American Journal of Botany 87(10): 1495–1506. 2000.

LATITUDINAL TRENDS IN WOOD ANATOMY WITHIN SPECIES AND GENERA: CASE STUDY IN *CORNUS* S.L. (CORNACEAE)[1]

SHUICHI NOSHIRO[2,4] AND PIETER BAAS[3]

[2]Forestry and Forest Products Research Institute, Tsukuba Norin, P.O. Box 16, Ibaraki 305–8687, Japan; and
[3]National Herbarium of the Netherlands, P.O. Box 9514, 2300 RA Leiden, The Netherlands

Latitudinal trends in wood anatomical characters in three Asiatic species of *Cornus* sensu lato (s.l.) were studied and compared with those for the whole genus based on an extensive sampling covering the specific distribution ranges and the generic data from a previous study. We studied 124 specimens of *C. controversa* growing between 31.5° and 45.3° N, 54 of *C. kousa* between 24.4° and 40.5° N, and 64 of *C. macrophylla* between 27.8° and 41.0° N. Characters studied were vessel element length, fiber length, vessel frequency, tangential vessel diameter, and vessel grouping index. At the species level no latitudinal trends were detected throughout the distribution ranges of the species. Neither tree size, altitude, nor climatic factors had a significant correlation with wood anatomical characters. In contrast, at the genus level, latitudinal trends were significant not just for the whole genus, but for both New and Old World species groups. At the genus level, latitude and three climatic factors all had a significant correlation with wood anatomical characters, but correlation coefficients with latitude were markedly high. The difference in latitudinal trends between the genus and species levels may be due to the radiation of *Cornus* along paleoclimatic gradients in the early Tertiary.

Key words: altitude; climate; Cornaceae; *Cornus*; ecological wood anatomy; genus-level trends; latitude; species-level trends.

The systematic wood anatomy of Cornaceae and allies (Noshiro and Baas, 1998) showed the existence of clear latitudinal trends in three genera with a wide geographical distribution: *Cornus* s.l., *Garrya*, and *Alangium* excluding sect. *Constigma*. Vessel element length and fiber length of these three genera and tangential vessel diameter of *Cornus* s.l. showed a nearly linear decrease with increasing latitude with values at ~40° about half those of equatorial values. When *Cornus* species were roughly divided into large trees, medium-sized trees, small trees, and shrubs, latitudinal trends for vessel element length were apparent within each size group.

Latitudinal trends in several wood anatomical characters seem to be a general phenomenon for woody dicotyledonous genera with a wide geographical distribution. The trends have been detected in *Ilex* (Baas, 1973), *Symplocos* (van den Oever, Baas, and Zandee, 1981) and 17 smaller genera of 14 families (van der Graaff and Baas, 1974). These studies only described correlations between latitude and wood anatomical characters and discussed the trends in terms of the tropical to the arctic climatic gradient. None has tried statistical comparison of wood anatomical variation with more precise climatic data.

At the species level, variation in wood structure has been studied more in relation to altitude than to latitude. Latitudinal and altitudinal trends in wood structure at the species level are either not detected, present but not pronounced, or obvious. Van der Graaff and Baas (1974) found no altitudinal trends in six species nor latitudinal ones in one species. Sastrapradja and Lamoureux (1969) did not find any altitudinal trends in *Meterosideros polymorpha* Gaud. in Hawaii either. On the contrary, Noshiro, Joshi, and Suzuki (1994) showed in *Alnus nepalensis* D. Don that six characters were correlated with altitude and/or stem diameter. Among *Rhododendron* species in Nepal, Noshiro, Suzuki, and Ohba (1995) and Noshiro and Suzuki (1995) showed that 13 wood anatomical characters had a highly significant correlation with altitude and/or tree size at the genus level, but that only one to eight characters had a significant correlation with altitude and/or tree size within four studied species. Contradictory results have been obtained for intraspecific variation, probably influenced by the sample size and statistical analyses employed. A more detailed study on latitudinal and altitudinal trends at the species level is therefore necessary.

To evaluate the meaning of the latitudinal and altitudinal trends in wood anatomical characters at the species level, it is also necessary to consider the climatic conditions of sampling localities along the latitudinal and altitudinal gradients and the ontogenetic changes as reflected by growth ring numbers in the studied material. The sampling should be extensive and preferably cover the whole range of distribution of the selected species. Samples for the genus-level study should also be available from wide latitudinal ranges so that differences or similarities in the species- and genus-level trends are comparable. *Cornus* sensu lato (s.l.) is an ideal taxon for such a study.

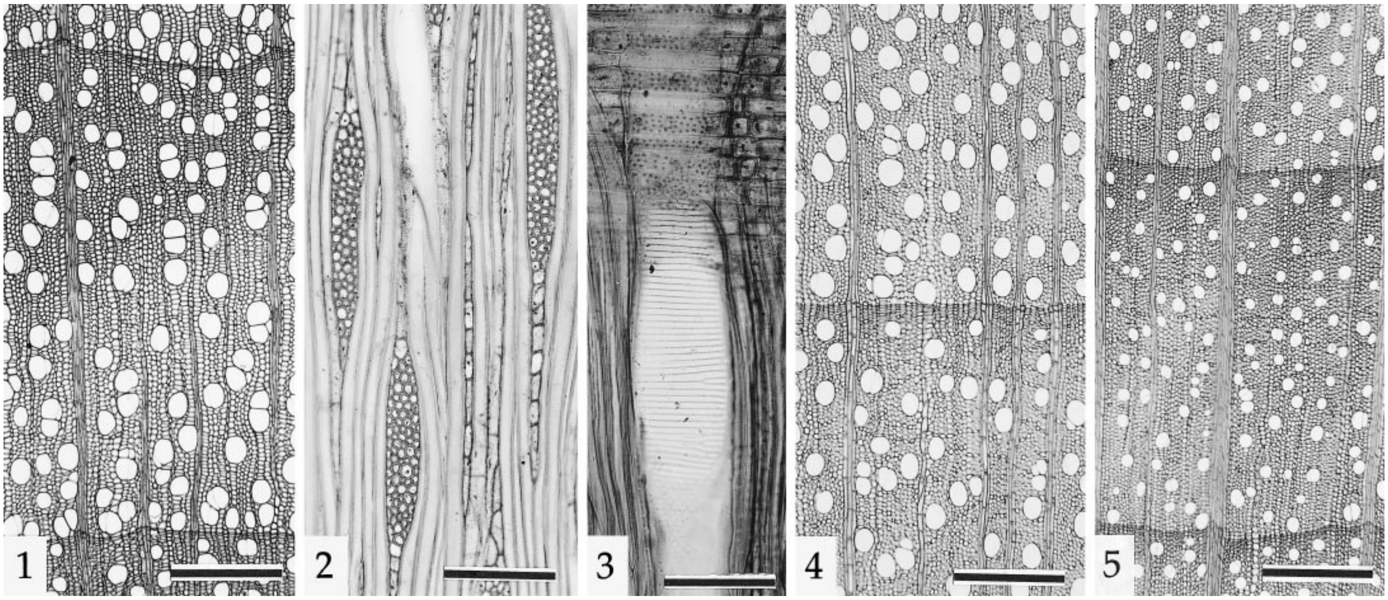
Cornus s.l. shows wood anatomical variation that is correlated with latitude, and its trends were distinct from those of the other genera (Noshiro and Baas, 1998). Wood anatomy supported the broad genus concept that Eyde (1987) advocated. Analyses of *rbcL* sequences of Cornaceae and allies (Xiang et al., 1993; Xiang and Soltis, 1998), *rbcL* and *matK* sequences (Xiang, Soltis, and Soltis, 1998), chloroplast DNA restriction sites (Xiang et al., 1996), and morphological characters (Murrell, 1993) also support the broad genus concept. *Cornus* s.l. consists of ~65 species of deciduous trees or shrubs, rarely herbs, mostly in the mesic temperate zone of the northern

---

[1] Manuscript received 29 April 1999; revision accepted 4 January 2000.

The authors thank Messrs. R. Hirano, T. Yoshino, and Drs. R. Funada, T. Furuno, T. Ito, M. Suzuki, K. Terada, M. Tsukagoshi, and K. Yoda for the supply of wood specimens, Mr. T. Sugawa for the supply of unpublished data, and Dr. Y. Ohtani for the supply of climatic data. Collection of Nepalese specimens was supported by the Monbusho International Scientific Research Program (Field Research) (Numbers 58041022, 60041018, 08041137 to H. Ohba and Number 63041060 to M. Suzuki) from the Ministry of Education, Science and Culture, Japan.

[4] Author for reprint requests (e-mail: noshiro@ffpri.affrc.go.jp).



Figs. 1–5. Three Asiatic species of *Cornus* s.l. **1.** Cross section of *C. controversa* (Noshiro 961011-2). Bar = 500 μm. **2.** Tangential section of *C. controversa* (Noshiro 961011-2). Bar = 200 μm. **3.** Radial section of *C. controversa* (Noshiro 961011-2). Bar = 100 μm. **4.** Cross section of *C. macrophylla* (Noshiro 980630-2). Bar = 500 μm. **5.** Cross section of *C. kousa* (Noshiro 980607-3). Bar = 500 μm.

hemisphere, with only two species in the equatorial part of the southern hemisphere.

Three Japanese species of *Cornus* s.l. are deciduous trees covering wide latitudinal and altitudinal ranges throughout Japan and are appropriate materials for the study of species-level latitudinal trends in wood structure along altitudinal and ontogenetic gradients. Climate data are available throughout Japan for the last 30 yr, so trends in wood structure can also be assessed critically along climatic gradients. *Cornus controversa* Hemsl. ex Prain (*Swida controversa* (Hemsl.) Soják) of sect. *Mesomora* is a tree up to 24 m tall and 70 cm in diameter, which grows widely in warm to cool temperate forests from Hokkaido to Kyushu in Japan, and in Korea, Taiwan, central and south China, and in the Himalayas. *Cornus kousa* (Buerg.) Nakai (*Benthamidia japonica* (Sieb. et Zucc.) Hara) of sect. *Syncarpea* is a medium-sized tree up to 15 m tall and 50 cm in diameter, in montane forests from Honshu to Kyushu, and in subtropical forests of Ishigaki Island of the Ryukyu Islands in Japan, and in Korea. *Cornus kousa* var. *chinensis* occurs widely in central and south China, and individuals on Ishigaki Island growing in subtropical forests may be included in this variety. *Cornus macrophylla* Wall. (*Swida macrophylla* (Wall.) Soják) of sect. *Kraniopsis* is a tree up to 20 m tall and 50 cm in diameter, in warm temperate forests from Honshu to Kyushu in Japan, and in Korea, Taiwan, central China to the Himalayas and Afghanistan. Wood structure of the three species is similar except for the vessel grouping (Figs. 1–5; Noshiro and Baas, 1998). All have diffuse porous wood, heterocellular multiseriate rays, diffuse-in-aggregates axial parenchyma, and scalariform perforation plates. Vessels often form short radial multiples in *C. controversa*, but are exclusively solitary in the other two species.

TABLE 1. Ranges of nonanatomical data and wood anatomical characters of three *Cornus* species. For wood anatomical characters, the ranges show minimum and maximum values of sample averages, and averages and standard deviations for sample averages are given in parentheses.

	C. controversa	*C. kousa*	*C. macrophylla*
Tree height (m)	4.5–24	3–12	5–20
Stem diameter (cm)	7–65	4–33	6–42
Altitude (m)	25–1580	200–1480	20–2630
Latitude (°N)	31.5–45.3	24.4–40.5	27.8–41.0
Annual range of temperature (°C)	616.3– 29.3	11.5–25.7	14.3–25.5
Warmth index (°C)	44–143	59–221	71–180
Annual precipitation (mm)	917–4002	1126–4291	1048–4291
Vessel element length (μm)	961–1488	944–1588	932–1545
	(1184 ± 108)	(1278 ± 132)	(1206 ± 141)
Fiber length (μm)	1357–2016	1407–2351	1534–2193
	(1699 ± 144)	(1938 ± 204)	(1894 ± 159)
Vessel frequency (no./mm^2)	20.8–69.4	22.8–78.3	25.6–55.7
	(39.6 ± 9.8)	(58.3 ± 12.3)	(37.9 ± 7.5)
Tangential vessel diameter (μm)	54.2–90.4	42.8–82.3	52.5–89.1
	(73.2 ± 6.7)	(56.7 ± 6.8)	(73.7 ± 7.9)
Vessel grouping index	1.03–1.61	1.00–1.07	1.00–1.07
	(1.21 ± 0.11)	(1.02 ± 0.02)	(1.02 ± 0.02)

In this study we aimed at clarifying species-level trends in wood structure of these three *Cornus* species. We will first clarify ontogenetic changes and within-growth-ring changes of vessel element and fiber characters, to determine background variation for the species-level analyses. We will then analyze species-level trends in wood structure in relation to latitude, altitude, and tree size, and compare the results with the climatic gradient within the distribution ranges. Using the data of the previous systematic study (Noshiro and Baas, 1998), the genus-level trends in *Cornus* s.l. will be analyzed against climatic factors, and their influence on wood structure will be evaluated. Finally, species-level trends will be compared with latitudinal trends at the genus level, and the evolutionary implication of wood structural diversification at the genus and species levels will be discussed. Because of the difficulty in quantifying ray characters, we studied only vessel and fiber characters.

MATERIALS AND METHODS

We studied 124 specimens of *Cornus controversa,* 54 of *C. kousa,* and 64 of *C. macrophylla.* Among the specimens, 25 of *C. controversa,* 18 of *C. kousa,* and 14 of *C. macrophylla* were xylarium specimens, and all the others were collected in their natural habitat, mostly by the first author. Specimens for each species had a latitudinal range of ~15° and an altitudinal range of over 1500 m, representing the distribution ranges of the three species in Japan (Table 1). All the specimens of *C. controversa* were collected in Japan between Hokkaido and Kyushu from a continuous distribution range. All the specimens of *C. kousa* were from the montane forest of Japan, but three samples were from the subtropical forest on Ishigaki Island with a disjunct distribution. Most specimens of *C. macrophylla* were collected in Japan between Honshu and Kyushu up to 1350 m, but five specimens were collected in Nepal between 2250 and 2630 m.

All the specimens the first author collected were outermost stem wood, mostly at breast height. Of 99, 38, and 50 specimens of the respective species, both stem diameter at breast height and tree height were recorded, but for the others only the diameter at breast height was known. Values for climatic factors were estimated from monthly and yearly records at meteorological stations nearest to the habitats, and temperature was adapted to the habitat condition with a lapse rate of 0.65°C/100 m. Among climatic factors, annual range of temperature, warmth index, and annual precipitation are compared with wood anatomical characters. The annual range of temperature is calculated as the difference in the mean monthly temperature between the warmest and coldest months. The warmth index is defined as the yearly sum of the mean monthly temperature minus 5°C for the months with the mean temperature above 5°C and is considered as a good index to describe distribution ranges of woody plants in East Asia (Kira, 1949). The list of materials with their localities and specimen numbers is given in the Appendix, and ranges of tree size, altitude, latitude, and estimated values for climatic factors of habitats are listed in Table 1.

Wood blocks were sectioned and macerated according to the standard techniques for light microscopy. Quantitative characters of vessel elements in cross sections were measured with an image analysis system. Two to three areas, 1.28 × 0.96 mm^2, were selected for the measurement of specimens, and extremely narrow rings were excluded whenever possible. Thirty elements per sample for vessel element length and fiber length were measured from macerations. Samples for maceration were collected from outermost growth rings. Vessel grouping was measured only for *C. controversa* and is expressed by the index of Carlquist (1988) where the total number of vessels is divided by the total number of vessel groups. All the studied preparations were deposited at TWTw, Tsukuba, Japan. For the genus-level trends of *Cornus* s.l., the same specimens as cited in Noshiro and Baas (1998) were used, but additional data for vessel element and fiber lengths are presented.

To assess ontogenetic changes in quantitative characters, vessel element length, fiber length, and tangential vessel diameter were studied in one tree of *Cornus controversa* from the data of Sugawa (1979; and unpublished data). The sample tree was 60 yr old and 32 cm in stem diameter at breast height and was collected at Shizuoka, Japan. To assess expected fluctuation in vessel element and fiber lengths from random samples within a growth ring, three blocks of 400–500 μm in radial thickness were collected and compared within a growth ring of one specimen each of the three *Cornus* species.

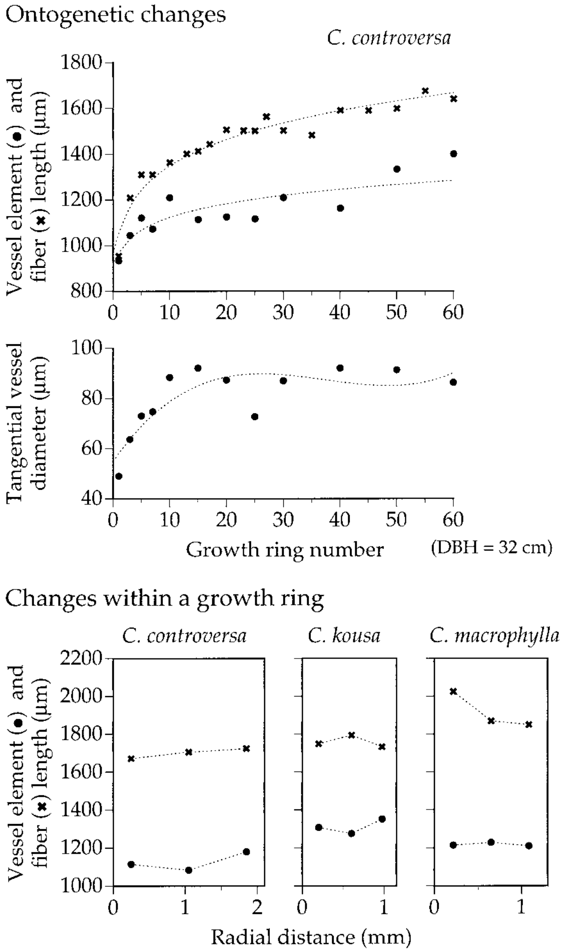


Fig. 6. Changes in ontogeny and within a growth ring of wood anatomical characters in *Cornus* species. Specimens for ontogenetic changes: *C. controversa,* TWTw 9342; those for changes within growth rings: *C. controversa,* Noshiro 961011-12, *C. kousa,* Noshiro 961016–3, *C. macrophylla,* Noshiro 961029-10.

RESULTS

Changes in ontogeny and within growth rings—The regression lines of vessel element length, fiber length, and tangential vessel diameter showed a steep increase during the first ten growth rings. Subsequently, there was a gradual increase in vessel element and fiber lengths, while tangential vessel diameter stayed nearly constant (Fig. 6). Wood formed after the 10th yr could thus be regarded as mature wood, though vessel elements and fibers gradually lengthened 20% of the 10th-yr value between the 10th and 60th growth rings. This boundary of the 10th yr between juvenile and mature wood agreed with the radial variation of vessel element and fiber lengths for one *Cornus controversa* and one *C. kousa* specimens studied by Furukawa et al. (1983). In our material the 10th growth ring nearly equalled 5 cm in diameter at breast

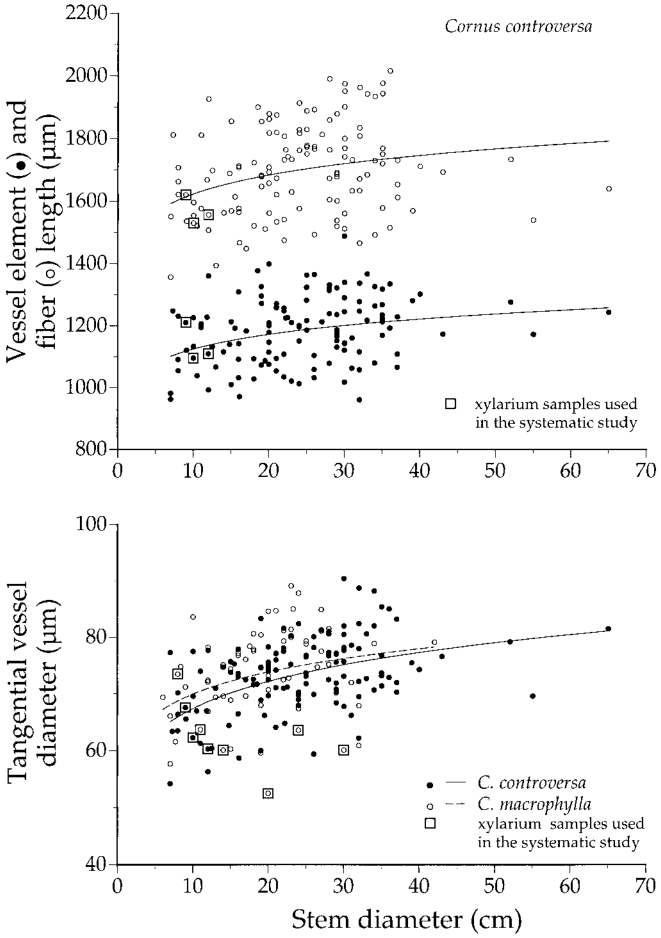


Fig. 7. Vessel element length, fiber length, and tangential vessel diameter plotted against stem diameter in *Cornus controversa* and *C. macrophylla,* and character distribution of xylarium specimens used in the systematic study of Cornaceae and allies (Noshiro and Baas, 1998).

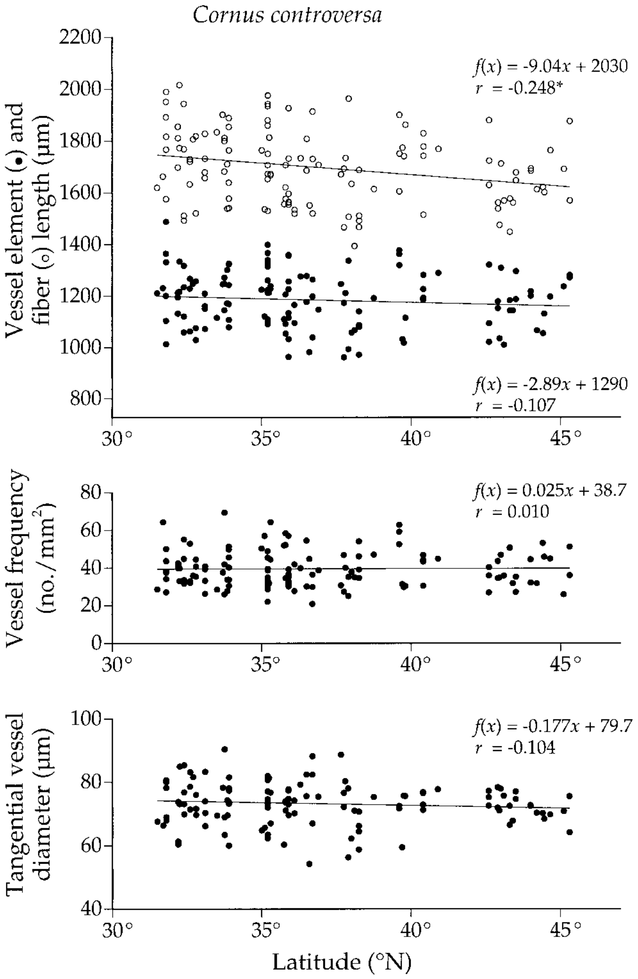


Fig. 8. Latitudinal variation in wood anatomical characters of *Cornus controversa.* Significance level: * = 1%.

height. Thus specimens over 5 cm diameter were provisionally treated as mature wood in this study. Among the specimens used for the species-level study, a gradual increase of cell dimensions was observed as stem diameter increased, but the difference in cell dimensions between stem diameter of 10 and 60 cm was within the variation range at stem diameter of 30 cm (Fig. 7). Ontogenetic trends in mature wood were therefore negligible in the following species-level analyses.

Within a growth ring, fiber length of woody dicotyledons can fluctuate up to five times the minimum value at about the growth ring boundary (Bisset and Dadswell, 1950; Hejnowicz and Hejnowicz, 1958; Swamy, Parameswaran and Govindarajalu, 1960; Süss, 1967). Vessel element length is more or less constant in diffuse-porous wood (Hejnowicz and Hejnowicz, 1958; Swamy, Prameswaran and Govindarajalu, 1960; Süss, 1967). In the three *Cornus* species, both vessel element and fiber lengths were fairly constant throughout a growth ring and fluctuated <10% of the minimum value (Fig. 6). Thus our sample of ~500 μm in radial thickness could be considered to yield the average value for the whole growth ring for vessel element and fiber lengths.

Trends in the three Cornus species—In contrast to the latitudinal trends for *Cornus* s.l., latitudinal trends at the species level were negligible. In *Cornus controversa,* vessel element length, fiber length, vessel frequency, and tangential vessel diameter all had nearly horizontal trends along latitude with only one significant correlation at the 1% level (Fig. 8). Fiber length showed a very weak, but recognizable, trend when compared with the other three characters, but the decrease from 31.5° N to 45.3° N was only 7.1% according to the linear regression, which was statistically significant here. All the other characters had <3.3% increase or decrease within the distribution range. Variation ranges for each character were constant throughout the distribution range of this species, except for the narrower range for tangential vessel diameter in the specimens of Hokkaido above 42.6° N.

Cornus kousa showed more marked latitudinal trends in the four wood anatomical characters than *C. controversa,* but this was likely because of the three samples from Ishigaki Island at ~24° N (Fig. 9). These three specimens had a disjunct distribution at low altitudes in a subtropical forest and tended to have longer vessel elements and fibers, lower vessel frequency, and wider vessels than the specimens from Kyushu to northern Honshu. If we exclude these specimens, three wood anatomical characters showed no latitudinal trends without any significant correlation. From 30.3° N to 40.5° N, vessel element length, fiber length, and vessel frequency decreased 5.2, 7.8,

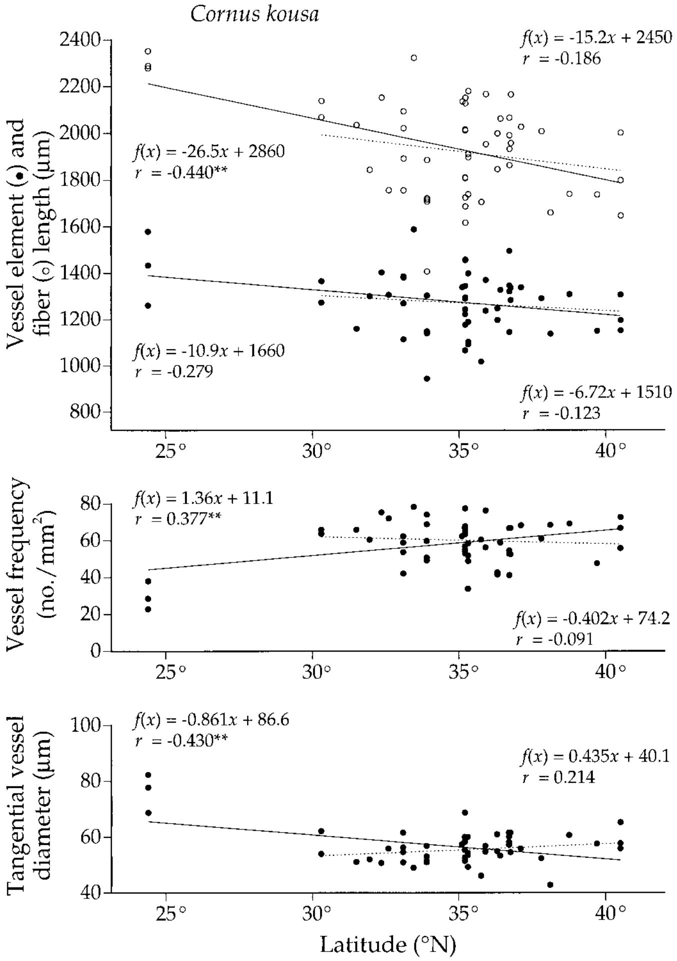


Fig. 9. Latitudinal variation in wood anatomical characters of *Cornus kousa*. Continuous lines are for the whole specimens, and dashed lines exclude specimens from Ishigaki Island. Significance level: ** = 0.5%.

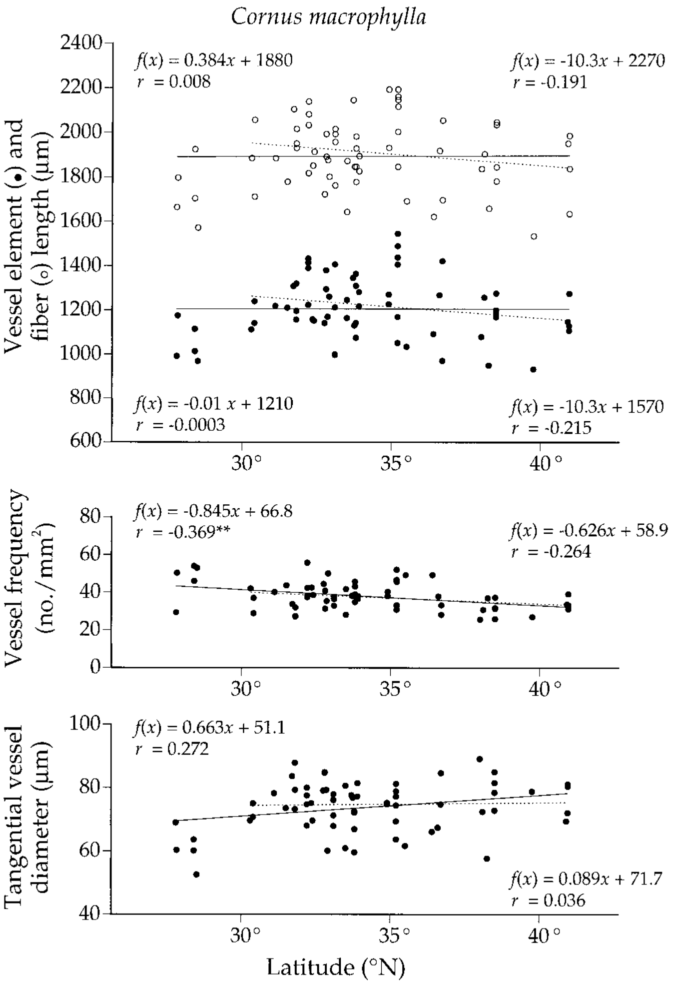


Fig. 10. Latitudinal variation in wood anatomical characters of *Cornus macrophylla*. Continuous lines are for the whole specimens, and dashed lines exclude Nepalese specimens. Significance level: ** = 0.5%.

and 6.6%, respectively, and tangential vessel diameter increased 8.3%, according to the linear regression. Because of the large number of specimens at ~35° N, variation ranges for each character tended to be largest around this latitude, almost equal to the total variation for each character.

In *Cornus macrophylla*, vessel element length and fiber length were more constant than in *C. controversa*, but vessel frequency and tangential vessel diameter, respectively, showed a medium decrease and increase, with vessel frequency having the only significant correlation (Fig. 10). From 27.8° N to 41.0° N, vessel frequency decreased 25.7%, and tangential vessel diameter increased 12.6%, according to the linear regression. Variation range was nearly constant throughout the distribution range of this species, but seemed to be displaced upward between 30° and 35° N. The specimens from Nepal at ~28° N that grew at very high altitudes between 2250 and 2630 m tended to have slightly shorter vessel elements and fibers and smaller vessels than the Japanese specimens. If we exclude the Nepalese specimens, latitudinal trends were more marked for vessel element and fiber lengths and less so for vessel frequency and tangential vessel diameter. Thus within the three *Cornus* species, latitudinal trends were almost negligible, except for *Cornus kousa* when the specimens on Ishigaki Island were included.

Nonanatomical factors besides latitude, i.e., tree height, stem diameter, altitude, annual range of temperature, warmth index, and annual precipitation, also had a very small correlation with wood anatomical characters of these three species (Table 2). In each species, two to four characters had a significant correlation with some of the nonanatomical factors at the 0.5% significance level, but correlation coefficients were all below 0.5, except for *Cornus kousa*. In *Cornus kousa*, trends were strongly biased by the disjunct specimens on Ishigaki Island at a low latitude, and exclusion of these specimens resulted in a fairly low correlation, all below 0.5, with only two significant correlations. In *C. macrophylla* also, coefficients were influenced by the Nepalese specimens from high altitudes, and exclusion of the Nepalese specimens resulted in one significant correlation at the 0.5% level between stem diameter and vessel frequency. Among the combinations, stem diameter and tangential vessel diameter had a comparatively higher correlation in *C. controversa* and *C. kousa*, and this probably reflected a gradual ontogenetic increase of tangential vessel diameter in mature wood that was not clearly indicated in the preliminary ontogenetic study (Fig. 7). Among wood anatomical characters, vessel element and fiber lengths were significantly highly correlated, and tangential vessel diameter

TABLE 2. Correlation table of nonanatomical data and wood anatomical characters of three *Cornus* species. H: tree height, D: stem diameter, Alt: altitude, Lat: latitude, ART: annual range of temperature, WI: warmth index, AP: annual precipitation, VEL: vessel element length, FL: fiber length, VF: vessel frequency, TVD: tangential vessel diameter.

C. controversa	*H*	*D*	*Alt*	*Lat*	*ART*	*WI*	*AP*	*VEL*	*FL*	*VF*	*TVD*
	N = 99	*N* = 124									
Tree height	–										
Stem diameter	0.640**	–									
Altitude	0.082	0.220	–								
Latitude	−0.018	−0.026	−0.468**	–							
Annual range of temperature	−0.032	−0.028	−0.089	0.792**	–						
Warmth index	−0.071	−0.120	−0.272**	−0.685**	−0.765**	–					
Annual precipitation	0.190	0.159	0.397**	−0.759**	−0.633**	0.524**	–				
Vessel element length	0.392**	0.271**	−0.021	−0.107	−0.149	0.125	0.175	–			
Fiber length	0.242	0.217	−0.111	−0.248*	−0.394**	0.335**	0.269**	0.675**	–		
Vessel frequency	−0.019	−0.302**	−0.079	0.010	0.035	0.034	0.058	0.146	−0.083	–	
Tangential vessel diameter	0.481**	0.437**	0.222	−0.104	−0.067	−0.064	0.067	0.410**	0.360**	−0.315**	–
Vessel grouping index	−0.104	−0.108	0.124	−0.055	0.002	−0.030	−0.061	−0.073	−0.148	0.380**	0.014

C. kousa	H	D	Alt	Lat	ART	WI	AP	VEL	FL	VF
	N = 38	*N* = 54								
Tree height	–									
Stem diameter	0.680**	–								
Altitude	−0.452**	−0.030	–							
Latitude	−0.117	0.066	−0.100	–						
Annual range of temperature	−0.231	−0.076	0.121	0.880**	–					
Warmth index	0.389	0.015	−0.585**	−0.723**	−0.794**	–				
Annual precipitation	−0.321	−0.084	0.601**	−0.514**	−0.364*	−0.023	–			
Vessel element length	0.334	0.010	−0.236	−0.279	−0.340	0.351*	−0.018	–		
Fiber length	0.243	−0.212	−0.363*	−0.440**	−0.501**	0.553**	−0.037	0.774**	–	
Vessel frequency	−0.365	−0.075	0.261	0.377**	0.376*	−0.535**	0.093	−0.128	−0.310	–
Tangential vessel diameter	0.543**	0.405**	−0.370*	−0.430**	−0.558**	0.639**	−0.111	0.371*	0.398**	−0.513**
Without individuals on Ishigaki Island; *N* = 51										
Vessel element length	–	−0.045	−0.159	−0.123	−0.219	0.265	−0.017	–		
Fiber length	–	−0.287	−0.243	−0.186	−0.281	0.405**	−0.037	0.782**	–	
Vessel frequency	–	−0.008	0.073	−0.091	−0.143	−0.056	0.107	0.073	−0.082	–
Tangential vessel diameter	–	0.468**	−0.182	0.214	−0.009	−0.002	−0.153	0.210	0.143	−0.155

Significance level: ** = 0.5%, * = 1%.

TABLE 2. Continued.

C. macrophylla	H	D	Alt	Lat	ART	WI	AP	VEL	FL	VF
	N = 50		*N* = 64							
Tree height	—									
Stem diameter	0.597**	—								
Altitude	−0.245	−0.015	—							
Latitude	0.132	0.046	−0.632**	—						
Annual range of temperature	0.215	−0.012	−0.539**	0.819**	—					
Warmth index	0.052	−0.002	−0.454**	−0.326*	−0.404**	—				
Annual precipitation	−0.039	−0.042	−0.001	−0.454**	−0.229	0.413**	—			
Vessel element length	0.204	0.065	−0.273	0.000	0.047	0.296	0.135	—		
Fiber length	0.166	0.045	−0.254	0.008	0.016	0.253	0.121	0.748**	—	
Vessel frequency	−0.104	−0.315	0.294	−0.369**	−0.338*	0.107	0.067	−0.122	−0.216	—
Tangential vessel diameter	0.358	0.266	−0.383**	0.272	0.362**	0.003	−0.009	0.480**	0.452**	−0.567**
Without individuals in Nepal; *N* = 59										
Vessel element length	—	0.098	0.010	−0.215	−0.241	0.233	0.049	—		
Fiber length	—	0.060	0.021	−0.191	−0.264	0.181	0.041	0.720**	—	
Vessel frequency	—	−0.436**	0.042	−0.264	−0.173	0.197	0.192	−0.029	−0.143	—
Tangential vessel diameter	—	0.356*	0.030	0.036	0.079	−0.130	−0.170	0.404**	0.369**	−0.470**

Significance level: ** = 0.5%, * = 1%.

showed a moderate correlation with vessel element length, fiber length, and vessel frequency. These trends among wood anatomical characters conformed to the genus-level ones described by Noshiro and Baas (1998) and seemed to be intrinsic trends in wood structure. Thus, except for a minor ontogenetic influence of stem diameter, nonanatomical factors did not influence wood structure of the three *Cornus* species at latitudes higher than 30° N.

DISCUSSION

Species-level trends in Cornus s.l. and other genera—The analysis of three *Cornus* species showed that their wood structure is variable, partly affected by ontogeny (cambial age), but that this variation cannot be explained in terms of climate gradients along either latitude or altitude. The three *Cornus* species did not show any latitudinal trends between 30° and 45° N, but specimens from south of this range in *Cornus kousa* and *C. macrophylla* clearly had distinct ranges of variation. If we could include specimens from China, south of 30° N, latitudinal or altitudinal trends could have been analyzed more accurately.

Latitudinally, most species of woody plants grow within a range of 15°, except for tropical coastal species, and an infraspecific study covering temperate to tropical areas is usually difficult. One exception is *Symplocos cochinchinensis* (Lour.) S. Moore studied by van den Oever, Baas, and Zandee (1981). Among its 22 specimens growing between 23° S and 33° N, however, no significant latitudinal trends existed either in vessel diameter, vessel element length, vessel frequency, bar number of perforation plates, or fiber length (according to a new simple correlation analysis of van den Oever et al.'s data). Though existence of latitudinal trends was not detected in this widely distributed species, further studies may uncover a threshold latitude for the expression of latitudinal trends.

Altitudinally, there may be a threshold altitude at 2000 m. *Alnus nepalensis* is the only species thus far known to have altitudinal trends conforming with the genus-level altitudinal or latitudinal ones (Noshiro, Joshi, and Suzuki, 1994). In this species, the population above 2000 m had more vessels, shorter vessel elements, and shorter fibers than that below 2000 m. Within either population, however, no altitudinal trends were detected except for vessel element length in the upper population. Thus difference in the population average above and below 2000 m mainly defined the altitudinal trends in this species. In *Symplocos cochinchinensis* specimens growing between 0 and 3900 m, vessel element and fiber lengths tended to be shorter in six specimens above 2000 m than in 12 specimens below 2000 m, but with a low significance level of 5%, according to the data of van den Oever, Baas, and Zandee (1981). Such a threshold altitude at 2000 m may also explain distinctive character values of Nepalese specimens of *C. macrophylla*.

Altitudinal trends in these species are, however, exceptional. The almost complete lack of latitudinal or altitudinal trends in wood structure of the three *Cornus* species throughout their distribution range agrees with the results of van der Graaff and Baas (1974) and Sastrapradja and Lamoureux (1969) and conforms with the results for four individual *Rhododendron* species (Noshiro and Suzuki, 1995). Thus, the wood structure of these species is not affected by either latitudinal or altitudinal gradients.

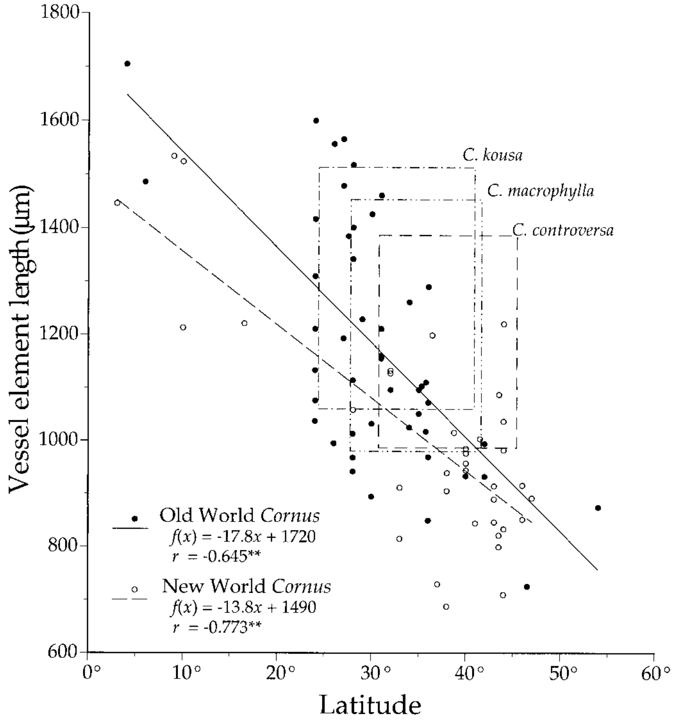


Fig. 11. Latitudinal trends in vessel element length of the genus *Cornus* in the Old and New Worlds and ranges of three Asiatic *Cornus* species excluding extreme values. Data are from Noshiro and Baas (1998) with additions. Significance level: ** = 0.5%.

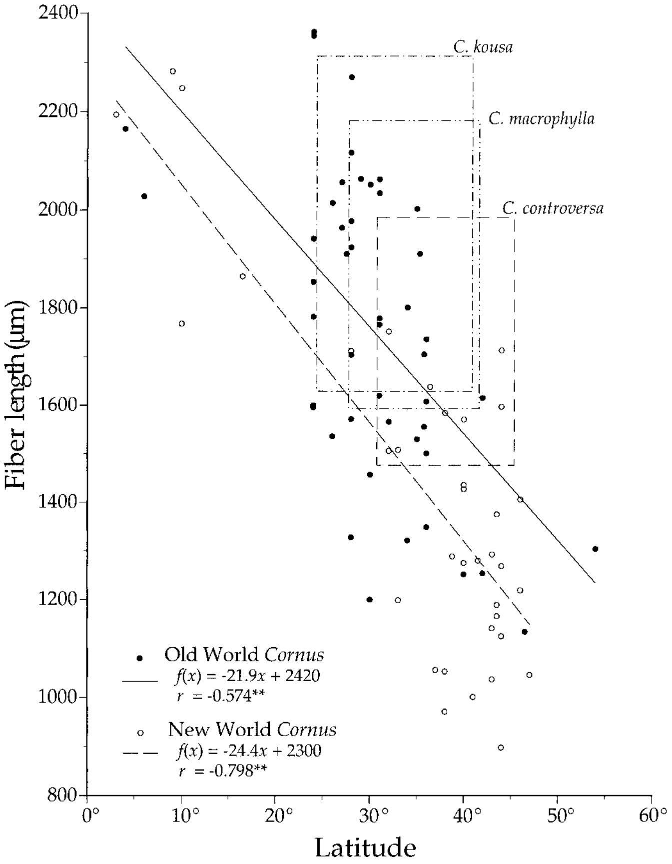


Fig. 12. Latitudinal trends in fiber length of the genus *Cornus* in the Old and New Worlds and ranges of three Asiatic *Cornus* species excluding extreme values. Data are from Noshiro and Baas (1998) with additions. Significance level: ** = 0.5%.

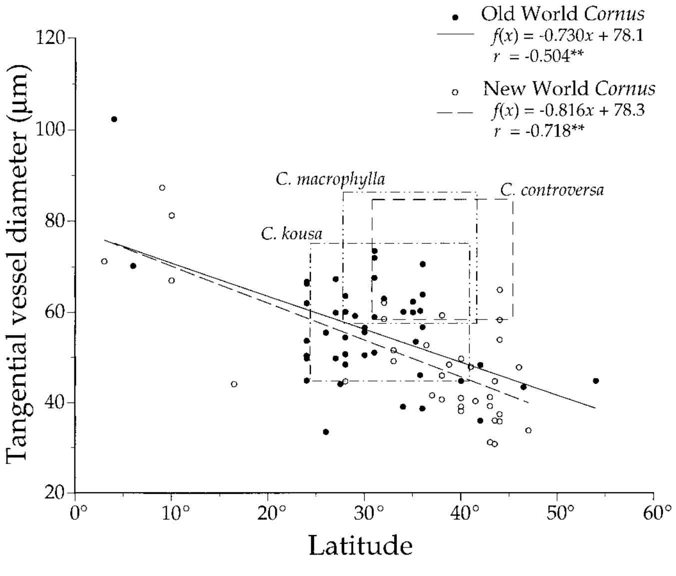


Fig. 13. Latitudinal trends in tangential vessel diameter of the genus *Cornus* in the Old and New Worlds and ranges of three Asiatic *Cornus* species excluding extreme values. Data are from Noshiro and Baas (1998). Significance level: ** = 0.5%.

Genus-level trends in Cornus s.l. and comparison with nonanatomical factors—Although latitudinal trends were clear within *Cornus* s.l. as a whole (Noshiro and Baas, 1998), trends can differ in the two species groups in the Old and New Worlds, which diverged from each other in the early Tertiary or before (Tiffney, 1985; Rogers, 1993). Latitudinal trends for the Old and New World specimens, depicted using the data of Noshiro and Baas (1998), were similar; both have a significant correlation at the 0.5% level (Figs. 11–13). According to the regression lines, from 0° to 50° latitude vessel element length decreases 52 and 46%, fiber length 45 and 53%, and tangential vessel diameter 47 and 52% in the Old and New Worlds, respectively. Thus, the Old World and New World species groups of *Cornus* s.l. have similar latitudinal trends in wood anatomical features, though it is not clear whether the separation of the two groups happened before the establishment of latitudinal trends or vice versa.

In our systematic wood anatomical study of Cornaceae and allies (Noshiro and Baas, 1998), the existence of latitudinal trends for *Cornus* s.l. was recorded, but the trends were not analyzed statistically against nonanatomical factors. At the genus level, nonanatomical factors, i.e., latitude and climatic factors, have a highly significant correlation with wood anatomical characters in *Cornus* s.l. (Table 3). Except for the vessel grouping index for *C. controversa*, all the other wood anatomical characters have a significant correlation with the four nonanatomical factors. Among the nonanatomical factors, latitude clearly has the highest correlation with wood anatomical factors. Distribution of climatic factors is strongly influenced by the distribution of land and sea (Monin, 1975; Crowley and North, 1991) and is not correlated linearly with latitude. A

TABLE 3. Correlation table of nonanatomical data and wood anatomical characters of *Cornus* s.l. Lat: latitude, ART: annual range of temperature, WI: warmth index, AP: annual precipitation, VEL: vessel element length, FL: fiber length, VF: vessel frequency, TVD: tangential vessel diameter.

N = 84	Lat	ART	WI	AP	VEL	FL	VF	TVD
Latitude	–							
Annual range of temperature	0.674**	–						
Warmth index	−0.718**	−0.478**	–					
Annual precipitation	−0.448**	−0.125	0.598**	–				
Vessel element length	−0.720**	−0.428**	0.522**	0.412**	–			
Fiber length	−0.718**	−0.415**	0.601**	0.545**	0.898**	–		
Vessel frequency	0.539**	0.414**	−0.492**	−0.447**	−0.494**	−0.606**	–	
Tangential vessel diameter	−0.644**	−0.432**	0.447**	0.456**	0.548**	0.555**	−0.721**	–
Vessel grouping index	−0.309**	−0.157	0.045	−0.018	0.254	0.115	−0.140	0.365**

Significance level: ** = 0.5%, * = 1%.

stronger correlation of wood anatomical characters with latitude than with climatic factors seems to indicate a direct influence of more latitudinally linear geophysical factors on wood structure, such as gravity, intensity of solar radiation, or length of photoperiod. Another possibility is that some unknown ecological parameters resulting from a combination of climatic and/or geophysical factors may have latitudinally linear trends and may affect wood anatomy in ways not clarified by simple correlation analysis of individual parameters. One or several of these parameters must have influenced wood structure along with the adaptive radiation of constituent species within *Cornus* s.l.

Latitudinal trends are similar to ecological trends along the mesic to xeric gradient shown in many systematic wood anatomical studies by Carlquist (1975b, 1988), in floristic wood anatomical studies such as Baas, Werker, and Fahn (1983), Baas and Schweingruber (1987), Carlquist (1975a), and Carlquist and Hoekman (1985), or in other systematic works such as Zhang, Baas, and Zandee (1992). This comparison is well illustrated in the diagram of Dickison (1989), where decrease in vessel element length and vessel diameter and increase in vessel frequency commonly occur in gradients toward the cool temperate or montane or xeric habitats from the tropical mesic one. In two phylogenetically divergent genera, *Hibbertia* (Dilleniaceae) and *Erythroxylum* (Erythroxylaceae), Rury and Dickison (1984) showed that not just wood anatomy, but plant stature and leaf morphology and anatomy were clearly correlated with a gradient of water availability. The adaptive merits of latitudinal or ecological trends in wood structure are obscure at present, especially for vessel element and fiber lengths (Baas, 1982). The similarity in latitudinal and altitudinal trends to mesic to xeric trends must be related with physiology and ecology of respective species, and their relationship should be clarified in relation to the phylogenetic diversification of species in respective genera.

Comparison of the genus- and the species-level trends in Cornus s.l.—*Cornus* s.l. as a whole has more marked latitudinal trends and its characters vary more than the three Asiatic species. Between 30° and 40° N, a latitudinal range common to the three species, vessel element length, fiber length, and tangential vessel diameter for the whole genus decreased 14.5% from 1149 μm, 15.6% from 1680 μm, and 14.8% from 55 μm, respectively, according to the linear regression for *Cornus* s.l. and using data from additional specimens to the materials studied by Noshiro and Baas (1998). Within the same latitudinal range, vessel element length, fiber length, and tangential vessel diameter decreased 2.5, 5.3, and 2.4% in *Cornus controversa*, 5.3, 7.8, and −8.33% in *C. kousa* excluding samples of the Ishigaki Island, and 4.3, 1.8 and −6.0% in *C. macrophylla* excluding Nepalese samples, respectively. For vessel frequency, trends differed between species and genus levels, and species-level trends had a linear increase or decrease, whereas the genus-level trend had a more or less curvilinear increase (Noshiro and Baas, 1998). The relative amount of variation at the species and genus levels can be compared by employing coefficients of variation, i.e., the standard deviation expressed as a percentage of the average corrected to exclude the effect of sample size. The coefficients for vessel element length, fiber length, vessel frequency, and tangential vessel diameter range from 9.1 to 11.7%, 8.5 to 10.6%, 19.7 to 24.8%, and 9.2 to 12.0%, respectively, for the three species, but these values are twice as large, 21.4%, 23.1%, 51.7%, and 24.4%, respectively, for *Cornus* s.l.

In the latitudinal plots of wood anatomical features, the values for the three Asiatic species are relatively high, compared with the regression lines for *Cornus* s.l. (Figs. 11–13). This trend is especially marked in the tangential vessel diameter of *Cornus controversa* and *C. macrophylla.* This difference probably derives from the small size of trees from southern localities used for the systematic study of Cornaceae and allies (Noshiro and Baas, 1998). In the present study, most samples were obtained from large mature individuals, whereas xylarium specimens from small individuals were used in the systematic study. Thus, among the samples for the species-level studies, xylarium specimens used in the previous systematic study are scattered at the lower end of the ontogenetic trends (Fig. 7). Moreover, the localities of the xylarium specimens were confined to the southern part of the specific distribution ranges, 31°–36° N for *C. controversa* specimens, 31°–36° N for *C. kousa* specimens, and 27°–36° N for *C. macrophylla* specimens. Even if such bias exists in xylarium specimens, the general latitudinal trends in wood anatomical characters are manifest. If we could have used only fully mature wood samples in the systematic study, the regression lines for the genus may have even been steeper than those shown in the systematic study.

Evolutionary scenario—*Cornus* s.l. has clear latitudinal trends in wood structure, mostly a highly significant linear decrease in fusiform cell size along the whole distribution range, whereas each species has narrower variation without any latitudinal or altitudinal gradients. Differences in latitudinal trends at the genus and species levels in *Cornus* s.l. remain to be explained.

Though at present climatic factors show a weaker correlation with wood anatomical features than latitude, historically climate must have influenced wood structure as a water transporting system. Paleoclimatological data indicate that in the mid-Cretaceous a warmer climate prevailed, especially at high latitudes, with a gentler latitudinal gradient than at present (Crowley and North, 1991). With a major climatic degradation at the end of Eocene, climate became cooler and seasonality became more manifest (Wolfe, 1978, 1992, 1994). Wood anatomical features of dicotyledons were affected by these changes in climate since the Cretaceous, and percentages of short vessel elements increased over time together with an increased incidence of distinct growth rings, implying increased seasonality (Wheeler and Baas, 1991, 1993). Quantitative wood anatomical ranges within a genus and its constituent species may have been narrow when the genus became a distinct entity in the late Cretaceous or early Tertiary, when the warmer climate prevailed and the latitudinal climatic gradient was gentle. With the development of more variable climate with distinct seasonality in the late Tertiary, these quantitative features likely became more variable with the adaptive radiation of various species.

Paleobotanical evidence shows diversification of *Cornus* s.l. in the Tertiary at least since the Eocene, but there seems to be no concrete Cretaceous record of this genus so far (Suzuki, 1982; Eyde, 1988; Taylor, 1990; Taylor and Taylor, 1993; Mai, 1995). Eyde (1988) reviewed reports of *Cornus* fossils and regarded Eocene fruit stones as the oldest authentic record of this genus. At present it is not clear when in the Tertiary diversification and adaptive radiation in *Cornus* s.l. was most active, and how these correlated with climatic degradation and steepening of latitudinal gradients.

Vessel elements and fibers in the secondary xylem of woody dicotyledons derive from fusiform initials in the cambium. Vessel element length nearly equals the length of fusiform initials in the cambium (Bailey, 1920). Bailey and Tupper (1918) and Bailey's students clarified evolution of various wood structural features of angiosperms in line with the reduction in tracheary element length from gymnosperms tracheids to angiosperms vessels. The present study suggests that, beside this large-scale evolutionary trend in the whole angiosperms, length of vessel elements or fusiform initials and other related quantitative features also have a distinct evolutionary history for individual genera involving ecological (latitudinal) adaptation.

LITERATURE CITED

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

———. 1982. Systematic, phylogenetic, and ecological wood anatomy—history and perspectives. *In* P. Baas [ed.], New perspectives in wood anatomy, 23–58. Martinus Nijhoff/Dr. W. Junk, The Hague, The Netherlands.

———, AND F. H. SCHWEINGRUBER. 1987. Ecological trends in the wood anatomy of trees, shrubs and climbers from Europe. *IAWA Bulletin new series* 8: 245–274.

———, E. WERKER, AND A. FAHN. 1983. Some ecological trends in vessel characters. *IAWA Bulletin new series* 4: 141–159.

BAILEY, I. W. 1920. The cambium and its derivative tissues. II. Size variation of cambium initials in gymnosperms and angiosperms. *American Journal of Botany* 7: 355–367.

———, AND W. W. TUPPER. 1918. Size variation in tracheary cells: I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. *Proceedings of the American Academy of Arts and Sciences* 54: 149–204.

BISSET, I. J. W., AND H. E. DADSWELL. 1950. The variation in cell length with one growth ring of certain angiosperms and gymnosperms. *Australian Forestry* 14: 17–25.

CARLQUIST, S. 1975a. Ecological factors in wood evolution: a floristic approach. *Americal Journal of Botany* 64: 887–896.

———. 1975b. Ecological strategies of xylem evolution. University of California Press, Berkeley, California, USA.

———. 1988. Comparative wood anatomy. Springer-Verlag, Berlin, Germany.

———, AND D. A. HOEKMAN. 1985. Ecological wood anatomy of the woody southern Californian flora. *IAWA Bulletin new series* 6: 319–347.

CROWLEY, T. J., AND G. R. NORTH. 1991. Paleoclimatology. Oxford University Press, New York, New York, USA.

DICKISON, W. C. 1989. Steps toward the natural system of the dicotyledons: vegetative anatomy. *Aliso* 12: 555–566.

EYDE, R. H. 1987. The case for keeping *Cornus* in the broad Linnaean sense. *Systematic Botany* 12: 505–518.

———. 1988. Comprehending *Cornus*: puzzles and progress in the systematics of the dogwoods. *Botanical Review* 54: 233–351.

FURUKAWA, I., M. SEKOGUCHI, M. MATSUDA, T. SAKUNO, AND J. KISHIMOTO. 1983. Wood quality of small hardwoods (II). Horizontal variations in the length of fibers and vessel elements in seventy-one species of small hardwoods. *Hardwood Research* Number 2: 103–134.

HEJNOWICZ, A., AND Z. HEJNOWICZ. 1958. Variations of length of vessel members and fibres in the trunk of *Populus tremula* L. *Acta Societatis Botanicorum Poloniae* 27: 131–159.

KIRA, T. 1949. Forest zones of Japan. Technological Association of Forestry, Tokyo, Japan.

MAI, D. H. 1995. Tertiäre Vegetationsgeschichte Europas. Gustav Fischer, Jena, Germany.

MONIN, A. S. 1975. The role of the oceans in climatic models. *In* Physical basis of climate and climate modelling, Report Number 16. GARP Publications Series., 210–205. World Meteorological Organization, Geneva, Switzerland.

MURRELL, Z. E. 1993. Phylogenetic relationships in *Cornus* (Cornaceae). *Systematic Botany* 18: 469–495.

NOSHIRO, S., AND P. BAAS. 1998. Systematic wood anatomy of Cornaceae and allies. *IAWA Journal* 19: 43–97.

———, L. JOSHI, AND M. SUZUKI. 1994. Ecological wood anatomy of *Alnus nepalensis* (Betulaceae) in East Nepal. *Journal of Plant Research* 107: 399–408.

———, AND M. SUZUKI. 1995. Ecological wood anatomy of Nepalese *Rhododendron* (Ericaceae). 2. Intraspecific variation. *Journal of Plant Research* 108: 217–233.

———,———, AND H. OHBA. 1995. Ecological wood anatomy of Nepalese *Rhododendron* (Ericaceae). 1. Interspecific variation. *Journal of Plant Research* 108: 1–9.

ROGERS, J. J. 1993. A history of the earth. Cambridge University Press, Cambridge, UK.

RURY, P. M., AND W. C. DICKISON. 1984. Structural correlations among wood, leaves and plant habit. *In* R. A. White and W. C. Dickison [eds.], Contemporary problems in plant anatomy, 495–540. Academic Press, Orlando, Florida, USA.

SASTRAPRADJA, D. S., AND C. LAMOUREUX. 1969. Variation in wood anatomy of Hawaiian *Metrosideros* (Myrtaceae). *Annales Bogorienses* 5: 1–83.

SUGAWA, T. 1979. Properties of the important Japanese woods. Anatomical properties (I) Fiber length of the important Japanese hardwoods. *Bulletin of the Forestry and Forest Products Research Institute* Number 306: 135–167.

SÜSS, H. 1967. Über die Längenänderungen der Parenchymstränge, Holzfasern und Gefässglieder von Laubhölzern im Verlauf einer Zuwachsperiode. *Holz als Roh- und Werkstoff* 10: 369–377.

SUZUKI, M. 1982. Some fossil woods from the Palaeogene of Northern Kyushu, II. *Botanical Magazie Tokyo* 95: 281–294.

SWAMY, B. G. L., N. PARAMESWARAN, AND E. GOVINDARAJULU. 1960. Variation in vessel length within one growth ring of certain arborescent dicotyledons. *Journal of the Indian Botanical Society* 39: 163–170.

TAYLOR, D. W. 1990. Paleobiogeographic relationships of angiosperms from the Cretaceous and early Tertiary of the North American area. *Botanical Review* 56: 279–417.

TAYLOR, T. N., AND E. L. TAYLOR. 1993. The biology and evolution of fossil plants. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

TIFFNEY, B. H. 1985. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. *Journal of the Arnold Arboretum* 66: 243–273.

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

VAN DEN OEVER, L., P. BAAS, AND M. ZANDEE. 1981. Comparative wood anatomy of *Symplocos* and latitude and altitude of provenance. *IAWA Bulletin new series.* 2: 3–24.

WHEELER, E. A., AND P. BAAS. 1991. A survey of the fossil record for dicotyledonous wood and its significance for evolutionary and ecological wood anatomy. *IAWA Bulletin new series* 12: 275–332.

———, AND———. 1993. The potentials and limitations of dicotyledonous wood anatomy for climatic reconstruction. *Paleobiology* 19: 487–498.

WOLFE, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *American Scientist* 66: 694–703.

———. 1992. Climatic, floristic, and vegetational changes near the Eocene-Oligocene boundary in North America. *In* D. R. Prothero and W. A. Berggren [eds.], Eocene-Oligocene climatic and biotic evolution, 421–436. Princeton University Press, Princeton, New Jersey, USA.

———. 1994. Tertiary climatic changes at middle latitudes of western North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108: 95–105.

XIANG, Q.-Y., S. J. BRUNSFELD, D. E. SOLTIS, AND P. S. SOLTIS. 1996. Phylogenetic relationships in *Cornus* based on chloroplast DNA restriction sites: Implications for biogeography and character evolution. *Systematic Botany* 21: 515–534.

———, AND D. E. SOLTIS. 1998. *RbcL* sequence data define a cornaceous clade and clarify relationships of Cornaceae sensu lato. *In* D. E. Boufford and H. Ohba [eds.], Sino-Japanese flora: its characteristics and diversification. University Museum, University of Tokyo, Bulletin Number 37, 123–137. Tokyo University Press, Tokyo, Japan.

———,———, D. R. MORGAN, AND P. S. SOLTIS. 1993. Phylogenetic relationships of *Cornus* L. sensu lato and putative relatives inferred from *rbcL* sequence data. *Annals of the Missouri Botanical Garden* 80: 723–734.

———,———, AND P. S. SOLTIS. 1998. Phylogenetic relationships of Cornaceae and close relatives inferred from *matK* and *rbcL* sequences. *American Journal of Botany* 85: 285–297.

ZHANG, S.-Y., P. BAAS, AND M. ZANDEE. 1992. Wood structure of the Rosaceae in relation to ecology, habitat and phenology. *IAWA Bulletin New Series* 13: 307–349.

APPENDIX

Cornus controversa Hemsl. ex Prain

JAPAN—Hokkaido: Sarufutsu, Soya, 110 m, 45.3° N, H 14 m, DBH 21 cm, Noshiro 970710–1; do., 150 m, 45.3° N, H 15 m, DBH 39 cm, Noshiro 970710–2; Toyotomi, Teshio, 120 m, 45.1° N, H 14 m, DBH 29 cm, Noshiro 970710–3; Nakagawa, Nakagawa, 90 m, 44.65° N, H 11 m, DBH 24 cm, Noshiro 970710–4; Shimokawa, Kamikawa, 330 m, 44.45° N, H 14 m, DBH 29 cm, Noshiro 970711–1; Uryu, 350 m, 44.4° N, DBH 8 cm, KYOw 9256; do., 380 m, 44.2° N, H 15 m, DBH 37 cm, Noshiro 970711–2; Aibetsu, Kamikawa, 450 m, 44° N, H 12 m, DBH 20 cm, Noshiro 970711–3; do., 400 m, 44° N, H 14 m, DBH 33 cm, Noshiro 970711–4; Biei, Kamikawa, 340 m, 43.5° N, H 15 m, DBH 29 cm, Noshiro 970712–8; do., 340 m, 43.5° N, H 13 m, DBH 19 cm, Noshiro 970712–9; Naka-furano, 380 m, 43.4° N, H 12 m, DBH 30 cm, Noshiro 970712–7; Mt. Ashibetsu, 300 m, 43.3° N, DBH 17 cm, TWTw 713; Furano, 350 m, 43.3° N, DBH 16 cm, TWTw 5794; Onbetsu, Shiranuka, 230 m, 43.1° N, H 11 m, DBH 15 cm, M.Suzuki s.n.; Tomakomai, 70 m, 43° N, H 12 m, DBH 16 cm, TWTw 16846; Hidaka, Saru, 530 m, 42.95° N, H 14 m, DBH 22 cm, Noshiro 970712–1; do., 330 m, 42.9° N, H 17 m, DBH 29 cm, Noshiro 970712–2; do., 330 m, 42.9° N, H 13 m, DBH 20 cm, Noshiro 970712–3; Monbetsu, Saru, 200 m, 42.6° N, H 10 m, DBH 18 cm, Noshiro 970712–4; do., 180 m, 42.6° N, H 12 m, DBH 23 cm, Noshiro 970712–5; do., 160 m, 42.6° N, H 17 m, DBH 29 cm, Noshiro 970712–6. —**Aomori**: Hiranai, 50 m, 40.9° N, H 12 m, DBH 30 cm, Noshiro 961024–8; Shingo, 310 m, 40.4° N, H 12 m, DBH 22.5 cm, Noshiro 961024–1; do., 355 m, 40.4° N, H 15 m, DBH 25 cm, Noshiro 961024–2; do., 390 m, 40.4° N, H 15 m, DBH 25 cm, Noshiro 961024–3.—**Akita**: Kosaka, 650 m, 40.4° N, H 13 m, DBH 36 cm, Noshiro 961024–4.—**Iwate**: Iwa-izumi, 70 m, 39.8° N, H 14 m, DBH 20 cm, Noshiro 961025–1; Tarou, 25 m, 39.75° N, H 18 m, DBH 30 cm, Noshiro 961025–2; Miyako, 60 m, 39.7° N, H 12 m, DBH 26 cm, Noshiro 961025–4; Oohasama, 500 m, 39.6° N, H 19 m, DBH 25 cm, Noshiro 961025–5; do., 500 m, 39.6° N, H 20 m, DBH 28 cm, Noshiro 961025–6; do., 600 m, 39.6° N, H 14 m, DBH 18.5 cm, Noshiro 961025–7.—**Miyagi**: Naruko, 500 m, 38.75° N, DBH 15.5 cm, TUSw 10559; Sendai, 158 m, 38.25° N, H 8.7 m, DBH 16.1 cm, A 15; do., 158 m, 38.25° N, H 8.55 m, DBH 14.8 cm, A 16; do., 158 m, 38.25° N, H 11.2 m, DBH 19.5 cm, A 18; do., 165 m, 38.25° N, DBH 34 cm, TUSw 10509; Shichikashuku, 450 m, 38° N, H 8 m, DBH 32 cm, Noshiro 4900.—**Yamagata**: Kaminoyama, 310 m, 38.1° N, DBH 13 cm, TWTw 16842; Oguni, 500 m, 37.9° N, H 4.5 m, DBH 12 cm, Noshiro 4888; Yonezawa, 495 m, 37.9° N, H 13 m, DBH 32 cm, Noshiro 980629–4; do., 730 m, 37.8° N, H 14 m, DBH 23 cm, Noshiro 980630–1.—**Fukushima**: Shinobu Spa, 410 m, 37.75° N, H 14 m, DBH 43 cm, Noshiro 980629–1; Mt. Azuma, 1020 m, 37.75° N, H 12 m, DBH 32 cm, Noshiro 980629–2; Inawashiro, 950 m, 37.65° N, H 14 m, DBH 32 cm, Noshiro 980629–3.—**Ibaraki:** Mt. Yamizo, 450 m, 36.9° N, H 11 m, DBH 20 cm, Noshiro 4912; Mt. Nantai, 300 m, 36.7° N, H 8 m, DBH 10.5 cm, Noshiro 960923–1; do., 330 m, 36.7° N, H 11 m, DBH 34 cm, Noshiro 960923–2; do., 490 m, 36.7° N, H 19 m, DBH 24 cm, Noshiro 960923–6; Hitachi, 280 m, 36.6° N, DBH 7 cm, TWTw 4294.—**Gunma**: Shimonita, 950 m, 36.3° N, H 16 m, DBH 52 cm, Noshiro 980607–2.—**Saitama**: Chichibu Tokyo Univ. For., 750 m, 35.9° N, DBH 10 cm, TWTw 568; do., 750 m, 35.9° N, DBH 14 cm, TWTw 1138; do., 750 m, 35.9° N, DBH 10 cm, TWTw 1389; do., 750 m, 35.9° N, DBH 22 cm, TWTw 4333; do., 750 m, 35.9° N, DBH 12 cm, TWTw 12002.—**Chiba**: Chiba Tokyo Univ. For., 300 m, 35.2° N, DBH 8 cm, TWTw 437; do., 200 m, 35.2° N, DBH 20 cm, TWTw 3411; do., 200 m, 35.2° N, DBH 10 cm, TWTw 13356.—**Kanagawa**: Hakone, 850 m, 35.2° N, H 12 m, DBH 30 cm, Noshiro 4933; do., 370 m, 35.2° N, H 16 m, DBH 34 cm, Noshiro 961011–1; do., 360 m, 35.2° N, H 12 m, DBH 28 cm, Noshiro 961011–2; do., 360 m, 35.2° N, H 10 m, DBH 21 cm, Noshiro 961011–3; do., 335 m, 35.2° N, H 18 m, DBH 33 cm, Noshiro 961011–7; do., 770 m, 35.2° N, H 13 m, DBH 35 cm, Noshiro 961011–10; do., 770 m, 35.2° N, H 12 m, DBH 37 cm, Noshiro 961011–11; do., 760 m, 35.2° N, H 12 m, DBH 35 cm, Noshiro 961011–12.—**Tokyo**: Hachijo Is., 520 m, 33.1° N, H 13 m, DBH 19 cm, TWTw 17361.—**Ishikawa**: Mt. Iou, 550 m, 36.5° N, H 15 m, DBH 32 cm, Noshiro 980517–1; do., 570 m, 36.5° N, H 12 m, DBH 29 cm, Noshiro 980517–2.—**Nagano**: Mugikusa Pass, 1580 m, 36.1° N, H 9 m, DBH 21 cm, Noshiro 960916–1; do., 1245 m, 36.1° N, H 12 m, DBH 29 cm, Noshiro 960916–2; Ina, 1320 m, 35.9° N, H 6 m, DBH 7 cm, TWTw 16302; do., 980 m, 35.9° N, H 8 m, DBH 16 cm, TWTw 16318; do., 1050 m, 35.8° N, H 8 m, DBH 21 cm, TWTw 16298; do., 940 m, 35.8° N, H 10 m, DBH 16 cm, TWTw 16299; Kiso, Ohtaki, 1100 m, 35.8° N, DBH 11 cm, TWTw 636.—**Gifu**: Neo, 450 m, 35.75° N, H 8 m, DBH 12 cm, TWTw 13917.—**Shizuoka**: Gotenba, 1200 m, 35.3° N, DBH 28 cm, TWTw 9342; Honkawane, 990 m, 35.25° N, H 15 m, DBH 27 cm, TWTw 17541. —**Wakayama**: Hongu, 350 m, 33.75° N, DBH 7.3 cm, OSAw 109; Kozagawa, 250 m, 33.7° N, DBH 30 cm, KYOw 9328.—**Shimane**: Izumo, 50 m, 35.3° N, DBH 11.8 cm, KYOw 1662; Tonbara, 450 m, 35.1° N, DBH 9.1 cm, KYOw 7516; Kijima, 720 m, 35° N, DBH 22.2 cm, KYOw 1710.—**Tokushima**: Ichiu, 1230 m, 33.9° N, H 8 m, DBH 19 cm, Noshiro 961028–2; do., 1350 m, 33.9° N, H 11 m, DBH 22 cm, Noshiro 961028–3; Mt. Marugasa, 1250 m, 33.9° N, H 15 m, DBH 28 cm, Noshiro 961028–5; do., 820 m, 33.9° N, H 24 m, DBH 65 cm, Noshiro 961028–7; Kisawa, 960 m, 33.9° N, H 17 m, DBH 25 cm, Noshiro 961029–1; do., 930 m, 33.9° N, H 14 m, DBH 35 cm, Noshiro 961029–3; do., 555 m, 33.85° N, H 20 m, DBH 40 cm, Noshiro 961029–11; Mt. Tsurugi, 1190 m, 33.85° N, H 20 m, DBH 55 cm, Noshiro 961029–7; Kaminaka, 460 m, 33.75° N, H 16 m, DBH 19 cm, Noshiro 961029–13; do., 490 m, 33.75° N, H 22 m, DBH 30 cm, Noshiro 961029–15.—**Kochi**: Kitagawa, 230 m, 33.5° N, H 16 m, DBH 32 cm, Noshiro 961030–2—**Ooita**: Mt. Kurodake, 890 m, 33.1° N, H 11 m, DBH 31 cm, Noshiro 961016–7; do., 890 m, 33.1° N, H 9 m, DBH 24 cm, Noshiro 961016–9; do, 800 m, 33.1° N, H 10 m, DBH 20 cm, Noshiro 961016–11; Ume, 355 m, 32.8° N, H 12 m, DBH 20 cm, Noshiro 961017–3; do., 510 m, 32.8° N, H 12.5 m, DBH 21 cm, Noshiro 961017–4; do., 510 m, 32.8° N, H 12 m, DBH 18 cm, Noshiro 961017–5.—**Miyazaki**: Hourigawa, Kitagawa, 200 m, 32.7° N, H 16 m, DBH 22 cm, Noshiro 961017–7; Shiiba, 1420 m, 32.6° N, H 18 m, DBH 31 cm, Noshiro 961015–1; do., 1420 m, 32.6° N, H 17 m, DBH 35 cm, Noshiro 961015–2; do., 980 m, 32.4° N, H 17 m, DBH 30 cm, Noshiro 961014–10; do., 1010 m, 32.4° N, H 12 m, DBH 26 cm, TWTw 17047; Nishi-mera, 250 m, 32.25° N, H 15 m, DBH 36 cm, Noshiro 961014–8; do., 280 m, 32.25° N, H 10 m, DBH 25 cm, Noshiro 961014–9; Saito, 210 m, 32.2° N, H 7.5 m, DBH 11 cm, Noshiro 961014–6; do., 220 m, 32.2° N, H 8 m, DBH 12.5 cm, Noshiro 961014–7; Kitago, 450 m, 31.8° N, H 10 m, DBH 26 cm, Noshiro 961013–1; do., 460 m, 31.8° N, H 8 m, DBH 28 cm, Noshiro 961013–2; do., 450 m, 31.8° N, H 15 m, DBH 24 cm, Noshiro 961013–3; Mt. Wanizuka, 880 m, 31.8° N, H 11 m, DBH 24 cm, Noshiro 961013–5; do., 850 m, 31.8° N, H 11 m, DBH 26 cm, Noshiro 961013–6; do., 840 m, 31.8° N, H 18 m, DBH 30 cm, Noshiro 961013–7; Obi, 600 m, 31.7° N, DBH 8 cm, TWTw 12290.—**Kumamoto**: Yabe, 1500 m, 32.6° N, H 17 m, DBH 37 cm, Noshiro 961015–3; Mizukami, 1130 m, 32.4° N, H 17 m, DBH 35 cm, Noshiro 961014–11; do., 1130 m, 32.4° N, H 22 m, DBH 35 cm, Noshiro 961014–12; Hitoyoshi, 700 m, 32.2° N, DBH 15 cm, TWTw 12289.—**Kagoshima**: Tarumizu, 450 m, 31.5° N, DBH 9 cm, TWTw 13510.

Cornus kousa Buerger ex Miq.

JAPAN—Aomori: Towada Lake, 540 m, 40.5° N, H 9 m, DBH 24 cm, Noshiro 961024–5; do., 540 m, 40.5° N, H 7 m, DBH 19 cm, Noshiro 961024–6; do., 403 m, 40.5° N, H 10 m, DBH 33 cm, Noshiro 961024–7.—**Iwate**: Shizukuishi, 450 m, 39.7° N, DBH 16 cm, TWTw 378.—**Miyagi**: Naruko, 500 m, 38.75° N, DBH 15 cm, TUSw 10558.—**Yamagata**: Kamino-yama, 330 m, 38.1° N, DBH 11 cm, TWTw 16843; Yonezawa, 750 m, 37.8° N, H 8 m, DBH 13 cm, Noshiro 980629–5.—**Tochigi**: Mt. Nasu, 800 m, 37.1° N, H 7 m, DBH 14 cm, Noshiro 4923; Funyu, 350 m, 36.75° N, DBH 10 cm, TWTw 1795; Ashio, 1250 m, 36.75° N, DBH 8 cm, TWTw 2560.—**Gunma**: Tone, 900 m, 36.7° N, DBH 20 cm, TWTw 132; Shimonita, 950 m, 36.3° N, H 10 m, DBH 16 cm, Noshiro 980607–1; do., 950 m, 36.3° N, H 8 m, DBH 13 cm, Noshiro 980607–3.—**Ibaraki:** Mt. Nantai, 620 m, 36.7° N, H 9 m, DBH 20 cm, Noshiro 960923–4; do., 550 m, 36.7° N, H 12 m, DBH 29 cm, Noshiro 960923–5; do., 530 m, 36.7° N, H 12 m, DBH 22 cm, Noshiro 960923–7.—**Saitama**: Chichibu Tokyo Univ. For., 850 m, 35.9° N, DBH 9 cm, TWTw 1172; do., 850 m, 35.9° N, DBH 12 cm, TWTw 12003.—**Chiba**: Chiba Tokyo Univ. For., 200 m, 35.2° N, DBH 9 cm, TWTw 427; do., 250 m, 35.2° N, DBH 16 cm, TWTw 3412.—**Kanagawa**: Hakone, 770 m, 35.2° N, H 12 m, DBH 32 cm, Noshiro 4934; do., 280 m, 35.2° N, H 7.5 m, DBH 14 cm, Noshiro 961011–5; do., 760 m, 35.2° N, H 10 m, DBH 28 cm, Noshiro 961011–9; do., 750 m, 35.2° N, H 10 m, DBH 23 cm, Noshiro 961011–13; do., 740 m, 35.2° N, H 9 m, DBH 33 cm, Noshiro 961011–14; do., 1285 m, 35.2° N, H 4 m, DBH 10.5 cm, Noshiro 961011–15; do., 1250 m, 35.2° N, H 6 m, DBH 28 cm, Noshiro 961011–16; do., 1270 m, 35.2° N, H 12 m, DBH 20 cm, Noshiro 961011–17.—**Ishikawa**: Kanazawa, 520 m, 36.4° N, DBH 8 cm, TWTw 14948.—**Gifu**: Neo, 850 m, 35.75° N, H 7 m, DBH 10 cm, TWTw 13932.—**Kyoto**: Asiu, Miyama, 550 m, 35.3° N, DBH 6 cm, TWTw 5891; do., 760 m, 35.3° N, H 3 m, DBH 8.5 cm, TWTw 14829; do., 600 m, 35.3° N, DBH 7.1 cm, KYOw 9573.—**Shimane**: Izumo, 200 m, 35.3° N, DBH 14.8 cm, KYOw 1663; Tonbara, Shimane, 450 m, 35.1° N, DBH 17.5 cm, TWTw 16845.—**Tokushima**: Mt. Marugasa, 1400 m, 33.9° N, H 7 m, DBH 13 cm, Noshiro 961028–1; do., 1350 m, 33.9° N, H 6 m, DBH 15 cm, Noshiro 961028–4; Koyadaira, 1340 m, 33.9° N, H 8 m, DBH 18 cm, Noshiro 961029–4; do., 1340 m, 33.9° N, H 5 m, DBH 13 cm, Noshiro 961029–5; do., 1300 m, 33.9° N, H 8 m, DBH 21 cm, Noshiro 961029–6.—**Kochi**: Higashi-tsuno, 920 m, 33.45° N, H 6 m, DBH 4 cm, TWTw 15893.—**Ooita**: Mt. Kuroiwa, 1270 m, 33.1° N, H 11 m, DBH 25 cm, Noshiro 961016–1; do., 1190 m, 33.1° N, H 6 m, DBH 15 cm, Noshiro 961016–3; Mt. Kurodake, 900 m, 33.1° N, H 7 m, DBH 17 cm, Noshiro 961016–5; do., 890 m, 33.1° N, H 7 m, DBH 18 cm, Noshiro 961016–6.—**Miyazaki**: Shiiba, 1440 m, 32.35° N, H 5 m, DBH 11 cm, TWTw 17070; Ebino, 1140 m, 31.95° N, H 7.5 m, DBH 11 cm, Noshiro 961014–1.– **Kumamoto**: Yabe, 1480 m, 32.6° N, H 11 m, DBH 28 cm, Noshiro 961015–4.—**Kagoshima**: Tarumizu, 700 m, 31.5° N, DBH 8 cm, TWTw 13511; Yaku Is., 1370 m, 30.3° N, H 7 m, DBH 16 cm, TWTw 16005; do., 1370 m, 30.3° N, H 5 m, DBH 6.5 cm, TWTw 16008.—**Okinawa**: Ishigaki Is., 230 m, 24.4° N, H 11 m, DBH 15 cm, Noshiro 9804001; do., 240 m, 24.4° N, H 12 m, DBH 23 cm, Noshiro 9804002; do., 220 m, 24.4° N, H 11 m, DBH 20 cm, Noshiro 9804003.

Cornus macrophylla Wall.

JAPAN—Aomori: Hiranai, 30 m, 40.95° N, H 9 m, DBH 19 cm, Noshiro 961024–10; do., 50 m, 40.95° N, H 13 m, DBH 27 cm, Noshiro 961024–11; do., 100 m, 40.95° N, H 11 m, DBH 31 cm, Noshiro 961024–12; do., 60 m, 40.9° N, H 9 m, DBH 13 cm, Noshiro 961024–9.—**Iwate**: Tarou, 20 m, 39.75° N, H 11 m, DBH 25 cm, Noshiro 961025–3.—**Miyagi**: Ishinomaki, 70 m, 38.5° N, H 12 m, DBH 23.3 cm, K.Yoda 163; do., 70 m, 38.5° N, H 8 m, DBH 22.7 cm, K.Yoda 172; do., 70 m, 38.5° N, H 13 m, DBH 28 cm, K.Yoda 174; do., 70 m, 38.5° N, H 8 m, DBH 17.5 cm, K.Yoda 187; Sendai, 100 m, 38.25° N, DBH 7 cm, TUSw 10560.—**Yamagata**: Kamino-yama, 340 m, 38.1° N, DBH 12 cm, TWTw 16844; Takahata, 380 m, 38° N, H 14 m, DBH 23 cm, Noshiro 980630–2.—**Ibaraki:** Mt. Nantai, 330 m, 36.7° N, H 9 m, DBH 20 cm, Noshiro 960923–3; do., 160 m, 36.7° N, H 18 m, DBH 26.5 cm, Noshiro 960923–8.—**Chiba**: Chiba Tokyo Univ. For., 180 m, 35.2° N, DBH 6 cm, TWTw 465; do., 150 m, 35.2° N, DBH 15 cm, TWTw 3410; do., 150 m, 35.2° N, DBH 11 cm, TWTw 13357.—**Kanagawa**: Hakone, 310 m, 35.2° N, H 16 m, DBH 22 cm, Noshiro 961011–4; do., 280 m, 35.2° N, H 9 m, DBH 16 cm, Noshiro 961011–6; do., 350 m, 35.2° N, H 20 m, DBH 34 cm, Noshiro 961011–8.—**Ishikawa**: Kanazawa, 148 m, 36.6° N, H 13 m, DBH 24 cm, TUSw 10564; do., 280 m, 36.4° N, DBH 7 cm, TWTw 14968.—**Shizuoka**: Ito, 40 m, 34.9° N, H 9 m, DBH 28 cm, Noshiro 4936.—**Hyogo**: Kawanishi, 350 m, 34.9° N, DBH 8.4 cm, OSAw 210.—**Wakayama**: Kozagawa, 250 m, 33.7° N, DBH 18 cm, KYOw 9329.—**Shimane**: Matsue, 370 m, 35.5° N, DBH 7.7 cm, KYOw 7501.—**Tokushima**: Mt. Marugasa, 1050 m, 33.9° N, H 10 m, DBH 21 cm, Noshiro 961028–6; Kisawa, 900 m, 33.9° N, H 12 m, DBH 23 cm, Noshiro 961029–2; Mt. Tsurugi, 1350 m, 33.8° N, H 7 m, DBH 12 cm, Noshiro 961029–8; do., 1340 m, 33.8° N, H 7.5 m, DBH 12 cm, Noshiro 961029–9; do., 1130 m, 33.8° N, H 17 m, DBH 22 cm, Noshiro 961029–10; Kaminaka, 240 m, 33.8° N, H 14 m, DBH 19 cm, Noshiro 961029–12; do., 460 m, 33.75° N, H 12 m, DBH 16 cm, Noshiro 961029–14.—**Kochi**: Touyou, 50 m, 33.5° N, H 8 m, DBH 32 cm, Noshiro 961030–1; Saga, Hata, Kochi, 280 m, 33.1° N, H 9 m, DBH 9 cm, TWTw 15794; Kawasaki For. Sta., 300 m, 32.9° N, DBH 14 cm, TWTw 910.—**Fukuoka**: Gougawayama Nat. For., 500 m, 33.5° N, DBH 18 cm, TWTw 2251.—**Ooita**: Mt. Kurodake, 910 m, 33.1° N, H 9 m, DBH 17 cm, Noshiro 961016–4; do., 890 m, 33.1° N, H 12 m, DBH 18 cm, Noshiro 961016–8; do., 890 m, 33.1° N, H 12 m, DBH 32 cm, Noshiro 961016–10; Ume, 180 m, 32.85° N, H 10 m, DBH 25 cm, Noshiro 961016–12; do., 300 m, 32.8° N, H 13 m, DBH 21 cm, Noshiro 961017–1; do., 300 m, 32.8° N, H 16 m, DBH 27 cm, Noshiro 961017–2.—**Miyazaki**: Hourigawa, Kitagawa, 610 m, 32.75° N, H 20 m, DBH 42 cm, Noshiro 961017–6; Shiiba, 900 m, 32.4° N, H 12 m, DBH 17 cm, TWTw 16940; do., 960 m, 32.35° N, H 12 m, DBH 14 cm, TWTw 17033; Saito, 70 m, 32.2° N, H 11 m, DBH 19 cm, Noshiro 961014–2; do., 70 m, 32.2° N, H 10 m, DBH 19 cm, Noshiro 961014–3; do., 70 m, 32.2° N, H 12 m, DBH 23 cm, Noshiro 961014–4; do., 210 m, 32.2° N, H 14 m, DBH 27 cm, Noshiro 961014–5; Mt. Wanizuka, 610 m, 31.8° N, H 14 m, DBH 22 cm, Noshiro 961013–4; do., 840 m, 31.8° N, H 11 m, DBH 24 cm, Noshiro 961013–8; do., 830 m, 31.8° N, H 11 m, DBH 20 cm, Noshiro 961013–9; Obi, 500 m, 31.7° N, DBH 10 cm, TWTw 12288.—**Kagoshima**: Tarumizu, 450 m, 31.5° N, DBH 8 cm, TWTw 13509; Mt. Inao, 220 m, 31.1° N, DBH 12 cm, TWTw 14326; Yaku Is., 100 m, 30.4° N, H 8 m, DBH 20 cm, TWTw 16119; do., 50 m, 30.4° N, H 10 m, DBH 20 cm, TWTw 16163; do., 620 m, 30.3° N, H 9 m, DBH 14 cm, TWTw 16052. **NEPAL**:—**Manang:** Chame, 2620 m, 28.5° N, H 5 m, DBH 20 cm, H. Ohba et al. 8340304.—**Kasuki**: Ghandruk, 2280 m, 28.4° N, H 15 m, DBH 30 cm, H. Ohba et al. 8340106; do., 2250 m, 28.4° N, H 10 m, DBH 24 cm, M.Suzuki et al. 8840442.—**Sankhuwasabha**: Chyangrima, 2410 m, 27.83° N, H 7 m, DBH 15 cm, Noshiro et al. 9840120; Kipu Pokhari, 2630 m, 27.8° N, H 6.5 m, DBH 15 cm, Noshiro et al. 9840170.