ELSEVIER

Scientia Horticulturae 92 (2002) 97–105

SCIENTIA HORTICULTURÆ

www.elsevier.com/locate/scihorti

Xylem conductivity and vulnerability in cultivars and races of avocado

Isabel Reyes-Santamaría[a], Teresa Terrazas[b,*], Alejandro F. Barrientos-Priego[c], Carlos Trejo[b]

[a]*Especialidad en Fisiología, Colegio de Postgraduados Montecillo, Edo. de México 56230, Mexico*
[b]*Especialidad en Botánica, Colegio de Postgraduados Montecillo, Edo. de México 56230, Mexico*
[c]*Postgrado en Horticultura, Departamento de Fitotecnia, Universidad Autónoma Chapingo, Chapingo, Edo. de México 56230, Mexico*

Accepted 21 May 2001

Abstract

Anatomical vessel features of Guatemalan, Mexican and West Indian races and cultivars Colín V-33, Fuerte and Hass of *Persea americana* Mill. were studied in 10-year-old trees grown in the field under similar environmental and management conditions with the main purpose to get insight on anatomical variation among genotypes. The cultivars differed anatomically from the races, showing an inverse relationship between races and cultivars with respect to vessel frequency and diameter, however, relative conductivity was similar among cultivars suggesting an adjustment between vessel diameter and frequency that maintains a similar relative conductivity among genotypes. The three races had the higher vessel frequency and the narrower vessel diameters as well as the lowest vulnerability index values compared to Hass and Fuerte cultivars. An important finding in this study was that cultivar Colín V-33, a dwarf genotype, had intermediate anatomical characteristics between races and the other cultivars suggesting a better adapted hydraulic system to water deficits. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: *Persea americana*; Wood anatomy; Vessels; Genotypes; Avocado

1. Introduction

It is well known that anatomical characteristics of water conduction systems in plants can have a profound impact on the hydraulic conductivity efficiency of the xylem. When xylem water columns experience extreme tension especially under environmental stress

* Corresponding author. Tel.: +52-595-20200; fax: +52-595-20247.
E-mail address: winchi@colpos.colpos.mx (T. Terrazas).

0304-4238/02/$ – see front matter
PII: S0304-4238(01)00284-9

conditions, cavitation occurs with air introduced into tracheids or vessels forming an embolism (Tyree and Sperry, 1989). Cavitation is common in nature as a result of water stress and freezing. It is of major importance in plant survival because embolized conduit systems increase resistance to water flow and trigger different plant physiological responses like stomatal closure, foliage loss and eventually death (Peña and Grace, 1986; Tyree and Sperry, 1988; Sperry and Pockman, 1993; Kavanagh and Zaerr, 1997). It is not yet clear what determines vulnerability to cavitation among species; an initial hypothesis is that large diameter conduits are more vulnerable to cavitation than small ones (Tyree and Sperry, 1989; Lo Gullo and Salleo, 1991; Hargrave et al., 1994). If the former is true then according to the Hagen–Poiseuille equation, the hydraulic conductance of a conduit with a diameter twice as wide as another would be 16-fold greater but it would be more prone to cavitation. However, this idea is not consistent since in several cases, species with larger diameter conduits are less vulnerable to cavitation than species with narrower vessels (Tyree and Sperry, 1988). Further studies have suggested that vulnerability to cavitation in many cases could be related to the structure of the pit membranes, the larger the pore the more vulnerable the conduit (Tyree and Sperry, 1989; Grace, 1993; Hargrave et al., 1994).

In fruit culture, grafting of different scions and rootstocks has been a traditional practice with the aim to confer dwarfing characteristics and resistance to environmental stress like salinity, drought, pests and diseases. The new characteristics obtained in the plant must be the result of an intense interaction between the rootstock and scion carrying different genetic information. Also chemical signals moving up and down through different conduction systems must have profound effects in assimilation, water relations and development (Lockard and Schneider, 1981; Iacono et al., 1998).

In this initial study, the purpose was to determine secondary xylem anatomical variation especially of those features related to water conduction in three races and three cultivars of mature avocado trees growing under similar environmental conditions. Also, we evaluated relative hydraulic conductivity and vulnerability index of the conduit system among genotypes. It was hypothesized that if anatomical differences exist among the genotypes both, relative conductivity and the risk of water column cavitation will be different.

2. Materials and methods

The plant material was collected in Fundación Salvador Sánchez Colín-Centro de Investigaciones Científicas y Tecnológicas del Aguacate experimental orchard, located at Coatepec Harinas, State of México, México (18°55′N, 99°46′W, 2240 m elevation) with a temperate subhumid climate (García, 1988). Avocado genotypes studied belong to the races: Guatemalan (*Persea americana* var. *guatemalensis* Williams), Mexican (*P. americana* var. *drymifolia* [Schlecht. and Cham.] Blake) and West Indian (*P. americana* var. *americana* Mill.) and the cultivars: Colín V-33, Fuerte and Hass. Four 10-year-old trees were sampled for each race and cultivar. The races were grown in the orchard from seeds collected in the wild, whereas cultivars were grafted on Mexican race seedling rootstock 57PBo3. Height and trunk diameter of sampled trees are shown in Table 1. All trees in the orchard are watered monthly from December to May and 3 kg per tree of 120–100–80

Table 1
Height and trunk diameter of sampled trees of *P. americana* Mill. races and cultivars grown at Coatepec Harinas, State of Mexico

Races	Height (m)	Diameter (cm)	Cultivars	Height (m)	Diameter (cm)[a]
West Indian	5	18	Colín V-33	2	16
	5	15		2	28
	5	22		2	23
	5	18		2	22
Guatemalan	5	21	Fuerte	5	27
	5	20		5	38
	5	20		5	28
	5	18		5	27
Mexican	5	32	Hass	5	31
	5	49		5	27
	5	24		5	58
	5	26		5	24

[a] Measured above the graft of the scion.

(N:P:K) are applied in June and October. The soil is of volcanic origin classified as Andisoil.

Wood samples were cut with a steel punch 30 mm in diameter at 0.35–0.45 m from soil in the races and above the graft of the scion in the cultivars (0.40–0.75 m from soil). The samples were fixed in formaldehyde–acetic acid–ethanol (Berlyn and Miksche, 1976) for 48 h and later stored in glycerin–ethanol–water (1:1:1) until sectioning. Transverse sections 20–30 μm thick were cut on a sledge microtome, stained with safranin and then mounted with synthetic resin. Wood macerations were made with Jeffrey's solution (Berlyn and Miksche, 1976) and mounted on temporary slides.

Vessel frequency (vessels mm^{-2}) represents the mean of 75 fields per sample and vessel diameter (μm) was measured at the widest part of the tangential vessel lumen as viewed in cross-section and did not include cell wall. Vessel element length (μm) was measured using macerations and included the tails. Average values for diameter and length are based on 75 individual vessel elements per sample. All measurements were performed with an image analyzer software Image-Pro Plus V.3.1.1 (Media Cybernetics, Silver Spring, MD, 1997).

Variation on efficiency and susceptibility to damage during water conduction was evaluated through relative hydraulic conductivity (Zimmermann, 1983) and vulnerability index (Carlquist, 1977). The relative hydraulic conductivity was estimated using the modified Hagen–Poiseuille equation (Fahn et al., 1986): $\mathrm{RC} = r^4\mathrm{VF}$, where RC is the relative conductivity, r the vessel radius and VF the vessel frequency. The vulnerability index was calculated: $V = \mathrm{VD}/\mathrm{VF}$, where V is the vulnerability index, VD the vessel diameter and VF the vessel frequency.

Basic statistics were calculated for each variable and results showed that 'Colín V-33' data did not adjust to a normal distribution; thus all variables were transformed to natural logarithm or square root to carry on the following analyses. Variance analyses were used to determine the existence of intra- and inter-genotype significant differences for the variables studied. These analyses were followed by the pairwise comparison analysis of Tukey.

A canonical discriminant analysis was applied to all variables and allowed us to identify a subset of characters that separate the genotypes to the maximum and identify the relative contribution from each variable to their separation. The distinction among genotypes was assessed using the *F*-test on the Mahalanobis distance. A discriminant classificatory

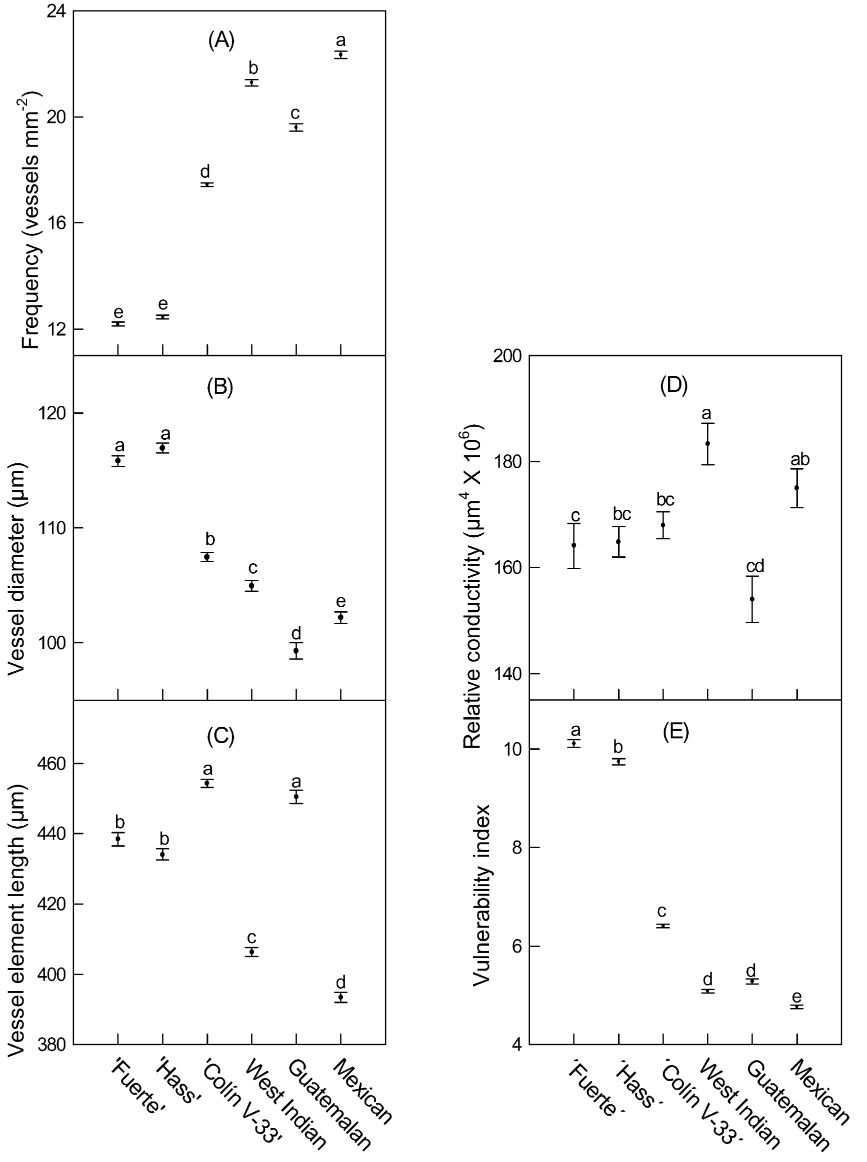

Fig. 1. Pairwise comparison (Tukey, $P = 0.05$) for the vessel features of avocado races and cultivars studied. Each point represents the mean of 75 observations ± standard error: (A) vessel frequency; (B) vessel diameter; (C) vessel element length; (D) relative conductivity; (E) vulnerability index.

analysis was applied to verify that individuals are classified in the pre-assigned genotype. All analyses were performed using SAS software (SAS, Cary, NC, 1989).

3. Results

Significant differences among the cultivar Colín V-33 and the three races, Guatemalan, Mexican and West Indian were found in all the variables measured, but Fuerte and Hass cultivars did not show any difference between each other. The three avocado races showed the highest vessel frequency 22, 21 and 20 vessels mm^{-2} for West Indian, Guatemalan and Mexican, respectively. The cultivar Colín V-33 had an intermediate vessel frequency (17 vessels mm^{-2}), whereas Fuerte and Hass cultivars showed the lowest frequency (12 and 12.5 vessels mm^{-2}, Fig. 1A).

Vessel diameter showed an inverse behavior and statistical significant differences were found among genotypes ($P < 0.0001$). 'Fuerte' and 'Hass' had the widest vessel diameters, with mean values of 116 and 117 μm, respectively, followed by 'Colín V-33' and races West Indian and Mexican with mean values of 107, 105 and 102 μm, respectively.

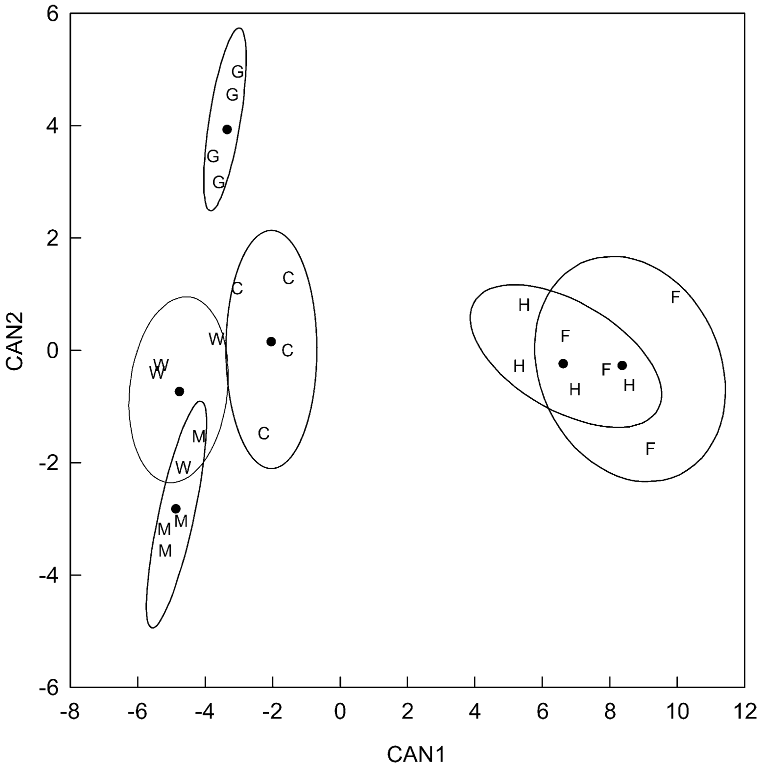

Fig. 2. Two-dimensional representation of canonical discriminant of five variables from three races (M: Mexican, G: Guatemalan, W: West Indian) and three cultivars (C: Colín V-33, F: Fuerte, H: Hass). See Table 2 for loadings, the first and second functions account for 97.31% of the variation.

Table 2
Function loadings from canonical discriminant analysis of the different genotypes of *P. americana* Mill. studied

Variables	Function 1	Function 2
Vulnerability index	0.972215[a]	−0.028209
Vessel frequency	−0.941428[a]	−0.096220
Vessel diameter	0.557256	0.240026
Vessel element length	0.208604	0.440074[a]
Relative conductivity	−0.037718	−0.244871

[a] The highest loadings.

The Guatemalan race possessed the narrowest vessel diameter with a mean value of 99 μm (Fig. 1B). The vessel element length did not follow any clear pattern (Fig. 1C). Guatemalan race and cultivar Colín V-33 had the longest elements followed by 'Fuerte' and 'Hass' which showed the same mean value, whereas West Indian and Mexican races possessed the shortest elements (Fig. 1C).

No differences in relative conductivity were found among cultivars between Mexican and West Indian races (Fig. 1D); however, significant differences in relative conductivity exist between Guatemalan race and the other races. Vulnerability index showed significant differences among most genotypes ($P < 0.0001$), having 'Fuerte' and 'Hass' the highest values (10.1 and 9.7, respectively), whereas 'Colín V-33' and the three avocado races having the lowest vulnerability values with a gradual reduction among them (Fig. 1E).

Canonical discriminant analysis results revealed that two functions accounted for 97.31% of the variance (Wilk's lambda $P < 0.0001$). The first function explained 85.55% of the variation with an eigenvalue of 39, whereas the second only accounted for 11.76% of the remainder variance with an eigenvalue of 5.36. Both functions contributed significantly to races and cultivars separation, except for Hass and Fuerte cultivars (Mahalanobis distance, $P > 0.63$) and West Indian and Mexican races (Mahalanobis distance, $P > 0.45$) (Fig. 2). The variables that contributed more ($P < 0.0001$) to the distinction of races and cultivars and with the highest loadings were vulnerability index and vessel frequency in the first function and vessel element length in the second function (Table 2). In the discriminant classificatory analysis, individuals were readily classified in the corresponding genotypes, with predicted group memberships of 75–100% (Table 3), except for 'Fuerte' where only 50% of the individuals were correctly classified.

Table 3
Predicted group memberships (%) of individuals of *P. americana* Mill. genotypes based on discriminant classificatory analysis

Race/cultivar	West Indian	Guatemalan	Mexican	Colín V-33	Fuerte	Hass	Total
West Indian	*75*	0	25	0	0	0	100
Guatemalan	0	*100*	0	0	0	0	100
Mexican	25	0	*75*	0	0	0	100
Colín V-33	0	0	0	*100*	0	0	100
Fuerte	0	0	0	0	*50*	50	100
Hass	0	0	0	0	25	*75*	100

4. Discussion

Anatomical characteristics responsible of water conduction are different between races and cultivars as revealed by statistical multivariate analyses, in spite of being grown under the same environmental and management conditions. Races showed a higher variability in vessel frequency and diameter than cultivars and this variability clearly affects relative conductivity and vulnerability index. Mexican and West Indian races possess a higher similarity in water conduction features than with Guatemalan race. These similarities confirmed other evidences suggesting that Guatemalan race has different ancestors than Mexican and West Indian races (Scora and Bergh, 1990). Baas (1982) mentioned that vessel features responsible for water conduction are genetically fixed in species, however, avocado races are more variable than cultivars, and probably these differences are related to many years of being used as food.

'Fuerte' is a hybrid between Mexican and Guatemalan races and 'Hass' has only 10–15% of Mexican race genes and the remaining of Guatemalan race (Bergh and Ellstrand, 1986). Both cultivars have the same progenitors and this explains, in part, the high similarity on vessel features revealed by statistical analyses. These cultivars showed fewer vessels and wider diameters than their progenitors, contrary to *Populus* clones (Peszlen, 1994) and *Eucalyptus hybrids* (February et al., 1995). A possible explanation about vessel frequency and diameter between these two cultivars and the races of origin is what is known as transgressive progeny, in which a combination of pure individuals not related in a cross could give a transgressive hybrid, where the individuals could bypass the parents in a positive or negative form. However, we consider that cultivars as Booth and Reed will behave as Fuerte and Hass compared to their progenitors. These speculations must remain hypothetical at present until more detailed studies are conducted. In the case of 'Colín V-33', it is an offspring of 'Fuerte' and probably some transgressive characteristics were lost due to segregation.

When dwarf trees are present, there is a strong correlation between tree height and vessel element size. Generally, shorter vessel elements and narrower diameters occur (Baas et al., 1984). This was not the case in cultivar Colín V-33, a dwarf mutant (Barrientos-Pérez and Sánchez, 1982) with the longest vessel elements of the genotypes studied and with vessel diameters intermediate between races and cultivars. Mean vessel element lengths found in the genotypes studied are shorter than those reported for *P. americana* (mean $= 500\,\mu m$) growing in the wild and with trees taller than 20 m (Rogel, 1985). There is an allometric relationship between vessel element length and tree height in *P. americana* as reported in other species (Zhang et al., 1992), but not for cultivar Colín V-33 as mentioned above.

Vessel frequency and diameter are inversely related in all genotypes studied, similar to other tree species (Carlquist, 1988; Terrazas and Dickison, 2001), except for vines (Ewers and Fisher, 1989). The avocado races showed narrow vessels and among them Guatemalan race has the narrowest vessels. These values may suggest that the water flow system in Guatemalan race has a lower probability to suffer a dysfunction. The narrow and abundant vessels theoretically could allow the functioning of the conduction system if many vessels are disabled by cavitation (Carlquist, 1977), as could be the case of 'Colín V-33'.

In spite of the differences in vessel frequency and diameter among genotypes, relative conductivity is similar among the cultivars suggesting an adjustment. It is common that species with narrow and abundant vessels show low vulnerability values (Carlquist, 1977). This indicates that among cultivars, ‘Colín V-33’ has a safer water flow system because of its low vulnerability index. These results support Hargrave et al. (1994) findings, who found that wider vessels are more susceptible to show dysfunction compared to vessels with narrow diameter. This interpretation supports the idea that cultivars Fuerte and Hass with wide vessels could be more susceptible to have embolism during periods of water stress (Hargrave et al., 1994) than the three races and cultivar ‘Colín V-33’. However, the former suggestion has to be taken with caution since water movement and balance are not only regulated by the anatomical characteristics. They may be also influenced by water potential gradient between the soil–plant–atmosphere, as well as for stomatal features and their sensitivity, especially when water content is limited in the soil.

It is known that low vulnerability values are present in plants that require low quantities of water to develop (Carlquist, 1977), thus avocado races may be better adapted to water stress since they possess abundant narrow vessels, which confer them less probability of catastrophic failure of the conducting tissue. The world’s most used cultivars are Hass and Fuerte, however, ‘Colín V-33’ is used to a limited extent in Mexico. This cultivar has the particularity of being dwarf (Barrientos-Pérez and Sánchez, 1982) and it has been used as interstock to reduce ‘Fuerte’ size (Barrientos-Priego et al., 1987). The anatomical features of the water conductive system of ‘Colín V-33’ confer it the same relative conductivity as the other cultivars, but may be less susceptible to cavitation. Further, water stress experiments are needed to support this assertion.

The anatomical differences of the vessels in the secondary xylem within and between races and cultivars suggest that the three avocado races studied are the ones that show higher vessel frequency, narrower vessel diameters, low vulnerability, and a more variable relative hydraulic conductivity. Among the cultivars, ‘Colín V-33’ was an intermediate between the races and cultivars with characteristics that may suggest a better performance under water stress conditions. This hypothesis is currently under study.

Acknowledgements

We thank to Fundación Salvador Sánchez Colín-CICTAMEX for sampling facilities, to CONACYT grant 28901B for financial support and to Colegio de Postgraduados for laboratory facilities. The senior author also thanks CONACYT for scholarship 70482.

References

Baas, P., 1982. Systematic, phylogenetic and ecological wood anatomy: history and perspectives. In: Baas, P. (Ed.), New Perspectives in Wood Anatomy. Martinus Nijhoff, Dordrecht, The Hague, pp. 23–58.

Baas, P., Chenglee, L., Xinying, Z., Keming, C., Yuefen, D., 1984. Some effects of dwarf growth on wood structure. Int. Assoc. Wood Anat. Bull. 45, 63–74.

Barrientos-Pérez, F., Sánchez, C.S., 1982. Height variability obtained from a new dwarf avocado tree population. Calif. Avocado Soc. Yrbk. 66, 155–160.

Barrientos-Priego, A.F., López, J.A., Sánchez, C.S., 1987. Effect of cv. Colín V-33 as interstock on avocado (*Persea americana* Mill.) growth cv. Fuerte. S. Afr. Avocado Grower’s Assoc. Yrbk. 10, 22–24.

Bergh, B., Ellstrand, N., 1986. Taxonomy of the avocado. Calif. Avocado Soc. Yrbk. 70, 135–145.

Berlyn, G.P., Miksche, J.P., 1976. Botanical Microtechnique and Cytochemistry. Iowa State University Press, Ames, IA.

Carlquist, S., 1977. Ecological factors in wood evolution: a floristic approach. Am. J. Bot. 64, 887–896.

Carlquist, S., 1988. Comparative Wood Anatomy. Springer, Berlin, New York.

Ewers, W.F., Fisher, B.J., 1989. Variation in vessel length and diameter in stems of six tropical and subtropical lianas. Am. J. Bot. 76, 1452–1459.

Fahn, A., Werker, E., Baas, P., 1986. Wood anatomy and identification of trees and shrubs from Israel and adjacent regions. Isr. Acad. Sci. Hum., Jerusalem, Israel.

February, E.C., Stock, W.D., Bond, W.J., Le Roux, D.J., 1995. Relationships between water availability and selected vessel characteristics in *Eucalyptus grandis* and two hybrids. Int. Assoc. Wood Anat. J. 16, 269–276.

García, E.,1988. Modificaciones al Sistema de Clasificación Climática de Köppen 4a. ed. México City.

Grace, J., 1993. Consequences of xylem cavitation for plant water deficits. In: Smith, J.A.C., Griffiths, H. (Eds.), Water Deficits Plant Responses from Cell to Community. BIOS Scientific Publishers, London, pp. 109–128.

Hargrave, K.R., Kolb, K.J., Ewers, F.W., Davies, S.D., 1994. Conduct diameter and drought-induce embolism in *Salvia mellifera* (Labiatae). New Phytol. 126, 695–705.

Iacono, F., Buccella, E., Peterlunger, E., 1998. Water stress and rootstock influence on leaf gas exchange of grafted and ungrafted grapevines. Sci. Hortic. 75, 27–39.

Kavanagh, K.L., Zaerr, J.B., 1997. Xylem cavitation and loss of hydraulic conductance in western hemlock following planting. Tree Physiol. 17, 59–63.

Lo Gullo, M.A., Salleo, S., 1991. Three different methods for measuring xylem cavitation and embolism: a comparison. Ann. Bot. 67, 417–424.

Lockard, R.G., Schneider, G.W., 1981. Stock and scion growth relationships and the dwarfing mechanism in apple. Hort. Rev. 3, 315–375.

Peña, J., Grace, J., 1986. Water relations and ultrasound emissions of *Pinus sylvestris* L. before, during and after a period of water stress. New Phytol. 103, 515–524.

Peszlen, I., 1994. Influence of age on selected anatomical properties of *Populus* clones. Int. Assoc. Wood Anat. J. 15, 311–321.

Rogel, G.M. de los A., 1985. Estudio anatómico de la madera de seis especies trópicales. Bol. Téc. INIF México 89, 1–70.

Scora, R.W., Bergh, B., 1990. The origins and taxonomy of avocado (*Persea americana* Mill.) Lauraceae. Acta Hortic. 275, 387–394.

Sperry, J.S., Pockman, W.T., 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. Plant Cell Environ. 16, 279–287.

Terrazas, T., Dickison, W.C., 2001. Wood anatomy of Anacardiaceae. IAWA J. 22, in press.

Tyree, M.T., Sperry, S., 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Plant Physiol. 88, 574–580.

Tyree, M.T., Sperry, S., 1989. Vulnerability of xylem to cavitation and embolism. Annu. Rev. Plant Physiol. Mol. Biol. 40, 19–38.

Zhang, S.-Y., Baas, P., Zandee, M., 1992. Wood structure of the Rosaceae in relation to ecology, habit and phenology. Int. Assoc. Wood Anat. Bull. 13, 307–347.

Zimmermann, M.M., 1983. Xylem Structure and the Ascent of Sap. Springer, Berlin.