

# The effect of three rootstocks on water use, canopy conductance and hydraulic parameters of apple trees and predicting canopy from hydraulic conductance

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## ABSTRACT

This study investigated the effect of the dwarfing M9, semi-dwarfing MM106 and local Hashabi rootstocks on the water use, canopy conductance ( $G_c$ ) and hydraulic conductance ( $k$ ) of apple orchards with the same scion, Golden Delicious. The average summer leaf area index (LAI) was 2.4, 2.7 and 1.7 for M9, MM106 and Hashabi, respectively. Irrigation in 1997 was less than water use until June, and excessive afterwards. In 1998, irrigation was doubled, and was excessive throughout the season. Sap flow ( $J$ ) in June–August 1998 totalled 476, 682 and 606 mm (or 0.60, 0.86 and 0.76 of class A pan evaporation) for M9, MM106 and Hashabi, respectively. Maximum sap velocity in the three rootstocks (approximately 70 cm h<sup>-1</sup>) occurred in the outer 30–60% of the stem, and its decrease with depth was greater in M9 than in the other rootstocks. Midday  $G_c$  during both summers was least for M9, intermediate for Hashabi and greatest for MM106. The  $k$  value of M9 and MM106 for the soil to stem, stem to leaves and soil to leaves pathways were determined from daily courses of water potential of leaves,  $\Psi_l$ , stem,  $\Psi_{stem}$  and  $J$ . Specific  $k$  ( $k_s$ , i.e. relative to stem sapwood area) did not significantly differ between the two rootstocks for soil to stem and soil to leaf pathways, but leaf specific  $k$  ( $k_l$ ) was greater for MM106 soil to stem (71% greater) and soil to leaf (63%) pathways, respectively. The inverse slopes of the relationships between midday canopy resistance ( $R_c$ ) and vapour pressure deficit ( $D$ ) for MM106 was 1.75 of that for M9, and the ratio of their Huber values, i.e. the ratio of sapwood to leaf area, was 1.6. These findings indicate that differences in water use are attributable to differences in  $k_l$ , and not to differences in wood properties ( $k_s$ ). Application of a model relating  $R_c$  to orchard area specific  $k$  ( $k_g$ ) showed that the slope of the relationships between midday  $R_c$  and  $D$  for the 1998 data could be predicted using common values of  $k_s$  (0.134 kg m<sup>-2</sup> s<sup>-1</sup> MPa<sup>-1</sup>) and midday  $\Psi_l$  (-1.34 MPa) for the three rootstocks. The implications of these findings, and the similarities in the differences between rootstocks of  $G_c$ ,  $k_l$ ,  $k_g$  and Huber values, are discussed with respect to rootstock water use and irrigation.

**Key-words:** *Malus domestica*; apple orchard; water relations; M9; MM106; irrigation; leaf area index.

## INTRODUCTION

Most modern orchard trees are composed of two different genetic components: a scion grafted onto a rootstock. Scions are selected for the quality and quantity of their fruit and rootstocks for their ability to grow strong, persistent root systems in the particular soil. In addition, some rootstocks are characterized as 'strong' or 'weak' based on the vigour of the scion that grows on them. The use of weak rootstocks has been instrumental in development of compact, high density orchards whose vegetative growth is slow, reducing operational costs, e.g. harvest and pruning.

Early work on xylem anatomy of apple (*Malus domestica* Borkh.) rootstocks led to the conclusion that water relations are involved in dwarfing (Beakbane & Thompson 1939), whereas other studies showed that mineral nutrition is not (Beakbane 1956). In dry conditions  $\Psi_l$ , leaf conductance ( $G_l$ ) and water uptake are lower for dwarfing rootstocks (Olien & Lakso 1984; Olien & Lakso 1986; Higgs & Jones 1990; Hussein & McFarland 1994), which has been attributed to possible decreased  $k$  (Olien & Lakso 1984; Olien & Lakso 1986; Higgs & Jones 1990), based on indirect estimates (Olien & Lakso 1984).

The ability of the hydraulic system to supply water to the leaves (Tyree & Ewers 1991) is indicated by  $k_l$ , and when climatic transpirational demand is high, lower  $k_l$  will lead to decreased plant water potential and content and lower  $G_l$ . The latter will control plant water deficits and maintain  $\Psi_l$  within a range that does not endanger the hydraulic system (Tyree & Sperry 1989). In many cases, reduced  $k_l$  will also reduce photosynthetic carbon uptake and growth (and perhaps yield) potential (Sperry 2000), and this has been suggested as a possible mechanism for dwarfing of apple trees by rootstocks (Higgs & Jones 1990). Limited carbon uptake does not necessarily decrease fruit yield, since the limited carbon resource is not distributed evenly between carbon sinks, and fruit load is usually a strong sink. Therefore, reduced photosynthetic productivity of dwarfing rootstocks may result in good yields and reduced vegetative growth.

Syvertsen (1981) found that citrus  $k$ , on a root projected area basis, was correlated with rootstock vigour. The influ-

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ence of  $k$  of the root system on plant productivity has been shown in a number of studies. The value of  $k$  has been shown to influence leaf expansion rates in grasses (Wahl & Ryser 2000) and cotton (Radin & Eidenbock 1984), other growth parameters in wheat (Richards & Passioura 1989) and photosynthetic capacity in a number of angiosperms and gymnosperms (Brodribb & Feild 2000; Sperry 2000; Hubbard *et al.* 2001). It would seem, then, that at least part of the reduced growth characteristic of dwarfing rootstocks is due to their reduced  $k$ .

Kamboj *et al.* (1997) reported a correlation between summer abscisic acid (ABA) to auxin ratios in shoot bark of ungrafted apple rootstock trees in England and rootstock vigour. A 4 year irrigation experiment with apple trees on vigorous and dwarfing rootstocks with restricted and unrestricted root volumes found that restriction decreases growth rates and yields drastically (by >50% after 4 years), and much more than rootstock dwarfing (Webster *et al.* 2000). For non-irrigated trees with restricted roots,  $\Psi_1$  and  $G_1$  were significantly lower than for the other treatments, so lower  $k$  could explain the decreased productivity. But when trees with restricted roots were well irrigated,  $\Psi_1$  and  $G_1$  were similar to that for trees with unrestricted roots (Atkinson *et al.* 2000), although productivity was still depressed. This led to the conclusion that other factors, such as hormones produced in the roots, also influence scion growth and productivity.

In the study reported here significant differences in water use were found in apple orchards with the same scion on three rootstocks of different degrees of vigour. Differences in canopy structure between the orchards were not large (Cohen *et al.*, unpublished), so they were assumed not to be the only reason for the differences in water use. The hypothesis investigated in this study is that the different values of  $k$  of the orchards caused the differences in water use. The information gathered on the influence of rootstock on orchard water use should be useful in determining orchard water requirements, since this data is lacking, as shown by the lack of reference to this aspect in current manuals on crop water requirements (e.g. Allen *et al.* 1998).

## THEORY

Sperry *et al.* (1998), Bond & Kavanagh (1999), Oren *et al.* (1999a) and Ewers, Owen & Sperry (2000) proposed that in some conditions (e.g. when the soil-plant continuum is in steady state and the canopy is highly coupled to the air)  $G_c$  ( $\text{mol m}^{-2} \text{s}^{-1}$ ) and  $k_g$  ( $\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ ) are in equilibrium, such that:

$$G_c = [k_g \times (\Psi_{\text{soil}} - \Psi_1 - g) \lambda \gamma / (\rho C_p D)] \times P / (RT), \quad (1)$$

where the subscript l denotes leaf,  $g$  is the gravity component of water potential [which was negligible in the current study because  $\Psi_{\text{soil}}$  (MPa) was taken as predawn  $\Psi_1$  measured at canopy height],  $\lambda$  is latent heat of evaporation ( $\text{J kg}^{-1}$ ),  $\gamma$  is the psychrometric constant ( $\text{Pa C}^{-1}$ ),  $\rho$  is

density of air ( $\text{kg m}^{-3}$ ),  $C_p$  is heat capacity of water in air ( $\text{J kg}^{-1} \text{C}^{-1}$ ),  $D$  is vapour pressure deficit of the air (Pa),  $P$  is atmospheric pressure,  $R$  is the gas constant ( $8.3144 \text{ Pa m}^3 \text{ mol}^{-1} \text{ K}^{-1}$ ) and  $T$  is temperature (K). Note that  $P/(RT)$  converts from the physical conductance units,  $\text{m s}^{-1}$ , to molar units (Anonymous 1989). If  $k_g$  and  $\Psi_{\text{soil}}$  are constant and  $\Psi_1$  is maintained constant by adjustment of  $G_c$ , then  $G_c$  is proportional to  $k/D$ , and as  $k$  does not change rapidly, the relationship of  $G_c$  to  $D$  will be inverse, with  $G_c$  intercept proportional to  $k_g$ .

The relationship of  $G_c$  to the logarithm of  $D$  has been found to fit experimental studies (e.g. Jones 1992; Granier, Huc & Barigah 1996). Oren *et al.* (1999a) and Ewers *et al.* (2000) recommended using the form:

$$G_c = a - b \ln(D), \quad (2)$$

and showed that the relationship of the slope (parameter  $b$ ) to the intercept (parameter  $a$ , or, taken as a proxy, the value of  $G_c$  at 1000 Pa) is approximately 0.6 for many cases. Using measured values of  $a$ ,  $k$  and  $\Psi_1$ , Eqns 1 and 2 can be used to predict  $b$  (Oren *et al.* 1999b).

In this study, we found that a better fit is obtained, especially at very high values of  $D$ , using

$$G_c = \exp(a - bD), \quad (3)$$

which can be used in the same manner for predicting  $b$  and is better defined when  $D$  approaches zero.

An alternative approach for analysing the relationship of canopy conductance to  $D$  is to consider the canopy resistance  $R_c$ , where  $R_c = 1/G_c$ , as a function of  $D$ . In this case a linear model gives a good fit (see Results and discussion), as might be expected from Eqn 1, i.e.

$$1/G_c = R_c = a + bD, \quad (4)$$

where  $a$  is the extrapolated minimum canopy resistance when  $D = 0$ . Substituting Eqn 4 in the model relating  $k$  to  $G_c$  response to  $D$  (Eqn 1) gives:

$$1/(a + bD) = k_g (\Psi_{\text{soil}} - \Psi_1) P \lambda \gamma / (\rho C_p R T D) \quad (5)$$

$$\text{or } a/D + b = \rho C_p R T / [P \lambda \gamma k_g (\Psi_{\text{soil}} - \Psi_1)] \quad (6)$$

and when  $a$  becomes very small relative to  $D$ :

$$b = \rho C_p R T / [P \lambda \gamma k_g (\Psi_{\text{soil}} - \Psi_1)]. \quad (7)$$

Equation 7 demonstrates that for steady-state flow and constant  $\Psi_{\text{soil}} - \Psi_1$ ,  $b$  is inversely proportional to  $k_g$ . The importance of Eqn 7 is that it can be used to predict the response of canopy conductance to  $D$  from hydraulic parameters only and is independent of  $D$ .

## MATERIALS AND METHODS

The measurements were carried out in commercial fruit-bearing apple orchards at Kibbutz Ortal (33°05' N; 35°45' E; 900 m above mean sea level), Israel. Tree scions were of the Golden Delicious 'Smoothie' variety on three rootstocks (MM106, virus free M9 and Hashabi, a local

rootstock) which produce canopies of different sizes. Canopies on the MM106 and Hashabi rootstocks are large, whereas those on M9 are small, and the standard planting distances are varied accordingly. Central leader training systems were used. Details of planting distances, row dimensions, LAI and planting date are given in Table 1. Details of leaf area index and canopy structure measurements are given elsewhere (Cohen *et al.* 1997b; Cohen *et al.*, unpublished).

Irrigation of the orchard was carried out using a computerized drip irrigation system. Drip lines were along the tree trunk axis of the row, with nozzles every 0.83 m. Irrigation frequency was three times per week. Irrigation amounts in 1997 were according to regional recommendations (see Klein 1993a, b) using class A pan crop factors that increase gradually, from 0.3 at the beginning of the season to 1.0 in August. Based on previous experience irrigation amounts for M9 were reduced by 20%. In 1998 an additional drip line was added to the experimental plot, which doubled the irrigation amounts.

The soil is very rocky, making soil water measurements problematic. During 1997 tensiometers were installed 25 cm from the nozzles at 40 and 80 cm depth, with three replicates. Measurements made before each irrigation throughout the season showed that soil water potential was usually greater than  $-10$  kPa, and after late July dropped below  $-15$  kPa three times during the season.

Sap flow measurements were made with a heat pulse systems (see Cohen, Fuchs & Green 1981, Cohen 1994 for details) using custom-made multiplexers and commercial dataloggers (types CR21X and CR10X; Campbell Sci., Logan, UT, USA). The system measures sap flow at six depths simultaneously. Three systems, each measuring eight trees per hour, were deployed in the orchards, one for each rootstock. Several times during the season the systems were moved to a second set of trees, although one tree was common to both sets, such that 15 trees in each rootstock were measured. Day-to-day variability in sap flux was smaller than tree-to-tree variability. Holes were drilled using a precision-tooled guide firmly strapped to the tree with a jack device to ensure that heater and probe bores are parallel ( $\pm 1$  mm) for the full depth of the sensor probe. Probes were inserted in the scion at least 10 cm above the graft but

below the first branch, from the south side of the tree. Sap flow in this direction was taken as the average for the tree (see Discussion). As all sap flow measurements were made in wood of the Golden Delicious variety, differences in thermal transport properties of the wood are unlikely to have introduced bias in the results. Calibration values for the system were taken from previous work (Cohen *et al.* 1981, Cohen 1994) and sapwood heat capacity from Jones, Hamer & Higgs (1988). Technical problems sometimes prevented measuring all eight trees per rootstock. In all cases data points presented (including  $G_c$ ) are averages of at least three trees.

Climate data was collected with a standard 3 m high meteorological mast in an open field that bordered the orchard, next to the class A pan used by the orchard irrigation manager. Solar radiation was measured with a solarimeter (type CM10; Kipp and Zonen, Delft, The Netherlands), temperature and humidity with a psychrometer (type HMP35C; Campbell Sci.) and wind speed with a cup anemometer (Met One model 014 A; Campbell Sci.). Data was logged with a CR10 datalogger (Campbell Sci.) every 30 min. When climate data was incomplete, data from two similar meteorological masts located within 5 km of the experimental site and at the same altitude were substituted. Instrumentation for solar radiation and relative humidity was calibrated once during the experimental period.

Over a period of several days measurements of  $G_1$  and  $\Psi_1$  were carried out on four trees of each of two rootstocks, M9 and MM106, in which sap flow was measured simultaneously. Leaves were measured in cycles of one and a half hours each. The  $\Psi_1$  measurements were made with two pressure chambers (Arimad, Kfar Haruv, Israel) on two sunlit, two shaded and four covered leaves from each tree (64 leaves per cycle) by two operators, with a third person selecting, cutting and delivering leaves for measurement from the tree to the pressure chambers in plastic bags. Measurements on leaves covered with aluminium foil-coated bags several hours prior to measurement were considered to represent  $\Psi_{stem}$  (Naor, Klein & Doron 1995). The value of  $G_1$  of the lower leaf surface was measured with two steady-state porometers (Li-Cor LI1600; Li-Cor, Lincoln, NE, USA) by two operators on three sunlit and three shaded leaves of the same eight trees (96 leaves per cycle).

**Table 1.** Structural parameters for the three orchards measured in 1997 and 1998. Sap flow was measured in 15 trees during the summer, but the intensive measurements of  $\Psi$  were made on four of the trees, whose parameters are reported separately. Width of bark, including phloem, averaged 2 mm and was excluded from the calculation of sapwood cross-sectional area. LAI values represent averages for both summers

Rootstock	Sample size	Sapwood cross section ( $\text{cm}^2 \text{ tree}^{-1}$ )	Planting distances (m)	Trees ( $\text{m}^{-2}$ )	LAI	Huber value (dimensionless)	Planting date	Row azimuth ( $^\circ$ )
M9	15	$51 \pm 2$	$3.5 \times 1.75$	0.163	2.4	$3.5 \times 10^{-4}$	1986	45
	4	$55 \pm 5$				$3.7 \times 10^{-4}$		
MM106	15	$125 \pm 6$	$4.5 \times 2$	0.111	2.5	$5.6 \times 10^{-4}$	1982	-8
	4	$145 \pm 12$				$6.4 \times 10^{-4}$		
Hashabi	15	$77 \pm 3$	$4 \times 2$	0.125	1.7	$5.7 \times 10^{-4}$	1987	-8

The value of  $G_c$  ( $\text{mol m}^{-2} \text{s}^{-1}$ ) was estimated from sap flow measurements assuming a high degree of coupling between the air and the canopy, as:

$$G_c = \lambda \gamma P J / (\rho C_p R T D), \quad (8)$$

where  $J$  is sap flux on an orchard surface area basis ( $\text{kg m}^{-2} \text{s}^{-1}$ ). Estimation of decoupling coefficients (not shown here) through analysis of the Penman-Monteith equation (after Jones 1992) and using measured  $G_1$  values, showed these to be very low ( $<0.2$ ), indicating that the canopy was highly coupled.

The value of  $k_g$  was determined from the relationship between sap flux ( $J$ ) and differences in water potential between the soil ( $\Psi_{\text{soil}}$ ), stem ( $\Psi_{\text{stem}}$ ) and leaves ( $\Psi_1$ ). For the pathway between the roots and the stem

$$k_{g,\text{soil-stem}} = J / (\Psi_{\text{soil}} - \Psi_{\text{stem}}). \quad (9)$$

In well-irrigated situations, when  $\Psi_{\text{soil}}$  is small and constant relative to leaf and stem, pre-dawn  $\Psi_1$  can be taken as a measure of  $\Psi_{\text{soil}}$ . For the pathway from stem to leaves on clear days, the  $\Psi$  of sunlit and shaded leaves must be considered. Assuming that average distances and hydraulic conductivity from stem to leaf are the same for all leaves; taking the leaves in parallel, it follows that:

$$k_{g,\text{stem-1}} = J / [\Psi_{\text{stem}} - (\alpha \Psi_{1,\text{sun}} + (1-\alpha) \Psi_{1,\text{shade}})], \quad (10)$$

where  $\alpha$  is the fraction of sunlit leaf area in the canopy (Moreshet *et al.* 1990).

Equations 9 and 10 were solved for individual sets of  $\Psi_1$  and  $J$  measurements, as well as by regression analysis when  $J$  was plotted as a function of weighted  $\Psi_1$  (Cohen, Fuchs & Cohen 1983; Moreshet *et al.* 1990).

## RESULTS

Climate data for the orchard during the summer season are presented in Table 2. The site, at 900 m elevation, is windy and cool relative to other parts of Israel. The Mediterranean climate is characterized by rainless summers with predominantly clear skies and high solar radiation, reaching midday averages close to  $1000 \text{ W m}^{-2}$  in the summer months. Rainfall in the winters before the 1997 and 1998 irrigation seasons was 823 and 879 mm, respectively. Mini-

mum wind speeds were measured in early morning (0430–0500 h) with maxima at approximately 1600 h when the local sea breeze arrives at the site.

Orchard structural parameters are given in Table 1. Planting distances for the different rootstocks reflect the anticipated vigour of the trees, so that orchard area per tree was least for the dwarfing rootstock (M9) and increased for Hashabi and MM106. Stem cross-sectional areas, measured at the point where sap flow was measured between the graft and first branch, reflect the reduced growth of M9. Differences in LAI (on an orchard basis) were small. Huber values, i.e. the ratio of sapwood area to leaf area, for MM106 and Hashabi were similar, but were approximately 37% less for M9 rootstocks.

During the irrigation season of 1997 the 'weak' M9 used much less water than the more vigorous MM106 and Hashabi (Fig. 1). Irrigation during May was 53, 56 and 55% of water use for Hashabi, M9 and MM106, respectively. Irrigation was approximately equal to water use in June, but exceeded it significantly later in the season. However, the tensiometer measurements did not indicate that soils were dry during the early part of the season (data not shown), so differences in water use between the rootstocks after May were probably not caused by differences in soil moisture. In order to ensure that soil moisture was not limiting, irrigation was doubled in 1998. This increased the water use of Hashabi, M9 and MM106 by 31, 58 and 51%, respectively, but irrigation still exceeded water use significantly (Table 3).

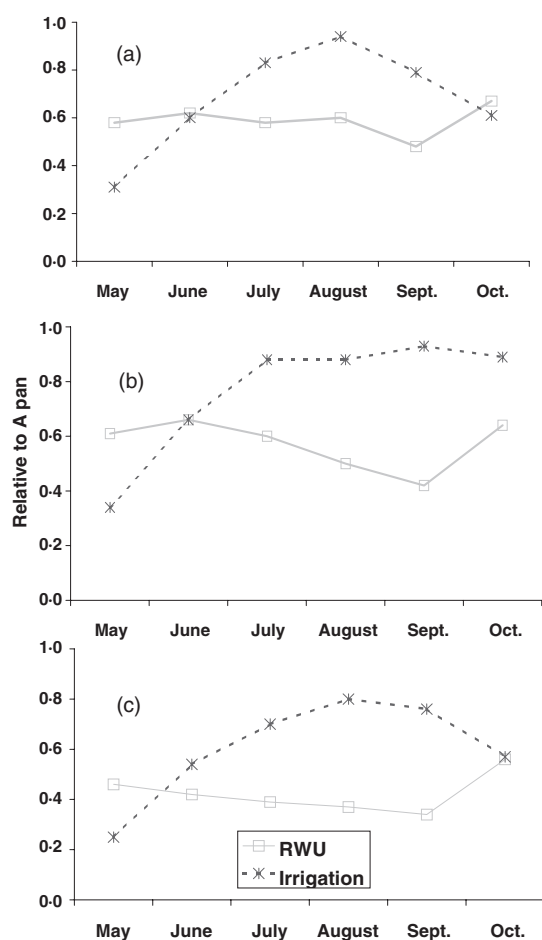
Bud break was in early April, and the measurements show that by May the water use was already high. Peak relative water use (relative to pan evaporation, Fig. 1) was in May for M9, and in June for the other two rootstocks. Relative water use decreased during the summer both in MM106 and M9, although for Hashabi there was no decrease until September. In October relative water use increased, apparently due to the large decrease in pan evaporation after September (see Table 2).

The value of  $G_1$  was measured in MM106 and M9 on three days in June and July of 1998 (Fig. 2). On the first two days  $G_1$  for sunlit leaves and on the second day for shade leaves were consistently higher in MM106. On the third day differences were not significant. The magnitude of the differences between rootstocks was small, approximately

**Table 2.** Climate data measured adjacent to the orchard during 1998. Values are from mean monthly half-hour averages from a full set of climate data logged every half hour

Month	Min $T_a$ (°C)	Max $T_a$ (°C)	Max rad ( $\text{W m}^{-2}$ )	Min wind ( $\text{m s}^{-1}$ )	Max wind ( $\text{m s}^{-1}$ )	Min RH (%)	Max RH (%)	A-Pan 1997 (mm)	A-Pan 1998 (mm)
May	13.6	22.8	831	2.2	4.5	43	70	264	*
June	15.7	25.8	990	2.4	5.8	47	82	250	257
July	17.9	28.2	988	2.9	6.1	45	79	280	294
August	19.3	29.9	933	2.0	5.4	42	82	238	246
September	18.2	27.0	793	2.3	5.4	40	74	236	227
October	14.0	24.0	747	1.6	4.2	37	65	124	*

\*not available. RH, relative humidity; A-Pan, class A pan evaporation.



**Figure 1.** Irrigation and relative water use (RWU, from sap flow measurements) of apple trees on Hashabi (a), MM106 (b) and M9 (c) rootstocks, during 1997, relative to Class A pan evaporation.

20%. On June 8 and July 14  $G_1$  peaked in morning hours and subsequently decreased. On June 9,  $G_1$  increased until midday.

The midday (1000–1400 h) hourly average  $G_c$  for June

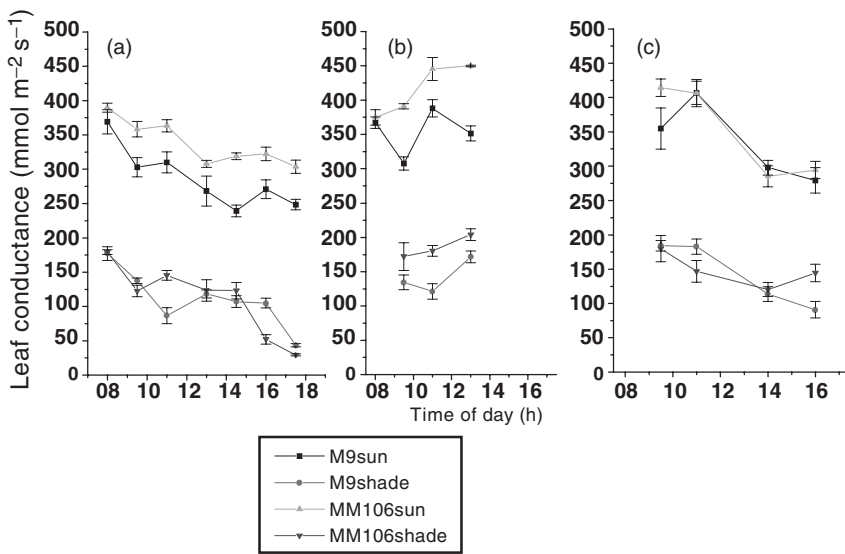
and July 1998, when water use was maximal and irrigation was in excess, is presented in Fig. 3a, plotted as a function of  $D$ . Data points when solar radiation was less than  $400 \text{ W m}^{-2}$  were not included, so  $G_c$  may be assumed to be non-light-limited. The  $G_c$  value of MM106 was highest, and that of M9 the lowest. Typical values for MM106, Hashabi and M9 at high  $D$  (3000 Pa) were 0.4, 0.3 and 0.2, and at low  $D$  (1000 Pa) 1.1, 0.7 and 0.4  $\text{mol m}^{-2} \text{ s}^{-1}$ , respectively. The value of  $G_c$  in 1997, when irrigation was lower, was generally lower. Figure 3b presents the same data, plotted as the inverse of  $G_c$ , i.e.  $R_c$ . This yields linear relationships.

Regression of the data in Fig. 3 and similar data for 1997, using Eqns 2, 3 and 4, and Eqn 4 with a forced zero intercept, yielded the parameters in Table 4. Results for Eqn 3 are plotted in Fig. 4. The  $G_c$  value of M9 in both years was similar, but for MM106 and Hashabi the lower irrigation of 1997 decreased the maximum  $G_c$ , i.e. that obtained at low  $D$ . For Eqn 2 (Table 4b), regression of parameters  $b$  on proxy values for  $a$  (i.e.  $G_c$  at 1000 Pa) for the six cases in Table 4b yielded a slope of 0.57, which is close to the value of 0.6 found in a survey of other species (Oren *et al.* 1999b). However, at very high  $D$  (which was double the maximum values reported by Ewers *et al.* 2000), Eqn 2 underestimates  $G_c$ . A better fit for  $G_c$  (i.e. higher  $r^2$ ) was obtained using Eqn 3, which also fit the data at high  $D$  better. Regression for  $R_c$  with Eqn 4 gave the highest  $r^2$  values (Table 4d), and improved the estimates at high  $D$ . The intercept  $a$  in Eqn 4 is the extrapolated minimum  $R_c$ , and, as shown in Eqn 7,  $1/b$  is proportional to  $k_g$ . The fits to the data from 1997 and 1998 (Table 4d) show that in both years  $k_g$  ( $=1/b$ ) increased from M9 to Hashabi to MM106, and that when irrigation was excessive (i.e. in 1998) minimum  $R_c$ ,  $a$ , decreased in the same manner. With lesser irrigation, in 1997, minimum canopy resistance had the opposite trend.

Intensive measurements of water relations of M9 and MM106 were made on a few days, and the most complete set is for 8 June 1998. Pre-dawn  $\Psi_1$  was  $-0.22 \pm 0.01$  ( $\pm$ standard error of the mean) and  $-0.29 \pm 0.01$  MPa for M9 and MM106, respectively, and the following day  $-0.19 \pm$

Rootstock	Month	Monthly total (mm)		Relative to class A Pan (crop coefficient)	
		Sap flow (measured)	Irrigation (applied)	Measured	Applied
Hashabi	June	189	360	0.74	1.40
	July	208	463	0.71	1.58
	August	208	540	0.85	2.20
	Total	606	1363	0.76	1.71
M9	June	155	288	0.60	1.12
	July	163	322	0.55	1.10
	August	158	322	0.64	1.31
	Total	476	933	0.60	1.17
MM106	June	225	344	0.87	1.34
	July	227	438	0.77	1.49
	August	231	440	0.94	1.79
	Total	682	1224	0.86	1.54

**Table 3.** Irrigation and water uptake, measured with sap flow sensors, of fully grown Golden Delicious apple trees on semidwarfing MM106, local Hashabi and dwarfing M9 rootstocks during the rainless summer. Site was Ortal (900 m above sea level). Data from 1998. Applied irrigation was approximately double the regional recommendations



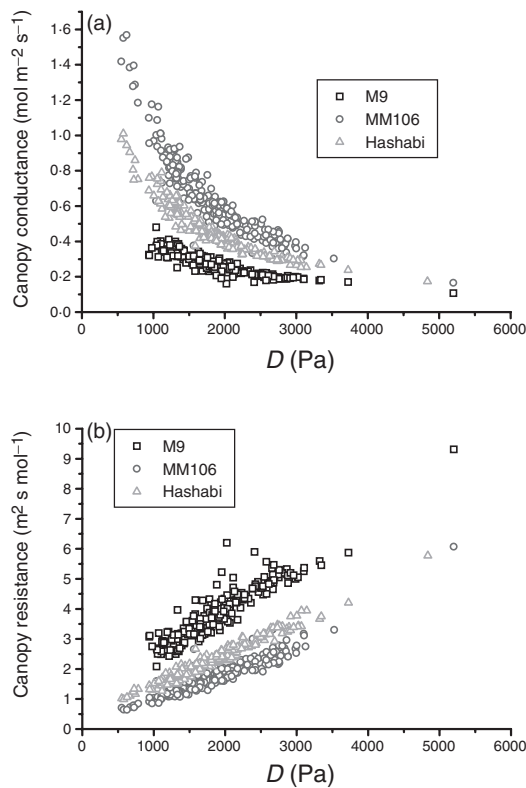
**Figure 2.** Leaf conductance ( $G_l$ ) measured in the two rootstocks on 8 and 9 June and 14 July 1998. Vertical bars indicate two standard errors of the means.

0.01 MPa for both. These values demonstrate that both plots were well watered and had similar soil water conditions. Daily courses of  $J$  and  $\Psi$  are presented in Fig. 5. Mean  $J$  per tree for M9 at midday was less than half that of MM106. A comparison of  $\Psi$  measured in the two rootstocks (Fig. 5b) shows that  $\Psi$  of stem and shaded leaves was

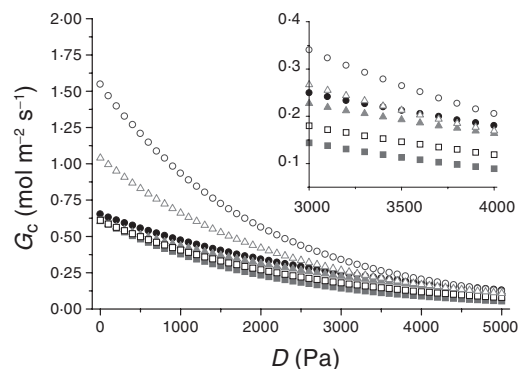
slightly lower in M9, but did not significantly differ for sunlit leaves.

The value of  $k_1$ , which expresses the ability of the hydraulic system to supply water to the leaves (Tyree & Ewers 1991), was determined from the slope of the relationship between  $J$  and  $\Psi$  (Eqn 9), where  $J_g$  was converted to  $J_l$  by dividing by LAI. The relationships are close to linear, especially for  $\Psi_{stem}$  (Fig. 6a,b).

Since water flows from soil to the stem, and from there to both sunlit and shaded leaves, the relationship between  $\Psi_{stem}$  and  $J_l$  indicates  $k_1$  from soil to stem (Moreshet *et al.* 1990). Figure 7 shows this relationship for the two rootstocks and demonstrates that  $k_{1,soil-stem}$  in M9 is approximately 56% that of MM106. For the path from stem to leaves,  $\Psi_l$  of sunlit and shaded leaves was weighted by the estimated relative areas of sunlit and shaded leaves (Eqn 10), computed after Cohen *et al.* (unpublished), and the difference between  $\Psi_{stem}$  and  $\Psi_l$  is plotted against  $J_l$  (Fig. 8). In



**Figure 3.** Midday canopy conductance  $G_c$  (a) and canopy resistance  $R_c$  (b) of irrigated Golden Delicious Apple trees on three rootstocks in 1998, as a function of vapour pressure deficit ( $D$ ).



**Figure 4.** Regression curves from fits of midday canopy conductance ( $G_c$ ) to vapour pressure deficit ( $D$ ) according to Eqn 3. Lines are shown for the three rootstocks in 1997 (closed symbols) and 1998 (open symbols). MM106, Hashabi and M9 indicated by circles, triangles and squares, respectively. Regression parameters are presented in Table 4a.

**Table 4.** Regression fits for the relationship of canopy conductance to  $D$  according to four models: (a)  $G_c = \exp(a - bD)$ ; (b)  $G_c = a - b \ln(D)$ ; (c)  $1/G_c = bD$ ; (d)  $1/G_c = a + bD$ , where  $G_c$  is canopy conductance in  $\text{mol m}^{-2} \text{s}^{-1}$  and  $D$  in Pa. Fits are for midday hourly mean conductance values for three to eight trees measured in June and July of 1997 and 1998. Irrigation in 1998 was excessive. Data points for 1998 are shown in Fig. 3 and regression curves for model a in Fig. 4.

Rootstock	Year	(a) $G_c = \exp(a - bD)$			(b) $G_c = a - b \ln(D)$			$n$	(c) $R_c = 1/G_c = bD$		(d) $R_c = 1/G_c = a + bD$		
		$a$	$b$	$r^2$	$a$	$b$	$r^2$		$b$	$r^2$	$a$	$b$	$r^2$
M9	1997	-0.489	$4.82 \times 10^{-4}$	0.92	1.98	0.230	0.90	192	2.21	0.93	0.517	1.96	0.95
Hashabi	1997	-0.506	$3.26 \times 10^{-4}$	0.89	1.91	0.211	0.87	152	1.58	0.71	1.09	1.09	0.92
MM106	1997	-0.424	$3.21 \times 10^{-4}$	0.90	1.94	0.211	0.86	199	1.46	0.61	1.10	0.941	0.93
M9	1998	-0.493	$4.08 \times 10^{-4}$	0.85	2.03	0.232	0.85	211	1.90	0.86	0.617	1.61	0.85
Hashabi	1998	0.0402	$4.54 \times 10^{-4}$	0.92	3.44	0.398	0.93	215	1.24	0.93	0.329	1.08	0.96
MM106	1998	0.439	$5.05 \times 10^{-4}$	0.87	5.28	0.620	0.88	234	0.936	0.88	$2.91 \times 10^{-2}$	0.921	0.88

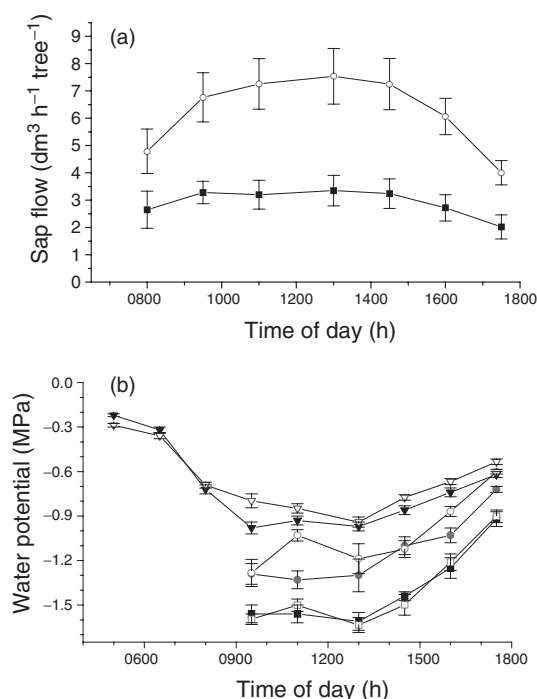
this case the offsets for the regression lines are taken as zero because at dawn, when  $J$  was zero,  $\Psi_{\text{stem}}$  and  $\Psi_1$  were the same. Differences in slope between rootstocks were smaller than those obtained from  $\Psi_{\text{stem}}$  (Fig. 7).

A summary of the calculated  $k_1$  values for the two components (soil-to-stem and stem-to-leaf) and for the total pathway is given in Fig. 9a. Values are averages calculated with synchronous data sets for  $J_1$  and  $\Psi_1$  collected on 8 and 9 June, using Eqns 9 and 10, and results were not significantly different from those obtained from slopes of linear regressions. Differences in  $k_{1,\text{stem-leaf}}$  between the two root-

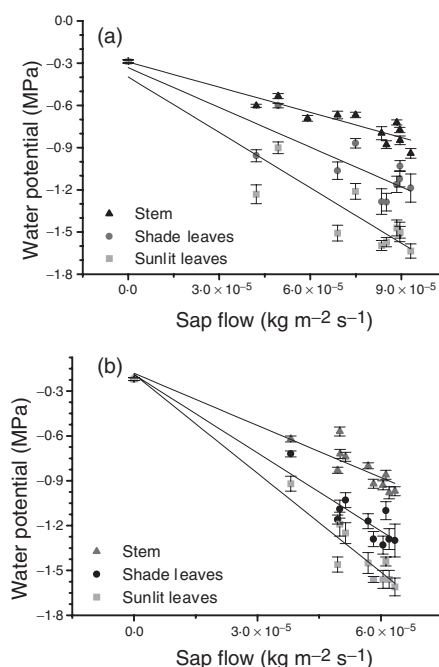
stocks were barely significant. However, for  $k_{1,\text{soil-stem}}$  differences were highly significant, and  $k_{1,\text{soil-stem}}$  for MM106 was 70% higher than for M9, causing total  $k_1$  to be significantly higher in MM106.

The value of  $k_s$  ( $=k_1/\text{Huber value}$ ), expressing the efficiency of the stem sapwood to transport water (Tyree 1999), is given in Fig. 9b. Total  $k_s$  and  $k_{s,\text{soil-stem}}$  were not significantly different between the rootstocks, whereas  $k_{s,\text{stem-leaf}}$  was higher for M9, but the difference was on the borderline of significance.

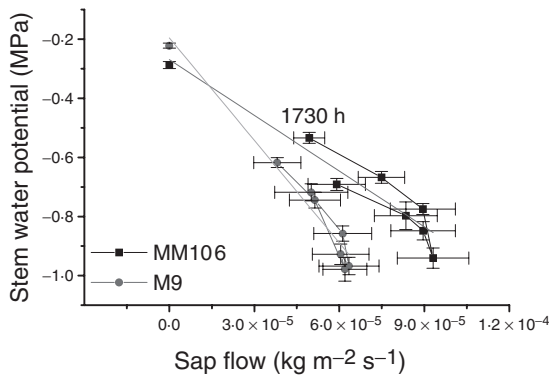
Average daily maximum sap velocity for 5 d in July 1998



**Figure 5.** Daily course of sap flow (a) and water potentials of sunlit and shaded leaves and stem (b) measured in MM106 and M9 on June 8/1998. Vertical bars indicate two standard errors of the means. Open symbols, MM106; closed symbols, M9. Stem, shade and sun leaf water potentials indicated by triangles, circles and squares, respectively.



**Figure 6.** The relationships of water potential  $\Psi$  to leaf specific sap flow  $J_1$  for sunlit and shaded leaves and stem of MM106 (a) and M9 (b) on 8 June 1998. Lines indicate linear regression fits. Vertical bars indicate two standard errors of the means. Negative inverse slopes for the regression fits were not significantly different from the leaf specific hydraulic conductance  $k_1$  values shown in Fig. 9a.

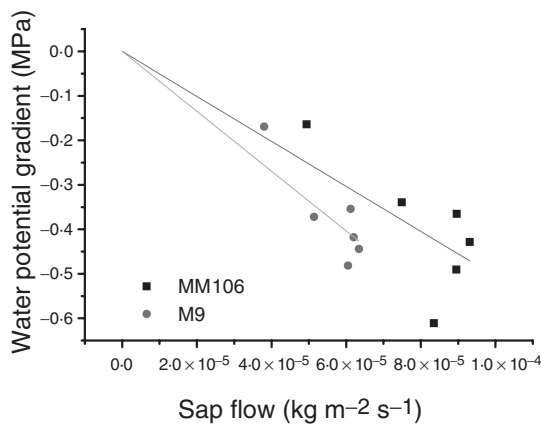


**Figure 7.** Relationship of stem water potential ( $\Psi_{\text{stem}}$ ) to leaf specific sap flow ( $J_l$ ) for the two rootstocks on 8 June. Vertical and horizontal bars indicate two standard errors of the means.

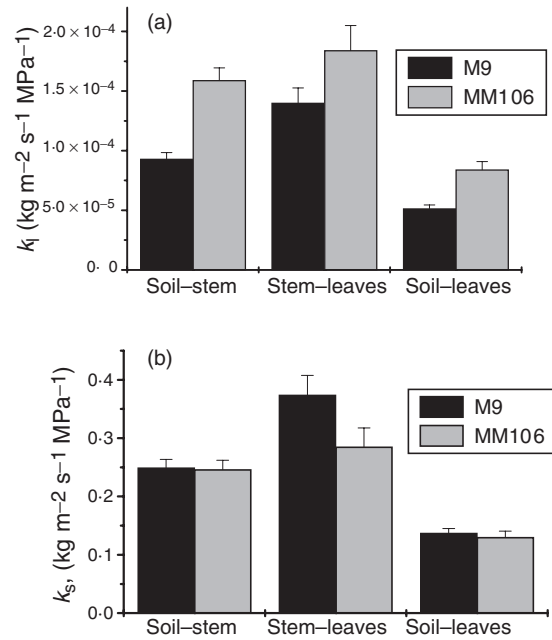
as a function of depth in the sapwood, is shown in Fig. 10. For sensor depth less than approximately half the radius, differences in velocity between the rootstocks were not significant. For MM106 and Hashabi rootstocks, velocity began to decline approximately 70% distance into the sapwood. For M9 the decline began less than half way into the sapwood. It should be noted, though, that the amount of sapwood area after a relative depth of 0.5 is only 25%.

**DISCUSSION**

This study found significant differences in water use between apple trees on three rootstocks, and especially reduced water use in the dwarfing M9 rootstock. Although it is well known that there are differences in water use of different rootstocks it is difficult to predict them and utilize this information for irrigation management. The problem will be more acute in the future, when water becomes more limited and methodologies for precision agriculture will



**Figure 8.** The water potential gradient from stem to leaves for M9 and MM106 as related to leaf specific sap flow ( $J_l$ ) for 8 June. Leaf water potential ( $\Psi$ ) was weighted according to sunlit and shaded fractions. The lines are from linear regression forced through the origin.

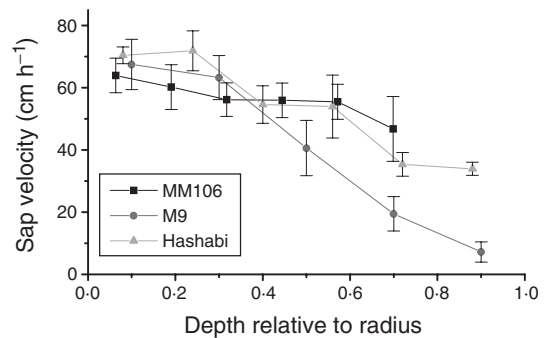


**Figure 9.** Hydraulic conductance for apple trees on two rootstocks on 8 and 9 June 1998. Conductance ( $k$ ) is expressed as (a) leaf specific  $k_l$  (relative to leaf area) and (b) as specific  $k_s$  (relative to sapwood cross-sectional area). Total  $k$  (soil-leaves) as well as two components, soil-to-stem and stem-to-leaves, are given. Vertical bars indicate one standard error of the mean.

allow irrigation amounts for individual trees to be based on remote measurements of canopy parameters such as tree volume (Meron, Cohen & Melman 2000).

**Measurement accuracy**

The accuracy of LAI measurement, discussed elsewhere (Cohen *et al.*, unpublished; Welles & Cohen 1996), is approximately 20%; the accuracy of the sap flow measure-



**Figure 10.** Sap velocity distribution in scion stems between the graft and first branch of the different rootstocks. Values are averages for peak midday flow rates measured on 5 d in mid-July 1998 in six to eight trees in each rootstock. Depth was measured from the beginning of the sapwood, i.e. from the end of the bark, and phloem and is plotted relative to sapwood radius. Mean radii were 4.0, 5.0 and 6.3 for M9, Hashabi and MM106, respectively. Vertical bars indicate two standard errors of the mean.

ments, which were made carefully (see Materials and methods), is better. A possible source of errors is the azimuthal variation in sap flow in the stem. Azimuthal variability of sap flow in apple trees has been shown to be significant in some studies (Cabibel 1994; Weibel & Devos 1994; Green, Clothier & McLeod 1997). Here, a check of differences in sap flow for different azimuthal directions was made in four trees on warm days in the autumn of 1998, before leaf fall. Climate was uniform, with cloudless skies, maximum half-hour average solar radiation on the different days between 758 and 776 W m<sup>-2</sup> and maximum temperatures of between 25.9 and 26.3 °C. Results, shown in Table 5, demonstrate that differences are not consistent from tree to tree and do not exceed 20%. Relative sap flow in different azimuths was similar in the morning and afternoon, indicating that the solar direction accounts for little of the variation. Cabibel (1994) and Green *et al.* (1997) attributed azimuthal variability to differences in root and soil water distribution, which under our conditions would not change during the day. Since all other measurements in this study were made with probes inserted from the south and differences between directions were not consistent, we assume that there was no bias due to azimuthal distribution.

**Hydraulic conductance (k)**

Whole plant *k*<sub>1</sub> reported for several annual crops (Tsuda & Tyree, 2000) and *k* on a per-tree basis for citrus trees (Moreshet *et al.* 1998) are of the same order of magnitude as *k*<sub>1</sub> reported here. Huber values (Table 1), approximately 5 × 10<sup>-4</sup>, are in the middle of the range of values reported for 28 temperate and tropical species (Patino, Tyree &

Allen Herre 1995). Differences between *k* of the lower and upper portions of the trees (i.e. soil-to-stem versus stem-to-leaves) were significant (Fig. 9), and *k* for the upper portion was higher, similar to reports for citrus (Moreshet *et al.* 1990), tropical pioneer and non-pioneer trees (Tyree, Patino & Becker 1998) and annuals (Tsuda & Tyree 2000).

Differences in water use between M9 and MM106, were similar to (and apparently attributable to) the differences in *k*<sub>1</sub> (Fig. 9a), mainly in the pathway from soil to stem. Differences in *k*<sub>s</sub> (Fig. 9b) were small and significant only for the pathway from stem to leaves. This indicates that the conductivity of the wood is similar in the two rootstocks, as evidenced also by the fact that the maximum sap velocities were the same for the three rootstocks (Fig. 10).

Sunlit  $\Psi_1$  during the day was similar in M9 and MM106, but shade  $\Psi_1$  and especially  $\Psi_{stem}$  was lower in M9. This suggests that minimum  $\Psi_1$  is controlled by the tree, although the minimum values, approximately -1.6 MPa, were higher than those observed to cause closure of stomata by  $\Psi_1$  (e.g. Landsberg, Blanchard & Warrit 1976). In many conditions  $\Psi_1$  and water use during midday hours are fairly constant in different environmental conditions, as observed in the current experiment for the different rootstocks (Fig. 5) and for other tree species (e.g. Hubbard *et al.* 2001; Cohen *et al.* 1997a). Such behaviour could help explain the high correlations between midday  $\Psi_{stem}$ , leaf conductance and productivity parameters found in apple and other deciduous orchard species (Naor 1998; Naor *et al.* 1995).

As minimum values of  $\Psi_1$  for sunlit and shaded leaves and  $\Psi_{stem}$  were similar for M9 and MM106 (Fig. 5), the distribution of maximum sap velocity in the stem (Fig. 10) is proportional to *k*<sub>s</sub> at the different depths within the stem and total *k*<sub>s</sub> is proportional to the sum of the velocities weighted by the sapwood cross-sectional area at each depth. As M9 was found to have reduced maximum velocities in the inner sapwood (Fig. 10), it is to be expected that its overall *k*<sub>s</sub> would be less than that for the other rootstocks. However, as noted above, the sapwood area with reduced sap velocity is small (approximately 25%), so the influence of the reduced velocity deep in the stem is small. The difference in sap velocity in the deep part of the stem may become more important as the tree ages and stem radius increases.

**Canopy conductance**

Parameters for the relationships between *G*<sub>c</sub> and *D* differed for the three rootstocks. M9 was seen to have especially reduced *G*<sub>c</sub> in dry midday conditions (i.e. high *D*, Figs 3 & 4). These results are only partly corroborated by the measurements of *G*<sub>1</sub> (Fig. 2), which showed reduced midday *G*<sub>1</sub> in M9, but to a lesser extent than the observed differences in *G*<sub>c</sub>. Further comparison of *G*<sub>c</sub> to *G*<sub>1</sub> measured with porometers would require a scaling-up effort based on detailed information on canopy structure. Such an exercise, carried out in the past for a citrus orchard (Cohen *et al.* 1987), estimated that differences in canopy structure due to differences in orchard hedgerow shape, dimensions and

**Table 5.** Ratio of sap flow measured in one direction to the average value for all sensors in the tree. Measurements were made on days with clear skies in October 1998, before leaf fall. Data are averages for two clear days except for Hashabi, tree ID 9, where one full day of data was collected. Solar azimuth directions in morning, midday and afternoon were south-east, south and south-west, respectively

	Tree ID	Probe azimuthal direction				Sap flow (L)
		North	South	East	West	
Hashabi:						
Morning	7		1.06	0.80	1.14	
	9	0.70	1.12	1.17		
Afternoon	7		0.87	0.93	1.19	
	9	0.76	1.10	1.15		
Day	7		0.93	0.89	1.19	24
	9	0.75	1.16	1.09		19
MM106:						
Morning	7			1.09	0.91	
	1	0.94			1.06	
Afternoon	7			1.10	0.90	
	1	1.15			0.85	
Day	7			1.10	0.90	37
	1	1.07			0.93	31

row azimuth could change water use by up to 20%. It is possible that a combination of relatively small differences in  $G_c$ , combined with differences in canopy structure, could lead to the large differences in water use observed here.

Changes in ratios of root-to-leaf area, whether caused artificially by defoliation, root pruning, storm damage, or differences in irrigation and fertilization during canopy development, have all been shown to result in differences in  $G_c$  and  $G_l$  and in the relationship of  $G_c$  to  $D$  (Meinzer & Grantz 1990; Meinzer *et al.* 1995; Pataki, Oren & Phillips 1998; Ewers *et al.* 2000; Oren *et al.* 2001) similar to the differences shown in Figs 3 and 4 for the three rootstocks. As shown in Eqn 7, the inverse of the slope of the linear relationship between  $R_c$  and  $D$ , in conditions where  $\Psi$  is constant, should be proportional to  $k$ . The ratio of the inverse of the slopes for midday  $R_c$  for MM106 and M9 in 1998 (Fig. 3b), 1.09 and 0.62 Pa mol<sup>-2</sup> s<sup>-1</sup>, i.e. 1.75, is similar to that obtained for the ratio between the two rootstocks of total  $k_1$  and  $k_g$ , 1.63 and 1.70, respectively (Fig. 9) and to the ratio between Huber values, 1.6 (Table 1). These parameters are not completely independent, as they all depend on leaf area data, but the correspondence between the ratios does encourage the use of Eqn 4 to express the relationship between  $G_c$  and  $D$ .

The relative differences in Huber values are in good agreement with the differences in  $k_1$  because the basic water transport efficiency (i.e.  $k_s$ ) of the two rootstocks examined was roughly the same (Fig. 9b). This correspondence indicates that the sapwood cross-sectional area gives a measure of the size of the total hydraulic system of the plant, especially the root system, as would be expected from the pipe model theory for water transport (Tyree & Ewers 1991). As  $k_s$  was not significantly different for the two rootstocks, Eqn 7 was used to predict the relationship of  $R_c$  to  $D$ , i.e. parameter  $b$  for Eqn 4, using the average total  $k_s$  and midday  $\Psi_1$  measured on 8 and 9 June 1998: 0.134 kg m<sup>-2</sup> s<sup>-1</sup> MPa<sup>-1</sup> and -1.36 MPa, respectively. First,  $k_s$  was converted to  $k_g$ , using sapwood cross-sectional areas and planting densities from Table 1, so that it would be comparable to  $G_c$ . Predicted  $b$ -values, 1.95, 1.70 and 1.19 s m<sup>2</sup> mol<sup>-1</sup> Pa<sup>-1</sup> for M9, Hashabi and MM106, were close to the values obtained from direct determinations for 1998 (Table 4c,d), yielding values for  $G_c$  at  $D = 3000$  Pa within 0.07 mol m<sup>-2</sup> s<sup>-1</sup> of those shown in Fig. 4 for 1998. The result for Hashabi is important because its  $k$  was not measured: therefore, this result is an independent check of whether Eqn 7 can yield useful results for other rootstocks using values of  $k_s$  and  $\Psi_1$  determined for M9 and MM106, and measurements of stem cross-section for the specific rootstock. Inversion of Eqn 7 to compute  $k_g$  for 1997 from the measured  $b$ -values and assuming  $\Psi_1 = -1.36$  MPa, indicates that average  $k_g$  in 1997 was approximately 75% of that in 1998.

Midday  $G_c$ , determined from  $k_s$  and  $D$ , together with an expression describing the relationship of conductance to irradiance (e.g. Jarvis 1976), could be used to predict orchard water use for orchards of different sizes and rootstocks. The parameter describing the difference between orchards would be the ratio of sapwood cross-sectional to

surface area. More work will be needed to determine the utility of this approach, but it may be useful meanwhile to pay more attention to Huber values and stem cross-sectional areas in future orchard water use studies.

## CONCLUSIONS

The current study has shown large differences in water use and in some hydraulic parameters of mature apple trees on three apple rootstocks: the dwarfing M9, semi-dwarfing MM106 and local Hashabi. The differences agreed qualitatively with the differences in vigour. The main rootstock difference found was that  $k_1$  of M9 was significantly lower than that of MM106, and that the difference was largest in the pathway from soil to stem. This, together with the tendency to maintain similar midday  $\Psi_1$  values, is apparently the reason for the large differences in water use between the rootstocks. However,  $k_s$  was found to be the same for both rootstocks. A model relating  $k_g$  to the response of  $G_c$  to  $D$  was applied, and analysis showed that using common  $k_s$  and midday  $\Psi_1$ , together with the relationship of scion sapwood cross-sectional to surface area, the differences in  $G_c$  response to  $D$  could be predicted for the three rootstocks. It appears likely that future research will enable these relationships to be used for irrigation management.

## ACKNOWLEDGMENTS

The authors wish to thank A. Wallach, Yan Li, A. Grava, Yefet Cohen, Fusheng Li and Dr Chongren Yao for technical assistance, to Kibbutz Ortal for use of their apple orchard, to Professor A. Erez for helpful discussions and to Professors G. Stanhill, S. Moreshet and Y. Cohen for reviewing the manuscript. This project was supported by grants numbers 306-0279 and 306-0353 from Chief Scientist's fund of the Israeli Ministry of Agriculture and by Research Grant Award No. IS-3284-01 from BARD, The United States - Israel Binational Agricultural Research and Development Fund. Contribution no. 608/01 from the Agricultural Research Organization, Institute of Soil, Water and Environmental Sciences, Bet Dagan, Israel.

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Received 1 August 2001; received in revised form 20 August 2001; accepted for publication 20 August 2001