REGULAR ARTICLE

Variations in the radial gradient of sap velocity in trunks of forest and fruit trees

Yehezkel Cohen · Shabtai Cohen · Tatiana Cantuarias-Aviles · Gabriel Schiller

Abstract We studied the radial pattern of sap velocity (v) in trunks of six forest species: *Cupressus sempervirens* L; *Eucalyptus camaldulensis* F. Muell; *Pinus halepensis* Mill. (Alleppo pine); *Quercus aegilops* L. ssp. *ithaburensis* [Decne] Boiss; *Quercus calliprinos* Webb; *Quercus rotundifolia* Lam. (Syn. *Quercus ilex* spp. *Rotundifolia*) and three fruit species: *Citrus sinensis* L. Osback; *Malus domestica* cv. Golden Delicious; *Persea americana* Mill. Data was selected from measurements made over a period of 15 years. For each species, at least data of 1–2 weeks measured on days with clear sky and after a rain event or irrigation were analyzed. Measurements were made with the T_{max} heat pulse method, and six points were measured along the radius of the trunk. Two types of radial pattern were found; in one type the highest v value was recorded near the cambium, decreasing toward the heartwood; and the other type had low v near the cambium increasing toward a depth of 12 to 20 mm below the cambium and decreasing with depth to the heartwood. There was large interspecies variability of v in both the pattern of radial gradient with depth and the distance between the cambium and the border of conducting sapwood. Variations in radial pattern of v between trees within species were generally small with a coefficient of variation of 4–20%. The mean fractions of volumetric flow in the 0–16 and 0–24 mm layers below the cambium were 59% and 79% of the total flow, respectively. The distance between the cambium and the border between conducting and non-conducting sapwood varied from 31 to 66 mm in the various species. The radial distribution of sap velocity with azimuth around the trunk had a coefficient of variation similar to that found between trees of the same species. The amplitude of the azimuthal variation changed during the day; it was high in the mornings and evenings and low at noon. The variation of sap velocity in three azimuths was more affected by the structure of each individual trunk than by the position with respect to the sun.

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Y. Cohen (✉) · S. Cohen
Department of Environmental Physics and Irrigation,
Institute of Soil, Water and Environmental Sciences,
Agricultural Research Organization,
Bet-Dagan P.O. Box 6, Israel
e-mail: vwhezi@volcani.agri.gov.il

G. Schiller
Institute of Plant Science,
Agricultural Research Organization,
Bet-Dagan P.O. Box 6, Israel

Present address:
T. Cantuarias-Aviles
Departamento de Produção Vegetal, USP/ESALQ,
Piracicaba, SP, Brazil

Introduction

Intensive studies have been conducted during the past 15 years on the radial gradient of sap flux density in tree trunks. Research on this topic has received attention because experimental results showed that determination of v in the trunk based on a single point (or small section) in the outer part of the sap wood introduces a large error in the estimation of total sap flow (Hatton et al. 1990; Cermak et al. 1992; Lu et al. 2000; Fiora and Cescatti 2006). The reason for the error is that in most regions with temperate climates the radial and circumferential sap velocity in the sapwood varies with time and amongst trees. A species-specific radial gradient in v was reported and, generally, v was highest near the cambium and declined, either moderately or steeply toward the heartwood (Wullschleger and King 2000; James et al. 2003). Some studies demonstrated diurnal and seasonal changes in the pattern of the radial gradient of v (Ford et al. 2004a).

Variability in radial and circumferential v caused large errors when measurements of v at a single depth, or single radial profile, were used to estimate whole-plant water use (Jimenez et al. 2000; James et al. 2002). The radial pattern is generally affected by soil water content, moisture content in the xylem, size of the stem, sap flow rate and climatic conditions. (Cermak and Kucera 1990; Kostner et al. 1996; Delzon et al. 2004; Ford et al. 2004b). Although the changes in radial pattern of v have been demonstrated in many species, some studies have observed consistent radial profiles of v among tree species with tracheid xylem anatomy (Phillips et al. 1996; Spicer and Gartner 2001).

A general conclusion from the above cited studies is that measurement of v in more than one point in the sapwood is necessary for accurate measurement of total tree transpiration, and as the radial gradient of v in the sapwood is steeper, as can occur in species with ring porous wood anatomy, the points of measurements should be denser (Clearwater et al. 1999).

The environmental effect on the radial gradient of v was intensively studied. A dependence of radial pattern of v on the distribution of water uptake by the root system was shown in several species (Ford et al. 2004a; Nadezhdina et al. 2007). The radial gradient was less steep as the soil water content in the upper soil layers declined, suggesting that v in the inner part of the sapwood decreases less than that in the outer part that is closer to the cambium. On the other hand, Kubota et al. (2005) reported that the relative reduction in v in *Fagus crenata* Blume (Japanese beech) was similar in both the outer and inner xylem irrespective of soil moisture distribution.

Radial gradients of sap velocity in forest and fruit trees have already been described in the 1980s in studies using the T_{max} or compensation heat pulse methods (Cohen et al. 1981; Green and Clothier 1988). Both studies considered the radial gradient in v and made use of multi-sensor probes that deploy sensors at different depths below the cambium to a distance of 40–50 mm. Multi sensor probes were also used by Hatton et al. (1990), using a heat pulse system, Cermak et al. (1992), using a segment heat balance system and Lu et al. (2000), using a thermal dissipation system. However, the consequences of variations in radial gradient in v on estimation of total sap flow were not considered sufficiently.

Our objectives in this paper are: firstly, to examine the assumption that the multi-sensor probes used in the previous studies indeed represent the entire conducting xylem area as it has been assumed, secondly, to determine the relative contribution of the annuli in accordance to their radial position in the sapwood; and thirdly, to study the effect of a few environmental variables on the pattern of the radial gradient of sap velocity in the tree trunk.

Materials and methods

In this work, we examined measurements made in nearly 15 studies that were conducted by the authors of the present study in which sap flow rate was determined in the trunks of forest and fruit trees.

The objectives of the studies conducted in forests were to determine the water regimes under Mediterranean climate conditions, as a guiding tool for sustainable forest management (Schiller and Cohen 1995). The studies were conducted in the northern and southern regions of Israel. The northern region is characterized by a Mediterranean sub-humid climate with winter rainfall between 500 and 700 mm. The southern region is characterized by semi-arid to arid climate with winter rainfall of less than 300 mm. Potential evaporation in the southern region during a typical summer day reaches approximately 11.5 mm.d^{-1}, which is

1–2 mm higher than the northern region. The measurements in *Quercus rotundifolia* were made in central Portugal which is also characterized by a Mediterranean climate with hot and dry summer and mean annual rainfall is 665 mm. Measurements in Israel were conducted in forest plots whose area varied from 1 to 10 ha and the trees were 15- to 20-year-old. More details on the experiment with *Q. rotundifolia* may be found in David et al. 2004.

The objective of the studies conducted in orchards was to determine the orchard's water requirement for optimizing irrigation management. Irrigation was applied during the rainless period (April to November) to maintain optimum tree water status. In the forest and orchard studies, sap flow rate was measured using a calibrated T_{max} heat pulse method (Cohen et al. 1981). Sap velocity (v) was determined in the tree's trunk at 0.4–1.5 m height using six-thermistor probes inserted radially into the trunk. The distance between the thermistors on the probe was 8 mm; the first sensor was positioned at 4 mm below the cambium and the last sensor at approximately 44 mm. The heat pulse was given by a line source heater inserted 15 mm upstream of the sensor probe. Both the sensor probe and the heater were inserted to 60 mm depth below the cambium. A 20 mm thick drill-guiding template was used to ensure the relative position between the heater and the sensors. Even when using this guiding template, earlier study (Cohen et al. 1981) indicated that holes in the trunk deeper than 60 mm deviated significantly from the 15 mm vertical distance between the probe and the heater.

Generally, before the beginning of the routine measurements, three probes were inserted at three orientations around the trunk in each tree to study the relative v between three azimuths. Measurements of v were made continuously during 3 days. After 3 days, two probes were removed from the trunk and the measurements continued with one probe for each tree. The data recorded by the single probe were corrected in accordance to its weight relative to the other two measured probes during the pre-measurements period. During the experimental period, v was measured in eight trees at hourly intervals continuously for 7 to 14 days.

For extrapolation of single tree transpiration rate to stand transpiration the sampled trees must represent the population of the site. Therefore, stem diameter at constant height above ground of all trees growing at the site were measured. According to the diameter distribution in the population, eight trees were selected to represent the population; in these trees the probes were installed. The results presented in this work show only data collected following a significant amount of rain in the forests or 1–3 days after irrigation in the orchards.

We analyzed results of six forest species *Cupressus sempervirens* L; *Eucalyptus camaldulensis* F. Muell; *Pinus halepensis* Mill.(Alleppo pine); *Quercus aegilops* L. ssp. *ithaburensis* [Decne] Boiss; *Quercus calliprinos* Webb; *Q. rotundifolia* Lam. (Syn. *Quercus ilex* spp. *Rotundifolia*), and three fruit species: *Citrus sinensis* L. Osbeck; *Malus domestica* cv. Golden Delicious; *Persea americana* Mill. With the exception of the *Eucalyptus* species, the studied forest tree species are considered Mediterranean-climate native species, which are characterized by relatively high drought avoidance or resistance and a relatively slow growth rate.

Results

The diurnal trend, on several days throughout the year, of sap flow in a typical Mediterranean species, *Q. calliprinos* is shown in Fig. 1. The sap flow rate reflects the changes in soil water content and climatic parameters throughout the year. Highest flow rate was obtained on DOY 118 at the end of the rainy season and the beginning of air warming. The relatively high sap flow rate on DOY 333 indicates the beginning of the rainy season and air-cooling. The highest accumulated daily sap flow rate, averaged for eight trees, was 64 kg tree^{-1}, from which extrapolation for stand transpiration was made. The example given above for *Q. calliprinos* was applied for all forest species given in this work to study the water regime of Mediterranean forests.

Several parameters related to water transport in the trunks of the studied species are shown in Table 1. The largest studied tree was *Q. rotundifolia* growing in a natural agro-forestry region in Portugal (David et al. 2004). The other native species were younger and smaller. Maximum sap velocity is the velocity at noon hours (1100–1400), the range shows minimum and maximum values for trees within species. A poor relationship ($R^2 = 0.247$) was found between trunk diameter and the depth of conducting sapwood,
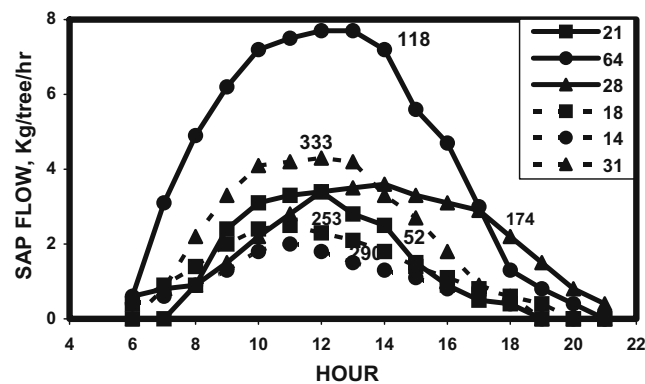
Fig. 1 Diurnal curves of sap flow in *Q. calliprinos* tree grown in sub-humid climate throughout the year, (Doy indicated for each line) the data in the figure are the average of eight trees, computed the range of sap velocity at noon time on DOY 118 was 0.36–0.64 m h^{-1}. Sap flow rates (kg day^{-1} tree^{-1}) for each DOY are given in the *right side* of the figure

computed by the regressions of normalized sap velocity and depth below the cambium.

The radial gradient of *v* in *P. halepensis* is shown in Fig. 2; the highest values of *v* were recorded near the cambium, and decreased with distance from the cambium. Figure 2 presents data of pine trees planted in two forests: one forest was planted in the Mediterranean sub-humid Ramat Hanadiv forest (500–700) mm annual rainfall) and the other forest was planted in the semi-arid Yatir forest (300 mm annual rainfall). In the trees grown in sub-humid climate, the extrapolated depth of the conducting sapwood reached 39.8 mm below the cambium (Fig. 2a and Table 1) while the extrapolated value for the trees in the semi-arid climate

was 52.7 mm (Fig. 2b and Table 1). Sap velocity at each depth was normalized to the maximum velocity measured along the radius. The normalized sap velocity, averaged over eight trees and plotted against depth below the cambium, fits a third order polynomial for trees in the sub-humid climate (Fig. 2c) and a second order for trees in the semi-arid climate (Fig. 2d), the correlation coefficient of the regressions in both was very high (Fig. 2c and d). The variations in the radial gradient, between trees in sub-humid climate were 7.8% and 8.5% for 4 and 12 mm depth below the cambium respectively; similar values were also obtained for trees in the semi-arid climate (Table 2). The most significant effect of semi-arid

Table 1 Age, stem diameter at the measurement point of sap flow, sap velocity at noon time (1100–1400) and computed depth of conducting xylem below the cambium

Species	Age of the trees in the experimental site (years)	Range of stem diameter (m)[a]	Range of maximum sap velocity (m h^{-1})[b]	Maximum depth of conducting xylem (mm)[c]
Cupressus sempervirens	15	0.12–0.13	0.19–0.30	37.4
Eucalyptus camaldulensis	10	0.15–0.19	0.30–0.58	52.5
Quercus calliprinos	20	0.14–0,19	0.36–0.64	48.0
Quercus ithaburensis	15	0.22–0.32	0.31–0.91	36.7
Quercus rotundifolia	~100	0.45	0.33–1.08	65.9
Pinus halepensis (sub-humid)	15	0.16–0.27	0.28–0.63	39.8
Pinus halepensis (semi-arid)	19	0.14–0.15	0.22–0.68	52.7
Malus domestica	9–11	0.13–0.17	0.22–0.78	54.1
Citrus sinensis	8	0.10–0.13	0.25–0.45	46.3
Persea americana	16	0.24–0.28	0.22–0.54	53.9

[a] The largest and smallest stem diameter of the trees.

[b] The highest and lowest maximum sap velocity measured at noon hour

[c] Distance (mm) between the cambium and the border between conducting and non-conducting xylem.
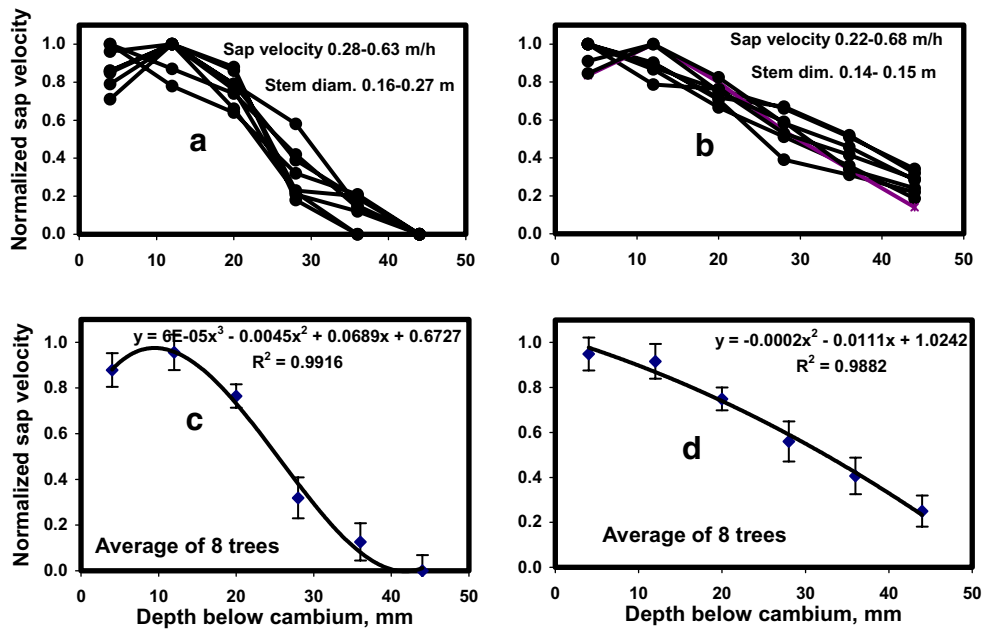
Fig. 2 Normalized sap velocity as a function of depth below the cambium in *P. halepensis* trees grown in sub-humid climate (**a**) and in semi-arid climate (**b**). Third and second order polynomial regressions of the mean are shown for trees in sub-humid climate (**c**) and in the semi-arid climate (**d**), respectively. *Bars* indicate the standard deviation (SD) of the mean

climate on the trees was that at 44 mm below the cambium (the deepest measured depth) v was 15–30% of the maximum value obtained near the cambium.

A similar radial pattern of sap velocity, to that described for Pine, was obtained in 10-year-old trees of *E. camaldulensis* (Fig. 3a). The variation in the radial gradient of v between eight trees varied between 3.2% to 19.8% for the various depths (Table 2), variations were usually higher in the deeper layers with low values of v. A second order polynomial fits the regression of the average normalized v and depth,

with high correlation coefficient. As in Pine trees in the semi-arid climate, the border between conducting and non-conducting sapwood in this species exceeded the depth of 44 mm. At 44 mm depth, the value of v was 40% to 55% of the maximum average value.

In all other forest and fruit species studied, sap velocity decreased with distance from the cambium into the xylem (Fig. 4). In *C. sinensis* and *Quercus ithaburensis* a linear regression adequately describes the reduction in sap velocity with depth. In the other four species shown in the figure, a second order

Table 2 Coefficient of variation of the average normalized sap velocity in eight trees

Species	Depth below cambium (mm)					
	4 mm	12 mm	20 mm	28 mm	36 mm	44 mm
Cupressus sempervirens	0	9.5	9.7	16.5	?	?
Eucalyptus camaldulensis	14.3	5.9	3.2	9.8	13.0	19.8
Quercus calliprinos	8.5	8.5	14.8	15.6	13.3	40.0
Quercus ithaburensis	0	9.6	19.8	27.4	?	?
Quercus rotundifolia	19.3	1.3	8.7	14.1	17.1	19.4
Pinus halepensis (sub-humid)	7.8	8.5	6.8	16	20.1	27.6
Pinus halepensis (semi-arid)	11.5	4.4	9.3	11.2	13.6	14.8
Malus domestica	0	17.1	16.7	19.1	23.8	23.7
Citrus sinensis	0	15.4	18.8	16.5	28.3	47.4
Persea Americana	11.5	4.4	9.3	11.2	13.6	14.8

Zero indicates that all eight trees had normalized value of sap velocity equal to one, *question mark* indicates coefficient higher than 50% due to low average value.

Fig. 3 Normalized sap velocity as a function of depth below the cambium in *E. camaldulensis* (**a**). Second order of polynomial regression was used to describe the relationship (**b**). *Bars* indicate the SD of the mean
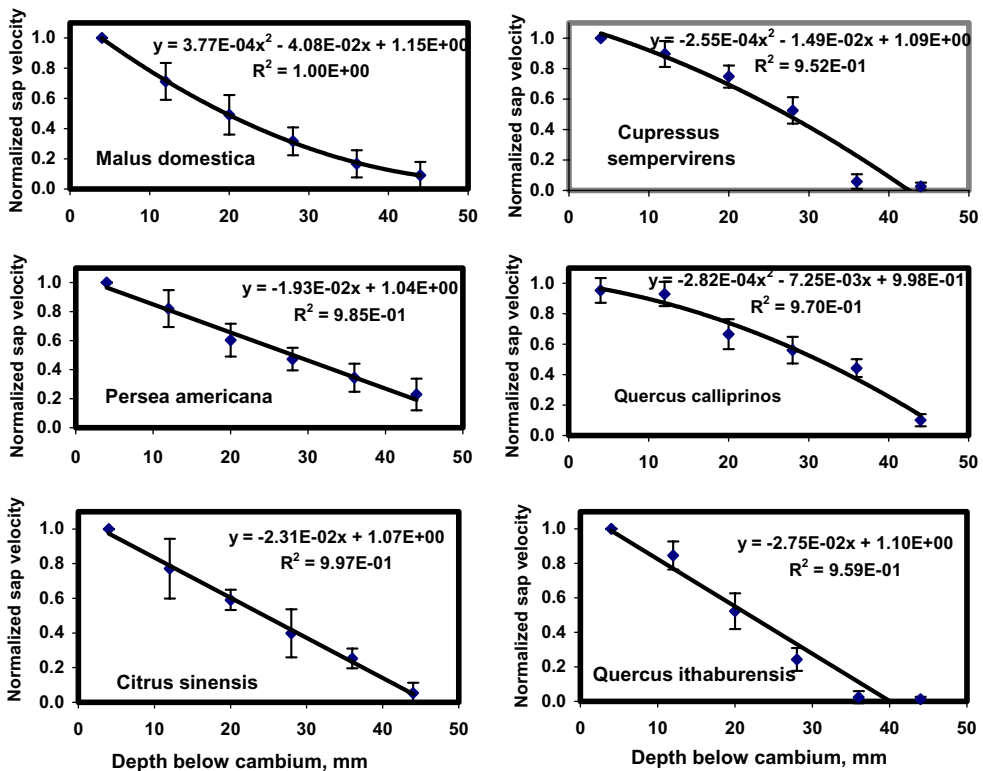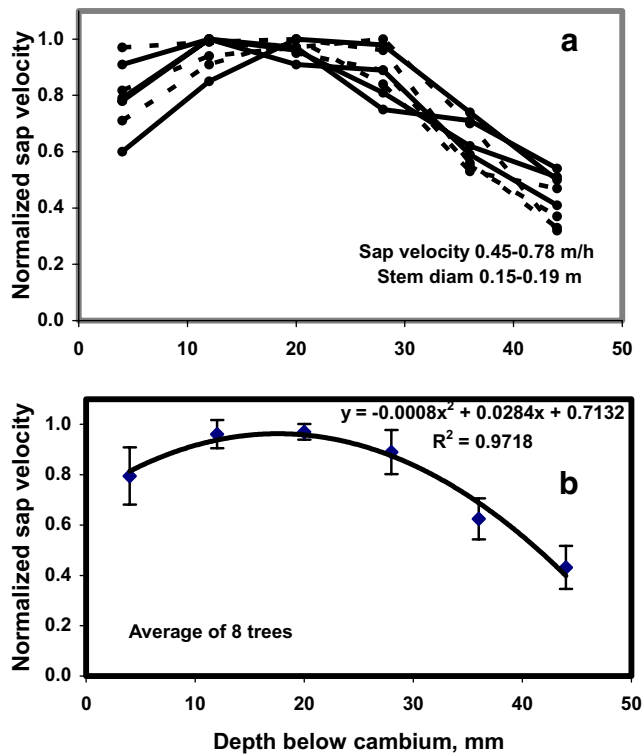
Fig. 4 Drop of sap velocity with depth below the cambium of three forest and three fruit trees. *Bars* indicate the SD of the average of eight trees, more physical parameters of water transport of the tree in Table 1

polynomial curve yields a higher coefficient than the linear curve. The results of the extrapolation of the curves to zero flow for all species are given in Table 1. Variations between trees in all depths are shown in Table 2. Zero value indicates that in all measured trees, maximum normalized v was recorded in one depth such as in *C. sempervirens* at 4 mm depth. Question mark indicates depth with very low value of v in which the coefficient of variation was 50% or more.

The distribution of the flow in the cross section for all studied species is shown in Table 3. The results shown in the table were computed from the normalized sap velocity data shown above. The distribution of the flow varied significantly between species. In the 0- to 16-mm layer below the cambium the flow in the various species was 40% to 72% of the total flow, and averaged 58.7% for all species. For the 0- to 24-mm layer the flow varied from 64% to 88% and the average for all species was 79%.

Radial gradients of sap velocity were also observed for different azimuths within the tree in all measured species, an example of azimuthal variations are given for *Q. rotundifolia* in Fig. 5a. The sap velocity was measured with 8 probes in different orientations around the 0.45-m diameter trunk In all orientations the sap velocity decreased with depth, except for the nearest point to the cambium at 4 mm depth . The coefficient of variation of sap velocity between different azimuths was close to that obtained for variations between trees (Table 2). A third order polynomial regression fits the average normalized v distribution with depth (Fig. 5b). However, the fitted polynomial could not be extrapolated to zero. Therefore, in order to determine the depth at which no sap flow occurs a "segmented" regression was used. The outer depths were fit with a quadratic equation and the inner depths were fit with a logarithmic model. The latter model gave a good fit for the inner four points ($R^2 =$ 0.999) and the model gave a precise value for the extrapolated depth of zero flow (Fig. 5c).

## Discussion

Radial gradient of sap velocity

We found two basic patterns in radial gradient of v in the trunk: a pattern with high v near the cambium and decreasing with depth toward the heartwood and a peak type pattern that is low near the cambium increasing to approximately 12 mm below the cambium and then decreasing toward the heartwood. Radial gradient patterns of sap velocity have been reported and discussed previously for various tree species (Granier et al. 1994; Wullschleger and King 2000; Nadezhdina et al. 2002; Gartner and Meinzer 2005). Our work showed that there is large interspecies variability with respect to sap velocity, the pattern of radial gradient of v, the distribution of the flow with depth below the cambium and the distance between cambium and the inner border of active sapwood. We also found that intra-specific variations in the radial pattern of v within species were small in all analyzed species. However, a few studies with other species have reported inconsistency in the radial pattern of v between trees and within a day or a season; and the pattern was correlated with vapor

Table 3 Normalized volumetric sap flow (percent of total flow in the cross section) at different depth intervals weighted for sapwood area at each depth

Species	Depth interval (mm)						
	0–8	8–16	16–24	24–32	32–40	40–48	48–56
Citrus sinensis	41	28	18	9	4	1	0
Cupressus sempervirens	37	30	21	10	1	0	0
Eucalyptus camaldulensis	22	23	21	17	11	6	0
Malus domestica	42	27	16	8	4	2	1
Persea americana	31	24	18	13	8	4	1
Pinus halepensis (sub-humid)	40	17	28	13	2	0	0
Pinus halepensis (semi-arid)	30	25	19	14	11	0	0
Quercus calliprinos	32	26	20	13	7	2	0
Quercus ithaburensis	42	30	19	9	1	0	0
Quercus rotundifolia	16	24	24	15	10	7	4

Results from analytical integration of the regression equations in Figs. 2, 3, 4 and 5.

Fig. 5 Drop in sap velocity with depth in 8 orientations around the trunk of a 0.45 stem diameter *Q. rotundifolia* tree (**a**) and the average for the tree (**b** and **c**). The depth distribution was fit to a third order polynomial (**b**) and to a segmented model (**c**) with a quadratic polynomial for the first four depths ($y=-2.65$ E-03 $x^2+8.58$ E-02 $x+2.92$ E-01, $R^2=9.42$ E-01) and a logarithmic function for the four deep points ($y=-0.7456$ Ln(x)$+3.1229$, $R^2=0.999$). *Vertical bars* indicate the SD of the mean
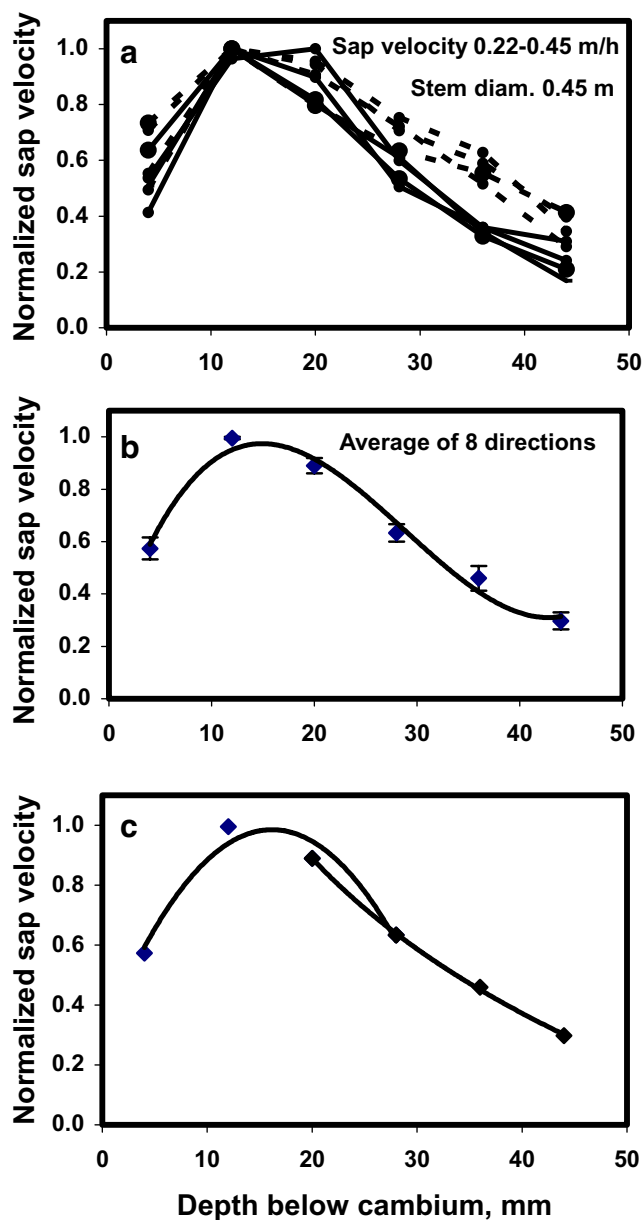
pressure deficit, PAR and soil water availability (Phillips et al. 1996; Nadezhdina et al. 2002; Delzon et al. 2004; Ford et al. 2004a; Poyatos et al. 2007). Other causes of spatial distribution of *v* in the sapwood may be embolism in the xylem, although its effect for short periods may not be significant (Clearwater and Goldstein 2005). A small number of sampling points of *v* in the sapwood area may also contribute to apparent tree-to-tree variations (Loustau et al. 1998). In this study we analyzed, for most of the species, only data from measurements made within a 2

week period for each species at noon-time, under stable climatic conditions and optimal soil water content. Additionally, in our study the number of sampling points in the sapwood area was relatively high (18 during the pre-measurement period and 6 continuously) and the sensors were placed precisely at the planned points in the sapwood. All these conditions could have been responsible for the relatively low variability by minimizing changes in atmospheric and soil conditions as well as errors caused by inaccuracy in sensor placement.

Conductive sapwood area

Our results showed differences in the radial gradient of v between *P. halepensis* trees growing at two different climatic conditions. The depth of conducting sap wood was larger in trees growing under a semi-arid climate than that under a sub-humid climate. Other studies with *Pinus* species also showed an increase in transport of water in the inner sapwood as a result of high atmospheric evaporative demand (Ford et al. 2004b). Their explanation was that under high evaporative demand the gradient in water potential between leaves and soil increases and this affects the transport of water in the inner sapwood layers, which is generally characterized by high resistance to water flow. The climatic conditions in the semi-arid site of our study with *P. halepensis*, together with limited rainfall, even during the rainy period, could have affected the flow in the inner sapwood in a similar way.

The relationship between the sap flow radial pattern and distribution of water uptake by the root system was reported in other studies (Burgess et al. 1998; Nadezhdina et al. 2007). A decrease in sap flow in the outermost xylem relative to the inner xylem as a result of water depletion in the upper soil layers was reported by Nadezhdina et al. (2007). They hypothesized that the variation in radial pattern of sap velocity in the tree trunk reflects a vertical distribution of water uptake that varies with water availability in different soil layers.

Our results in *Eucalyptus* trees support their findings; the radial profile of v in trees growing in a "liman" (flood water irrigated plot) in the Negev Highland was limited to a maximum depth of 32 mm below the cambium (Cohen et al. 1997). But the radial gradient of the *Eucalyptus* trees examined in this study reached 52.5 mm depth below the cambium (Table 1). Continuous monitoring of soil water content in the "liman" showed high water content in the soil profile, indicating continuously high water availability. On the other hand, for the *Eucalyptus* trees analyzed here, which were grown in a sub-humid climate, the upper soil layer was dry during the rainless summer and autumn period. We assume that the dry upper soil layer promoted root development into the deeper wetter soil layers, which might explain the larger conducting area of the sapwood.

In seven of the nine species analyzed in this study we measured sap flow at the point where the last sensor of the probe was placed, i.e., 44 mm below the cambium. Therefore, we suggest that the border between conducting and non-conducting sapwood in these species may be deeper than 44 mm. Extrapolation of the functions describing the change of v with depth yielded the depth of zero-flow for each species. The largest distance between the cambium and the depth of zero flow was 65.9 mm, obtained for *Q. rotundifolia*. The implication of these findings is that by measuring to the depth of 44 mm only and not extrapolating, we underestimate the total flow in the trunk by ignoring part of the conducting sapwood area. Although the sap velocity and the total area of the unmeasured inner conducting sapwood may be small, extrapolation of the measurements to zero flow, based on several points along the cross section of the trunk, seems very important for minimizing this error in estimating tree and stand transpiration.

We may add that if the conducting sapwood area is deeper than 50–60 mm below the cambium (which rarely happened), the use of a measurement technique which requires an accurate distance between the line-heater and sensor probe (e.g. the T_{max} method) is not recommended unless appropriate drilling techniques are developed. This is because a deviation which increases with distance from the cambium may occur between the two holes due to drill beat vibrations. In this case it seems that a system that does not requires a precise symmetry between the sensors and heater is preferable.

Functions describing the depth distribution of sap velocity

We have found that the depth distribution of sap velocity in the sapwood was adequately described by a linear equation in three species, and by second and third order polynomials in the other six species. In one case, i.e. the large *Q. rotundifolia* tree, the polynomial did not extrapolate to zero, and a logarithmic equation was applied.

The mechanisms that can lead to inactivation of xylem are embolisms and tyloses (Tyree and Zimmermann 2002). One assumption might be that these increase with xylem age, which would lead to the decrease in velocity with depth in the sapwood. Since wider vessels are more susceptible to embolism, an embolism-based inactivation would probably result in a decrease

in vessel diameter with depth. By application of the Poiseuille equation, it is easy to show that if the decrease in mean vessel diameter with depth is linear, this case would lead to a polynomial relationship between sap velocity and depth. On the other hand, if the relative decrease in active vessels (irrespective of their width) is constant with depth, an exponential relationship might result. The linear case, on the other hand, might result from a linear decrease in active vessel density with depth. Since most cases studied here fit the polynomial case, we take this as evidence for a change in mean diameter of active vessels with depth and age of the sapwood.

Azimuthal variations

Azimuthal variations are often explained by differences in the direction of sun exposure (Granier 1987) and/or by heterogeneity in soil structure, that may effect root distribution in the soil (Nadezhdina et al. 2007), or by the position of the sensors in the trunk relative to large branches (Lu et al. 2000) and height of the measurement point along the stem (Kostner et al. 1998). In the present study, we did not find consistent differences in the pattern between azimuths around the trunk as previously reported by Nadezhdina et al. (2007). Our earlier study with mature Citrus trees showed that the ranking of sap velocity in three orientations was more affected by the structure of each individual trunk than by the position with respect to the sun (Cohen et al. 1981). Due to these earlier findings we established in our studies a sampling procedure which included an orientation correction factor, as described in the methods section. Our analysis in this study showed that the variations in radial pattern of normalized v between azimuths around the trunk were similar to the variations between trees within species and the variations between azimuths had no preferential orientations. In view of our results and the earlier findings it is necessary to consider the azimuthal variations in sap velocity to be similar in importance to those of variations between trees.

Conclusions

Radial and azimuthal variations of sap velocity in tree trunks must carefully be considered in order to improve accuracy in measuring tree and stand transpiration. This improvement may be achieved by using multi-sensor probes, radially inserted in the trunk for measurements of sap velocity at several points. The use of a multi-sensor probe and extrapolation of the results to zero flow allows accurate determination of the entire conducting sapwood area. Our results suggest that extrapolation of sap flow measurement from one single point, in order to obtain transpiration at a single plant level, and ignoring the radial and azimuthal distribution of sap velocity may be associated with large errors.

Variations in volumetric sap flow within species between forest and fruit trees may reach 200–300%. However, variations in the radial pattern of sap velocity between trees within species, particularly at points with relatively high sap velocity, were small (generally around 10% or less) and the variations in radial pattern between azimuths within a single tree had a similar magnitude to that between trees. These results may affect the number of samples required for accurate measurements.

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