and shrubs from the savanna forest region in eastern Sumbawa and Timor. Communs For. Res. Inst., Bogor 33: 1–146.

MILLER, H. J. 1975. Anatomical characteristics of some woody plants of the Angmagssalik district of Southeast Greenland. Meddr Grønland 198(6): 1–30.

MILLER, R. B. 1975. Systematic anatomy of the xylem and comments on the relationships of Flacourtiaceae. J. Arnold Arbor. 56: 20–102.

MILLER, R. B. 1976. Wood anatomy of the species of *Juglans*. Bot. Gaz. (in the press).

MOORE, D. M. 1968. The vascular flora of the Falkland Islands. Br. Antarct. Surv. scient. Rep, 60.

NICHOLSON, D. I. 1965. A study of the virgin forest near Sandakan North Borneo. *In*: Symposium on ecological research in humid tropics vegetation (Kuching, 1963). Governm. Sarawak & Unesco Coöp. Office of S.E. Asia.

NOVRUZOVA, Z. A. 1968. [The water-conducting system of trees and shrubs in relation to ecology]. Izv. Akad. Nauk. Azerb. SSR, Baku, 230 pp.

OHWI, J. 1965. Flora of Japan.

OSTENFELD, C. H. & J. GRÓNTVED. 1934. The flora of Iceland and the Faeroes.

OZENDA, P. 1958. Flore du Sahara septentrional et central.

PHILIPSON, W. R. & B. G. BUTTERFIELD. 1967. A theory on the causes of size variation in wood elements. Phytomorphology 17: 155–159.

PHILIPSON, R. W., J. M. WARD & B. G. BUTTERFIELD. 1971. The vascular cambium. Its development and activity.

POORE, M. E. D. 1968. Studies in Malaysian rain forest I. The forest on triassic sediments in Jengka forest reserve. J. Ecol. 56: 143–196.

REYES, L. J. 1938. Philippine woods. Commonw. Philipp. Dept. Agric. Commerce, Tech. Bull. 7.

RICHARDSON, S. D. 1964. The external environment and tracheid size in conifers. *In*: M. H. Zimmerman (ed.), The formation of wood in forest trees: 367–388.

RØNNING, O. I. 1964. Svalbards Flora.

SANIO, K. 1872. Über die Grösse der Holzzellen bei der gemeinen Kiefer (*Pinus sylvestris*). Jb. wiss. Bot. 8: 401–420.

SCHULZ, J. P. 1960. Ecological studies on rain forest in Northern Suriname. Verh. K. Ned. Akad. Wet., Afd. Natuurk. 53(1): 1–267.

SLEUMER, H. 1954. Flacourtiaceae. Fl. Mal. I, 5(1): 1–106.

SLEUMER, H. 1968. Die Gattung *Escallonia* (Saxifragaceae). Verh. K. Ned. Akad. Wet., Afd. Natuurk. 58(2): 1–146.

SLEUMER, H. 1971. Icacinaceae. Fl. Mal. I, 7(1): 1–87.

SLEUMER, H. (in preparation). A monograph of Neotropical Flacourtiaceae. *In*: Flora Neotropica.

SOLEREDER, H. 1899, 1908. Systematische Anatomie der Dicotyledonen (und Ergänzungsband).

SPECHT, R. L. & C. P. MOUNTFORD. 1958. Records of the American–Australian scientific expedition in Arnhem land 3: 185–325.

STEENIS, C. G. G. J. VAN. 1969. Plant speciation in Malesia, with special reference to the theory of non-adaptive saltatory evolution. Biol. J. Linn. Soc. 1: 97–133.

STEENIS, C. G. G. J. VAN. 1976. Autonomous evolution in plants. Differences in plant and animal evolution. Gdns' Bull., Singapore (in the press).

STERN, W. L. 1974. Comparative anatomy and systematics of woody Saxifragaceae. *Escallonia*. Bot. J. Linn. Soc. 68: 1–20.

STERN, W. L., E. M. SWEITZER & R. E. PHIPPS. 1970. Comparative anatomy and systematics of woody Saxifragaceae. *Ribes*. *In*: N. K. B. Robson, D. F. Cutler & M. Gregory (eds.), New Research in Plant Anatomy., Bot. J. Linn. Soc. 63, Suppl. 1: 215–237.

STOCKER, O. 1956. Die Abhängigkeit der Transpiration von den Umweltfaktoren. *In*: W. Ruhland (ed.), Handbuch der Pflanzenphysiologie 3: 436–488.

SÜSS, H. & W. R. MÜLLER-STOLL. 1973. Zur Anatomie des Ast-, Stamm- und Wurzelholzes von *Platanus* x *acerifolia* (Ait.). Willd. Öst. bot. Z. 121: 227–249.

VERSTEEGH, C. 1968. An anatomical study of some woody plants in the mountain flora in the tropics (Indonesia). Acta bot. neerl. 17: 151–159.

VIROT, R. 1975. Epacridaceae. Flore de la Nouvelle Calédonie et dépendances 6.

WADE, L. K. & D. N. MCVEAN. 1969. Mt. Wilhelm studies I. The alpine and subalpine vegetation. Res. school Pacific studies. Dept. Biography and Geomorphology Publ. BG/1.

WEBER, H. 1969. Zur natürlichen Vegetationsgliederung von Südamerika. *In*: E. J. Fittkau, J. Illies, H. Klinge, G. H. Schwabe & H. Sioli (eds.), Biogeography and ecology in South America II: 475–518.

ZEEUW, C. DE. 1965. Variability in wood. *In*: W. A. Côté (ed.), Cellular ultrastructure of woody plants: 457–471.

ZIMMERMANN, M. H. & C. L. BROWN. 1971. Trees. Structure and Function.