A COMPARISON OF THE ECOLOGICAL WOOD ANATOMY OF THE FLORAS OF SOUTHERN CALIFORNIA AND ISRAEL

by

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Summary
A comparison is made between ecological trends in wood anatomy found in southern California and Israel and adjacent regions. Trends for type of vessel perforation, vessel member length and the occurrence of helical thickenings show striking parallels. Characters like vessel diameter and frequency and incidence of (fibre-)tracheids show only weakly similar trends. Vessel grouping and ring-porosity do not show any parallel in the data for southern California and Israel. The differences between the two floras can largely be attributed to different floristic composition and the alternative possibilities for safe and efficient xylem sap transport and drought resistance in different taxa.

Key words: Ecological wood anatomy, vessels, fibres, tracheids, desert shrubs, halophytes, chaparral, riparian species.

Introduction
The ecological trends in wood anatomy of the trees and shrubs from southern California and Israel and adjacent regions (Carlquist & Hoekman, 1985; Baas et al., 1983; Fahn et al., 1985) lend themselves well for comparison. Both regions harbour various desert vegetation and sclerophyllous maquis or chaparral as well as riparian trees and shrubs. The different floristic compositions of the two regions makes a comparison all the more interesting, because the existence of parallel trends would eliminate the influence of the floristic composition, which always weakens the general validity of conclusions in studies confined to one region.

Both the wood anatomical terminology and the plant ecological conventions of the independent studies cited above differ widely, however, and emphases have been put on different aspects, so that the results for the two regions are not easily comparable. Partly this is due to differences of opinion by the respective authors, partly it is inherent in individuality of any comparative or descriptive study carried out by different people. Without resolving any disagreements at this stage, we consider it appropriate to compare our data directly, so that the interpretative parts of both studies can be tested for their general validity.

Definition of tracheids and fibre types
Carlquist and Hoekman (1985) define tracheids in such a way that they include all fibrous elements designated as fibre-tracheids by Fahn et al. (1985). In the latter study an extended version of the IAWA glossary of terms (1964) for fibre-tracheids was followed, identical to the one advocated by Baas (1985) and similar to the characterisation given for 'fibres with distinctly bordered pits' in the explanatory notes of the IAWA Standard List of Wood Anatomical Characters suitable for Computerized Hardwood Identification (Miller, 1982). With perhaps few exceptions this renders the 'true tracheids' sensu Carlquist (1984) and Carlquist and Hoekman (1985) synonymous with the 'fibre-tracheids' sensu Baas (1985) and Fahn et al. (1985); in this study the term fibre-tracheids was avoided in the descriptions but used in the ecological comparisons for fibres with numerous and distinctly bordered pits in both the radial and tangential walls).

Vasicentric tracheids in the definition of Carlquist (1985) and Carlquist and Hoekman (1985) include all the imperforate trachey elements intermingled with vessels designated as 'vascular tracheids intergrading with very narrow vessels' by Fahn et al. (1985). Moreover it includes the vasicentric tracheids in the IAWA glossary such as occur in Quercus. The category of vascular tracheids, defined on a topographic criterion by Carlquist (1985) was not recognised as a separate category by Fahn et al. (1985). In the ecological comparisons Baas et al. (1983) and Fahn et al. (1985) did not emphasise the occurrence of vascular or vasicentric tracheids, but the syndrome of two vessel size classes with which it is usually associated.
Table 1. Comparison of some ecological trends in the wood anatomy of the floras of southern California and Israel and adjacent regions.

<table>
<thead>
<tr>
<th>Wood anatomical character</th>
<th>California</th>
<th>Desert scrub</th>
<th>Desert wash</th>
<th>Halophytes</th>
<th>Chaparral</th>
<th>Riparian</th>
</tr>
</thead>
<tbody>
<tr>
<td>Equivalent in Israel</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vessel diameter (µm)¹</td>
<td>C</td>
<td>26</td>
<td>42</td>
<td>29</td>
<td>29</td>
<td>51 (56)</td>
</tr>
<tr>
<td></td>
<td>I*</td>
<td>71</td>
<td>110</td>
<td>53</td>
<td>75</td>
<td>83</td>
</tr>
<tr>
<td>Vessel frequency² (N × mm⁻²)</td>
<td>C</td>
<td>360</td>
<td>148</td>
<td>158</td>
<td>299</td>
<td>163 (249)</td>
</tr>
<tr>
<td></td>
<td>I*</td>
<td>113</td>
<td>53</td>
<td>92</td>
<td>159</td>
<td>65</td>
</tr>
<tr>
<td>Vessel member length (µm)</td>
<td>C</td>
<td>190</td>
<td>185</td>
<td>100</td>
<td>261</td>
<td>418 (324)</td>
</tr>
<tr>
<td></td>
<td>I*</td>
<td>201</td>
<td>170</td>
<td>121</td>
<td>265</td>
<td>308</td>
</tr>
<tr>
<td>Ring-porous or semi-ring-porous (% of species)³</td>
<td>C</td>
<td>90 (70)</td>
<td>82 (50)</td>
<td>50 (50)</td>
<td>98 (29)</td>
<td>100 (13)</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>38</td>
<td>10</td>
<td>11</td>
<td>63</td>
<td>58</td>
</tr>
<tr>
<td>Scalariform perforations (% of species)</td>
<td>C</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>13</td>
</tr>
<tr>
<td>Vasicentric and/or vascular tracheids (% of species)⁴</td>
<td>C</td>
<td>41</td>
<td>33</td>
<td>0</td>
<td>64</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>71</td>
<td>28</td>
<td>74</td>
<td>47</td>
<td>8</td>
</tr>
<tr>
<td>'True tracheids' or fibre-tracheids (% of species)⁵</td>
<td>C</td>
<td>40</td>
<td>12</td>
<td>0</td>
<td>24</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>31</td>
<td>3</td>
<td>8</td>
<td>32</td>
<td>8</td>
</tr>
<tr>
<td>Helical sculpturing (% of species)</td>
<td>C</td>
<td>29</td>
<td>0</td>
<td>25</td>
<td>56</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>36</td>
<td>13</td>
<td>8</td>
<td>53</td>
<td>17</td>
</tr>
<tr>
<td>Vessel grouping⁶ (see legend)</td>
<td>C</td>
<td>2.62 (26%)</td>
<td>3.61 (18%)</td>
<td>2.6 (25%)</td>
<td>4.76 (41%)</td>
<td>1.77 (0%)</td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>45%</td>
<td>33%</td>
<td>53%</td>
<td>28%</td>
<td>8%</td>
</tr>
</tbody>
</table>

C = data for southern California from Carlquist & Hoekman (1985) for trees and shrubs. Data for riparian *shrubs only, between brackets.

I = data for Israel from Fahn et al. (1985) and Baas et al. (1983) for trees and shrubs. * = data for shrubs only.

¹ Average inside vessel diameter for Californian trees and shrubs (data for shrubs only between brackets); maximum vessel diameter averaged for the individual florulas minus twice the average vessel wall thickness for shrubs from Israel.

² Total vessel number per sq.mm for California; number of distinct vessels per sq.mm as seen in transverse section for Israel (all distinct vessels in a multiple or clusters counted as individual vessels).

³ Percentage of ring-porous and semi-ring-porous species; between brackets the percentage of species with distinctly ring-porous wood.

⁴ Includes all types of non-ground tissue tracheids, irrespective of definition: vasicentric and vascular tracheids sensu Carlquist & Hoekman (1985) as well as sensu IAWA Committee (1964).

⁵ See text for definitions of 'true tracheids' or fibre-tracheids.

⁶ Average number of vessels per multiple followed by the percentage of species with an average of more than 3.0 vessels per group between brackets for California; percentage of species with over 80% of the vessels in multiples for Israel.
Methods

Data on vessel diameter, vessel grouping and vessel frequency were derived in different ways in the two studies. Carlquist and Hoekman (1985) gave average inside vessel diameter; Baas et al. (1983) and Fahn et al. (1985) only gave full ranges of vessel diameter and used maximum vessel diameter in the ecological comparisons, because the wider vessels have a disproportionately great part in sap conduction due to the Hagen-Poiseille relationship between conductivity and the fourth power of the vessel radius. Moreover, not enough measurements were carried out to calculate a meaningful average; such average values would anyway have little functional significance in the large proportion of woody plants in Israel with two vessel size classes. Precise data on average vessel diameter and density of all vessels as provided by Carlquist and Hoekman (1985) are necessary to compute mesomorphy and vulnerability indices, which were not given for the florulas in Israel and its adjacent areas.

Vessel grouping was expressed as average number of vessels per pore group by Carlquist and Hoekman (1985), while Baas et al. (1983) and Fahn et al. (1985) gave less precise indications of vessel grouping by calculating the percentages of solitary vessels and of vessels in multiples.

Comparisons

In Table 1 a number of selected wood anatomical characters which play an important part in the discussions of ecophylectic and functional aspects in Baas et al. (1983), Fahn et al. (1985) and Carlquist and Hoekman (1985) are compared for similar ecological categories in southern California and Israel. Only part of the ecological categories discussed in the two studies have been included, because others are not represented by enough taxa in one of the regions or are not quite comparable. The category of halophytes has been included, despite the fact that from southern California only four species of halophytes are listed. In the woody flora of Israel and adjacent regions halophytes form a major component and represent the most xeric extreme in the flora.

Data for southern California are derived from tables 1–3 in Carlquist and Hoekman (1985); data for the Middle East are from tables 5.1 to 5.5 as well as from the specific descriptions in Fahn et al. (1985). Note should be taken of the fact that in this paper desert categories are combined in a different manner than in Baas et al. (1983) and Fahn et al. (1985). This was done to increase the comparability with the ecological groups recognised by Carlquist and Hoekman (1985).

Trends for average vessel diameter in southern California show only a limited similarity with those for maximum vessel diameter (averaged for florulas) for shrubs in Israel. In southern California the riparian species have the highest values, while in Israel the shrubs from desert wadis have the widest vessels. Both regions have in common that chaparral and desert scrub show little difference in vessel diameter. The category of halophytes has the narrowest vessels in the flora of Israel, while in California this position is taken by the desert scrub elements. Data for both florulas support the generalisation that vessels of xeric species tend to be narrowest. Yet differences in maximum vessel diameter give another pattern than differences in average diameter for the hydrophyllc and desert wash (= wadis) category. Such differences also exist in comparisons by Barajas-Morales (1985) of tropical rainforest and dry deciduous forest, where vessels are on average much narrower in the dry forest trees, and by Baas et al. (1983) of maximum vessel diameter data for the rainforests and monsoon forests of Java, where the latter showed the highest values.

For functionally relevant information on vessel diameter, the data in both studies are probably insufficient: frequency distributions of all diameter classes would be more meaningful, but are cumbersome to acquire, especially for a large number of species.

Vessel frequency values differ widely in all categories, due to the different counting methods employed. Perhaps differences in stem diameter have also played a role in the differences (some species had to be represented by herbarium twigs in the study by Carlquist and Hoekman, 1985). Yet there is a parallel in that vessels are most numerous in the xeric categories of chaparral and desert shrubs (with extremes in the halophytes of Israel and in the desert scrub of southern California) and least numerous in wadis and riparian situations (the small number of halophytes from southern California renders the average value for vessel frequency rather insignificant).

Vessel member length shows a perfect parallel in both florulas: in the sequence riparian – chaparral – desert scrub – desert wash – halophytes there is a consistent decline in average vessel element length. With the exception of the desert wash category being intercalated between the more arid desert scrub and halophytic flora, this sequence represents a mesic-xeric gradient.

Scalariform perforations are in both regions confined to the least arid categories of chaparral and riparian species. In the former vegeta-
tion type which is subjected to prolonged dry seasons, scalariform perforations are moreover exceedingly rare.

Ring-porous tendencies differ very much in the different regions. Not only in absolute figures, but also in mesic-xeric tendencies the floras have nothing in common. Especially the desert wash vegetation shows opposing trends: it has a high proportion of species with ring-porous or semi-ring-porous wood in southern California, while in Israel it ranks lowest in ring-porous tendencies.

Similarly, the occurrence of vasicentric and vascular tracheids (irrespective of the definitions employed, the combined categories in the studies by Carlquist and Hoekman and Fahn et al. are synonymous!) shows different ecological trends, except for the low incidence of these elements in riparian trees and shrubs in both regions and their intermediate frequency in desert wash or wadi elements.

‘Tracheids’ or ‘fibre-tracheids’ show some differences in their incidence of the comparable vegetation types in Israel and southern California, but show similar tendencies in other respects: both regions share a fairly high incidence of fibres with distinctly bordered pits in the desert scrub and chaparral.

Helical sculpturing, on the other hand, shows striking parallels in both regions: chaparral ranks highest, followed by desert scrub and riparian species; halophytes and desert wash rank lowest.

Vessel grouping is expressed in such different ways for the two floras that a comparison is difficult to make. To increase comparability in Table 1, also the percentage of species with an average of 3.0 or higher for number of vessel per multiple has been given for southern California to have some way to compare them with data by Fahn et al. (1985) on the percentage of species with over 80% of their vessels in multiples. High degrees of vessel grouping occur in the chaparral of southern California and in the halophytes and desert scrub of Israel. The chaparral or maquis of Israel ranks only fourth in vessel grouping. Both regions share a minimum degree of vessel grouping in the riparian category.

Discussion

As emphasised by Carlquist and Hoekman (1985), there are many alternative ways for a plant to survive in situations of water stress. A safe, yet sufficiently efficient hydraulic architecture is only one of the syndromes integrated with different adaptations in leaf structure and phenology, root systems, photosynthetic and metabolic pathways, etc. Even hydraulic safety and efficiency per unit volume of sapwood can be achieved in various ways. Keeping these alternative strategies in mind, it can hardly be expected that all the characters of Table 1 would show parallel trends in the woody floras of southern California and Israel and adjacent regions. Moreover, the ecological categories in both regions, although comparable, are far from identical in their environment throughout the year. Yet, there are parallels in some characters, especially in vessel member length, incidence of scalariform perforations and helical vessel wall sculpturing. Characters like vessel diameter and frequency, and incidence of (fibre-)tracheids show only partial parallels but also notable differences. In yet other characters the patterns seem even more incompatible.

Different floristic composition in combination with the limited ranges of variation within certain families (or put in other words: different possibilities of ecological xylem strategies of these families) are the main basis of these differences. In the data for the flora of Israel, the high number of tropical elements in the desert wadis as well as the high number of Chenopodaceae in drier desert types and in salt marshes heavily influenced the statistics for the various subtypes of desert vegetation (Fahn et al., 1985), while a high number of Rosaceae and Papilionoideae strongly influenced the data for the maquis or chaparral. In southern California woody Chenopodaceae are absent, but woody Compositae (Asteraceae) are much more numerous. All Chenopodaceae have vascular tracheids in a vasicentric position intergrading with very narrow vessels, while only a minority of woody Compositae show such tracheids. Rosaceae and Papilionoideae play about an equal part in the floras of both regions, but in southern California Rosaceae are equally well represented in the desert scrub and chaparral, while in Israel the family is largely restricted to the latter vegetation type.

If different trends in widely separated regions do not have to surprise us on account of available alternative strategies and different floristic compositions, the trends unaffected by floristic composition for vessel member length, scalariform perforations and helical sculpturing increase in their general validity as postulated in various previous studies (e.g., Carlquist, 1975; Baas, 1976). We are far removed from a consensus of opinion on the functional significance of vessel member length and helical sculpturing. The elimination of scalariform perforations from all vegetation types except those from temperate to subtropical mesic biotopes and cold temperate to arctic or tropical alpine regions can satisfactorily be explained.
in terms of decreased resistance to flow, while their retention in frost-prone areas may be advantageous to prohibit the spreading of embolisms and consequently favour their dissolution at a later stage.

Although approached in different ways both studies on the ecological wood anatomy of trees and shrubs from southern California and Israel and adjacent regions show interesting adaptations to safe and efficient water transport. Experimental studies will have to shed light on the roles of tracheids of various kinds, helical sculpturing and different vessel size classes (for the latter see important results by Ellmore and Ewers, 1985, reported in this issue). For the controversial issue of element length, we should perhaps not only consider the possible functional significance of fully differentiated xylem elements of a given length, but also the dynamics of cambial multiplicative and additive divisions in combination with loss of initials (cf. Berlyn, 1982), and the possible advantage of short initials in extreme (dry or cold) environments.

References

— 1985. Vasicentric tracheids as a drought survival mechanism in the woody flora of southern California and similar regions; review of vasicentric tracheids. Also 11: 37–68.