WOOD ANATOMY AND ITS RELATION TO PLANT SIZE AND LATITUDE IN *Buddleja* L. (BUDDLEJACEAE)

Teresa Terrazas, Silvia Aguilar-Rodríguez and Lauro López-Mata

SUMMARY

Wood anatomy of the genus Buddleja was studied to gain insight about its relationship with habit and latitude. Habit was positively associated with most characteristics, showing the highest correlation coefficients with vessel element length and fibre length. Four features were negatively correlated with latitude, confirming observations for other taxa and only ray width was positively correlated. Wood has a discrete variation among habit categories as revealed by canonical discriminant analysis. Moreover, variance analysis confirmed significant differences in fibre length and vessel element length between species that are small shrubs and trees taller than 10m. These results suggest that Buddleja species growing in harsher environments, as the small shrubs, show less variation in wood cell size, while species growing in more diverse environments may have more diverse habits and consequently greater wood cell size variation.

ANATOMÍA DE LA MADERA DE *Buddleja* L. (BUDDLEJACEAE) Y SU RELACIÓN CON EL TAMAÑO DE LA PLANTA Y LA LATITUD

Teresa Terrazas, Silvia Aguilar-Rodríguez y Lauro López-Mata

RESUMEN

Se estudió la anatomía de la madera del género Buddleja para tener una perspectiva de su relación con el hábito y con la latitud. El hábito se asoció positivamente con la mayoría de los caracteres de la madera y mostró los coeficientes de correlación más altos con la longitud de los elementos de vaso y de las fibras. Cuatro caracteres se correlacionaron negativamente con la latitud, confirmando las observaciones realizadas en otros taxa y únicamente el ancho de los radios se correlacionó positivamente. La madera tiene una variación discreta entre las categorías del hábito, como lo revela el análisis canónico discriminante. El análisis de varianza confirmó diferencias significativas en las fibras y la longitud de los elementos de vaso entre especies que tienen hábito de arbustos pequeños y los árboles de >10m de alto. Estos resultados sugieren que las especies de Buddleja que tienen hábito arbustivo crecen en ambientes más extremos y muestran menos variación en el tamaño de las células xilemáticas, mientras que las especies que crecen en ambientes heterogéneos pueden tener diferentes hábitos y como consecuencia la variación en el tamaño celular de la madera es mayor.

Introduction

Ecological wood interpretations focused in floristic and systematic approaches. The floristic interpretations identify wood convergences in species coexisting in natural plant communities (Baas and Carlquist, 1985; Barajas-Morales, 1985; Carlquist and Hoekman, 1985a; Guthrie, 1989; Lindorf, 1994). Carlquist (1966) was one of the first to introduce ecological aspects into systematic studies and suggested carrying them out among the members of an order, family or genus to support the relationships between them. Although there are numerous studies in this field (Baas, 1973, 1983; Dickison, 1978; Carlquist, 1982, 1984 1986, 1992; Carlquist and Hoekman, 1985b; Carlquist and Wilson, 1995), a few studies evaluated the correlation between wood characters and latitude or habit using statistical methods, showing that wood features such as vessel element length and diameter are associated with latitude, elevation, and species habit or height (Baas, 1973; van der Graaff and Baas, 1974; van den Oever *et al*., 1981; Zhang, 1992; Terrazas, 1994; Noshiro *et al*., 1995; Sidiyasa and Baas, 1998; Noshiro and Baas, 2000; Liu and Noshiro, 2003; Terrazas and Loza-Cornejo, 2003; Motomura *et al*., 2007).

The genus *Buddleja* is distributed worldwide, up to 40º in latitude and from sea level to mountainous areas surpassing 3500masl (Leeuwenberg, 1979). Species of *Buddleja* are mainly shrubs, although trees and lianas are not uncommon. While wood anatomy for the genus has been studied by several authors (Mennega, 1980; Carlquist, 1997; Aguilar-Rodríguez and Terrazas, 2001) none of these studies have used statistical methods to examine correlations between wood characters and

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Teresa Terrazas. Bióloga, Universidad Nacional Autónoma de México (UNAM). Ph.D., University of North Carolina, Chapel Hill, EEUU. Investigadora, Instituto de Biología, UNAM, México. Dirección: Apartado Postal 70-233, 04510 México, D.F., México. e-mail: tterrazas@ibiologia.unam.mx

Silvia Aguilar-Rodríguez. Bióloga, UNAM, México. Doctora en Ciencias, Colegio de Postgraduados (COLPOS), Montecillo, México. Profesora, UNAM, México. e-mail: siagro@campus.iztacala.unam.mx

Lauro López-Mata, Biólogo, UNAM, México. Ph.D., University of North Carolina, Chapel Hill, EEUU. Profesor-Investigador, Programa de Botánica, COLPOS, Montecillo, México. e-mail: lauro@colpos.mx

ANATOMIA DA MADEIRA DE *BUDDLEJA* L. (BUDDLEJACEAE) E SUA RELAÇÃO COM O TAMANHO DA PLANTA E A LATITUDE

Teresa Terrazas, Silvia Aguilar-Rodríguez e Lauro López-Mata

RESUMO

Estudou-se a anatomia da madeira do gênero Buddleja para ter uma perspectiva de sua relação com o hábito e com a latitude. O hábito se associou positivamente com a maioria dos caracteres da madeira e mostrou os coeficientes de correlação mais altos com a longitude dos elementos de vaso e das fibras. Quatro caracteres se correlacionaram negativamente com a latitude, confirmando as observações realizadas em outros taxa e unicamente a dimensão dos rádios se correlacionou positivamente. A madeira tem uma variação discreta entre as categorias do hábito, como revela a análise canônica discriminante. A análise de variança confirmou diferenças significativas nas fibras e a longitude dos elementos de vaso entre espécies que têm hábito de arbustos pequenos e as árvores de >10m de altura. Estes resultados sugerem que as espécies de Buddleja que têm hábito arbustivo crescem em ambientes mais extremos e mostram menos variação no tamanho das células xilemáticas, enquanto que as espécies que crescem em ambientes heterogêneos podem ter diferentes hábitos e como conseqüência a variação no tamanho celular da madeira é maior.

latitude or habit. In this study, simple correlation analysis was used to evaluate if associations are significant between wood trials and latitude and habit, and a multivariate analysis was used to examine which quantitative wood features of 26 species contribute to discriminate species by their habit, with the main hypothesis that wood variation has a discrete variation among habits.

Materials and Methods

Buddleja wood samples collected in the field and from xylaria were studied (Table I). Sections 20-30µm thick were cut with a sliding microtome, stained with safranin and mounted in synthetic resin (Johansen, 1940). Wood macerations were made with Jeffrey's solution (Johansen, 1940) and temporary slides used to quantify vessel element length and fibre length.

Anatomical characters of the samples were quantified following the recommendations of the International Association of Wood Anatomists (IAWA, 1989). For each quantitative character, 25 measurements were made per sample. There is a tendency in most species to show wide and narrow vessels, thus they were measured separately. Tangential intervessel pit diameter and fibre length, diameter, lumen and wall thickness, as well as ray height and width were also measured. All characteristics were quantified with an image analyzer IMAGE-Pro Plus version 3.1 (Media Cybernetics, 1997) adapted to an Olympus BX-50 microscope.

Latitude and habit were gathered mostly from xylaria information or obtained from taxonomic monographs for *Buddleja* (Norman, 1966, 2000; Leeuwenberg, 1979) or from floras (Standley, 1924; Bruce and Lewis, 1960; Urban, 1964; Stewart and Johnston, 1970; Tutin, 1972; Smith *et al*., 1976; Huanca, 1993). Habit was classified into five categories: 1) small shrubs, 0.5-1.0m high; 2) large shrubs, 1-5m high; 3) small trees, 5-10m high; 4) trees >10m high, and 5) lianas.

To fulfill the assumptions of multivariate analyses, variables were transformed with natural logarithm or square root (Zar, 1999). Spearman correlation analysis was performed to detect associations with latitude and habit. Based on correlation analysis, a canonical discriminant analysis (CANDISC) was applied to all species, including eight anatomical characteristics (Table

TABLE I
LIST OF *Buddleja* SPECIES STUDIED WITH XYLARIA NUMBER AND COUNTRY PROVENANCE

B. alternifolia Maxim.	Uw840, FPRLw13170 - China
B. americana L.	CTFw23035 - Venezuela; MEXU 876 - Mexico
B. asiatica Lour.	Kw13213 - India; BFHw13082 - Burma
B. colvilei Hook. f.	Kw13216 - Bengala
B. cordata Humb. Bonpl. & Kunth	Aguilar 72, 252 - Mexico
B. crispa Benth.	Kw23025 - China
B. curviflora Hook. f. & Arn.	Tw14289; TWTw14276; TWTw15792 - Japan
B. davidii Franch.	RBRJw3.932, FPRLw12697, China; BFHw17007 - Japan
B. elegans Cham. & Schltdl.	Uw1372 - Brazil
B. globosa Hope	BFHw17597 - Peru; Uw532 - Argentina; FPRLw21364 - Chile; Kw23026 - Los Andes
B. incana Ruíz & Pav.	Tw26409 - Peru
B. longifolia Humb. Bonpl. & Kunth	BFHw10071 - Peru
B. macrostachya Benth.	Kw13218 - India
B. madagascariensis Lam.	Tw48506 - Morocco
B. marrubifolia Benth.	Tejero 4035 - Mexico
B. nitida Benth.	BFHw16102, BFHw19812 - Costa Rica; Aguilar 284a, 284b - Mexico
B. nivea Duthie	Uw166, Uw167 - China
B. paniculata Wall.	Kw13219, FPRLw3033 - Burma
B. parviflora Humb. Bonpl. & Kunth	Aguilar 53, Kw13221, Kw13222, Uw15970, MEXU 934 - Mexico
B. polystachya Fresen.	Kw13223 - Ethiopia
B. pulchella N. E. Br.	Uw22028 - Tanzania
B. saligna Willd.	Uw902 - cultivado; Kw13224, Uw22040 - South Africa
B. salviifolia Lam.	Uw22041 - South Africa
B. scordioides Humb. Bonpl. & Kunth	Ávila s/n, Aguilar 270, 271, 273 - Mexico
B. sessiliflora Humb. Bonpl. & Kunth	Aguilar 71, 253 - Mexico
B. thyrsoides Lam.	Uw20839 - Brazil

TABLE II
SPEARMAN CORRELATION COEFFICIENTS (R) AMONG ELEVEN WOOD CHARACTERS AND LATITUDE AND HABIT CATEGORIES OF *Buddleja*

Wood	Latitude	Habit categories
Vessel with narrow diameter[1]	-0.17 n.s.	0.44 ***
Vessel with wide diameter[1]	-0.35 *	0.62 *
Vessel element length[1]	-0.40 **	0.74 ***
Intervessel pit diameter[1]	-0.38 **	0.52 ***
Porosity	-0.25n.s.	-0.06 n.s.
Fibre length[1]	-0.37 *	0.76 ***
Fibre diameter[1]	-0.20 n.s.	0.53 ***
Fibre lumen diameter[1]	-0.24 n.s.	0.48 **
Fiber wall thickness[1]	-0.13 n.s.	0.36 *
Ray height	-0.02 n.s.	0.09 n.s.
Ray width[1]	0.31 *	-0.03 n.s.

[1] Used in CANDISC
* P<0.05, **P<0.001, ***P<0.0001, n.s.= nonsignificative.

TABLE III
ANATOMICAL CHARACTERS USED IN CANONICAL DISCRIMINANT ANALYSIS AND THEIR PARTIAL CONTRIBUTION TO THE FUNCTIONS EXPRESSED BY STANDARDIZED COEFFICIENTS OF DISCRIMINANT FUNCTIONS

Characters	Discriminant Function 1	Discriminant Function 2
Vessel with narrow diameter	0.213	-0.415
Vessel with wide diameter	-0.666	-0.579
Vessel element length	0.095	-2.146
Intervessel pit diameter	0.126	0.210
Fibre length	1.584	1.147
Fibre diameter	0.066	0.411
Fibre lumen diameter	0.418	0.898
Ray width	0.068	0.171

TABLE IV
MAHALANOBIS DISTANCE FOR SQUARE DISTANCE AMONG HABIT CATEGORIES

Habit categories	Small shrubs (0.5-1.0m)	Large shrubs (1-5m)	Small trees (5-10m)	Large trees (>10m)
Small shrubs	—			
Large shrubs	0.013	—		
Small trees	<0.0001	0.0004	—	
Large trees	0.0003	0.0007	0.0764	—
Vines	<0.0001	<0.0001	<0.0001	<0.0001

II). This analysis allowed us to identify if those eight wood variables with the highest correlation coefficients separate habit categories and identify the relative contribution of each character to such a separation. Significant differences among means of those anatomical characters identified by CANDISC were evaluated by variance analyses for each habit category, and differences among means were compared and segregated by Tukey test (P<0.05). All statistical analyses were performed with SAS software (SAS, 1989).

Results

Table II shows the correlation coefficients of anatomical characters with latitude and habit. The magnitude of the association was greater for habit than for latitude. Habit was positively correlated with eight characters, being the highest coefficients those for vessel element length and fibre length. There was a negative association between habit and latitude (r_s= -0.40, P<0.007); thus, some species are smaller in size the higher their latitude. Porosity type did not show a significant correlation with either latitude or habit.

The canonical discriminant analysis showed that two discriminant functions explained 84% of total variation (Table III), contributing significantly to the separation among habit categories (Wilks' λ: P<0.0001, N= 32). The first function (eigenvalue of 2.26) explained 45.26% of the total variation and the second (eigenvalue of 1.91) explained 38.34% of the remaining variation. According to the Mahalanobis distance, most of the centroids of each habit were significantly different (Table IV). The biplot for the first two discriminant functions showed that most individuals were assigned to the correct habit, except for one individual of *Buddleja sessiliflora* that was classified as a large shrub (Figure 1).

Variance analyses revealed significant differences between habit and narrow vessel diameter (F= 8.45, gl= 4, P= 0.0001, N= 43), vessel element length (F= 17.73, gl= 4, P<0.0001, N= 43), intervessel pit diameter (F= 6.07, gl= 5, P<0.0006, N= 43), fibre lumen (F= 9.76, gl= 4, P<0.0001, N= 43), fibre diameter (F= 5.05, gl= 4, P<0.0022, N= 43), and fibre length (F= 19.47, gl= 4, P<0.0001, N= 43). There were no differences in fibre wall thickness, ray height or ray width (P>0.06) with regard to habit. Figure 2 summarizes the multiple comparisons of means for six wood features among habit categories. The narrowest vessel diameter was seen in shrubs (Figure 2a). Vessel element length and fibre length are smaller in small shrubs to larger in tall trees, except for fibre length in vines (Figure 2b-f). For example, small shrubs had the shortest vessel elements and fibres (224 ±76µm and 489 ±137µm, respectively) whereas mean vessel element length in tall trees was 295 ±73µm and fibre length was 638 ±138µm. Fibre diameter and lumen diameter contributed to distinguish shrubs from trees >10m high. Anatomical differences among trees, shrubs and lianas are shown in Figure 3a-c, whereas pit diameter and fibre lumina differences between trees and shrubs are illustrated in Figure 3d-g.

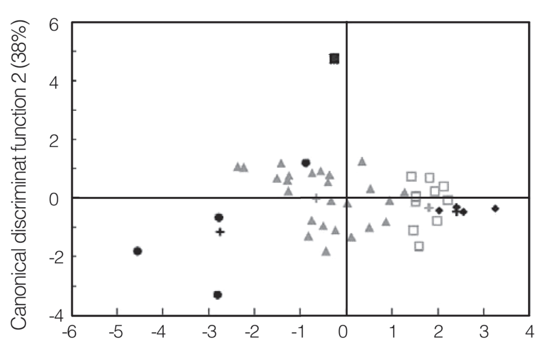

Figure 1. First two functions from canonical discriminant analysis of 26 species plotted for habit categories of *Buddleja*. Circles: small shrubs (0.5-1.0m), triangles: tall shrubs(1.1-5.0m), open squares: small trees (5.1-10m), diamonds: trees (>10 m); solid square: liana; +: centroids of each habit category.

Discussion

The correlation coefficients showed that anatomical wood characters and species habit are positively correlated in *Buddleja*, showing an allometric relationship, similar to that observed in other species (Chalk, 1983; Rury, 1985; Zhang, 1992; Terrazas, 1994; Noshiro and Baas, 1998; Terrazas and Loza-Cornejo, 2003; Motomura *et al.*, 2007). These analyses indicate that habit explains more of wood cell size variation than latitude. It suggests that microclimatic factors such as temperature and rainfall influ-

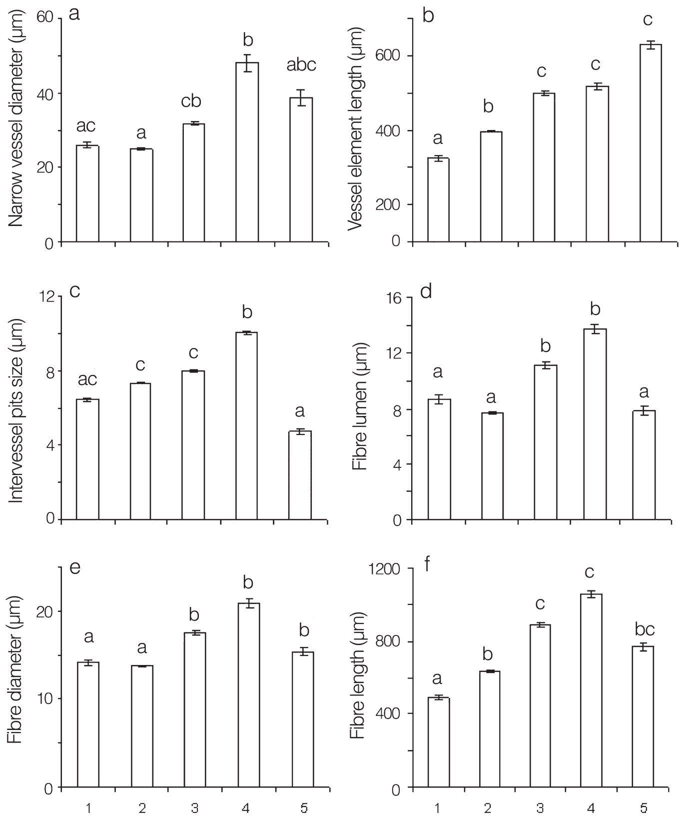

Figure 2. Mean (µm) and standard deviation (bars) of five wood features for habit categories of *Buddleja*. a: narrow vessel diameter, b: vessel element length, c: intervessel pit size, d: fibre lumen, e: fibre diameter, f: fibre length. Habit categories by height are 1: small shrubs (0.5-1.0m), 2: tall shrubs (1.1-5.0m), 3: small trees (5.1-10m), 4: trees (>10m), and 5: liana. Different letters indicate statistical significant differences (P<0.05, Tukey).

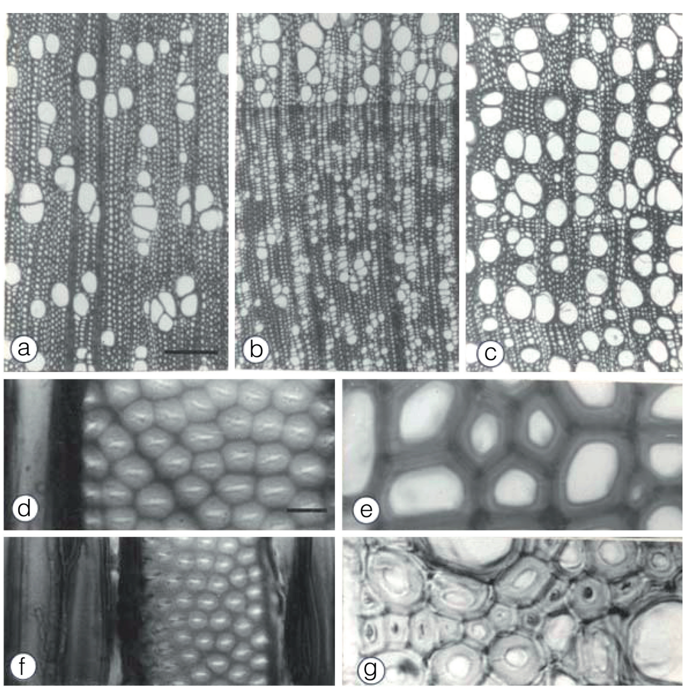

Figure 3. *Buddleja* wood variation of selected characters. a: transverse section of *B. americana*, diffuse porosity; b: transverse section of *B. davidii*, ring porosity; c: transverse section of *B. pulchella*, diffuse porosity; d: tangential section of *B. americana*, intervessel pits; e: transverse section of *B. nitida*, fibre lumina; f: tangential section of *B. polystachya*, small intervessel pits; g: transverse section of *B. saligna*, narrow fibre lumina. Scale bar: 2-4= 200µm; 5-8= 10µm.

ence wood structure, whereas latitudinal provenances do not clearly display this variation (van den Oever *et al.*, 1981; Zhang *et al.*, 1988; Aguilar-Rodríguez *et al.*, 2006). The individual distribution of several shrubby species, for example *B. alternifolia* with heights up to 5m, growing at high latitude (39º42'N, in Asia) may have influence on the low correlation coefficients between latitude and the anatomical characters. Zhang (1992) reported that in the family Rosaceae the percentage of variance explained by macroclimatic factors (latitude) was lower than in other groups of plants, as vessel element and ray size were mainly influenced by habit. Species of *Rhododendron* that grow as shrubs tend to have smaller vessel size (Noshiro and Suzuki, 2001).

Numerous studies mention that tracheary elements and ray height have the largest size in trees and the smallest size in short species (Carlquist, 1966; Dickison and Phend, 1985; Rury, 1985). Although this allometric relationship between various wood features and plant size seems to be typical, few studies confirm statistically such a relationship (Zhang, 1992; Terrazas, 1994; Noshiro *et al.*, 1995; Noshiro and Baas, 1998, 2000; Terrazas and Loza-Cornejo, 2003; Motomura *et al.*, 2007). Terrazas (1994) reported positive correlations between habit and some wood characters in Anacardiaceae. Tracheary elements were longer and wider, with the largest pits in the tallest species, and shorter, narrower tracheary elements with smaller pits in shorter species. However, ray height and width in *Buddleja* did not show a significant association with habit. A similar finding was reported for Anacardiaceae (Terrazas, 1994) but not for Rosaceae (Zhang, 1992), where both characters were significantly larger with smaller plant size. In *Pachycereus pecten-aboriginum* no allometric relationship between element vessel length and habit was detected (Arias and Terrazas, 2001).

Some wood characters in the liana *B. pulchella* show a different behavior. This vine possesses the longest vessel elements and wider diameters; however, fibres are shorter than those of the trees in the genus *Buddleja*. Bamber and Ter Welle (1994) mentioned that in lianas vessel diameter and ray height are longer and fibres are shorter. They also compared cell dimensions between lianas and trees, showing that vessels are wider and nearly three times longer in lianas than in trees. This difference was not observed in *Buddleja,* with a mean diameter of wide vessels of 95 ±10µm in *B. pulchella* and of 88 ±37µm in the arboreal species, suggesting that strong dimorphism in vessel diameter may occur mostly in lianas from tropical regions.

Porosity in the genus *Buddleja* does not have a significant association with habit, unlike the family Rosaceae, where the shrubby forms are associated with ring porosity and shorter vessel elements (Zhang, 1992). However, *Buddleja* shrub species commonly possess ring- or semiring-porous wood, and in the arboreal species >10m high, wood generally is diffuse-porous.

Although *Buddleja* wood is homogeneous (Carlquist, 1997; Aguilar-Rodríguez and Terrazas, 2001) most of its species can be separated by their habit, as suggested by canonical discriminant analysis. Vessel element length and fibre length distinguish shrubs from trees. These results suggest that *Buddleja* species which grow as small shrubs in restricted environments show a narrower variation in tracheary elements size, while species with a wide distribution, such as *B. sessiliflora,* differ in size and may grow to different heights. This species is widely distributed in the North American region, and grows as shrub or small tree depending on the environment (Norman, 2000). Zhang *et al.* (1988) suggested that wood may show more phenotypic than genotypic variation, related to growth in individuals. It is concluded that in species with wide distribution, variation in size of wood characters does not show a discrete relation with habit.

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