

RESEARCH PAPER

Air method measurements of apple vessel length distributions with improved apparatus and theory*

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Abstract

Studies showing that rootstock dwarfing potential is related to plant hydraulic conductance led to the hypothesis that xylem properties are also related. Vessel length distribution and other properties of apple wood from a series of varieties were measured using the 'air method' in order to test this hypothesis. Apparatus was built to measure and monitor conductivity to air of fresh wood segments of different lengths. Theory for determining vessel length distribution was improved to give a single parameter uni-modal vessel length probability density function. The function, derived by combining the exponential extinction (with extinction coefficient k) of wood conductivity to air (C) as wood length (x) increases (i.e. $C=C_0 \exp(-kx)$) with the differential double difference formula, is $P_x=x \times k^2 \exp(-kx)$, where P_x is the fraction of vessels of length x . The main parameter of the distribution, k , was found to be the inverse of the mode of the distribution, i.e. the most common vessel length, L_0 . L_0 for ten apple rootstock and scion varieties varied from 5.6 ± 0.1 cm ($\pm$ SE) for MM.111 to 9.0 ± 1.0 for Prunifolia ($P < 0.05$). Average maximum vessel length was approximately 50 cm, and differences were not significant. Effective vessel radii ranged from 14 for Prunifolia to 24.3 ± 0.7 μ m for M.26, with standard errors less than 12% of the mean. Specific conductivity of a 15 cm wood segment ranged from 2×10^{-4} to $1.6 \pm 0.2 \times 10^{-2}$ $\text{dm}^3 \text{ s}^{-1} \text{ kPa}^{-1} \text{ m}^{-1}$ for maruba and M.26, respectively, with standard errors up to 63% of the mean. Vessel density at the air entry point ranged from 18 ± 3 to 42 ± 6 vessels mm^{-2} for M.26 and MM.106, respectively, with stand-

ard errors as high as 89% of the mean. It was concluded that there is no general relationship between the wood properties investigated and rootstock size class, and that plasticity increases from vessel lengths to radii to specific conductivity and vessel densities.

Key words: Dwarfing, *Malus domestica*, probability density function, rootstock, scion.

Introduction

The domestic apple (*Malus domestica*), a hybrid of several wild species, is grown extensively in cool temperate regions of the world. Apple cultivation can be traced at least to the 10th century BC and many varieties have been developed. Grafting of apples on rootstocks also dates to antiquity, with early records from Greece in the 3rd century BC (Sauer, 1993). For more than a century rootstocks have been used to control scion size, as well as to give the tree resistance to a wide range of pests and diseases. Although rootstocks are necessarily related to the scion species and usually are from the same genus, they may be from different species.

Direct (Cohen and Naor, 2002; Atkinson *et al.*, 2003) and indirect (Higgs and Jones, 1990; Olien and Lakso, 1984, 1986) evidence indicates that hydraulic conductance of dwarfing apple rootstocks is lower than that of strong rootstocks, and similar findings have been reported for citrus (Syvertsen, 1981). Hydraulic conductance can reduce vegetative growth in a wide range of plant species (Wahl and Ryser, 2000; Radin and Eidenbock, 1984; Richards and Passioura, 1989; Brodribb and Feild, 2000;

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Hubbard *et al.*, 2001; Sperry, 2000). Ryan and Yoder (1997) presented a theory relating hydraulic limits to tree height and growth in forest species. However, attempts to prove that theory in specific cases have not always been successful (McDowell *et al.*, 2002).

Due to the considerable genetic variability of apple varieties, which has inevitably developed over the many centuries of cultivation, and due to the findings of differences in hydraulic properties of full-sized trees, it was expected that there might be significant differences in wood structure between varieties. Of course, it is of interest to determine which wood structural parameters are constant for apple and its relatives, and which are more plastic. It was hypothesized that some of the wood parameters would be related to rootstock dwarfing potential.

Methods for determining vessel length distribution have been described by Zimmermann and Jeje (1981) and Ewers and Fisher (1989). These involve measurement of air conductivity or counting of coloured vessels in wood samples of varying length and discrete numerical analysis of the measurements (see also Tyree, 1993). A tremendous amount of work would be needed in order to differentiate between small differences in length distributions with existing methodology. In the current study, theory is developed to analyse series of air conductivity measurements in order to determine the main parameters of the vessel size distribution and an average vessel radius. These parameters are easily treated with standard statistics so that small differences in vessel size distribution can be determined.

Theory

Air conductivity of capillaries and wood

Siau (1984) reviewed the physics of airflow in capillaries relevant to the computation of wood conductivity (also called permeability) to air and relating airflow to capillary dimensions. For details of equations 1, 4 and 5 the reader is referred to that text. In order to determine if airflow is laminar or turbulent, the Reynold's number (Re) should be computed, i.e.

$$Re = \frac{2\rho Q}{\pi r \eta} = \frac{2r\bar{v}\rho}{\eta} \quad (1)$$

where ρ is fluid density (kg m^{-3}), Q is volumetric flow rate ($\text{m}^3 \text{s}^{-1}$), r is capillary radius (m), η is air viscosity ($1.81 \times 10^{-5} \text{ Pa s}$ at 20°C), and $\bar{v}$ is average linear fluid velocity (m s^{-1}) in the capillaries. The left hand form of the equation is for a single capillary, while the right hand form is more general. When $Re < 2000$, fluid flow is laminar and the following equations 2–5 apply.

If the number of capillaries (N) and their approximate radii, r , in a piece of wood are known, then

$$\bar{v} = \frac{Q}{N\pi r^2} \quad (2)$$

Combining equations 1 and 2 gives the form for a wood sample containing N vessels,

$$Re = \frac{2\rho Q}{N\pi r \eta} \quad (3)$$

Thus if approximate values of r are known, for example, from microscopic observations of the wood, the Reynolds number can be determined from the volumetric airflow rate.

Gas conductivity, C , ($\text{m}^2 \text{s}^{-1}$) can be written as

$$C = \frac{QLP}{A\Delta\bar{P}} \quad (4)$$

where L is length of the wood segment (m), A is its cross-sectional area (m^2), P is pressure (Pa) at which the flow rate Q is measured, $\bar{P}$ is the average pressure in the segment, and ΔP is the pressure difference across the segment.

Analysis of Poiseuille's law for gas flow in capillaries leads to the equation:

$$r = \left[\frac{8Q\eta LP}{N\pi\Delta\bar{P}} \right] \quad (5)$$

where r is the effective radius of a single capillary.

Wood conductivity to air for a random distribution of vessel lengths

Air forced through freshly cut wood at low pressures ($< 100 \text{ kPa}$) passes only through open vessels, since airflow through the walls of vessels is blocked by wet pit membranes (the primary cell wall inside pits; Skene and Balodis, 1968). The conductivity, C , of the wood to air is proportional to the number of vessels extending from one cut end of the wood to the other (Siau, 1984). For a uni-modal distribution of vessel lengths, modal length L_o , and vessels randomly distributed in the wood, it would be expected that the decrease in C over a small segment of wood would be proportional to the wood length, dx , since vessels are increasingly closed as the wood length increases. In an analysis similar to that for extinction of radiation in a turbid medium, this can be described as

Table 1. Parameters of the uni-modal vessel length distribution, and formulae for their computation where C is conductivity to air, C_0 and k are constants determined by linear regression, x is length, and D is a conversion factor expressing the density of vessel elements at unit conductivity.

Parameter	Description	Formula	Equation
C	Conductivity of open vessels	$C = C_0 \exp(-kx)$	7
C_0	Conductivity intercept	From linear regression	7
L_m	Maximum vessel length	$\ln(DC_0)/k$	8
P_x	Vessel length distribution function	$x k^2 \exp(-kx)$	10
L_0	Mode or most common vessel length	$1/k$	11
N_0	Number of vessels at air entry point	DC_0	

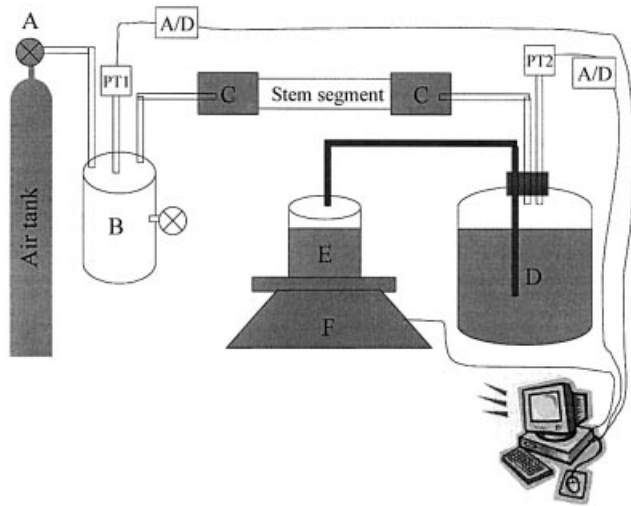


Fig. 1. Schematic diagram of the apparatus used to measure stem segment conductivity to air. A, valve and pressure regulator; B, ballast air tank with air bleed valve; C, high pressure air tight connectors to the stem segment; D, water tank; E, beaker; F, precision balance; PT, pressure transducer; A/D, analog to digital converter.

$$dC = C_0 - C = C_0(-kdx) \text{ or } dC/C_0 = -kdx \quad (6)$$

where C_0 is the conductivity of a thin length of wood (i.e. $x=0$) and k is an extinction coefficient. For a finite length of wood, x , equation 6 is integrated, such that:

$$\int_{C_0}^C dC/C = \int_0^x -kdx$$

and

$$\ln C - \ln C_0 = -kx \text{ or } \ln C = \ln C_0 - kx$$

$$C = C_0 \exp(-kx) \quad (7)$$

Equation 7, which was presented in a different form by Bramhall (1971), based on the observed air conductivity of dry wood, can be applied to data for the conductivity of wood at different wood lengths. Linear regression of $\ln(C)$ on x yields values for C_0 and k . If a conversion

factor, D , i.e. the number of vessels per unit conductivity, is known (i.e. $D = N/C$, and N is the number of vessels counted at the outlet end of a paint perfused wood segment of known conductivity) then the number of active vessels at the air entry point is DC_0 . Similarly, using the same conversion factor we can solve for the maximum vessel length, L_m ,

$$L_m = \ln(DC_0)/k \quad (8)$$

Uni-modal vessel length distribution

Several authors have discussed the use of the double difference method to determine vessel length distributions from measurements of numbers of open vessels or air conductivity at different lengths in the wood (see Tyree, 1993; and papers cited therein). The double difference method, expressed in differential form (Zimmermann and Jeje, 1981) is:

$$P_x = x (d^2C/dx^2)/C_0 \quad (9)$$

where P_x is the fraction of vessels of length x . Differentiation of equation 7 twice and substitution in equation 9 gives the continuous distribution function:

$$P_x = x k^2 \exp(-kx) \quad (10)$$

Integrating equation 10 from zero to infinity gives a value of one, which demonstrates that equation 10 is a true probability density function. Note that the vessel length distribution (equation 10) does not depend on the conductivity (i.e. C_0) or density of vessels in the piece of wood measured.

The maximum value of this distribution, i.e. the mode, L_0 , represents the most common vessel length in the wood. Analysis of the derivative of equation 10 gives the mode as the inverse of k , i.e.

$$L_0 = 1/k \quad (11)$$

It is important to note that L_0 is independent of the conversion factor D , so that no paint perfusion and counting of vessels is needed for its determination. The salient features of the uni-modal vessel length distribution are summarized in Table 1.

Materials and methods

The measurement apparatus and procedure

A schematic diagram of the apparatus constructed for measurements of conductivity to air is shown in Fig. 1. Air from the pressure tank was transferred to an intermediate ballast tank where precise pressure was measured with a pressure transducer, PT1 (part no. PX136-100GV, Omega Engineering, Stamford, Conn, USA). The air bleed in the ballast tank facilitated maintenance of a constant pressure. Pressurized air from the ballast tank was forced through the stem segment and the outgoing air was transferred to a sealed water tank where the air pressure was measured with PT2. Displaced water from the water tank was collected in a beaker on a precision balance, i.e. a 4-place, 200 g balance for low flow rates and a 2-place, 5000 g balance for high flow rates. Gas volume flow was measured by volume displacement of water, so 1 kg of water corresponds to 1.0 l of water at the pressure measured by P_{T2} . Hence the volumetric flow rate of air at atmospheric pressure (Q) is given by:

$$Q = F(P_{T2} + P^0) / P^0$$

where F is the rate of water displacement in kg s^{-1} , P^0 is atmospheric pressure, and P_{T2} is the pressure of air in the sealed water tank. P_{T1} , P_{T2} and the balance output were connected to RS-232 ports of a computer so that all three could be continuously monitored and logged online with a program written for that purpose. Re was low (i.e. $Re \ll 2000$, see Results), indicating that airflow in the vessels was laminar, so the results were analysed with equations 2–5.

Initial measurements with stem segments where air was forced through one end and the other end was immersed in water showed that maximum vessel lengths exceeded 40 cm, but flow rates were very low for long segments. In addition, most of the plants available for experimentation did not have unbranched stem segments much longer than 30 cm.

The measurement sequence was as follows. An approximately 30 cm unbranched stem or branch segment was cut directly from the plant. Segment diameters were all between 8 and 15 mm. Both ends of the segment were trimmed with a fresh razor blade to ensure that air flow would be directly proportional to applied pressure, as observed by Zimmermann and Jeje (1981) and observed here with samples in which air flow was measured at a series of pressures. The segment was then put in the apparatus (Fig. 1) and air pressure brought to the desired value, approximately 60 kPa (Ewers and Fisher, 1989). Computations show that in this system any water in the open vessels would be pushed out in the first few seconds. Water displacement rate and pressures were monitored until a steady-state value was reached. After reading the steady-state value a 2 cm piece of the segment at the air outlet side was removed and the process was repeated. The pressure measured by P_{T2} was negligible relative to atmospheric pressure until stem segments were less than 10 cm. When stem segments were short, water displacement rates became large and the higher weight-capacity balance was used. The apparatus was useful until stem length was 4–6 cm. The system generally reached steady state within 5–30 min depending on the water displacement rate (i.e. for lower rates more time was necessary).

After the final measurement, when stem segment length was 4–6 cm the remaining stem segment (i.e. stub) was perfused with water (to drive air out of the vessels) for approximately 20 min with a high pressure flow meter (Tyree *et al.*, 1995). Following perfusion, the stub was kept in water to prevent embolism and then it was infiltrated with an aqueous latex paint-pigment solution (approximately 0.2%) from the air entry side at a pressure of less than 0.2 MPa using a pressure chamber or by gravity using a siphon. When using the siphon the stub was left for a few days or until flow stopped. With the pressure chamber the stub was perfused with more than 100 ml of

the paint solution within 1 h. After perfusion with the paint, the outlet end of the stub was shaved clean with a sliding microtome and the number of painted vessels at the air exit point were counted under a dissecting microscope. This number was used to determine the conversion factor, i.e. the number of vessels per unit conductivity (parameter D).

For the early experiments in the series reported here a latex enamel paint solution was used to colour the vessels. The solution was ineffective, as seen by later measurements with latex paint-pigment solution, in which much higher vessel counts were found, so these early vessel count data were discarded. Filtering the latex paint-pigment solution through a series of filters showed that the colored particles were larger than 0.45 μm and smaller than 1 μm . Since vessels width was of the order of 40 μm (see Results) and pit diameter is smaller than 0.4 μm (Sperry and Tyree, 1988) it follows that the coloured solution moved freely through open vessels, i.e. between vessel elements through perforated plates, but did not pass between vessels through the pit membranes.

Plant material

Measurements of air conductivity were performed on stem or branch segments of a series of eight unworked (i.e. non-grafted) apple rootstocks and two scions (Table 2). Five of the rootstocks (M.9, M.26-EMLA, MM.111-EMLA, MM.106-EMLA, and G.16) were from stool bed propagated cuttings raised in a nursery for a year and then transferred to a greenhouse at the US Forest Service Aiken Laboratory in Burlington, VT in spring of 2001. The Maruba rootstock was raised similarly and transferred from Geneva, NY to the greenhouse in summer, 2000. The two remaining rootstocks, Prunifolia and Antanovka, were grown from seed at the Elmore Roots organic nursery in Elmore VT, and transferred to the greenhouse in autumn 2001 in a dormant state. They were in full leaf before measurement. The greenhouse was heated all winter and supplemental lighting extended the photoperiod to prevent dormancy. All measurements were made from March to June 2002.

In addition to the rootstock plants, two scions, Golden Delicious and Liberty, were measured. Branches 10–15 mm in diameter were cut from trees in the University of Vermont's Horticultural Research Complex in Burlington and transferred to the laboratory in water, where they were immediately connected to the measurement apparatus. These measurements were also made in late May and early June; well after the trees had leafed fully.

Data were analysed with Microsoft Excel. SAS software was used for analysis of variance (ANOVA) and for the Student–Newman–Keuls (SNK) multiple range test for determining significantly different means.

Results

Reynolds numbers for air flow in the vessels of the wood samples were estimated using an assumed r value of 10 μm (see Results for vessel diameters below). The low r value used was intended to overestimate, i.e. give worst case Re values, since for a given number of capillaries (N) and volumetric flow rate (Q), air velocity and Re are inversely proportional to r (equations 2 and 3). In all cases Re was between 3 and 130, with low values for long wood segments and higher values for short segments. The generally low values for Re (i.e. $Re \ll 2000$) indicate that airflow in the vessels was laminar, as required for analysis of the results with equations 2–5. The increase in Re as length decreased was because a relatively constant

Table 2. Details of the apple (*Malus domestica* Borkh.) rootstocks and other varieties studied

The final two columns give the number of individuals measured in the current study.

Variety	Type	Size class	Parentage/Latin name	Conductivity measurements	Vessel counts
G.16-L10	Rootstock	3	Ottawa 3× <i>Malus floribunda</i> ^a	3	1
M.9-EMLA	Rootstock	3	Unknown ^a	3	3
M.26-EMLA	Rootstock	4	M.16×M.9 ^a	3	3
MM.106-EMLA	Rootstock	7	Nothern Spy×M.1 ^a	3	3
MM.111-EMLA	Rootstock	8	Nothern Spy×M1.793 ^a	3	1
Golden Delicious	Scion	N/A	<i>Malus domestica</i> Borkh.	2	3
Liberty	Scion	N/A	<i>Malus domestica</i>	2	2
Maruba	Rootstock	10	<i>Malus prunifolia</i> Borkh. var. ringo (<i>Maruba kaido</i>)	1	0
Prunifolia	Rootstock	10 (seedling)	<i>Malus prunifolia</i> Borkh.	3	1
Antanovka	Rootstock	10 (seedling)	<i>Malus antanovka</i>	1	0

^a Source: Cornell University, New York State Agricultural Experimental Research Station, Geneva, NY fact sheet at: <http://www.nysaes.cornell.edu/hort/breeders/appelroots/Factsheets/FSAccess.htm>. This web site, which contains additional information on the rootstocks, explains that rootstocks are ranked 'by size class from smallest (1) to largest (10). Size classes are estimated as the relative per cent tree size of an own-rooted (full-sized) tree, e.g. size class 1 represents a rootstock that produces a tree 10–20% the size that an own-rooted tree would produce under similar conditions'.

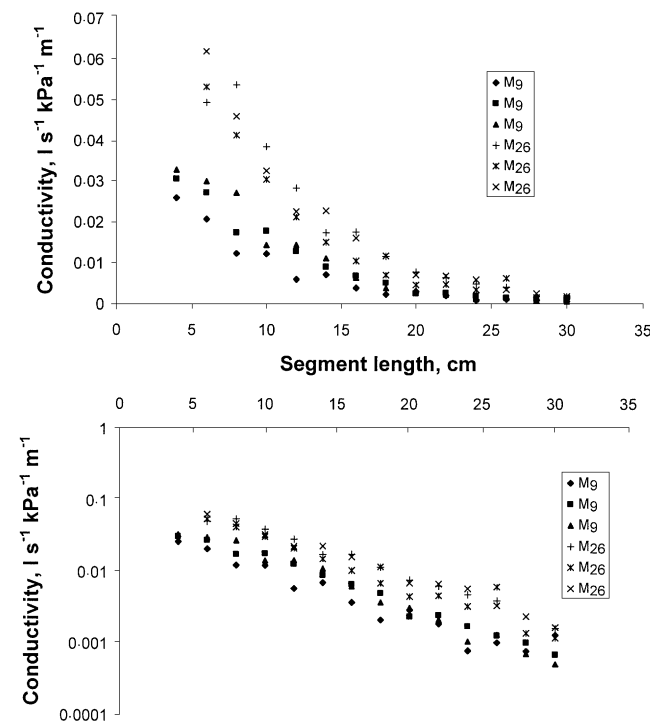


Fig. 2. Air conductivity per unit stem cross-sectional area as a function of segment length for three plants each from two rootstocks. The values on the graph are on normal and logarithmic y axes.

inlet air pressure was applied, and resistance decreased with decreasing length so that air velocity increased with decreasing segment length. Sperry and Tyree (1988) and Sperry *et al.* (1988) used a similar apparatus for air conductivity measurements, but worked at higher pressures at which flow is not laminar, so they used a modified form of equation 4.

A total of 27 samples were measured, with an average of 13 lengths measured for each sample. In 16 cases the r^2 for

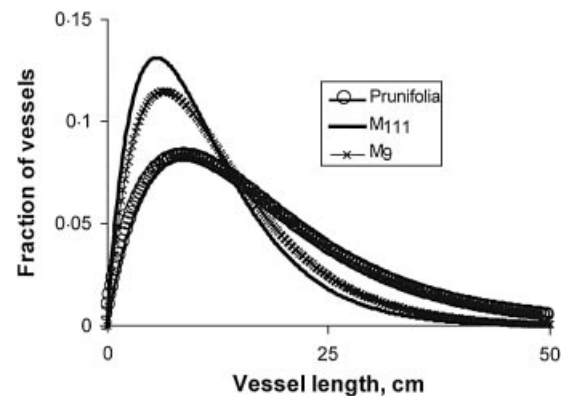


Fig. 3. Vessel length distribution function for three apple rootstock varieties, as determined by linear regression of the logarithm of wood conductivity on stem segment length. The curves are from equation 10.

the linear regression of log conductivity on length exceeded 0.95, of the remainder six exceeded 0.9, and two 0.8 (total 24 samples). The remaining three series, which showed high variability in conductivity, were discarded, and their low r^2 was attributed to problems with the apparatus. Vessels were successfully paint perfused and counted for 17 samples. Details of the measurement series are given in Table 2.

Figure 2 shows linear and logarithmic-linear plots of specific conductivity as a function of segment length for three plants of each of two rootstocks. The results show no evidence of a bimodal distribution of vessel lengths as observed for lianas and several other species (Zimmermann and Jeje, 1981; Ewers and Fisher, 1989). The log-linear plot is linear, as expected by the model. In addition, the two rootstocks have different conductivities but similar slopes in the log-linear plot. The similar slopes indicate similar vessel lengths (equations 7 and 11).

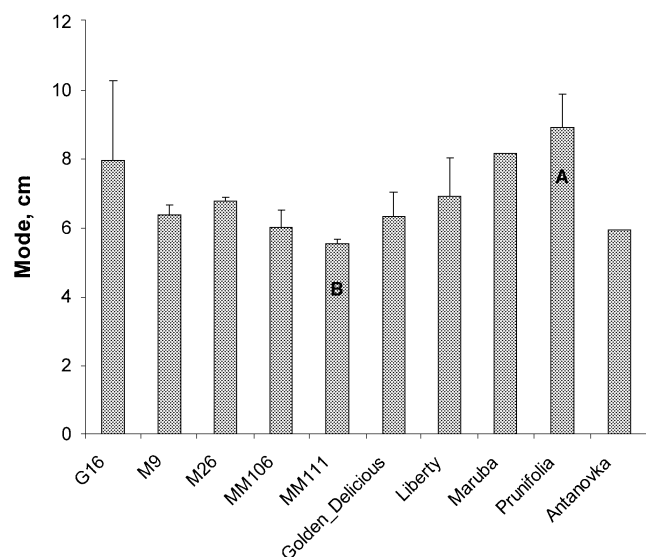


Fig. 4. Mean and standard error of mode (most common) vessel length for a series of apple rootstocks and two scions. For descriptions of the different varieties see Materials and methods. ANOVA showed that there were significant differences at $\alpha < 0.05$. Letters indicate significantly different classes from the SNK test. Unmarked columns belong to the class AB.

Figure 3 shows the distribution function for vessel lengths as determined from equation 10 for three rootstocks. As noted above, the difference between the distributions is expressed by one parameter, the slope of the relationship between the logarithm of conductivity and length, or its inverse, the mode vessel length.

Figure 4 shows mean and standard error of the mode, or most common, vessel length for the series of apple rootstock and scion varieties. The means vary from 5.6 ± 0.1 cm ($\pm$ standard error) for MM.111 to 9.0 ± 1.0 for Prunifolia, which were also the only ones whose modes differed significantly ($P < 0.05$). All standard errors were less than 1 except for G16, whose standard error was 2.3 cm, or 29% of the mean. Maximum vessel lengths, determined from equation 8 for individuals where conductivity was measured and vessels counted, were highly uniform, with averages for seven of the eight varieties studied ranging from 48.2 ± 0.9 to 53 ± 4 cm, and the two values for the eighth, Prunifolia, were 56 and 78 cm.

Figure 5 shows effective vessel radius estimates (from equation 5). In this case the variation between the varieties was larger, and radius varied from 14 – 24.3 ± 0.7 μm for Prunifolia (where only one vessel count was made) and M.26, respectively, and the five standard errors calculated were all less than 12% of the means.

Figure 6 shows the interpolated value for specific conductivity to air of 15 cm stem or branch segments. This length was the approximate mid-point of the usual measurement series done. Here the variations between rootstocks are much larger, ranging over two orders of

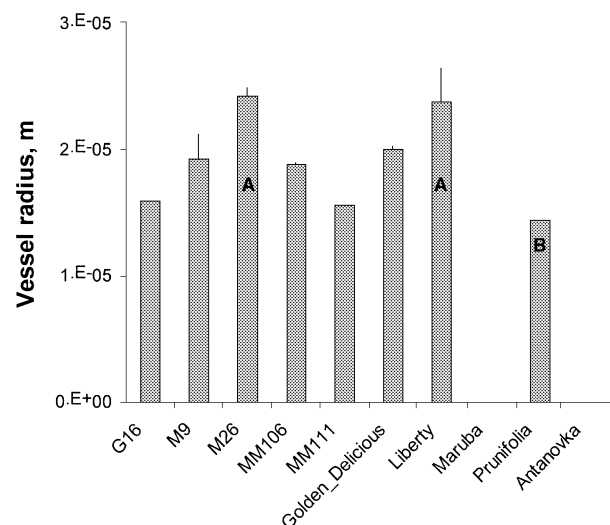


Fig. 5. Estimated vessel radius for the different apple varieties. Vertical bars indicate 1 SE of the mean. For G16L10 and EMLA111 only one stub vessel count was used so no standard error could be determined. For Maruba and Antanovka no counts were available. ANOVA showed that differences were significant at $\alpha < 0.01$. Letters indicate significantly different classes from the SNK test. Unmarked columns belong to the class AB.

magnitude from 2×10^{-4} to $1.6 \pm 0.2 \times 10^{-2}$ $\text{dm}^3 \text{s}^{-1} \text{kPa}^{-1} \text{m}^{-1}$ for maruba and M.26, respectively. Differences between individuals were also large, as indicated by the standard errors, which ranged from 10–63% of the means for MM.111 and Prunifolia, respectively. The large standard errors prevented some of the large differences observed in Fig. 6 from being statistically significant and probably indicate that there is considerable plasticity in this parameter. Even so, conductivity of Maruba was significantly lower than that of M.26 and Liberty.

Extrapolated estimates of vessel density at the air entry point are presented in Fig. 7. Means varied from 18 ± 3 to 42 ± 6 vessels mm^{-2} for M.26 and MM.106, respectively. Standard errors varied from 13% to 89% of the mean for MM.106 and Prunifolia, respectively. Thus, none of the differences observed in Fig. 7 are statistically significant.

Figure 8 shows the specific conductivity as a function of vessel density extrapolated to the air entry point. The slope of the relationship for each variety, when drawn to the origin, should be roughly proportional to the effective vessel radius (equation 5, Fig. 5). One exceptional point is the M9 sample that had higher vessel density, but conductivity similar to that of the other two M9 samples (vessel density 53 mm^{-2} , conductivity $0.066 \text{ kPa}^{-1} \text{s}^{-1} \text{m}^{-1}$). That particular point had an r^2 value of 0.99 for the log-linear relationship, so the conductivity measurement cannot be discounted, and 3451 coloured vessels were counted in the stub. Sometimes vessel counts are problematic due to proliferation of partially painted vessels (Ewers and Fisher, 1989).

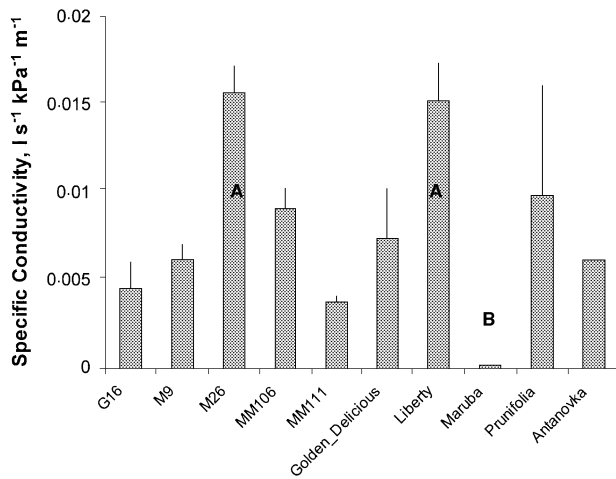


Fig. 6. Stem cross-section specific conductivity for 15 cm stem or branch sections of the different apple rootstocks and varieties. Values were calculated from the regressions of logarithm of conductivity on section length. Since all stem sections were measured from 30 cm down to about 4 or 6 cm, these are interpolated values. Vertical bars indicate 1 SE of the mean. ANOVA showed that differences were significant at $\alpha < 0.02$. Letters indicate significantly different classes from the SNK test. Unmarked columns belong to the class AB.

Discussion

The air method for determining vessel length distribution has been shown to yield results similar to those found with other methods (Zimmermann and Jeje, 1981; Ewers and Fisher, 1989), and has been used successfully to measure vessel size distributions in many plant species (Ewers *et al.*, 1990). Previously, analysis of the results was done by applying the discrete form of the double difference method to measured conductivities or, for the paint method, to counts of numbers of coloured vessels in paint perfused wood samples. In that analysis, small differences in the numerically determined discrete values of the second derivative of the measured relationship between wood conductivity and length sometimes led to a highly irregular discrete distribution function. This irregularity has been taken as evidence for non-random distribution of vessel ends in wood, and two algorithms, those of Zimmermann and Jeje (1981) and Ewers and Fisher (1989), have been suggested for smoothing the results to determine the 'true' discrete distribution function. Tyree (1993) analysed the two algorithms and demonstrated that the latter is more appropriate for wood samples. The approach suggested in the current study ignores the possibility of a non-random placement of vessel ends and smooths the data with linear regression. It has the advantage of giving one parameter, i.e. the mode, per measurement series, which can then be submitted to statistical analysis. For example, it would be hard to compare two species whose mode vessel length differs by 2 cm with the discrete methodology, while with the current analysis, standard errors less than this were obtained with only three repetitions. A future study may

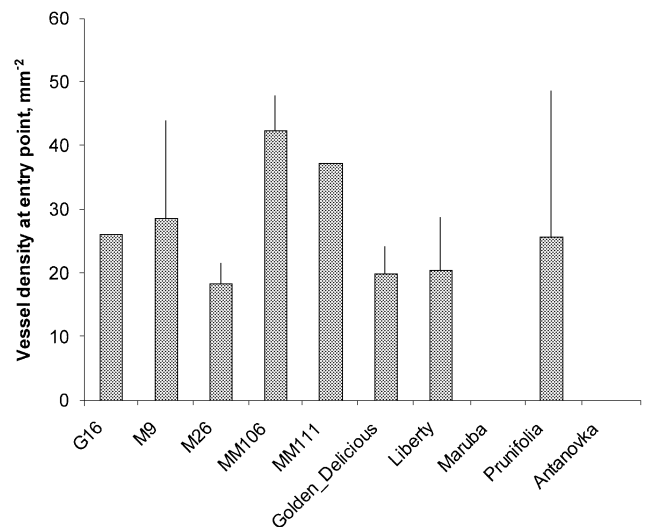


Fig. 7. Vessel density at the stem air (or paint) entry point. Values are number of vessels per mm². The values are based on the linear regression fits to the logarithmic plots of conductivity on stem segment length, and the ratio of number of paint-filled vessels to conductivity for the final stem stub, which varied between 4 cm and 6 cm in length. ANOVA showed that the differences were not significantly different.

address the possibility that the irregular results obtained previously with the discrete double difference analysis result from experimental errors using standard deviations in conductivity observed in the current study.

A logarithmic decrease with length of dry wood conductivity (or permeability) to gases was observed by several workers in a number of hardwood and softwood species when constant pressures were applied (Siau, 1984). In dry wood air passes from vessel to vessel through pit membranes. In wet wood and low air pressures, as noted, pit membranes are blocked by strongly adhered water, so that air flow is only through vessels that are open at both ends. For wet wood airflow is through a group of parallel capillaries, while for dry wood the capillaries are leaky. Although Bramhall (1971) reasoned that the number of vessels conducting air would decrease with decreasing length of dry wood and that this would lead to the observed logarithmic decline in conductivity, the reasoning applies strictly to the case of wet wood for the reason stated above. The results (e.g. Fig. 2) are empirical evidence that the theory is correct.

The observed log-linear decline of air-conductivity of stem segments with increasing stem length for freshly cut wood samples implies a log-linear decline of open vessels. Recently, Tyree *et al.* (2003) confirmed from paint-infusion studies on petioles that open vessel counts decline in a log-linear fashion. Prior to that, raw counts were not presented as log counts of paint-filled vessels versus distance from the infusion surface.

Previously, analysis of the relationship between conductivity and length was not translated to a continuous

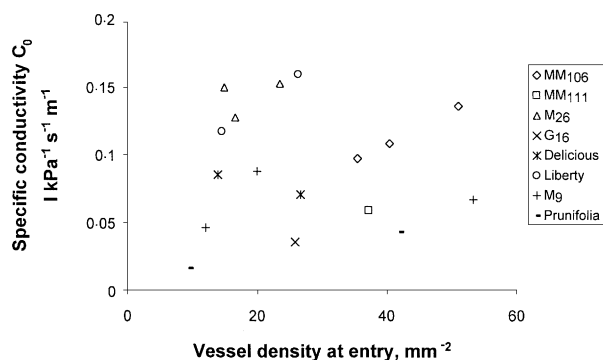


Fig. 8. Specific conductivity to air (C_0 , $\text{l kPa}^{-1} \text{s}^{-1} \text{m}^{-1}$) as a function of vessel density (vessels per mm^2) extrapolated to the stem air (or paint) entry point. The values are based on the linear regression fits to the logarithmic plots of conductivity on stem segment length, and the ratio of number of paint-filled vessels to conductivity for the final stem stub, which varied between 4 cm and 6 cm in length. Each data point represents one stem (or branch) sample.

vessel length distribution function. The analysis presented here has specific advantages to the discrete double difference method, since all that is required for determination of the vessel size distribution (equation 10) is the slope of the relationship between conductivity and length, which can be obtained with a few measurements. For the current work with apple samples, it was found that measurements of samples of lengths between 10 cm and 25 cm gave a clear relationship with a high r^2 and essentially the same results as obtained for the full series of measurements. In addition, the slope could be obtained with fewer measurements, i.e. with removal of 5 cm segments at each step. This would facilitate rapid characterization of more samples for better determination of inter-specific variability.

Uni-modal distributions of vessel lengths have been found in many diffuse porous tree species (Ewers *et al.*, 1990), so the distribution presented here should have considerable utility. Experimentally determined uni-modal vessel length distributions reported in the past all appear to fit the general form shown in Fig. 3, although some, where the mode is close to zero, do not indicate that they approach zero for very short lengths. The latter condition is a feature of the probability density function found in the current study (equation 10). Additional experimentation will be necessary to clarify this point. One possibility is to see if the log-linear plot remains linear as wood length approaches zero.

In lianas and ring porous species two types of vessels are common, each with a characteristic length distribution. Future work should lead to a bi-modal distribution function and statistical methods for testing if a set of conductivity measurements are indicative of a uni- or bi-modal distribution. Alternatively, casual observation of wood cross-sections under the microscope will indicate if the

wood is ring porous or contains more than one kind of vessel.

Passialis and Grigoriou (1999) found that apple branch wood is diffuse porous with vessel widths of $46 \pm 13 \mu\text{m}$, but the variety was not noted. This is in agreement with the effective diameters that were found here, 29–48 μm (Fig. 5). Similar values have been reported for other tree species and Siau (1984) presented similar values of conductivity to air ($0.005\text{--}0.03 \text{ dm}^3 \text{s}^{-1} \text{kPa}^{-1} \text{m}^{-1}$ for 15 cm length) for most of the specimens of conifer wood that he measured. Vessel lengths and diameters are in the range reported for other diffuse porous species (Ewers *et al.*, 1990).

The current study was part of an investigation of properties of different apple rootstocks that might explain the differences in observed hydraulic conductivity of dwarfing and non-dwarfing rootstocks (Cohen and Naor, 2002, and references therein). The results obtained for mode and maximum vessel length do not indicate a clear relationship to dwarfing properties of the rootstocks, but rather point to more or less constant vessel lengths in apple varieties and its closely related species used as rootstocks. In addition to low inter-varietal and inter-species variability, inter-specific variability for individuals of the same variety was low.

Greater variability was observed for vessel radius and vessel density, with the latter having high variability between individuals, such that inter-varietal differences in means, although large, were not statistically significant. The greatest variability was observed in specific conductivity of the wood (interpolated for a 15 cm segment), which varied by two orders of magnitude. But for these parameters too, there was no clear relationship with dwarfing potential.

Conclusions

Measurements of wood properties including vessel size distributions, effective vessel radii, specific conductivity to air, and vessel density, were determined from air conductivity measurements in a series of apple rootstocks and two scion varieties. Inter-individual, and inter-varietal variability was low for modal and maximal vessel length, and increased for vessel radius, specific conductivity to air, and vessel density. Although significant differences between some varieties were found for modal vessel length, effective radius, and specific conductivity, no general relationship to rootstock size class was observed.

The observed log-linear relationship of wood conductivity to air was combined with the double difference theory for determining vessel length distribution to give a continuous theoretical probability density function for vessel lengths. The inverse of the log-linear relationship was found to be the modal vessel length. Some other details of the function were examined, and it was used

successfully to analyse the measurement series for the different apples.

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