AN ANATOMICAL STUDY OF SOME WOODY PLANTS OF THE MOUNTAIN FLORA IN THE TROPICS (INDONESIA)

CHR. VERSTEEGH

Laboratorium voor Plantkunde, Wageningen.

SUMMARY

An anatomical investigation of 68 wood species, mainly from the mountains of Indonesia, was made. The mountain species show less specialized characters viz. tracheids and/or scalariform perforations are common, whereas in the lowland species tracheids are usually replaced by woodfibres and scalariform perforations are completely wanting. A correlation with taxonomical classification is absent. The possibility is considered that these characters have a relation to ecological circumstances.

1. INTRODUCTION

During the past five decades, anatomists have established "trends of evolution" in the structures of the plant stele. These trends were established mainly on anatomical investigations of woods of temperate regions as well as economically more or less important tropical species from the lowlands. With regard to wood anatomy some of these lines of structural evolution may be summarized briefly as follows: 1. Vessel elements with a scalariform perforation plate are more primitive than elements with a simple perforation plate; 2. Microporous vessels preceded the macroporous vessels; 3. Evolution has proceeded from tracheids to fibre-tracheids to wood fibres; 4. The diffuse arrangement of wood parenchyma cells is to be considered more primitive than the banded apotracheal and the paratracheal types; 5. Heterogeneous wood-rays are more primitive than homogeneous wood-rays.

The work of BAILEY & TUPPER (1918) and FROST (1930a, b) indicated that e.g. the type of perforation plate on the vessel members is a very strong phyletic character. "There is no evidence that this character is readily modified by changes in the environment" (TIPPO 1938). On the other hand it is well known that anatomical characters may vary between closely allied taxa (METCALFE & CHALK 1950).

On the other hand CHALK (1962) points out that some of the more obvious differences between woods, such as the occurrence of the above mentioned simple or scalariform perforation plates, represent only different degrees of specialisation and may have nothing to do with phylogenetic affinity.

In view of these facts an investigation was made of anatomical characteristics of the secondary xylem of Angiosperms occurring in the mountain areas of Indonesia. Only those samples were examined of which locality was exactly known or could be traced, a.o. with the aid of KOORDERS & VALETON (1894–1914).

2. MATERIALS AND METHODS

Wood samples were obtained from the following institutes:

- The Royal Tropical Institute, Amsterdam, nrs. 5, 7, 8, 42, 47, 53, 67, 68.
- Rijksherbarium, Leiden, nrs. 3, 17, 23, 52.
- Forest Utilization of the Agricultural University, Wageningen, nrs. 1, 6, 11, 13, 21, 22, 26, 29, 30, 31, 33, 34, 35, 36, 38, 39, 40, 43, 46, 48, 49, 51, 54, 58, 59, 61, 63.
- Laboratorium voor Plantkunde of the Agricultural University, Wageningen, nrs. 10, 14, 15, 16, 18, 19, 20, 24, 25, 27, 28, 32, 37, 50, 57, 60, 62, 64, 66.

(Numbers in table 1 provided with an asterisk are not investigated, but taken from MOLL & JANSSONIUS 1906–1936).

The wood samples were boiled for several hours, or subjected to formalin-alcohol, to make them softer. A few species with great difference in hardness of the xylem elements, were embedded in polyaethylene-glycol, before sliding them. Traverse, tangential and radial sections, varying from 15–20 microns, were made with a sliding microtome. Some sections were stained with Haemalaun (JOHANSEN 1940): maceration slides were made according to Jeffry (JOHANSEN 1940). All the sections were embedded in Kaiser's gelatineglycerine after treatment (JOHANSEN 1940).

For our research of the occurrence of tracheids in tropical wood species we have used the definition of tracheids, as explained in the "International Glossary of terms in Wood Anatomy" (1957). Thus xylem elements with large bordered pits on the radial walls only, are also to be considered as tracheids.

3. RESULTS

The results are given in *table 1*. The species investigated, are arranged alphabetically into families, which themselves are also arranged in an alphabetic order.

4. DISCUSSION

In tropical Asia, some families of the Angiosperms happen to be found in the mountainous regions only, e.g. like: *Theaceae*, *Winteraceae*, *Ericaceae*, *Hamamelidaceae*, *Cunoniaceae*, *Fagaceae* and *Myricaceae*. All these families possess tracheids, scalariform perforations of the vessels etc., characters occurring in the less specialized plants (CHALK 1962).

The *Araliaceae*, *Apocynaceae*, *Boraginaceae*, *Sapindaceae* and *Lauraceae*, belong, ıegarding to wood characteristics, usually to the rather highly developed plants. They grow mainly at lower altitudes. The axial system usually consists of wood fibres. Moreover paratracheal parenchyma and metatracheal parenchyma often occur, while the perforations of the vessels are round. The species of the *Araliaceae* occurring in the mountainous areas, like *Macropanax dispermum* (4) and *Schefflera elliptica* (5), however, have scalariform vessel perforations. The *Boraginaceae* are usually to be found in the plains at low altitude; they have an axial system, composed of wood fibres; the vessel perforations are not scalariform but round. *Ehretia acuminata* var. *pyrifolia* (8) however, possesses an axial system of both wood fibres and tracheids; it grows at a higher altitude in the mountain areas.

Dodonaea viscosa (54) occurs from 1–2000 meter above sea-level; it possesses all the characteristics of the higher developed plants, but it still has scalariform perforations of the vessels. At sea-level this tree is very small, whereas it becomes very tall in mountainous regions. So in fact it appears to be a species of the mountains. We have investigated a wood sample out of the Anggi lakes (West Nw. Guinea), 1750 meter above sea-level. In a maceration slide the elongated ends of the vessels (tails) and some scalariform perforations are to be seen.

In contrast with most of the *Apocynaceae*, which belong to the higher developed wood-species as far as the xylem is concerned and thus possessing an axial system consisting of wood fibres, *Rauwolfia reflexa* (2), a mountain species, has an axial system consisting of tracheids only.

Also the *Lauraceae*, usually growing rather low in the mountain areas, are highly developed with an axial system of wood fibres, whereas in all the mountain species, like *Actinodaphne procera* (31), *Lindera polyantha* (34), *Litsea mappacea* (38), *Litsea cassiaefolia* (35), *Cinnamomum sintok* (33), *Phoebe grandis* (40) and *Persea rimosa* (39), we come upon vessels with scalariform perforations which never occur in the species of the low-lying plains.

Thus *Litsea mappacea* (38) and *Litsea cassiaefolia* (35), two mountain species, possess an axial system of wood fibres, in which vessels with scalariform perforations are to be found, whereas the xylem of *Litsea glutinosa* (37) and *Litsea firma* (36), two species of the plains, also possess an axial system of wood fibres, but scalariform perforations of the vessels are lacking. In addition the mountain species *Cinnamomum sintok* (33) and the plain species *Cinnamomum culilawan* (32), were compared with each other. *Cinnamomum culilawan* has an axial system of wood fibres without scalariform vessel perforations, whereas

LEGENDS

+	= present
—	= absent
±	= questionable
½	= paratracheal parenchyma surrounding the vessels only parly
T	= tracheids, vascular tracheids or fibre tracheids
WF	= wood fibre (libriform)
MeP	= megapor vessels, diameter more than 100 microns
MiP	= micropor vessels, diameter less than 100 microns
ScPV	= vessels with scalariform perforations
RPV	= vessels with round or oval perforations
PaPa	= paratracheal parenchyma
ApBa	= apotracheal banded
DiPa	= diffuse parenchyma
HeWR	= heterogeneous woodrays
HopWR	= homogeneous woodrays, composed of procumbent cells
HouWR	= homogeneous woodrays, composed of upright cells
*	= material described by Janssonius.

Table 1

	Altitude above sea-level in meters	T	WF	MeP	MIP	ScPV	RPV	PaPa	ApBa	DiPa	HeWR	HopWR	HouWR
ACTINIDIACEAE													
1. Saurauia umbellata K. & V.	1000–1800	+	–	–	+	+	–	½	–	+	–	–	+
APOCYNACEAE													
*2. Rauwolfia reflexa T. & B.	1300	+	–	–	+	–	+	–	–	+	+	–	–
ARALIACEAE													
3. Harmsiopanax aculeata Warb.	2940	–	+	–	+	+	+	–	–	+	+	–	–
*4. Macropanax dispermum O.K.	1750	–	+	–	+	+	+	½	–	+	+	–	–
5. Schefflera elliptica Harms	±1500	–	+	+	–	+	+	½	–	+	+	–	–
AQUIFOLIACEAE													
6. Ilex pleiobrachiata Loes.	1400–1700	+	–	–	+	+	±	–	–	+	+	–	–
7. Ilex versteeghii M. & P.	montane	+	–	–	+	+	±	–	–	+	+	–	–
BORAGINACEAE													
8. Ehretia acuminata R. Br. var. pyrifolia Johnst.	1150	+	+	+	+	–	+	½	–	+	–	+	–
CAPRIFOLIACEAE													
*9. Viburnum lutescens Bl.	1250	+	–	–	+	+	–	½	+	+	+	–	–
CASUARINACEAE													
10. Casuarina equisetifolia L.	0	+	–	+	–	+	+	–	+	–	–	+	–
11. Casuarina montana Lesch.	800–2700	+	–	–	+	+	+	–	+	–	–	+	–
CELASTRACEAE													
*12. Perrottetia alpestris Loes.	±1500	–	+	–	+	+	–	–	–	–	+	–	–
CORNACEAE													
13. Mastixia trichotoma Bl.	900–1500	+	–	–	+	+	–	–	–	+	+	–	–

CUNOCIACEAE													
14. Ceratopetalum succirubrum C.T. White	500	+	−	−	+	+	+	−	+	−	−	+	−
15. Schizomeria serrata Hochr.	montane	−	+	+	+	+	+	−	−	+	+	−	−
16. Weinmannia blumei Planch.	1000	+	−	−	+	+	−	½	−	+	+	−	−
DAPHNIPHYLLACEAE													
17. Daphniphyllum spec.	3380	+	−	−	+	+	−	−	−	−	+	−	−
ERICACEAE													
18. Rhododendron laetum Sleum.	1800–2300	+	−	−	+	+	−	½	−	+	+	−	−
19. Rhododendron leucogigas Sleum.	±1200	+	−	−	+	+	−	½	−	+	+	−	−
20. Rhododendron zoelleri Warb.	1500–2000	+	−	−	+	+	−	½	−	+	+	−	−
21. Vaccinium latissimum J.J.S.	600–1500	+	±	−	+	+	+	−	−	+	+	−	−
22. Vaccinium varingiifolium Miq.	600–1500	+	±	−	+	+	−	−	−	+	+	−	−
EUPHORBIACEAE													
23. Claoxylon spec.	3000	−	+	+	+	+	+	−	−	+	+	−	−
FAGACEAE													
24. Castanopsis acuminatissima A. DC.	800	+	+	+	−	−	+	½	+	+	+	−	−
25. Lithocarpus molucca Hats.	±100	+	+	+	−	−	+	½	+	+	−	+	−
26. Nothofagus? rubra v. Steen.	±2000	−	+	+	+	−	+	−	+	+	+	−	−
27. Trigonobalanus verticellata Form.	1700	+	−	+	−	−	+	½	+	+	+	−	−
HAMAMELIDACEAE													
28. Altingia excelsa Noronha	±1200	+	−	−	+	+	−	−	−	+	+	−	−
29. Distyllum stellare O.K.	1000–2250	+	−	−	+	+	−	−	+	+	+	−	−
ICACINACEAE													
30. Platea latifolia Bl.	1000–1600	+	−	−	+	+	−	−	−	+	+	−	−
LAURACEAE													
31. Actinodaphne procera Nees.	1000	−	+	+	+	+	−	½	−	+	−	+	−
32. Cinnamomum culilawan Bl.	150	−	+	+	−	−	+	½	−	+	−	+	−
33. Cinnamomum sintok Bl.	700–1700	−	+	+	−	+	+	½	−	+	+	−	−
34. Lindera polyantha Boerl.	1500	−	+	+	−	+	+	½	−	+	+	−	−
35. Litsea cassiaefolia Bl.	±3000	−	+	−	+	+	+	½	−	−	+	−	−

	Altitude above sea-level in meters	T	WF	MeP	MiP	ScPV	RPV	PaPa	ApBa	DiPa	HeWR	HoPWR	HouWR
36. Litsea firma Hook. f.	210	−	+	+	−	−	+	½	−	−	+	−	−
37. Litsea glutinosa Hook. f.	50	−	+	+	−	−	+	½	−	−	+	−	−
38. Litsea mappacea Boerl.	1250–2000	−	+	+	−	+	+	½	−	+	−	+	−
39. Persea rimosa Kosterm.	1000	−	+	−	+	+	+	+	−	−	−	−	−
40. Phoebe grandis Merr.	110	−	+	−	+	+	+	½	−	+	+	−	−
MONIMIACEAE													
*41. Kibara coriacea Endl.	1000	−	+	−	+	+	+	½	−	+	+	−	−
MYRICACEAE													
42. Myrica javanica Reinw.	1500–3000	+	−	+	+	+	+	½	−	+	+	−	−
43. Myrica longifolia T. & B.	montane	+	−	−	+	+	+	½	−	+	+	−	−
MYRSINACEAE													
*44. Ardisia macrophylla Reinw.	900	−	+	−	+	+	+	½	−	+	+	−	−
*45. Ardisia marginata Bl.	1800	−	+	−	+	+	+	½	−	+	+	−	−
46. Maesa latifolia DC.	1000	−	+	−	+	+	+	½	−	+	+	−	−
47. Myrsine avenis DC.	1300–3000	−	+	−	+	+	+	½	−	+	+	−	−
MYRTACEAE													
48. Baeckea frutescens L.	±1500	+	−	−	+	−	+	½	+	+	+	−	−
49. Leptospermum flavescens J.E.Sm.	2000	+	−	+	−	−	+	½	−	+	+	−	−
50. Rhodamnia cinerea Jack.	±1200	+	−	+	−	−	+	½	+	+	+	−	−
NYSSACEAE													
51. Nyssa javanica Wang.	±1000	+	−	+	−	+	−	−	−	+	+	−	−
RUBIACEAE													
52. Amaracarpus spec.	3100	−	+	−	+	+	−	½	−	+	+	−	−
SABIACEAE													
53. Meliosma ferruginea Bl.	900	−	+	+	−	+	−	+	−	+	+	−	−

SAPINDACEAE													
54. Dodonaea viscosa Jack.	1750	−	+	−	+	−	+	½	−	−	−	+	−
SAXIFRAGACEAE													
55. Dichroa sylvatica Merr.	1500	−	+	−	+	+	+	½	−	+	+	−	−
56. Hydrangea paniculata Sieb.	montane	+	−	−	+	+	−	−	−	+	+	−	−
57. Itea macrophylla Wall.	600–1800	+	−	−	+	+	−	−	−	+	+	−	−
58. Polyosma integrifolia Bl.	1300	−	+	−	+	+	−	−	−	+	+	−	−
STAPHYLEACEA													
59. Turpinia sphaerocarpa Hassk.	1500	+	−	+	−	+	−	½	−	+	+	−	−
STYRACACEAE													
60. Bruinsmia styracoides Boerl. & Kds.	1100	+	−	+	−	+	−	½	−	+	+	−	−
SYMPLOCACEAE													
61. Symplocos spicata Roxb.	1300–2000	+	−	−	+	+	−	½	−	+	+	−	−
62. Symplocos spec.	montane	+	−	−	+	+	−	½	−	+	+	−	−
TERNSTROEMIACEAE													
63. Ternstroemia penangiana Chois.	1000	+	−	+	+	+	−	−	−	+	+	−	−
THEACEAE													
64. Gordonia papuana Kob.	1100	+	−	−	+	+	−	½	−	+	+	−	−
*65. Pyrenaria bracteosa DC.	1000	+	−	−	+	+	−	−	−	+	+	−	−
66. Pyrenaria serrata Bl.	1600	+	−	−	+	+	−	−	−	+	+	−	−
TRIMENIACEAE													
67. Trimenia spec.	montane	−	+	−	+	+	+	−	−	+	+	−	−
WINTERACEAE													
68. Drimys piperita Hook. f.	montane	+	−	−	−	−	−	−	−	+	+	−	−

Cinnamomum sintok has an axial system of wood fibres with scalariform vessel perforations.

Baeckea frutescens (48) is to be found from sea-level up to an altitude of 2400 meter. This species is also to be considered as a mountain species as it remains only a low shrub at sea-level, whereas it becomes a tall tree in the mountain areas. In the *Myrtaceae* of the low-lying plains, the axial system consists either of wood fibres or of tracheids, but in the mountain species only tracheids are to be found.

All the *Casuarina* species possess tracheids, but when we compare *Casuarina montana* (11), a mountain species, with *Casuarina equisetifolia* (10), a species of the plains, it appears, that *C. montana* possesses predominantly scalariform vessel perforations, whereas the latter only occasionally occur in *C. equisetifolia* (MOLL & JANSSONIUS 1906–1936).

Though the present investigation is far from complete, as no material could be obtained of many species of the mountain areas, it is evident, that at least the wood of the examined mountain species, but possibly of all species in the mountain areas, possesses one or more "less specialized" anatomical characteristics – in the sense of CHALK (1962) – even when the species is regarded to belong to a "highly developed" taxon.

Based on the characters given by CHALK (1962) it appears that 83% of the 303 European Angiospermous species investigated by GREGUSS (1959), must be considered to be less specialized. In this connection it is mentioned that Gymnosperms are to be seen as primitive plants as compared to Angiosperms and consequently possess primitive characters. This applies to the Gymnosperms of both the tropical and the temperate zones. It is remarkable that Gymnosperms in the tropics occur almost exclusively in the mountain regions, though there are some exceptions like *Agathis borneensis* and *Dacrydium elatum*, species occurring at sea level. However, in those cases the species is to be found on sandy soils, often with a hard and impenetrable "padas"-layer at a depth of 1½–2 m, *i.e.* the species grows on a dry soil. In the temperate regions Gymnosperms are also found either at higher altitude or at lower altitude on soils with a low water capacity.

As evaporation and transpiration in the mountain area are less than in the low-lands (COSTER 1937) and consequently water transport is less intensive, the vessels of the former mostly are smaller than those of the latter. The same holds for plants of dry soils.

Data presented here indicate that there is a correlation between wood structure and environment. Therefore it is necessary when describing a wood specimen to give as much information on the habitat as possible, since deviation from the "normal" histology of the secondary xylem may reflect adaptation to an extreme habitat. The investigations are in progress.

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