LACK OF LATITUDINAL TRENDS IN WOOD ANATOMY OF *Dodonaea viscosa* (Sapindaceae), a species with a worldwide distribution

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Latitudinal or altitudinal variation in several anatomical characters of wood is common for woody dicotyledonous genera with a wide distribution, but whether such variation exists at the species level is disputed. Latitudinal and altitudinal trends in wood anatomy of *Dodonaea viscosa* were studied, using 102 samples collected between 41.2° S and 33.3° N latitude and 7–2750 m altitude. We studied variation in four quantitative features: vessel element length, fiber length, vessel frequency, and tangential vessel diameter. Ontogenetic trends were minimal with a slight decrease or increase in the innermost stem and were negligible among the studied specimens. Throughout the distributional range of the species, no latitudinal trends were detected in either the Northern or Southern Hemispheres. Altitudinal trends were also nonexistent, except for two features in specimens from China and Japan. Absence of latitudinal or altitudinal trends in this widely distributed species suggests that in some species the species-level variation in wood anatomy is not controlled by ecological gradients.

**Key words:** altitude; *Dodonaea viscosa*; ecological wood anatomy; latitude; Sapindaceae; species-level trends.

Among woody dicotyledons, quantitative features of wood structure vary along latitudinal or altitudinal gradients differently within a genus and within a species. Within genera with a wide latitudinal distribution, such as *Hex* (Baas, 1973), *Symplocos* (van den Oever et al., 1981), and *Cornus* (Noshiro and Baas, 1998, 2000), latitudinal trends in several anatomical characters of wood are manifest, and features such as vessel element or fiber lengths halve from the equator to 40° latitude. Within genera with a wide altitudinal distribution, such as *Symplocos* (van den Oever et al., 1981) and *Rhododendron* (Noshiro et al., 1995), several anatomical characters of wood are significantly correlated with altitude. Within species, on the contrary, latitudinal or altitudinal trends in wood structure were not detected in the seven species studied by van der Graaff and Baas (1974), *Metrosideros polymorpha* Gaud. in Hawaii, USA (Sastrapradja and Lamoureux, 1969), or three Japanese *Cornus* species (Noshiro and Baas, 2000). However, significant latitudinal or altitudinal trends have been detected in a few species, e.g., *Acacia melanoxylon* R. Br. from Australia (Wilkins and Papassotiriou, 1989), *Alnus nepalensis* D. Don (Noshiro et al., 1994), and four *Rhododendron* species (Noshiro and Suzuki, 1995) from Nepal. Thus, whether wood structure generally varies with latitude and altitude at the species level is questionable.

The variable results for the species-level variation probably derive from differences in sample size and statistical analyses. In the study of three *Cornus* species from Japan, Noshiro and Baas (2000) studied 54–124 specimens per species from specific distributional ranges and compared quantitative features of wood structure with latitude, altitude, tree size, and climatic factors. Although the three *Cornus* species varied greatly in the studied features throughout the latitudinal or altitudinal range of species, none of the nonanatomical factors were significantly correlated with the wood anatomical features. The three species ranged in distribution, however, up to 15° in latitude and mostly to 1500 m in altitude. Their range was less than the latitudinal range of 27° for *Acacia melanoxylon* (Wilkins and Papassotiriou, 1989) and the altitudinal range of 2000 m for *Alnus nepalensis* (Noshiro et al., 1994) and up to 2700 m for 4 *Rhododendron* species (Noshiro and Suzuki, 1995).

*Dodonaea viscosa* Jacq. sensu lato (s.l.), a treelet or shrub up to 8 m (occasionally to 20 m) high and 20 cm (occasionally to 40 cm) in diameter at breast height (DBH), has an exceptionally wide range of distribution between 44° S and 33° N latitude and from sea level to 3600 m altitude (Fig. 1; Leenhouts, 1983, 1994). Thus, this species seems to be an ideal taxon for investigating species-level trends in quantitative features of wood anatomy along wide latitudinal and altitudinal gradients.

Leenhouts (1983, 1994) regarded *Dodonaea viscosa* s.l. as consisting of *D. viscosa* sensu stricto confined to tropical coastal areas and *D. angustifolia* L. f. occurring in other areas. However, we used the wider species concept following the opinions of West (1984, 1985), Smith (1985), Liu et al. (1985), Wagner et al. (1990), and Davies and Verdcourt (1998). Also, most wood specimens are identified at a wider species concept. Wood anatomy of *D. viscosa* is described in regional atlases (for example, Kanehira, 1921; Rock, 1972; Patel, 1975; Neumann et al., 2001) as well as in systematic studies of the wood anatomy of Sapindaceae (Li et al., 1995; Klasssen, 1999). These studies used less than 10 specimens and did not consider within-species variation.

In this study we aimed at clarifying species-level trends in wood structure of *D. viscosa* using a large number of wood specimens to cover the distributional range of this species be-
between 41.2° S and 33.3° N (Fig. 1). We first described the wood structure of this species and ontogenetic trends in features of its wood anatomy to define background variation for the species-level analyses. We then analyzed latitudinal trends in wood structure in the Northern and Southern Hemispheres and studied altitudinal trends.

MATERIALS AND METHODS

We studied 102 specimens, mostly from various institutional wood collections (Stern, 1988) with additional materials collected in China by the first author and in Japan by the second (Fig. 1; see list of localities and specimen numbers in the Appendix, http://ajbsupp.botany.org/v90/). Whenever possible, we recorded the stem diameter of samples before preparing blocks for sectioning.

We studied four quantitative features of wood structure: vessel element length, fiber length, vessel frequency, and tangential vessel diameter. Wood blocks were sectioned and macerated according to standard techniques for light microscopy. Before sectioning, the wood blocks were softened by 8% ethylenediamine, which improved section results without affecting anatomical features (Kukachka, 1978; Carlquist, 1982). Vessel frequency and tangential vessel diameter were measured in cross sections with an NS 15000 Image Processor (Microvision Instruments, Evry Cedex, France) or an image analysis system consisting of a digital microscope camera (Polaroid PDMC Ie, Polaroid, Cambridge, Massachusetts, USA), a personal computer (PowerPC G3, Apple Computer, Cupertino, California, USA), and image analysis software (ImageJ ver. 1.27, Wayne Rasband, National Institute of Mental Health, Bethesda, Maryland, USA). Two cross-sectional areas, $1.28 \times 0.96$ or $2.42 \times 1.82$ or $0.97 \times 0.73$ mm², were selected for the measurement of vessels to include at least 30 vessels per cross-sectional area. For lengths of vessel elements and fibers, 50 elements per sample were measured from macerations. Samples for maceration were collected from the outermost part of the specimens.

Ontogenetic trends in vessel features were measured in one sample, TWTw 15086, which was 7 cm at DBH and was collected on Iriomote Island in Japan. All the studied preparations are deposited at TWTw, Tsukuba, Japan. Correlation between vessel features and stem radius was studied in 71 specimens having a measurable stem radius. Latitudinal trends were analyzed separately among 36 specimens from the Southern Hemisphere and among 66 specimens from the Northern Hemisphere because of differences in climatic or geophysical conditions between these hemispheres. Altitudinal trends were first analyzed among 21 specimens from China and Japan, then with additional 23 specimens from other areas. The quantitative features were plotted using the linear or power curve fitting of the DeltaGraph version 4.5 (SPSS, Chicago, Illinois, USA). Statistical analyses were carried out with analytical tools in Microsoft Excel X (Microsoft, Redmond, Washington, USA). The relative amount of variation is expressed using coefficients of variation, i.e., standard deviation expressed as a percentage of the average corrected to exclude the effect of sample size.

RESULTS

General wood anatomy of Dodonaea viscosa—Wood diffuse-porous (Figs. 2, 5–7). Growth rings usually faint and irregularly spaced or absent, defined by banded parenchyma or change in fiber diameter. Vessels more or less evenly distributed, 21–148 vessels/mm², 25–57 µm in tangential diameter; round to oval to slightly angular in outline; moderately thick walled; solitary or in radial multiples of 2–4. Vessel element length 199–395 µm; perforation plates simple. Intervessel pits dense (Fig. 3), alternate, round, 3–6 µm in horizontal diameter with nearly horizontal slit-like apertures, non-vestured. Fibers very thick walled, 472–803 µm in length, with sparse minute simple pits in radial walls, non-septate. Axial parenchyma mainly vasicentric and diffuse (Figs. 2, 5–7), occasionally winged-aliform to confluent (Fig. 2), or in seemingly marginal, irregularly zonate bands (Fig. 6); prismatic crystals often in long chains of up to 30 or more, in chambered diffuse parenchyma cells (Fig. 4). Rays mostly homocellular, occasionally heterocellular with 1–3 rows of square to upright cells, 1–3 cells wide (Figs. 3, 4); pits to vessels distinctly bordered, round, 3–4 µm in diameter.

The occurrence of banded parenchyma and chambered,
Fig. 2–7. Wood structure of *Dodonaea viscosa*. 2–4. Cross, tangential, and radial sections of a specimen from Tahiti (SJRw 26400). 5–7. Cross sections of specimens from Bolivia (MADw 44337), New Zealand (USw W0019197), and Zaire (Tw 38616). Figures 2, 5–7, scale bar = 200 μm; Fig. 3, scale bar = 100 μm; Fig. 4, scale bar = 50 μm.

crystalliferous parenchyma cells varies greatly, but we could not detect any correlation between their occurrence and habitat ecology or ontogeny of specimens.

**Changes in ontogeny**—Ontogenetic trends studied along the longest radius in one of the largest specimens were nearly negligible (Fig. 8). Fiber length and tangential vessel diameter slightly increased between stem radius of 2 and 10 mm and became constant at ~650 and ~47 μm, respectively. For both features, the values at 2-mm radius were 7.5–11% lower than those at 10- to 45-mm radius. On the other hand, vessel element length and vessel frequency were nearly constant throughout the stem radius, at ~300 μm and 40 vessels/mm², respectively. Thus, some features seem to have matured already at 2-mm radius and others after 10 mm. Among 71 specimens with a measurable stem radius, vessel element length, fiber length, and vessel frequency slightly decreased, whereas tangential vessel diameter slightly increased (Fig. 9). The decrease or increase was steep up to 10-mm radius and thereafter was more gradual. The variation found between 10- and 20-mm radius equaled the total variation in the whole specimens. In conclusion, the studied features hardly varied radially.

**Trends along latitude**—All the studied features had nearly constant trends against latitude in both the Southern and Northern Hemispheres (Fig. 10). Throughout the distribution range of this species, vessel element length and fiber length ranged between 200 and 400 μm and between 470 and 800 μm with coefficients of variation 16–17% and 13%, respectively, but the linear regression lines were nearly horizontal against latitude. Because of the relatively large sample size at ~20° N (21 samples from Hawaii, USA, and 18 from China and Japan), the variation was nearly equal to the variation range for all the specimens. Vessel frequency seemed to be greater and varied more in the Northern Hemisphere than in the Southern Hemisphere, with averages of 80 and 70 vessels/mm² with coefficients of variation 40% and 33%, respectively, but their difference was not significant. Tangential vessel diameter had similar ranges of variation in both hemispheres, between 25 and 55 μm with coefficients of variation of 18–
Among the studied features, ranging between 30 and 50 mm, the most constant for this, the trends are nearly horizontal throughout the altitudinal range. Tangential vessel diameter is the most constant element and fiber lengths were nearly constant, staying at below 150 mm (Fig. 11). If we excluded these specimens, vessel element length and fiber length and those between vessel frequency and tangential vessel diameter were supported by significant correlations between these features in the wood structure of this species (Table 1).

Trends along altitude—Among specimens from China and Japan, vessel element length and fiber lengths seemed to increase from 0 to 200 m altitude, with low values in several specimens below 150 m (Fig. 11). If we excluded these specimens, vessel element length and fiber lengths were nearly constant, staying at ~330 and ~720 μm, respectively. Vessel frequency seemed to have higher values between 400 and 1000 m, but except for this, the trends are nearly horizontal throughout the altitudinal range. Tangential vessel diameter is the most constant among the studied features, ranging between 30 and 50 μm through the studied altitudes. For all the specimens, none of the studied features had a significant correlation ($P = 0.5$) with altitude. Thus, altitudinal trends were negligible through the range studied.

![Image](54x330 to 306x720)

DISCUSSION

The quantitative features of the wood anatomy of *Dodonaea viscosa* varied to a certain extent, but they did not vary along any latitudinal or altitudinal trends through a distribution range from 41.2° S to 33.3° N and from 7 to 2750 m. In the distributional range of *Dodonaea viscosa*, climatic conditions of habitats vary greatly (Table 2). One-third of specimens grow in tropical areas with minimum monthly temperature above 20°C, annual range of temperature less than 10°C, and yearly precipitation above 1000 mm. Some specimens grow in savanna to desert areas with yearly and monthly precipitation less than 500 mm and 70 mm, respectively. One-tenth of specimens grow in temperate areas with minimum monthly temperature below 10°C. One-fourth of specimens experiences winter drought with minimum monthly precipitation less than 20 mm. Thus, in spite of a wide climatic range of its habitats, species-level variations in quantitative features of wood anatomy of *Dodonaea viscosa* are nonexistent as in several other dicotyledonous species.

Three examples of significant species-level variation are *Acacia melanoxylon* (Wilkins and Papassotiriou, 1989), four *Rhododendron* species (Noshiro and Suzuki, 1995), and *Alnus nepalensis* (Noshiro et al., 1994). In *Acacia melanoxylon*, latitudinal trends uncovered in vessel diameter and vessel frequency were attributed to the more xeric conditions at increasing latitudes, but the trends were far gentler than those detected at the genus-level as in *Ilex* (Baas, 1973), *Symplocos* (van den Oever et al., 1981), and *Cornus* (Noshiro and Baas, 1998, 2000). In four *Rhododendron* species, altitudinal trends detected in one or two vessel features varied between species and were less pronounced than those within this genus. *Alnus nepalensis* had the most obvious altitudinal trends so far detected, but tree height of the specimens was significantly correlated with habitat altitude and likely contributed to the altitudinal trends.

Species-level variations in wood anatomy have so far been studied in species with a much narrower distribution range than *Dodonaea viscosa* and were confined to either the Northern or Southern Hemisphere. The specimens of the three *Cornus* species were mostly from the latitudinal range of 15° in an altitudinal range of 1500 m along the Japan Archipelago (Noshiro and Baas, 2000). The specimens of *Acacia melanoxylon* were from the latitudinal range of 27° from eastern...
Australia (Wilkins and Papassotiriou, 1989). Altitudinally, specimens of four *Rhododendron* species and *Alnus nepalensis* had a similar range to *Dodonaea viscosa*, 1500 to 2700 m and 2000 m, respectively, but all the specimens were from Nepal between 27° N and 29° N (Noshiro et al., 1994; Noshiro and Suzuki, 1995). Specimens of *Meterosideros polymorpha* had an altitudinal range of 2000 m, but all were from Hawaii (Sastripradja and Lamoureux, 1969). One exception is *Symplocos cochinchinensis* (Lour.) S. Moore, studied by van den Oever et al. (1981) and reanalyzed by Noshiro and Baas (2000); its 22 specimens were distributed from 26° S to 33° N and from 0 to 3900 m but had no latitudinal or altitudinal trends. These narrow ranges of species distribution with a limited range of habitat conditions could account for the nonexistence or rare occurrence of species-level variation.

Most species with a limited range of distribution must have experienced frequent contraction and expansion of their distribution range through glacial fluctuations. More than 10 glacial and interglacial fluctuations occurred during the Quaternary period (Bradley, 1999), greatly influencing the ranges of species distribution, especially of temperate species. During the 20 000 yr since the Last Glacial Maximum, distributional ranges of species are estimated to have shifted over 15° latitude and 1000 m altitude in North America (Delcourt and Delcourt, 1987, 1993), Europe (Huntley, 1988), and Japan (Tskakada, 1988). In species having a regional distribution, populations must have experienced frequent merging and divergence along with these fluctuations during the Quaternary period, resulting in higher incidences of genetic shuffling and a leveling of variations within species. Delcourt and Delcourt
Fig. 11. Altitudinal trends of vessel features in *Dodonaea viscosa* specimens from China and Japan and other areas with provisional curve fits for specimens from China and Japan and those for whole specimens.

Table 2. Climatic factors of the habitats of *Dodonaea* specimens deduced from the records of nearest meteorological stations.

<table>
<thead>
<tr>
<th>Climatic factor</th>
<th>Range</th>
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<tbody>
<tr>
<td>Mean monthly temperature (°C)</td>
<td>Maximum</td>
</tr>
<tr>
<td></td>
<td>16.9–34.1</td>
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<tr>
<td></td>
<td>Minimum</td>
</tr>
<tr>
<td></td>
<td>5.8–27.5</td>
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<tr>
<td>Annual range of temperature (°C)</td>
<td>Maximum</td>
</tr>
<tr>
<td></td>
<td>0.4–22.1</td>
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<tr>
<td>Mean monthly precipitation (mm)</td>
<td>Maximum</td>
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<tr>
<td></td>
<td>25–391</td>
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<tr>
<td></td>
<td>Minimum</td>
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<td></td>
<td>3–167</td>
</tr>
<tr>
<td>Yearly precipitation (mm)</td>
<td>Maximum</td>
</tr>
<tr>
<td></td>
<td>197–2748</td>
</tr>
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</table>

(1993) discussed floristic changes through glacial-interglacial cycles in North America, considering global climatic and environmental changes through the Quaternary period and a model of response of conifers to glacial-interglacial cycles presented by Critchfield (1984). They postulated that glacial-age conditions would lead to fragmentation and isolation of populations, leading to loss of genetic variability and promotion of interpopulation heterogeneity, and that glacial-interglacial transition of increased seasonality would facilitate individualistic plant migrations, intermingling of floras with redistribution of genetic variation, extinction of some species, and subsequent wave of speciation. For species other than *Dodonaea viscosa*, and probably for *Symplocos cochinchinensis*, the resulting homogeneous genetic background can be used to account for lack of obvious species-level variation.

In *Dodonaea viscosa*, the species range not only covers all the continents, but extends from coastal to mid-continental areas, such as in Africa, Australia, and South America, and into high mountains up to 3600 m altitude. Even during the Quaternary period, distribution shifts caused by glacial fluctuations cannot have been enough to merge populations throughout the
world. The worldwide distribution of this species seems to depend on wind or water dispersal of its broad-winged fruits, but the documentation for this is lacking (Leenhouts, 1994). Even if the distribution mechanism of this species is extremely efficient, genetic shuffling as postulated for most temperate species during the Quaternary period must have exerted little effect on the whole species, considering the regional diversification of infraspecific taxa as in Australia (West, 1984, 1985) or in Africa (Davies and Verdecourt, 1998). Thus, the lack of latitudinal and altitudinal trends in several anatomical features of the wood of Dodonaea viscosa support the notion that woody dicotyledonous species have a rather rigid plan in wood structure to cope with the variable habitat conditions even though they are genetically diversified.

Another way of interpreting the divergent trends in species-level variation is to consider that some species are inherently variable in wood structure against latitudinal or altitudinal gradients and others are not. Besides Acacia melanoxylon (Whitkins and Papasotiriou, 1989), four Rhododendron species (Noshiro and Suzuki, 1995), and Alnus nepalensis (Noshiro et al., 1994) mentioned earlier, Liquidambar styraciflua is known to have latitudinal trends in length of fibers, which lengthen in southern latitudes (Hunter and Goggans, 1969). Winstead (1972) and Randel and Winstead (1976) studied variation in fiber length in seedlings originally collected over an area ranging from New Jersey and Illinois, USA, to Honduras and Nicaragua, then grown under various controlled conditions. They showed that seedlings from southern latitudes (in the Northern Hemisphere) always have longer fibers irrespective of growth conditions and concluded that ecotypic differentiation in this species, not acclimatization, causes latitudinal variation in fiber length. Winstead (1978) further showed that similar ecotypic differentiation occurs also in Acer negundo from Quebec, Canada, to Texas, USA, resulting in longer fibers in southern latitudes. Although correlation with other anatomical features of wood are not clarified, these studies indicate that significant latitudinal trends exist in the wood anatomy of some species backed by genotypical diversification. However, latitudinal trends in fiber length of these species were far less than genus-level trends so far clarified.

The lack of latitudinal and altitudinal trends in the wood anatomy of Dodonaea viscosa added support for differences in structural diversification of wood at the genus and species levels. Although functionally adaptive xylem evolution and dominant role of macroclimatic adaptation at the genus level are largely documented (Carquist, 1975, 2001; Baas, 1982; Baas and Schweingruber, 1987; Dickison, 1989; Wheeler and Baas, 1991), it remains a mystery why the species-level trends in widely distributed species do not conform to the genus-level trends. The process of diversification in wood anatomy should be studied by further clarifying the genetic basis for wood formation while considering past adaptation to ecological gradients of diversing species.

LITERATURE CITED


