Trees (2006) 20: 253–261
DOI 10.1007/s00468-005-0007-5

ORIGINAL ARTICLE

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Anatomical wood variation of *Buddleja cordata* (Buddlejaceae) along its natural range in Mexico

Received: 30 June 2003 / Accepted: 6 May 2005 / Published online: 25 December 2005

Abstract *Buddleja cordata* is an evergreen species of wide distribution in Mexico that is represented by shrubs and trees. Wood variability of *B. cordata* was evaluated in relation to plant size as well as latitude, altitude, soils, and climatic data. Canonical correlation analysis (CCA) showed that two canonical correlations are significant (Wilks' λ, $p<0.0001$) and explained 76% of total variance. Redundancy analysis revealed that the first pair of canonical variates are significant, thus the canonical variate, named distribution, represents a gradient of maximum temperature of the warmest period, annual temperature range, and latitude in its area of distribution; whereas the canonical variate named wood represents vessel density, fiber length, and plant size, best associated to the environmental gradient. Vessel density expressed by its distribution in latewood and porosity type showed that ring-porosity is common in individuals from high latitudes. Temperatures below zero or lack of rainfall during several months might induce porosity variability in *B. cordata* as suggested by CCA, but was not related to phenology since the species is evergreen along its latitudinal range. Plant size was also influenced by extreme temperature and rainfall. Shorter plants are distributed in the northern population or driest sites located in north-central Mexico, and in addition, fiber length followed an allometric relation with individuals' height. Wood characters in *B. cordata* as for simple perforation plate, helical thickenings, type of intervascular and vessel-ray pits, scanty paratracheal parenchyma, and heterogeneous type IIB rays were not correlated with plant size, climate, and soil parameters or species distribution. These features are common with other species of *Buddleja*.

Keywords Allometric variation · *Buddleja cordata* · Canonical correlation · Diffuse porosity · Mexico · Ring porosity

Introduction

Buddleja cordata Humb. Bonpl. & Kunth is an evergreen, dioecious species that varies from shrubs to trees ranging from 1 to 20 m height and 10 to 45 cm in diameter at trunk base (Norman 2000; Rzedowski and Rzedowski 2001); however some individual trees are able to reach more than 80 cm in diameter at breast height (Aguilar-Rodríguez, unpubl. data). *B. cordata* is widely distributed in Mexico from the northern states of Sinaloa, Chihuahua, and Durango to the southern states in Oaxaca and Chiapas (Fig. 1). This species grows in a wide range of habitats; e.g., pine-oak, fir, and cloud forests, as well as in valleys of high elevation, in desert scrub with cacti and mesquite, and in chaparral with juniper (Norman 1966, 2000). Moreover, *B. cordata* is favored by disturbance, frequently occupying the openings of these plant communities or associated with crop fields. Due to the wide distribution and ecological tolerances that *B. cordata* possesses, the potential for variation among morphological, physiological and genetic traits is extremely high. As a consequence, *B. cordata* is an outstanding system to evaluate the hypotheses that have been postulated for some genera and families in relation to wood variability associated to habitat and habit features (Baas 1986; Noshiro and Baas 2000).

The influence of latitude, temperature, and humidity on secondary xylem structure has been studied in different taxa (Chalk 1983), mostly at family or genus levels (Carlquist 1966; Dickison et al. 1978; van der Oever et al. 1981; Baas 1986; Carlquist and Hoekman 1985; Dickison and Phend 1985; Rury 1985; Noshiro and Baas 1998). However, research at the species level is insufficient due to different tendencies in relation to tracheary element features

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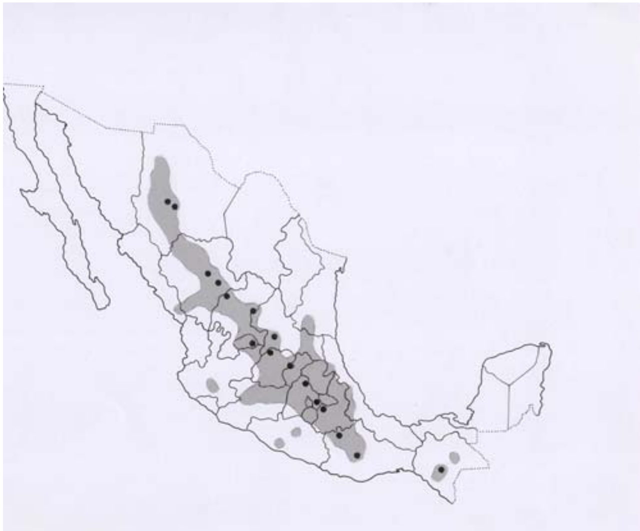

Fig. 1. Distribution of *B. cordata* in Mexico and provenances sampled for this study

(Sastrapradja and Lamoureux 1969; Parameswaran and Conrad 1982; Li-Hsia and Tseng-Chieng 1986; Xinying et al. 1988; Wilkins and Papassotiriou 1989; Lindorf 1997; Noshiro and Baas 2000; Arias and Terrazas 2001). Soil interaction with wood variability is poorly documented in the literature. Yaltirik (1970) found that a high concentration of calcium ions is associated with shorter vessel elements in *Acer* trees growing in areas with alkaline soils. Dünisch and Bauch (1994) evaluated the influence of mineral elements in *Picea abies* wood development, detecting that fertilized trees during lower rainfall showed an increment of periclinal divisions in the vascular cambium. Villagra and Roig-Juñent (1997) compared wood features of two species growing under different edaphic conditions and found an increment in the number of narrower vessels in *Prosopis argentinean* related to a water deficit in sandy soils. Other studies had focused on the influence of flooded soils on wood structure (Sidiyasa and Baas 1998; Yáñez-Espinosa et al. 2001). The ability of *B. cordata* to inhabit a wide distribution range raises the following question: are there anatomical wood differences related to latitude, elevation, climate (temperature and rainfall), and soil features or to plant size?

Materials and methods

Forty-two wood samples of *B. cordata* from 17 natural provenances were collected from Chiapas (16°47′N) to Chihuahua (27°54′N) Mexico (Fig. 1) in latitude and from 1350 to 3040 m in elevation (Table 1). The climate where *B. cordata* inhabits is defined as temperate with summer rainfall and dry season during part of the winter and spring, but slight rains may occur during the winter. Mean annual temperature varies from 12 to 19°C and annual rainfall from 544 to 1286 mm (García 1973; Quintas 2000). This species also grows in a dry climate where thorn–shrub communities develop (Norman 2000) with mean annual rainfall lower than 500 mm (García 1973). The predominant vegetation at the collection sites corresponded to oak forest, pine-oak and xeric thorn (Rzedowski 1986). At most sites litosol soils prevailed with exposed outcrop rocks.

Table 1 *Buddeja cordata* plant features, climate and soil parameters. Provenances arranged in descending latitudinal order. Acronyms: height (*H*, m), latitude (LAT, north), longitude (LONG, west), elevation (*E*, m), mean annual temperature (MAT), isothermality (ISO), temperature seasonality (TS), maximum temperature of the warmest period (MTWP), minimum temperature of the coldest period (MTCP), annual temperature range (ATR), annual rainfall (AR), rainfall seasonality (RS), rainfall of the driest quarter (RDQ), electrical conductivity (EC, Mmhos/cm), nitrogen (N,%), phosphorus (P, ppm)

Provenance	Plant and location							Climate						Soil		
	H	LAT	LONG	*E*	MAT	ISO	TS	MTWP	MTCP	ATR	AR	RS	RDQ	EC	N	P
Chihuahua 1	4, 3	27°54′06″	107°56′52″	2014	13	0.55	1.74	29.9	−2.7	33	836	94	49	0.16	0.70	24
Chihuahua 2	3, 4	27°54′05″	107°56′51″	2014	13	0.55	1.74	29.9	−2.7	33	836	94	49	0.16	0.06	16
Durango 1	4, 3	25°18′73″	104°38′30″	1350	19	0.59	1.59	35.5	2.2	33	391	104	0	0.16	0.26	13
Durango 2	1.5, 1.5,1.5	24°04′15″	104°39′28″	2084	16	0.60	1.31	30.2	0.9	29	553	108	0	0.16	0.12	7
Durango-Zacatecas	2.5, 4, 5	23°44′72″	104°00′53″	1938	17	0.62	1.2	30.7	2.7	28	492	111	0	0.16	0.26	16
Zacatecas	3, 5, 3	23°11′30″	102°53′05″	2336	16	0.61	1.03	28.1	2.6	25	422	94	0	0.16	0.19	11
Aguascalientes	3, 3	22°24′43″	102°16′91″	1983	17	0.63	0.99	30.3	3.1	27	443	91	0	0.16	0.21	16
San Luis Potosí	4, 3	22°15′02″	101°06′42″	2073	17	0.63	0.93	30.0	4.2	26	368	77	27	0.14	0.25	18
Querétaro 1	2.5, 6	20°22′	100°16′	2330	15	0.64	0.71	26.8	4.1	23	744	98	32	0.12	0.27	37
Querétaro 2	3, 2	20°22′	100°16′	2330	15	0.64	0.71	26.8	4.1	23	744	98	32	0.11	0.29	41
Tlaxcala	7, 7, 5	19°35′	98°37′	2630	13	0.68	0.63	24.1	1.0	23.1	662	83	26	0.15	0.46	108
México	4, 4	19°30′	98°47′	2460	15	0.68	0.73	26.3	0.9	25	647	85	0	0.10	0.23	7.8
Puebla	15, 15, 7	19°21′	98°39′	3040	12	0.68	0.47	20.6	2.6	18	950	88	31	0.13	0.16	43
Puebla-Oaxaca	8, 8	18°31′22″	97°27′15″	1760	18	0.67	0.64	28.6	6.7	22	544	92	0	0.17	0.02	4
Oaxaca	10, 8, 8	17°33′25″	97°23′1″	2333	15	0.69	0.50	26.3	4.8	21	701	91	0	0.19	0.26	16
Chiapas 1	8, 10, 9	16°50′29″	92°41′38	2219	14	0.71	0.48	23.0	5.0	18	1286	73	85	0.28	1.15	45
Chiapas 2	10, 8, 9	16°47′30″	92°35′49″	2700	12	0.74	0.39	20.8	3.2	18	1278	72	88	0.07	0.21	2

In each provenance samples of two to three healthy trees were collected (Table 1). Samples, including wood and bark, were cut at breast height (1.3 m) for trees and at the base of the thickest branch for shrubs. Only mature and reproductive individuals were collected to assure that juvenile wood was excluded. Samples were fixed and stored with glycerin–ethanol–water (1:2:3) solution until sectioning. Herbarium vouchers were deposited in CHAPA and IZTA. Height and diameter for each individual tree or shrub collected were recorded. Soil samples 15–20 cm deep were collected in dark-plastic bags and transported to the laboratory for further analysis. Each site was georeferenced with a GPS Magellan model Map 410.

Sections 20 μm thick were obtained with a sliding microtome, stained with safranin, and mounted in synthetic resin (Johansen 1940). Macerations were prepared using Jeffrey's solution (Berlyn and Miksche 1976). Temporary slides were prepared to gather data on vessel element and fiber lengths, as well as to corroborate the occurrence of vascular tracheids. Species wood description followed IAWA recommendations (IAWA Committee 1989). Due to vessel diameter dimorphism two categories were established and thus wide and narrow vessels were measured separately. In ring and semiring-porous woods, wide vessels corresponded to earlywood and narrow vessels to latewood, but in diffuse-porous, they were intermixed in early and latewood. Vessel density (number of vessels/mm^2), was counted only in latewood. Intervascular pit diameter, fiber total diameter, lumen diameter, and a single wall thickness, as well as ray height and width were also measured in cross and tangential sections. For each wood character 25 measurements or counts were gathered per individual. All measurements were obtained using an image analyzer IMAGE-Pro Plus version 3.1 (Media Cybernetics 1997) adapted to an Olympus BX-50 microscope with a Hitachi KP-D51 color digital camera and a screen resolution of 640×480 pixels. The semiautomatic option and the proper magnification lens (e.g., 10x objective for vessel and fiber length, 20x or 40x for vessel lumen diameter, and 100x for intervascular pit diameter and a single wall thickness) were used to obtain the precision needed. Fiber length/vessel element length ratio was calculated (Chattaway 1936) to evaluate the amount of intrusive growth. In the species wood description, values represent the mean and the standard deviation of all provenances.

Based on georeferenced locations for each population and the nearest weather stations, 18 climate variables were generated by Bioclim version 2.0 (Busby 1986). Soil samples were analyzed for five chemical parameters, texture, and electrical conductivity for each site following the standard analytical methods of the Soil Fertility Laboratory at Colegio de Postgraduados (Etchevers 1988). Selected climate and soil variables are provided in Table 1.

Multivariate data analyses were performed with SAS (1989). Data distribution did not meet the assumptions of multivariate normality, thus measurements were transformed to logarithm, square root, or arc cosine accordingly (Zar 1999). Porosity type is a categorical variable and was not included in the multivariate analysis, thus Spearman correlation was applied with latitude and climatic variables. Principal component analysis (PCA) was applied as a exploratory technique to detect a data subset that characterizes the variability among wood variables and plant size as well as climatic, soil, and location parameters. A canonical correlation analysis (CCA) was applied to determine the association between wood variables and plant size with environmental variables and to best explain the results of PCA analysis. The CCA is a technique for analyzing two or more sets of variables, which organizes sampling entities (wood characters) along pairs of continuous ecological gradients. This analysis allows identifying those variables that have the highest contribution within each canonical variate (Tabachnick and Fidell 1989).

Results

Anatomical description

Growth rings are conspicuous or inconspicuous. In ring-porous wood, earlywood has wider vessels, mostly solitary or in groups of two to six vessels; in some provenances narrower vessels are present at the beginning of earlywood (Fig. 2A); latewood shows vessels grouped in radial rows of two to ten vessels (Figs. 2A–C) or in clusters in oblique or tangential distribution (Fig. 2D). In diffuse-porous wood, there are few solitary vessels, mostly distributed in radial rows of two to seven vessels (Fig. 2E–G) or in clusters of 4–6 vessels mainly with tangential distribution (Fig. 2H). Pores are oval and rarely angular. Tangential diameter of wider vessels is 67±18 μm and of narrower vessels 36±9 μm. Most provenances have a bimodal distribution in vessel diameter (Fig. 2). Vessel element length has a mean of 353±77 μm. Perforations plates are simple (Fig. 3A). Intervascular pitting is alternate; pits are slightly crowded, oval in tangential outline, with diameter of 8.0±0.9 μm, and oval to lenticular aperture (Fig. 3B). Vessel-ray pits have reduced borders or simple, diameter is similar to intervascular pits (Fig. 3C). Helical thickenings are fine, close-spaced, occurring in wide and narrow vessel elements (Fig. 3D). Vascular tracheids have a mean of 330±70 μm. Ground tissue is composed of nonseptate libriform fibers, but some septate fibers are scattered in ground tissue. Fiber length has a mean of 865±164 μm; with fiber diameter of 17±0.5 μm, lumen diameter of 10.7±2 μm, and wall thickness of 3.0±0.5 μm. *F/V* ratio is 2.2–3.0. Parenchyma is scanty paratracheal, with two to four cells per strand without deposits. Rays are heterogeneous with 4–8/mm. Uniseriate rays are few with two to six cells high. Multiseriate rays have two to three cells wide (Fig. 3D), mostly two (37±6 μm wide); total height has a mean of 423±136 μm; multiseriate rays have a central portion of entirely procumbent cells and uniseriate marginal extensions of upright and square cells, commonly one to two cells. Cellular ray inclusions are absent.

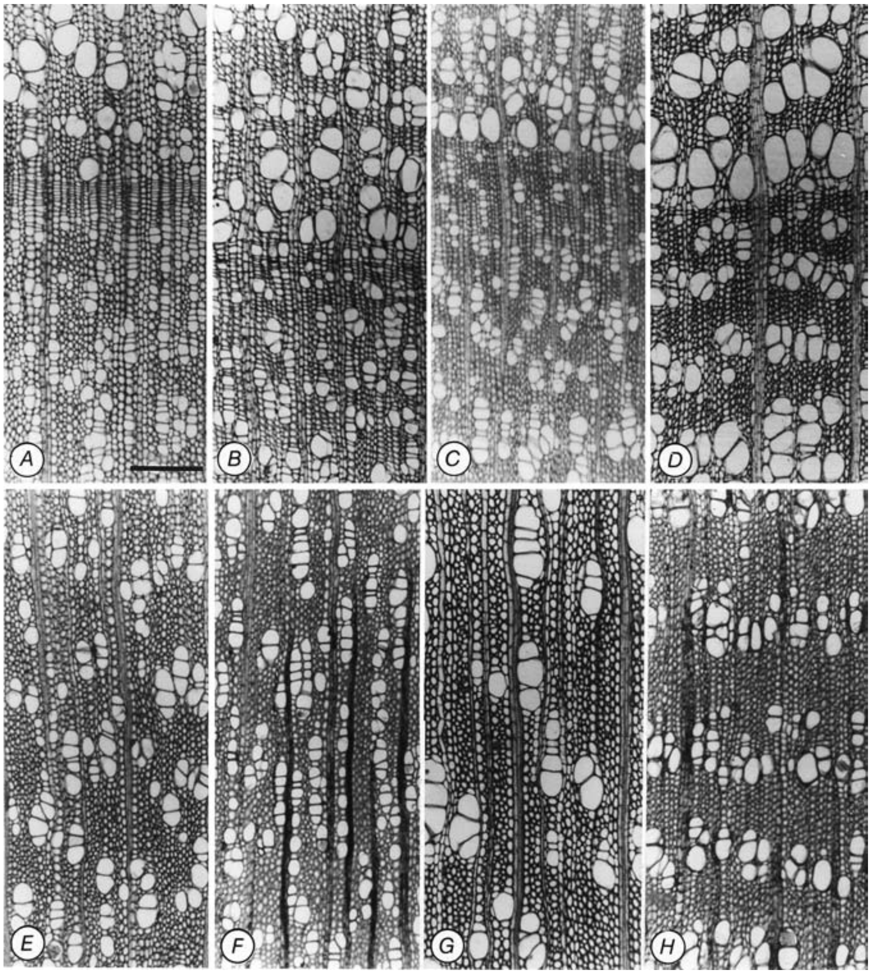

Fig. 2. Porosity of *B. cordata*. A–D. Ring-porous. A–C. Vessels in latewood mostly in radial rows. **A**. Chihuahua 1 (Aguilar 258). **B**. Durango 2 (Aguilar 261). **C**. Zacatecas (Aguilar 263). **D**. Vessels in latewood in oblique or tangential distribution, Oaxaca (Aguilar 286). E–H. Diffuse-porous. E–G. Most vessels in radial rows and few solitary. **E**. Querétaro 1 (Aguilar 267). **F**. Querétaro 2 (Aguilar 268). **G**. Chiapas 1 (Aguilar 282). **H**. Vessels with tangential distribution, Tlaxcala (Aguilar 281). Scale bar = 200 μm

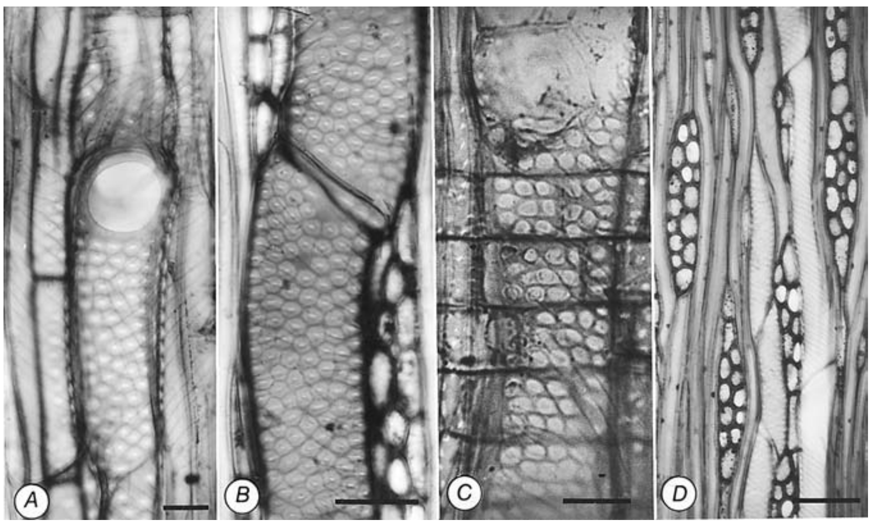

Fig. 3 *B. cordata* wood. **A**. Simple perforation plate (Aguilar 263). **B**. Intervascular pits (Aguilar 258). **C**. Vessel-ray pits (Aguilar 267). **D**. Biseriate rays (Aguilar 281). Scale bar A = 30 μm, B-D = 50 μm

Statistical analyses

Table 2 shows mean (± SD) values for the anatomical quantitative characters and *F*/*V* ratio ordered along the latitudinal gradient from north to south for all provenances. Porosity has a negative correlation with latitude ($r_s = -0.75$, $p < 0.0004$), temperature seasonality ($r_s = -0.75$, $p < 0.0003$), maximum temperature of the warmest period ($r_s = -0.67$, $p < 0.002$), and annual temperature range ($r_s = -0.73$, $p < 0.0005$), and is positively associated with isothermality ($r_s = 0.74$, $p < 0.0005$). No correlation was detected with plant size, mean annual temperature, min-

Table 2 Means and 1 SD for wood characters by provenance. Vessel density (vede), diameter of wide vessels (diwv), diameter of narrow vessel (dinv), vessel element length (vele), intervascular pit diameter (ipid), fiber lumen (filu), fiber diameter (fidi), fiber wall thickness (fiwt), fiber length (file), ray height (rahe), ray width (rawi), libriform fiber length / vessel element length (*F/V*)

Provenance	Vede	diwv µm	dinv µm	vele µm	ipid µm	filu µm	fidi µm	fiwt µm	file µm	rahe µm	rawi µm	*F/V*
Chihuahua 1	16±4	76±14	42±9	378±69	9.1±0.15	10±2	15±2	2.8±0.05	851±103	311±98	39±6	2.25
Chihuahua 2	13±4	81±14	40±9	365±88	9.0±0.09	11±3	17±3	2.9±0.06	988±86	317±80	37±6	2.71
Durango 1	16±5	69±15	39±10	297±60	8.0±0.09	11±3	17±3	2.9±0.06	755±79	409±99	37±4	2.54
Durango 2	19±4	68±12	36±8	249±52	7.3±0.08	9±2	15±3	2.7±0.08	603±110	359±79	34±5	2.42
Durango-Zacatecas	24±8	56±18	32±8	303±66	7.3±0.07	9±2	15±2	3.0±0.05	793±114	361±73	32±7	2.62
Zacatecas	17±4	57±17	31±6	294±83	8.2±0.08	9±2	15±2	2.9±0.05	759±122	386±87	29±5	2.58
Aguascalientes	21±5	51±13	30±6	280±68	8.3±0.07	9±2	15±2	2.9±0.06	842±113	411±84	30±6	3.01
San Luis Potosí	22±3	65±13	38±6	290±48	9.5±0.11	12±2	17±2	2.5±0.05	803±91	351±124	33±5	2.77
Querétaro 1	15±4	52±11	28±5	306±67	8.6±0.10	10±2	16±2	3.1±0.05	841±109	387±73	43±8	2.75
Querétaro 2	12±4	72±16	36±9	276±65	8.2±0.08	11±2	17±2	2.9±0.05	813±110	398±71	41±8	2.94
Tlaxcala	13±4	59±14	33±6	340±66	8.6±0.06	12±2	18±2	3.0±0.05	936±109	394±80	34±5	2.75
México	12±3	38±6	25±6	360±56	8.4±0.12	9±2	13±2	2.3±0.07	960±82	372±94	28±4	2.67
Puebla	7±2	80±15	40±8	341±62	9.2±0.14	13±3	20±3	3.5±0.05	860±97	573±145	48±10	2.52
Puebla-Oaxaca	10±3	75±13	38±5	344±74	8.5±0.05	11±2	18±2	3.4±0.08	877±96	507±181	43±8	2.55
Oaxaca	10±3	86±13	37±6	308±68	8.5±0.05	11±1	17±1	3.2±0.05	894±107	493±110	41±11	2.90
Chiapas 1	7±2	70±16	41±8	377±72	8.8±0.06	14±2	20±2	3.3±0.05	1081±150	550±156	44±7	2.87
Chiapas 2	6±2	81±14	44±8	415±81	8.5±0.09	11±1	18±1	3.4±0.04	1090±118	534±128	33±6	2.63

imum temperature of the coldest period, annual rainfall, rainfall seasonality, and rainfall of the driest quarter ($p>0.05$).

PCA revealed that three components accounted for 63.5% of the total variation of the secondary xylem of *B. cordata* wood. The first component explained 41.3% of the variation and 13 variables showed loadings greater than 0.200. The highest loadings were for four variables: vessel density, plant height, as well as maximum temperature of the warmest period (MTWP), annual temperature range (ATR), and isothermality (ISO) (Table 3). The second component explained 11.5% of the residual variation and the variables, minimum temperature of the coldest period (MTCP) and rainfall of the driest quarter (RDQ) showed the highest loadings. In the third component 10.6% of the remaining variation was explained by the soil variables electrical conductivity, phosphorus and nitrogen (Table 3).

Figure 4 shows the biplot of the two first components for the individuals of provenance. Along the first component, shorter individuals (<8 m height) with more abundant vessels in the latewood (12–24 vessels/mm^2), shorter fibers (<800 µm), narrower fiber diameter (15–17 µm), and lower rays (311–317 µm) were grouped in the left-hand region. Also individuals with mostly ring to semiring-porous wood were distributed in those localities with MTWP varying from 28 to 35°C and a high ATR (26–33°C). Taller individuals (>8 m height) with diffuse-porous wood and fewer vessels (6–10 vessels/mm^2), tending to show longer fibers (860–1090 µm), wider fiber diameter (18–20 µm) and taller rays (>534 µm) were grouped in the right-hand region of this axis. The provenances in which those individuals are distributed have MTWP varying from 21–23°C and an ATR of 18°C. Along the second component northern provenances are separated by MTCP –3°C and commonly zero rainfall during the driest quarter (RDQ), except for two localities of Chihuahua with 49 mm during that quarter.

The CCA showed that two canonical correlation coefficients are statistically significant (Wilks' λ, $p<0.0001$, $n=5$). The first canonical correlation explained 66% of the total variance and the second contributed 8% of the remaining variance. The first pair of canonical variates suggests that an increase in annual temperature range, maximum temperature of the warmest period, a decrease in rainfall as well as an increment in latitude have an effect on fiber length, vessel density and plant size (Table 4).

Discussion

The PCA revealed that 18 of the 32 variables included in this analysis had the highest loading. Plant size together with five climate variables, latitude and three soil parameters explained the highest percentage of variation present in *Buddleja cordata* wood, especially vessel density as well as fiber diameter, fiber length and ray height. Although most populations of *B. cordata* grow in temperate climates, variability exists in rainfall and temperature along the year and the analyses suggest that plant size and some wood features (vessel density, fiber size and ray height) are affected by these changes. Individuals of *B. cordata* collected from the most northern provenances were shrubs which grow under a temperate subhumid climate with summer rainfall and mean annual temperature of approximately 13°C, with minimum temperature of the coldest period from December to April below 0°C, and annual rainfall of 800 mm; these provenances possess ring-porous wood and in the latewood vessels tend to show longer and more abundant

Table 3 Eigenvectors of PCA for wood, height, and provenance variables for each plant collected

Variables	PRIN 1	PRIN 2	PRIN 3
Variation explained (%)	41.34	11.55	10.61
Eigenvalue	13.22	3.69	3.39
Vessel density	−.241[a]	−.026	0.081
Diameter of wide vessel	0.116	0.176	−.107
Diameter of narrow vessels	0.117	0.250	−.055
Vessel element length	0.168	0.138	−.123
Intervessel pit diameter	0.137	0.198	0.198
Fiber lumen	0.202	0.112	0.157
Fiber wall thickness	0.167	−.111	−.026
Fiber diameter	0.226	0.049	0.122
Fiber length	0.208	0.088	−.019
Ray height	0.206	−.172	−.005
Ray width	0.127	0.043	0.174
Plant height	0.233[a]	−.021	0.024
Latitude	−.229	0.219	0.019
Elevation	0.175	−.001	−.122
PH	−.165	−.175	0.324
Electrical conductivity	0.002	0.035	0.428[a]
Organic matter	0.102	0.156	0.361
Nitrogen	0.105	0.168	0.371[a]
Phosphorus	0.041	0.059	0.390[a]
Potassium	0.106	−.203	0.284
Sand	−.149	0.212	0.126
Slime	0.141	−.231	−.078
Clay	0.099	−.108	−.079
Mean annual temperature	−.175	−.252	0.155
Isothermality	0.234[a]	−.204	−.014
Temperature seasonality	−.220	0.253	−.010
Maximum temperature of the warmest period	−.249[a]	0.009	0.079
Minimum temperature of the coldest period	0.095	−.404[a]	0.116
Annual temperature range	−.245[a]	0.164	−.005
Annual rainfall	0.225	0.179	−.062
Rainfall seasonality	−.211	−.104	−.013
Rainfall of the driest quarter	0.184	0.300[a]	0.007

[a]Indicates the highest values for each component

radial groups with shorter and narrower fibers. In contrast, *B. cordata* trees collected in most southern provenances grow in temperate subhumid climates with summer rainfall, but with mean annual temperature of 14°C, with low-annual temperature range of 18°C along the year, and anual rainfall reaches 1300 mm with more than 80 mm of rain during the driest quarter. In these southern provenances individuals commonly possess diffuse porosity and shorter vessel groups, as well as longer and wider fibers. Ring and semiring-porous wood were also observed in some sites from the Central highlands like Zacatecas and Northeastern states. These provenances are characterized by a drier climate with the highest mean annual temperature (17°C), a lower annual rainfall (<500 mm), and zero rainfall during the driest quarter.

Differences in humidity and temperature are reflected in wood porosity present in the provenances of *B. cordata* along the distribution range and are not related to species leaf phenology because all individuals are evergreen. The typical ring-porous wood is distinctive of those individuals growing in provenances where cambial activity cessation occurs, caused by freezing, heat stress or drought (Chalk 1983). These factors surely contributed to cambial inactivity in the northern and central provenances of *B. cordata*. True ring-porous wood occurred in the northern provenances with temperatures below zero, whereas in the North-Central provenances water stress is an additional factor that contributes to porosity type and vessel trait modifications. Bissing (1982) found that porosity type and abundance of solitary vessels varied with water availability and the results mentioned for *B. cordata* support this assertion. Higher abundance of vessel grouping is interpreted as a way to avoid embolisms (Baas 1986). Changes in wood porosity not related to *B. cordata* phenology make this species an interesting system to study cambial activity associated with water conduction and photosynthesis.

Plant height and fiber length in *B. cordata* as shown by CCA supports an allometric relationship also reported for other genera (Rury 1985; Zhang 1992; Terrazas 1994; Noshiro and Baas 1998; Terrazas and Loza-Cornejo 2003). However, these results differ from those found for plant height and fibers length in three species of *Cornus* (Noshiro and Baas 2000). No tendency was detected for fiber intrusive growth in relation to *B. cordata* provenance distribution or plant size. However, a *F*/*V* ratio between 2.2 and 3.0 has been interpreted as an adaptation to favor longer fibers to acquire an optimum mechanical system (Carlquist 1988). Latitude is also an important source of variation closely related with temperature and rainfall as shown by CCA. Chalk (1983) mentioned a tendency to decrease cellular element size of secondary xylem as latitude increases. This tendency is confirmed in *B. cordata*. On the other hand, fiber length and ray height showed a negative correlation with latitude and the four climate variables detected by CCA, in contrast to the report for fiber length in *Cornus macrophylla* (Noshiro and Baas 2000). In *Acacia melanoxylon* there is a positive correlation between vessel element lengths, proportion of fibers, and multiseriate rays with latitude; but a negative correlation with vessel denstiy and diameter, proportion of uniseriate rays, and axial parenchyma (Wilkins and Papassotiriou 1989). Notably, in *B. cordata* axial parenchyma does not vary as function of latitude or elevation.

The influence of elevation on wood has been studied in different taxa, however the results do not show a consistent pattern (Noshiro and Baas 2000). In *Metrosideros polymorpha* physiological and morphological variation along an altitudinal gradient was found, and size of this species decreases as elevation increases (Cordell et al. 1998). GarcíaXinying et al. (1988) found positive correlations between elevation and vessel element length, vessel diameter, fiber–tracheid length and diameter, and ray height for an elevation range between 1000 and 1800 m. In *B. cordata*

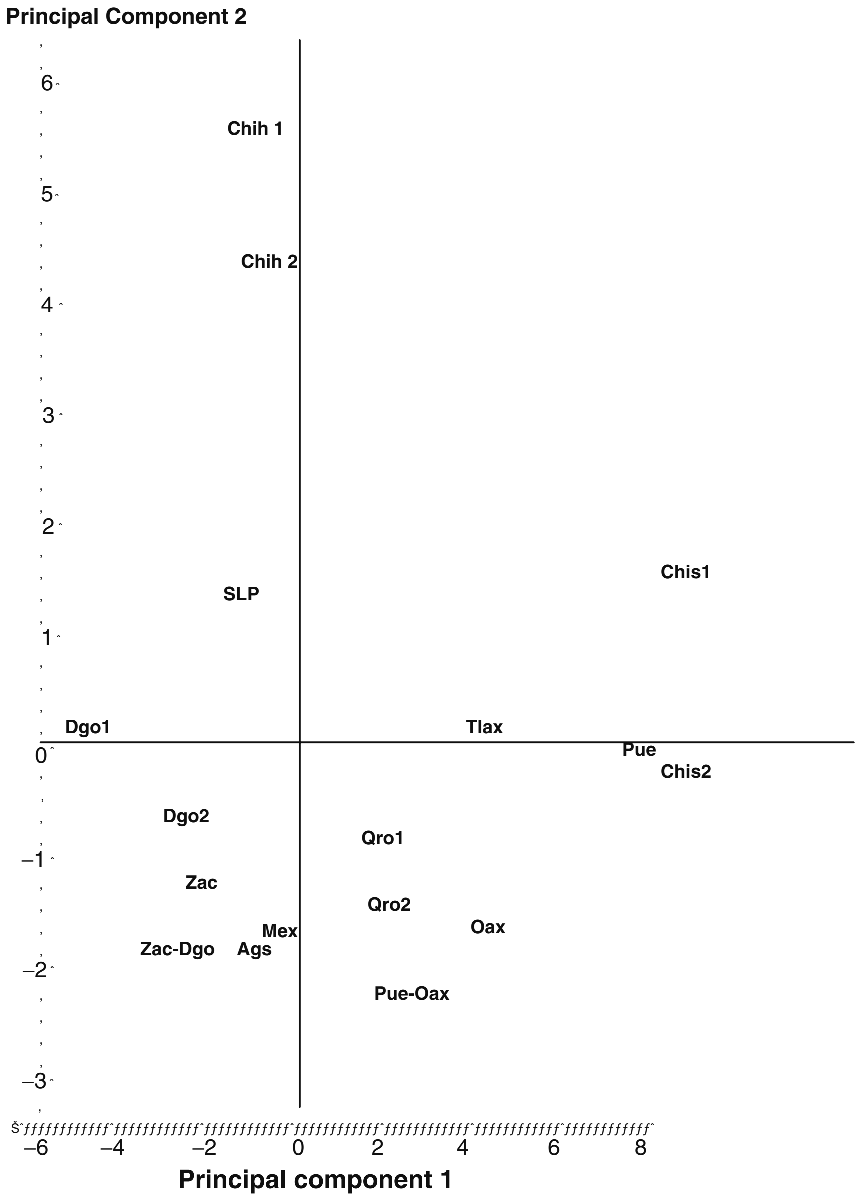

Fig. 4. Principal component analysis based on wood, climate, and soil variables, plotted for provenances where individuals of *B. cordata* were collected; see Table 1 for provenance information. Provenances: Chih1 = Chihuahua 1, Chih2 = Chihuahua 2, Dgo1 = Durango 1, Dgo2 = Durango 2, Dgo-Zac = Durango-Zacatecas, Zac = Zacatecas, Ags = Aguascalientes, SLP = San Luis Potosí, Qro1 = Querétaro 1, Qro2 = Querétaro 2, Tlax = Tlaxcala, Mex – México, Pue = Puebla, Pue-Oax = Puebla-Oaxaca, Chis1 = Chiapas 1, Chis2 = Chiapas 2

elevation is not an important source of variation according to PCA and CCA, despite an elevation range from 1350 m in Durango to 3040 m in Puebla, as is also the case in *Dodonaea viscosa* despite its world-wide distribution (Liu and Noshiro 2003). Moreover, each species attains different strategies to adjust wood anatomy to environmental conditions associated with elevation or latitude which may be related to its genetic background.

The soil parameters, electrical conductivity, phosphorus and nitrogen had the highest loadings in the third component, explaining only 10% of the remaining variance; however they were not recovered by CCA as important variables to explain wood variation in *B. cordata*. Although minerals are associated with cellular division and differentiation in the vascular cambium, this relationship is also affected by environmental conditions (Dünisch and Bauch 1994); for example, at high latitudes, low temperatures delay the carbon and nitrogen cycles in the surface soil (Currie 1999), thus electrical conductivity, phosphorus and nitrogen may influence *B. cordata* wood through climate. This suggests that *B. cordata* is able to grow under different soil properties without influencing wood traits directly.

We conclude that *B. cordata* wood characters such as the occurrence of simple perforation plates, alternate intervascular pits, vessel–ray pits with reduced borders, vessel elements with helical thickenings, scanty paratracheal parenchyma, and heterogeneous rays are not significantly influenced by plant size, climate, or species distribution. These wood features have been reported as distinctive for *Buddleja* wood (Aguilar-Rodríguez and Terrazas 2001), thus we suggest they have taxonomic value. Moreover, *F/V* ratio has not been influenced by plant size, climate or species distribution. Nonetheless, there is an evident

Table 4. Canonical correlation analysis (CCA) of environmental variables (distribution) versus wood characters (wood)

	First canonical variate		Second canonical variate		
	Correlation	Coefficient	Correlation	Coefficient	
Wood					
Vessel density	0.913[a]	0.835	0.268	0.906	
Diameter of wide vessel	−0.297	0.088	−0.68[a]	0.55	
Diameter of narrow vessels	−0.31	0.096	−0.574	0.426	
Fiber length	−0.734[a]	0.538	0.284	0.612	
Ray height	−0.727[a]	0.528	−0.199	0.568	
Ray width	−0.394	0.155	−0.535	0.441	
Plant height	−0.766[a]	0.586	−0.07	0.591	
Percent of variance	0.666		0.083		Total = 0.75
Redundancy	0.661		0.08		Total = 0.74
Distribution					
Latitude	0.831[a]	0.691	−0.059	0.695	
Maximum temperature of the warmest period	0.832[a]	0.692	0.018	0.693	
Annual temperature range	0.842[a]	0.71	0.032	0.71	
Temperature seasonality	0.766	0.587	−0.104	0.598	
Annual rainfall	−0.768[a]	0.591	−0.231[a]	0.644	
Percent of variance	0.654		0.078		Total = 0.73
Redundancy	0.73		0.08		Total = 0.81
Canonical correlation	0.982		0.942		

[a]Indicates the highest values

allometric relationship between plant size and fiber length and ray height. Porosity and vessel grouping varied negatively with latitude as well as with temperature and rainfall distribution along the year. The few studies of wood variation at the species level have revealed contrasting results. Tracheary element size responds differently to environmental factors in which species are distributed, as it has been the case in *B. cordata*. In some northern provenances, low temperatures probably favored *B. cordata* vascular cambium inactivity as PCA and CCA suggested. In these provenances a distinctive ring-porous wood occurs, whilst in more central localities, the lack of rainfall during the driest months of the year probably is the main factor that induces vascular cambium inactivity, as well as a higher variation in ring porosity type and vessel grouping in latewood. To understand the influence of climate (e.g. temperature and rainfall) on wood features of species widely distributed in the intertropical region, reciprocal transplants among selected provenances of particular species should be conducted.

Acknowledgements This work was partially supported by Consejo Nacional de Ciencia y Tecnología scholarship to Silvia Aguilar-Rodríguez (118733) and Colegio de Postgraduados. We appreciate the contribution of J. Daniel Tejero Díez (Universidad Nacional Autónoma de México- FES Iztacala) for identifying all the material collected for this study and to Araceli Cortés González for dark-room assistance

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