Hydraulic conductance and rootstock effects in grafted vines of kiwifruit

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Abstract

Whole-plant hydraulic conductance, shoot growth, and leaf photosynthetic properties were measured on kiwifruit vines with four clonal rootstocks to examine the relationship between plant hydraulic conductance and leaf stomatal conductance ($g_s$) and to test the hypothesis that reduced hydraulic conductance can provide an explanation for reductions in plant vigour caused by rootstocks. The rootstocks were selected from four species of Actinidia and grafted with Actinidia chinensis var. chinensis ‘Hort16A’ (yellow kiwifruit) as the scion. Total leaf area of the scion on the least vigorous Actinidia rootstock, A. kolomikta, was 25% of the most vigorous, A. hemsleyana. Based on shoot growth and leaf area, the selections of A. kolomikta and A. polygama are low-vigour rootstocks, and A. macrosperma and A. hemsleyana are high-vigour rootstocks for A. chinensis. Whole-plant hydraulic conductance, the ratio of xylem sap flux to xylem water potential, was lower in the low-vigour rootstocks, reflecting their smaller size. However, leaf-area-specific conductance ($K_l$) and $g_s$ were both higher in the low-vigour rootstocks, the opposite of the expected pattern. Differences in $K_l$ were found in the compartment from the roots to the scion stem, with no difference between rootstocks in the conductance of stems or leaves of the scion. There was no evidence that the graft union caused a significant reduction in hydraulic conductance of vines with low-vigour rootstocks. Leaf photosynthetic capacity did not vary between rootstocks, but photosynthesis and carbon isotope discrimination ($\Delta^{13}C$) under ambient conditions were higher in the low-vigour rootstocks because $g_s$ was higher. $g_s$ and $\Delta^{13}C$ were positively correlated with $K_l$, although the mechanism for this relationship was not based on stomatal regulation of a similar xylem water potential because water potential varied between rootstocks. For Actinidia rootstocks, changes in $K_l$ do not provide a direct explanation for changes in vigour of the scion. However, depending on the rootstock in question, changes in hydraulic conductance, biomass partitioning, and crown structure are involved in the response.

Key words: Actinidia, hydraulic conductance, kiwifruit, photosynthesis, rootstock effects, stomatal conductance, water relations.

Introduction

Clonal rootstocks are widely used to control the vegetative vigour of fruit trees and improve fruit yield and quality (Webster, 1995; Castle, 1995). The mechanisms for these commercially useful rootstock effects are complex and poorly understood, but a common hypothesis is that rootstocks that reduce scion vigour have low hydraulic conductance (Syvertsen and Graham, 1985; Atkinson and Else, 2001). Low root conductivity may reduce water transport to the shoots, ultimately decreasing stomatal conductance ($g_s$), photosynthesis, and shoot growth for a given investment in root biomass. In this study, the hydraulic architecture and leaf physiology of grafted kiwifruit (Actinidia) plants were compared with a range of new rootstocks that vary in the degree of vegetative vigour they impart to the scion. The aim was to learn more about the physiological mechanism for the control of kiwifruit scion vigour by the rootstock, and in particular to examine the relationship between the hydraulic architecture of the vine and leaf stomatal conductance and photosynthesis.
Previous explanations for rootstock effects on fruit trees have included the influence of the rootstock on water and mineral transport to the shoots (Jones, 1976; Olien and Lakso, 1986), growth regulator signals (Beakbane, 1956; Jones, 1986; Soumelidou et al., 1994b; Kamboj et al., 1999; Sorce et al., 2002), and the direct influence of the graft union on phloem and xylem transport (Simons, 1986; Soumelidou et al., 1994a, b; Atkinson et al., 2003). Particular attention has been focused on the hydraulic conductivity of the roots and graft union and their influence on water transport. Citrus rootstocks that promote vigour in the scion have high root conductivity, higher rates of leaf gas exchange, increased leaf N and P concentration and higher shoot to root ratios when grown as ungrafted plants (Syvertsen, 1981; Syvertsen and Graham, 1985). Leaf water potential ($\Psi_1$) and $g_s$ are lower in scions grafted onto dwarfing apple rootstocks when they are subjected to drying soil (Olien and Lakso, 1986; Higgs and Jones, 1990). The ability of apple rootstocks to control scion vigour has therefore been related to the way they respond to drought (Atkinson et al., 2000). Two recent studies of dwarfing apple rootstocks have both highlighted reductions in hydraulic conductance caused by low-vigour rootstocks. Cohen and Naor (2002) found that, in an orchard situation with plant spacing caused by low-vigour rootstocks, ‘Kaimai’ does not, however, reduce scion vigour. Flower-promoting kiwifruit rootstocks, including ‘Kaimai’, tended to have a higher total cross-sectional area of xylem vessels in the stele, implying higher root axial conductivity (Wang et al., 1994a). The roots of flower-promoting rootstocks also contain more starch and mucilage-containing crystalline idioblast cells, leading Wang et al. (1994a) to speculate that reserve mobilization and plant water status in spring had important effects on scion flower production. Several other groups have demonstrated significant rootstock effects on shoot growth and flower production in Actinidia (Viti et al., 1990; Cruz et al., 1997), but there are currently no practical rootstocks available for controlling scion vigour. There is also no information on the physiological mechanism by which an Actinidia rootstock might reduce scion vigour. The indication from the apple and citrus research described above is that such a rootstock will have low root conductance and reduce water transport to the shoot.

The hypothesis was that $K_r$ would be lower in grafted Actinidia plants with rootstocks that caused a reduction in scion vigour. Preliminary measurements with four clonal rootstocks grafted with the same scion showed that the rootstocks did have significant effects on scion water relations and $g_s$, and there were clear reductions in vigour in two of the four rootstocks. Studies of tree hydraulic architecture have recently emphasized the existence of a common relationship between $K_r$ and stomatal regulation of transpiration (Meinzer et al., 2001; Hubbard et al., 2001). The stomata are thought to respond to hydraulic and chemical signals in a way that integrates the hydraulic conductance of the soil to leaf pathway, thus maintaining a constant $\Psi_1$ and maximizing photosynthesis while minimizing the risk of hydraulic failure through cavitation (Bond and Kavanagh, 1999; Sperry, 2000). The response of $g_s$ to $K_r$ may help explain the effects of these Actinidia rootstocks on scion vigour.

### Materials and methods

#### Plant material

Cuttings for four rootstock clones were taken in 1995 and rooted in a nursery. The four rootstocks were part of a larger trial of eight genotypes selected to encompass a range of Actinidia species and growth forms. Actinidia hemslneya Dunn ‘Kaimai’ (formerly known as ‘TR2’) is a registered rootstock cultivar known to promote flowering and vigour in green kiwifruit (Wang et al., 1994b). The other three clones, of unknown potential as rootstocks, were selected...
from three different species held in the *Actinidia* germplasm collection at the HortResearch Te Puke Research Orchard. The species were *Actinidia macroasperma* C.F. Liang, *Actinidia polygama* (Sieb. et Zucc.) Maxim., and *Actinidia kolomikta* (Maxim. et Rupr.) Maxim. Hereafter, each clonal selection will be referred to by its species name. As ungrafted plants the *A. hemsleyana*, *A. macroasperma*, and *A. polygama* clones grow as vigorous, deciduous vines at the Te Puke site. The *A. kolomikta* clone, a deciduous species from colder continental climates in northeast Asia, grows slowly and is difficult to establish as a mature vine at the Te Puke site. The scion used on all rootstocks was *Actinidia chinensis* Planch. var. *chinensis* ‘Hort16A’, a commercial cultivar of yellow fleshed kiwifruit (Ferguson and Retamales, 1999).

Scion wood was whip and tongue grafted onto the rootstocks in 1996 at a height of 0.5 m. The grafted plants were planted in the orchard in August 1997 with 5.6 m between plants and 4.6 m between rows. The experimental design was a randomized complete block, with one grafted plant of each rootstock randomly arranged within six replicate blocks. Similar grafted vines were used as buffer rows around the entire experiment and male vines for pollination were interspersed among and around the blocks. The scions were trained on to a pergola structure 1.85 m high, with a single stem from the graft to pergola height and two leaders trained north and south in the row direction and managed according to normal commercial practice (Fig. 1), except that no growth regulators were used to promote bud burst or fruit growth. During winter the vines were pruned to remove excess growth and long one-year-old shoots tied down to form the fruiting crown for the next season. Vines on weaker rootstocks had fewer long shoots, so higher proportions of older shoots with short one-year-old laterals were therefore retained as the fruiting crown. After flowering the fruit were thinned to remove misshapen fruits and to maintain a minimum ratio of approximately two leaves per fruit on the weaker rootstocks. The vines were sprinkler irrigated beneath the canopy every 3–4 d during the summer to prevent significant soil water deficits developing. The measurements reported in this study were taken over two years from November 2000 until January 2003, a period that spans most of three growing seasons. The majority of measurements were made in the season that began in spring 2001 and ended with harvest in May 2002.

**Leaf area, plant size, and yield**

Leaf area index (LAI) was calculated from gap fraction data extracted from monthly digital hemispherical canopy photographs taken with a Nikon Coolpix 990 camera and an FC-EB fish-eye adapter, beginning in October 2001. The proximity of shelter trees to the western edge of the experimental plots meant that two photographs were taken per plant, one under the western edge of the crown and one under the centre, and only the eastern side of each photograph used for analysis. Black and white photographs were taken under overcast conditions with the compression level set to fine. To avoid bias by canopy density, exposure was determined by pointing the camera at the sky (no canopy) and observing the exposure level with the camera in automatic mode and exposure compensation set to -1.0, then fixing this observed exposure in manual mode for photographs under the canopy. Publicly available software (Gap Light Analyser 2.0, Simon Fraser University, British Columbia) was used to extract the gap fraction for each 10° zenith and 15° azimuth sector. Mean transmission was calculated for 10° zenith angle intervals from 10° to 60°, after discarding any sectors that fell outside the crown of the plant. Leaf angle was measured directly on the scion using a compass-protractor and LAI was then calculated from the transmission data based on the assumption of an ellipsoidal leaf angle distribution and a mean leaf angle of 25.4° (Norman and Campbell, 1989; Campbell, 1990). Photographic LAI estimates were verified against direct measurements of LAI made by counting or harvesting leaves. For pergola-grown kiwifruit canopies the relationship between LAI estimated from the photographed gap fraction and that measured directly had a slope of 1.0±0.05 and an R² >0.9 (M Clearwater, unpublished data).

Six emerging shoots were labelled during budburst on three replicate vines of each rootstock (72 shoots in total). Three shoots per plant were from buds emerging on parent shoots longer than 0.3 m, and three from parent shoots less than 0.3 m. Starting on 14 September 2001, and at approximately weekly intervals until 1 November, the width of each leaf on the shoot was measured using a ruler as soon as the leaf was large enough to handle (approximately 10 mm wide). Area per leaf was calculated from a regression developed by periodically harvesting leaves of a range of sizes from other shoots and relating leaf area to leaf width, and leaf area per shoot by summing the individual leaf areas. During measurements, the shoot apical bud was classified as alive or dead. Normal shoot development of kiwifruit includes a proportion of shoots with apical buds that cease growth and abort, resulting in a ‘terminated’ shoot.

Projected crown area (A crown) for each plant was estimated at the end of the 2002 and 2003 seasons from measurements of the width of the crown perpendicular to the row direction at 0.5 m intervals, and calculating crown area as the sum of the measured widths multiplied by 0.5 m. Total crown leaf area (A leaf) was calculated as crown area multiplied by LAI for the relevant month. Each year in early May the fruit from each vine was harvested and the weight of each fruit recorded. In July, when the vines were dormant, stem diameter was measured at marked points 0.15 m above and below the graft union.

![Fig. 1. A diagram showing the position of water potential measurements and the simplification of vine hydraulic conductance into an Ohm’s law analogue of three resistors (expressed as conductances) in series. K root-stem includes the roots, graft union, and scion main stem, K stem-shoot the scion leader, canes, and current year stems, and K leaf the leaf petiole and lamina. ($\Psi_\text{stem}$ and $\Psi_\text{shoot}$ were measured using the pressure chamber and non-transpiring leaves, and $\Psi_\text{soil}$ with transpiring leaves. $\Psi_\text{water}$ was measured as dawn leaf water potentials and was not significantly different from zero.](https://academic.oup.com/jxb/article-abstract/55/401/1371/478968)
After accounting for average bark thickness the Huber value was calculated as the ratio of sapwood area above the graft to leaf area.

**Photosynthesis**

During the first measurement season leaf samples were taken every 6 weeks for specific leaf area (SLA) and δ¹³C determination, beginning in November 2000. Five fully expanded, sun-exposed leaves were selected from shoots that began growth in spring. After removing the petioles, lamina area was measured using a leaf area meter (LI3100, Li-Cor, Nebraska). The leaves were then dried at 65 °C for 24 h, dry weight was recorded and the samples finely ground in a ring grinder. Subsamples of leaf tissue were sent to the University of Waikato Stable Isotope Unit where the δ¹³C/δ¹²C ratio was measured in a mass spectrometer (Tracermass, Europa Scientific Ltd, Crewe, UK) and discrimination expressed relative to that of the PeeDee belemnite standard (δ₁³C). Discrimination relative to CO₂ in the air was calculated as Δ¹³C=(δ₁³C−δ₀), where δ₀ is the δ of the source air (Farquhar et al., 1982), which was assumed to be –8‰.

The photosynthetic response of leaves to light and CO₂ was recorded between December 2001 and January 2002 using a portable photosynthesis system equipped with an LED light source (LI6400 and 6400-02B, Li-Cor, Nebraska). Five light-response and 8–12 CO₂-response curves were recorded for each rootstock. Each curve was recorded on a newly selected, fully expanded, sun-exposed leaf on a shoot that began growth in spring, with leaves selected from at least three different plants per rootstock. For light-response curves leaf temperature was between 20 °C and 25 °C, and the vapour pressure deficit (D) between 0.5 and 1.0 kPa. For the CO₂-response curves leaf temperature was controlled at 20 °C, D between 1.0 and 2.0 kPa, and light intensity held at 1500 μmol m⁻² s⁻¹. Light-response curves were fitted with a non-rectangular hyperbola (Ogren and Evans, 1993), and the parameters δ₈₉ (light-saturated rate of photosynthesis), φ (apparent quantum efficiency), R₉₉ (dark respiration), and θ (convexity) estimated by non-linear regression (Photosyn Assistant, Dundee Scientific, Dundee, UK). Plots of photosynthesis as a function of intercellular CO₂ concentration (cₙ) were fitted with the mechanistic model of (von Caemmerer and Farquhar 1981) and the parameters Jₙ₉ and Vₙ₉ estimated by non-linear regression (Photosyn Assistant, Dundee Scientific, Dundee, UK). For comparison with the δ¹³C discrimination measurements of the previous summer, the leaves used for CO₂-response measurements were retained, dried at 60 °C for 24 h and five from each rootstock sent for δ¹³C analysis as described above.

Photosynthesis and stomatal conductance of leaves under ambient conditions was recorded during January 2002. For these measurements, the light source was removed from the photosynthesis system, chamber temperature set to ambient air temperature (15–25 °C) and reference CO₂ concentration controlled to give values in the leaf chamber between 350 and 370 μmol mol⁻¹. On ten sunny or partially cloudy days photosynthesis was recorded between 10.00 h and 15.00 h on randomly selected, sun-exposed leaves on the same type of shoots and the same plants as those used for response curves. Usually six measurements were made on a plant before moving to the next rootstock and scion within the randomized block, then the procedure was repeated periodically through the day. During measurements, leaf temperature varied between 20 °C and 30 °C, D between 0.8 kPa and 2.5 kPa, and irradiance between 20 μmol m⁻² s⁻¹ and 2200 μmol m⁻² s⁻¹, with the variation in irradiance resulting from variation in leaf orientation and cloud cover. To compare ambient photosynthesis between rootstocks under light-saturated conditions, the data were filtered to exclude measurements when irradiance at the leaf surface was <1500 μmol m⁻² s⁻¹ and mean photosynthesis (A), gs, and leaf internal CO₂ concentration (ci) compared using analysis of variance (ANOVA) with vine nested within rootstock. For this comparison there were between 112 and 142 individual measurements spread over three plants per rootstock treatment. Mean irradiance for each rootstock was also compared to confirm that there was no bias in leaf irradiance during measurements.

**Hydraulic conductance**

Whole-plant hydraulic conductance was calculated periodically from February 2002 to January 2003 from measurements of whole vine sap flux and xylem water potential (the evaporative flux method; Tsuda and Tyree, 2000). Measurements were made at approximately monthly intervals through parts of two summers because of initial difficulty encountered measuring sap flow. The earliest measurements were on 8 November, when the leaf area index was approximately 80% of its maximum, and the last measurements were on 2 May, at the time of harvest and before significant leaf drop. Sap velocity was measured continuously every half hour using the heat pulse velocity method (Green et al., 2003), with thermocouples spaced at 5, 10, 15 and 20 mm depth within the sapwood. Two Teflon probe sets were installed in the scion of one plant of each rootstock treatment and connected to a CR10 datalogger and AM25T multiplexer (Campbell Scientific, Logan, UT). Replication was achieved by installing the equipment in a new randomized block three times during the experiment. Probes were installed at least 0.2 m above the graft union and below the pergola height. Bark thickness and stem diameter were recorded each time a probe was installed or removed. Attempts to use the heat pulse compensation method were unsuccessful because of the high velocity of sap flow in the small diameter but very porous kiwifruit stems. Cross-over times were too short to detect during periods of high evaporative flux. Heat pulse velocity was instead measured using the Tmax method, with the probes and datalogger configured to record the time until the maximum temperature rise downstream of the heater probe (Green et al., 2003). Heat pulse velocity was converted to sap velocity and volumetric sap flux for the plant (Eplant, kg s⁻¹) by dividing total stem sapwood area (Asapw) into an annulus for each thermocouple and summing annulus area multiplied by sap velocity for each annulus. Sap velocity was usually highest close to the cambium and declined moderately towards the centre of the stem, but the entire radius was conducting. Transpiration was also expressed per unit leaf area (Eleaf) by dividing Eplant by Aleaf.

For estimates of hydraulic conductance, xylem water potentials were measured using a pressure chamber on relatively sunny days on the same vines as used for sap velocity measurements. The flow pathway was partitioned into three compartments by measuring water potential at three different positions within the plant (Fig. 1), xylem water potential as close as possible to the main stem (Ψstem), xylem water potential midway between the centre and edge of the crown (Ψcrown), and leaf water potential also in the mid-crown area (Ψleaf). Ψcrown, Ψstem and Ψleaf were measured with the pressure chamber using leaves that had been prevented from transpiring by covering with aluminium foil the previous night or early in the morning of the same day. Ψleaf was measured on a leaf from the same or a nearby shoot to that used for Ψleaf except that the leaf was transpiring normally. Pressure chamber measurements on non-transpiring leaves reflect the water potential of the xylem in the stem to which the leaf is attached, whereas measurements on transpiring leaves reflect a bulk average of xylem and tissue water potential within the leaf itself (Meinzer et al., 2001). Measurements were taken every 1–2 h, while the vines were still exposed to sun, usually between 10.00 h and 17.00 h. Two measurements were made per position, one on each side of the vine, and further measurements were made if the first two did not agree. Dawn water potentials (Ψsun) were made on covered leaves on some days, but with the irrigation, summer rainfall of the region, and positive nocturnal root pressures, there were no

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Table 1. Properties of A. chinensis var. chinensis `Hort16A’ scions grafted onto clonal rootstocks from four other Actinidia species

All measurements except transpiration per unit leaf area ($E_{leaf}$) were made on the fully replicated and blocked trial ($n=6$) during the 2001–2002 season. The leaf area measurements were made in January 2001, fruit numbers and sap wood areas ($A_{sapw}$) were recorded at the end of the season. $E_{leaf}$ was estimated for the subset of plants used for sap flow measurements over two seasons. Values (means ±1 SE) in the same row with different letters are significantly different ($P<0.05$).

<table>
<thead>
<tr>
<th>Property</th>
<th>Rootstock</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>A. kolomikta</td>
</tr>
<tr>
<td>Crown area $A_{crown}$ (m$^2$)</td>
<td>16.2±1.2 a</td>
</tr>
<tr>
<td>Total leaf area (m$^2$)</td>
<td>28.6±3.0 a</td>
</tr>
<tr>
<td>Fruit m$^{-2}$ leaf area</td>
<td>25.5±2.4 a</td>
</tr>
<tr>
<td>Scion $A_{sapw}$ (cm$^2$)</td>
<td>8.7±0.9 b</td>
</tr>
<tr>
<td>Scion $A_{sapw}/$stock $A_{sapw}$</td>
<td>0.79±0.05 a</td>
</tr>
<tr>
<td>Huber value ×10$^5$</td>
<td>3.08±0.14 a</td>
</tr>
<tr>
<td>$E_{leaf}$ (mmol H$_2$O m$^{-2}$s$^{-1}$)</td>
<td>2.76±0.25 a</td>
</tr>
</tbody>
</table>

Significant differences between rootstocks and soil water potential was assumed to be zero.

The water potential values were averaged for each time and position and matched with the corresponding average sap flux measurement for the vine during the same half hour. Hydraulic conductance ($K$, kg MPa$^{-1}$ s$^{-1}$) for each portion of the pathway from soil to leaf was calculated as:

$$K=E_{plant}/\Delta\Psi$$  \hspace{1cm} (1)

where $\Delta\Psi$ was the difference in water potential across each portion of the pathway ($\Psi_{stem}$ for $K$ from soil to stem, $\Psi_{shoot}$=\$\Psi_{stem}$ for $K$ from stem to shoot, $\Psi_{leaf}$=\$\Psi_{shoot}$ for $K$ of the leaves, and $\Psi_{leaf}$ for $K$ of the whole pathway from soil to leaf; Fig. 1). Leaf-area-specific conductance ($K_l$), scion sapwood area specific conductance ($K_{sapw}$) and crown area specific conductance ($K_{crown}$) were calculated from $K$ as:

$$K_l=K/A_{leaf}$$  \hspace{1cm} (2)

$$K_{sapw}=K/A_{sapw}$$  \hspace{1cm} (3)

$$K_{crown}=K/A_{crown}$$  \hspace{1cm} (4)

(Tsuda and Tyree, 2000; Cohen and Naor, 2002). All conductance values were expressed in units of kg MPa$^{-1}$ m$^{-2}$ s$^{-1}$. Where necessary, an additional subscript was used to denote the relevant portion of the flow pathway for a particular conductance estimate, for example, $K_{soil-stem}$ for leaf-specific conductance from soil to the stem or $K_{plant}$ for leaf-specific conductance for the whole pathway. If it is assumed that transpiration per unit leaf area is the product of stomatal conductance times an effective vapour pressure deficit at the leaf surface, then from equations 1 and 2:

$$K_l=g_sD_l/(-\Delta\Psi P_{m_w})$$  \hspace{1cm} (5)

(Hubbard et al., 2001). Atmospheric pressure ($P$) and the molecular weight of water ($m_w$) are included to account for the expression of $D_l$ in kPa and $g_s$ in mol m$^{-2}$ s$^{-1}$. Equation 5 shows that, for a linear relationship between $K_l$ and $g_s$, the quotient of $D_l$ and $\Delta\Psi$ should remain constant.

**Results**

**Plant area and leaf area**

The crown area and leaf area index of the A. chinensis scion varied strongly in response to the rootstock on which it was grafted (Table 1; Fig. 2). Scions growing on the lowest vigour A. kolomikta stock occupied half the area, had half the leaf area index, and therefore had one-quarter of the total leaf area of scions on the most vigorous A. hemsleyana rootstock (Table 1). A. polygama and A. macrosperma rootstocks produced plants of intermediate size and leaf area index. Overall, A. kolomikta and A. polygama can be considered low-vigour rootstocks, and A. macrosperma and A. hemsleyana high-vigour rootstocks for this A. chinensis scion. Reductions in leaf area were not accompanied by equivalent reductions in flower numbers. Although a higher proportion of fruitlets were thinned from the low-vigour vines after anthesis (data not shown), these vines still carried higher crop loads relative to total leaf area (Table 1).

Differences in crown size and leaf area were related to differences in the rate of early shoot development and the proportion of terminating shoots (Fig. 3). When vigorous,
non-terminating shoots were considered, there was little difference in the rate of shoot leaf area development between rootstocks (Fig. 3A). However, less vigorous shoots that eventually terminated developed more slowly and the final total leaf area on each shoot was lower on the two low-vigour rootstocks (Fig. 3B). Of the 18 monitored shoots for each rootstock, 16 shoots (89%) had terminated on both the *A. kolomikta* and *A. polygama* stocks, while 8 and 5 shoots (44% and 28%, respectively) had terminated on the *A. macrosperma* and *A. hemsleyana* rootstocks by the end of measurements on November 1. The scion on the low-vigour rootstocks therefore had a higher proportion of terminating shoots, and their terminating shoots grew more slowly and had less leaf area per shoot. The leaf area index thus increased more slowly at the beginning of the season (Fig. 2). The low number of non-terminating shoots that extend beyond the existing crown also explains the low crown area on the low-vigour stocks (Table 1).

While the low-vigour stocks supported a reduced leaf area, the sapwood area of the scion main stem was not reduced when compared with the vigorous stocks (Table 1). The ratio of scion sapwood area to leaf area (the Huber value) was therefore three times higher with the low-vigour rootstocks (Table 1). By contrast with the usual taper in diameter from rootstock to scion, the *A. polygama* rootstock produced a relatively narrow rootstock stem, but a wider scion stem, and the highest ratio of scion sapwood area to rootstock sapwood area (Table 1).

**Photosynthesis and stomatal conductance**

The scions on the two low-vigour rootstocks had significantly lower SLA early in the season (Fig. 4A). $\Delta^{13}$C measured on the same leaf sample also showed consistent differences between rootstocks (Fig. 4B). *A. polygama* contrasted strongly with the other rootstocks by imparting the highest and least seasonally variable discrimination to the scion. $\Delta^{13}$C was lower with the three other rootstocks, but increased as the season progressed. In these three rootstocks discrimination was consistently ranked according to the leaf area and vigour of the scion: $\Delta^{13}$C *A. hemsleyana* (most vigorous) $<$ *A. macrosperma* $<$ *A. kolomikta* (least vigorous) (Fig. 4B).

During the middle of the growing season no significant difference in the photosynthetic response to light or CO$_2$ could be detected between rootstocks. Fitted parameters for the light response averaged ($\pm$ SE) over the four rootstocks were $A_{\text{max}} 19.5 \pm 0.8$, $\Phi 0.057 \pm 0.003$, $R_{\text{d}} 1.2 \pm 0.2$, $\Theta 0.40 \pm 0.03$. For the CO$_2$ response the average parameters were $V_{\text{cmax}} 37 \pm 1$ and $J_{\text{max}} 112 \pm 4$. While there were no clear differences in photosynthetic capacity, there were pronounced differences between rootstocks in the stomatal conductance and photosynthesis of scion leaves during photosynthesis on clear, sunny days. Under ambient conditions with high irradiance, $g_s$, A, and $c_i$ were higher on the two low-vigour stocks (Table 2). The leaves on the *A. polygama* stock were noticeable in having the highest $g_s$ and $c_i$ of all the stocks. Measurement of $\Delta^{13}$C on a sample
of leaves used for the CO₂ response curves confirmed the same pattern of discrimination as observed during the previous season (compare Table 2 and Fig. 4B).

**Hydraulic conductance**

Xylem water potential measured on fine days did not correspond to the vigour imparted by the rootstock. The scion on *A. kolomikta*, a low-vigour stock, had the most negative water potentials, while the scion on *A. polygama*, also a low-vigour stock, had the least negative water potentials (Fig. 5). The same pattern was observed regardless of the position in the crown, but differences were more pronounced the closer that measurements were made to the rootstock and the Ψ stem position. Approximately 50% of the total pressure drop from roots to the leaves occurred between the soil and the scion stem, less than 10% between the scion main stem and the leaves, and the remaining 40% in the leaves (Fig. 5).

The hydraulic conductance (*K* plant) of the rootstock and scion reflected the overall size of the plants. There were no consistent seasonal or daily changes in *K* plant, nor was there any clear hysteresis in plots of transpiration against Ψ. The values presented here are, therefore, the overall averages for the measurement period. Larger plants (*A. hemsleyana* and *A. macroasperma*) had higher conductance up to the leader (*K* soil-stem), the shoots (*K* stem-shoot) and the leaves (*K* leaf; Table 3). However, when conductance was expressed relative to the leaf area supplied (leaf-specific hydraulic conductance, *K* s), whole-plant conductance (*K* plant) was higher in the low-vigour rootstocks because of differences in the compartment from soil to scion stem (*K* soil-stem; Table 3). *K* soil-stem of the *A. polygama* rootstock/scion combination was 56% higher than that of *A. kolomikta*, which in turn was 37% higher than that of *A. macroasperma* and *A. hemsleyana*. However, there were no significant differences between rootstocks in *K* stem-shoot and *K* leaf. When conductance was expressed relative to scion sapwood area above the graft (specific conductance, *K* s plant), conductance was lowest in the low-vigour rootstocks (Table 4). This result reflects the large sapwood area of the stems of the low-vigour vines relative to the sap flux through these vines (Table 1). Conductance expressed relative to projected area occupied by the crown (*K* g) was lowest with the *A. kolomikta* rootstock, particularly up to the main stem (*K* g soil-stem; Table 4). Overall the low-vigour rootstocks had lower hydraulic conductance relative to ground area occupied by their scion.

For all measures of conductance, the conductance from the main stem to shoots in the mid-canopy was an order of magnitude higher than conductance from soil to the stem and conductance of the leaves (Tables 3, 4). This means that most of the resistance to flow was located between the soil and scion main stem, and within the leaf.

Ambient leaf photosynthetic parameters were correlated with differences in hydraulic properties caused by the rootstocks (Fig. 6). *c* i measured using gas-exchange equipment was correlated with Δ¹³C, indicating that the observed differences in *A* and *g* s under ambient conditions provide an explanation for the carbon isotope signature of the scion (Fig. 6A). Both *g* s and Δ¹³C were strongly

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**Table 2. Photosynthesis (A), stomatal conductance (g s) and leaf internal CO₂ concentration (c i) of leaves in full sunlight (irradiance >1500 μmol m⁻² s⁻¹) under ambient conditions, for *A. chinensis* var. chinensis ‘Hort16A’ scions grafted onto clonal rootstocks from four other *Actinidia* species (means ±1 SE, *n*=112 – 142)**

<table>
<thead>
<tr>
<th>Photosynthetic property</th>
<th>Rootstock</th>
<th><em>A. kolomikta</em></th>
<th><em>A. polygama</em></th>
<th><em>A. macroasperma</em></th>
<th><em>A. hemsleyana</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>A (μmol CO₂ m⁻² s⁻¹)</td>
<td></td>
<td>14.0±0.2 a</td>
<td>14.2±0.3 a</td>
<td>12.8±0.3 b</td>
<td>12.7±0.4 b</td>
</tr>
<tr>
<td>g s (mmol m⁻² s⁻¹)</td>
<td></td>
<td>239±6 b</td>
<td>301±10 a</td>
<td>197±8 c</td>
<td>213±10 c</td>
</tr>
<tr>
<td>c i (μmol mol⁻¹)</td>
<td></td>
<td>234±2 b</td>
<td>252±2 a</td>
<td>223±3 c</td>
<td>230±3 bc</td>
</tr>
<tr>
<td>Δ¹³C (%)</td>
<td></td>
<td>20.9±0.2 ab</td>
<td>21.8±0.3 a</td>
<td>20.2±0.5 bc</td>
<td>19.2±0.4 c</td>
</tr>
</tbody>
</table>

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**Fig. 5. Xylem water potential (Ψ) at three different positions within the *A. chinensis* scion on four clonal *Actinidia* rootstocks. Values are the averages for all dates and times that hydraulic conductance was measured, *n*=37 measurement times for each bar, ±1 SE. Lines below each group indicate the least significant difference (P <0.05) between rootstocks for each position.
correlated with \( K_{l,soil-stem} \) (Fig. 6B, C). \( g_s \) was not significantly correlated with \( K_{l,stem-shoot} \) or \( K_{l,leaf} \). In low-vigour rootstocks high \( g_s \) was associated with high \( K_{l,soil-stem} \), particularly in the \( A. polygama \) rootstock that had the highest \( g_s \) and \( K_{l,soil-stem} \) (Fig. 6B). Leaf level stomatal behaviour therefore appeared to be coupled to leaf-specific hydraulic conductance, with variation in conductance caused by differences between rootstocks in the pathway from the roots to the scion main stem.

**Discussion**

\( K_{l,plant} \) was higher in \( Actinidia \) plants with rootstocks that reduced scion vigour, and lower in plants with increased vigour, the opposite of the expected pattern. This result contrasts with the two recent studies of apple rootstocks that measured low \( K_{l} \) in plants with dwarfing rootstocks (Cohen and Naor, 2002; Atkinson et al., 2003). The \( g_s \) of sunlit leaves was also higher in the low-vigour plants and there was a positive linear relationship between \( g_s \) and \( K_{l,soil-stem} \). As a result there were consistent differences between rootstocks in the photosynthesis and carbon isotope composition of scion leaves.

Co-ordination between \( g_s \) and \( K_{l} \)

The links between stomatal function, hydraulic capacity, and regulation of the transpiration rate have been widely demonstrated in other species (Meinzer, 2002). The stomata of many species respond to sudden changes in \( K_{l} \) caused by defoliation (Pataki et al., 1998), shading (Whitehead et al., 1996), or partial cutting of the xylem (Sperry et al., 1993). Under ideal conditions, \( g_s \) declines with decreasing \( K_{l} \), resulting in near homeostatic regulation of leaf water potential at a constant value (Hubbard et al., 2001). It is thought that the mechanism for this regulation is a feedback response of the stomata to some

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**Table 3.** Hydraulic conductance (\( K_g \) kg MPa\(^{-1}\) m\(^{-2}\) s\(^{-1}\) \( \times 10^4 \)) and leaf-area-specific conductance (\( K_{l,sp} \) kg MPa\(^{-1}\) m\(^{-2}\) s\(^{-1}\) \( \times 10^4 \)) of grafted Actinidia plants with four clonal Actinidia rootstocks

Conductance values are presented for the three contiguous sections of the pathway illustrated in Fig. 1 and for the entire hydraulic pathway from soil to leaf (in bold). The rootstocks are arranged in order of total leaf area, from least vigourous (\( A. kolomikta \)) to most vigorous (\( A. hemsleyana \)). Values in the same row followed by different letters are significantly different (\( P <0.05 \); \( n=27\pm37 \); \( \pm 1 \) SE.

<table>
<thead>
<tr>
<th>Conductance</th>
<th>Rootstock</th>
<th>( A. kolomikta )</th>
<th>( A. polygama )</th>
<th>( A. macrosperma )</th>
<th>( A. hemsleyana )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( K_{g} ) soil-stem</td>
<td>30±2 a</td>
<td>57±4 b</td>
<td>66±4 b</td>
<td>99±5 c</td>
<td></td>
</tr>
<tr>
<td>( K_{g} ) stem-shoot</td>
<td>473±97 a</td>
<td>508±148 a</td>
<td>816±207 ab</td>
<td>1192±279 b</td>
<td></td>
</tr>
<tr>
<td>( K_{g} ) leaf</td>
<td>48±4 a</td>
<td>48±4 a</td>
<td>106±10 b</td>
<td>177±32 c</td>
<td></td>
</tr>
<tr>
<td>( K_{l} ) plant</td>
<td>17±4 a</td>
<td>23±4 a</td>
<td>35±2 b</td>
<td>56±4 c</td>
<td></td>
</tr>
<tr>
<td>( K_{l} ) soil-stem</td>
<td>1.11±0.08 b</td>
<td>1.73±0.12 a</td>
<td>0.82±0.05 c</td>
<td>0.80±0.04 c</td>
<td></td>
</tr>
<tr>
<td>( K_{l} ) stem-shoot</td>
<td>17.04±3.65</td>
<td>15.55±4.56</td>
<td>9.96±2.52</td>
<td>9.28±2.13</td>
<td></td>
</tr>
<tr>
<td>( K_{l} ) leaf</td>
<td>1.75±0.13</td>
<td>1.46±0.12</td>
<td>1.32±0.12</td>
<td>1.42±0.17</td>
<td></td>
</tr>
<tr>
<td>( K_{l} ) plant</td>
<td>0.61±0.04 a</td>
<td>0.69±0.04 a</td>
<td>0.44±0.02 b</td>
<td>0.45±0.03 b</td>
<td></td>
</tr>
</tbody>
</table>

**Table 4.** Sapwood area specific conductance (\( K_{s} \) kg MPa\(^{-1}\) m\(^{-2}\) s\(^{-1}\) \( \times 10^4 \)) and crown area specific conductance (\( K_{c} \) kg MPa\(^{-1}\) m\(^{-2}\) s\(^{-1}\) \( \times 10^4 \)) of grafted Actinidia plants with four clonal Actinidia rootstocks

Conductance values are presented for the three contiguous sections of the pathway illustrated in Fig. 1 and for the entire hydraulic pathway from soil to leaf (in bold). The rootstocks are arranged in order of total leaf area, from least vigourous (\( A. kolomikta \)) to most vigorous (\( A. hemsleyana \)). Values in the same row followed by different letters are significantly different (\( P <0.05 \); \( n=27\pm37 \); \( \pm 1 \) SE.

<table>
<thead>
<tr>
<th>Conductance</th>
<th>Rootstock</th>
<th>( A. kolomikta )</th>
<th>( A. polygama )</th>
<th>( A. macrosperma )</th>
<th>( A. hemsleyana )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( K_{g} ) soil-stem</td>
<td>2.5±0.1 a</td>
<td>3.6±0.3 b</td>
<td>6.4±0.4 c</td>
<td>7.2±0.3 c</td>
<td></td>
</tr>
<tr>
<td>( K_{g} ) stem-shoot</td>
<td>38.6±7.6 a</td>
<td>31.4±9.1 a</td>
<td>82.8±21.6 b</td>
<td>86.1±19.6 b</td>
<td></td>
</tr>
<tr>
<td>( K_{g} ) leaf</td>
<td>4.0±0.3 a</td>
<td>3.0±0.3 a</td>
<td>10.5±1.1 b</td>
<td>12.8±1.5 b</td>
<td></td>
</tr>
<tr>
<td>( K_{l} ) plant</td>
<td>1.4±0.1 a</td>
<td>1.4±0.1 a</td>
<td>3.4±0.2 b</td>
<td>4.0±0.2 c</td>
<td></td>
</tr>
<tr>
<td>( K_{l} ) soil-stem</td>
<td>1.7±0.1 a</td>
<td>3.1±0.2 bc</td>
<td>2.8±0.2 b</td>
<td>3.3±0.2 c</td>
<td></td>
</tr>
<tr>
<td>( K_{l} ) stem-shoot</td>
<td>26.2±5.0</td>
<td>26.8±7.2</td>
<td>36.7±9.8</td>
<td>40.0±9.1</td>
<td></td>
</tr>
<tr>
<td>( K_{l} ) leaf</td>
<td>2.8±0.2 a</td>
<td>2.7±0.2 a</td>
<td>4.6±0.5 b</td>
<td>5.9±0.7 c</td>
<td></td>
</tr>
<tr>
<td>( K_{l} ) plant</td>
<td>1.0±0.1 a</td>
<td>1.3±0.1 b</td>
<td>1.5±0.1 c</td>
<td>1.9±0.1 d</td>
<td></td>
</tr>
</tbody>
</table>
Hydraulic conductance and rootstock effects in kiwifruit

Hydraulic architecture and the rootstock effect

In the low-vigour A. kolomikta and A. polygama rootstocks, total leaf area was reduced by approximately 70\% compared with the vigorous stocks, but hydraulic conductance ($K_{plant}$) by only 55\%. Hydraulic conductance per unit leaf area ($K_{l,plant}$) was therefore increased. Atkinson et al. (2003) proposed that low graft union conductance provided a mechanistic explanation for the effect of dwarfing rootstocks in apple. In the present study, a destructive harvest was not possible and the conductance of the graft union could not be measured in isolation. Calculations of $K_{s,plant}$ for the scion main stem show significant differences because rootstock effects on stem diameter were not in proportion with changes in $K_{plant}$ (lower $K_{plant}$ but increased sapwood area with the low-vigour stocks). However, the sapwood of these Actinidia species, as with other lianas, is highly porous with large diameter vessels (Dichio et al., 1999; Clearwater and Clark, 2003). The conductance of the stem from the leader to the mid-canopy was an order of magnitude higher than the conductance of the leaves or roots (Tables 3, 4), and the main stem also probably contributes only a small proportion to overall resistance and any differences in $K_{plant}$ between rootstocks. The same pattern is found in ungrafted plants of other species, with the largest resistance often found in the roots (Sperry et al., 2002). Therefore, low $K_s$ in the low-vigour rootstocks is not reliable evidence that changes in the anatomy or conductance of the main stem were important components of the rootstock effects. Furthermore, if a change in hydraulic conductance of the graft union or main stem was the primary mechanism for Actinidia rootstock effects, equal or reduced $K_{l,plant}$ would be expected in the low-vigour rootstocks, as observed for the dwarfing apple rootstocks (Cohen and Naor, 2002; Atkinson et al., 2003). Alternative explanations must therefore be sought for the effect of these rootstocks on scion behaviour.

The high $K_{l,soil-stem}$ and $g_s$ of the scion growing on the A. polygama rootstock suggest an increase in root hydraulic capacity relative to shoot leaf area. Leaf-specific conductance differed in the soil to stem portion ($K_{l,soil-stem}$) of the pathway, rather than in the stems and leaves ($K_{l,stem}$ and $K_{s,leaf}$) of the scion. The most significant resistance in the pathway from soil to main stem is likely to be the roots (Sperry et al., 2002). Less negative $\Psi_{stem}$ aspect of leaf water status (an hydraulic signal), resulting in changes in $g_s$ that minimize fluctuations in $\Psi_{leaf}$ (Bond and Kavanagh, 1999; Hubbard et al., 2001). In the present study the mechanism was not a feedback response to bulk $E_{leaf}$ or $\Psi_{leaf}$ because these variables differed between the rootstocks. $\Psi_{leaf}$ differed significantly between rootstocks and was not correlated with $g_s$. The stomata may instead have been responding to some other aspect of leaf water status, or to an unknown chemical signal exchanged between the rootstock and scion. Regardless of the mechanism involved, the changes in leaf photosynthesis and carbon isotope composition and their relationship with $K_l$ suggest a consistent, long-term stomatal response to a change in vine hydraulic architecture caused by the rootstock. If the mechanism does involve a chemical signal then it may also be relatively conserved between genotypes. The rootstocks used in this study were from four different species belonging to two sections of the genus Actinidia (Leiocarpae and Strigosae) with widely different geographical distributions within eastern Asia. The scion was a clone from a fifth species and a separate section (Stellatae) (Ferguson, 1990). Further experiments with these rootstocks will include comparisons of xylem sap composition and the possible nature of xylem transported signals passed from the rootstock to the scion.

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**Fig. 6.** Relationships between stomatal conductance ($g_s$), carbon isotope discrimination ($\Delta^{13}C$), and hydraulic conductance. (A) $\Delta^{13}C$ as a function of leaf internal CO$_2$ concentration ($c_i$) estimated from ambient photosynthesis measurements. (B, C) $g_s$ and $\Delta^{13}C$ as functions of leaf-area-specific hydraulic conductance from the soil to the scion main stem ($K_{l,soil-stem}$). $c_i$ and $g_s$ are from Table 2, $\Delta^{13}C$ is the February measurement from Fig. 4 (the same time of year but a year earlier than the $g_s$ measurements), and $K_{l,soil-stem}$ is from Table 3. Bars indicate $\pm$ 1 SE.
also indicates that the root conductance of the *A. polygama* rootstock was high compared with the rate of transpiration, despite the increase in *g* s. Root conductance should be a function of root biomass and root conductance per unit biomass. Species with high root conductance tend to be faster growing and produce roots with a higher surface area or length per unit dry mass (Tyree *et al*., 1998; Comas *et al*., 2002). There are also trade-offs between root morphology, anatomy, and root longevity, with faster turnover expected in high-conductance species (Eissenstat, 1997). It is therefore possible that the grafting of *A. chinensis* onto the *A. polygama* stock resulted in an increased proportion of total carbon gain being allocated to the roots. Root respiration, root turnover, or partitioning to total root biomass may be higher with the *A. polygama* rootstock relative to the supported leaf area. Further measurements are needed to determine if there is a causal relationship between carbon partitioning to roots and reductions in vigour of the scion.

Of the four rootstocks, *A. kolomikta* caused the most extreme reduction in scion leaf area index and plant size, and had the most negative water potentials. The results for this rootstock illustrate the need to consider changes in crown architecture when interpreting leaf level responses to changes in plant hydraulic architecture (Meinzer *et al*., 1993). The Ohm’s law analogy used in this study simplifies the crowns into two resistors connected in series (the stems and leaves), when in fact it represents a complex series parallel network. A change in the distribution of flow through this network affects the interpretation of estimates of hydraulic conductance. To illustrate this effect, consider Equation 5 and the linear relationship between *K* l,soil-stem and *g* s (Fig. 6B). For *Ψ* stem to be significantly more negative with *A. kolomikta* then *D* l must also have increased, otherwise there would not have been a linear relationship between *K* l,soil-stem and *g* s across the different rootstocks. With *A. kolomikta* the LAI was low, a higher proportion of leaves must have been exposed to direct sunlight, *E* leaf was higher, and it was therefore concluded that the effective average driving force for transpiration across all leaves (*D* l) was increased. Boundary layer conductance may also be lower with a more open crown, thus further increasing transpiration. Although calculated *K* l,plant was higher with *A. kolomikta*, these vines may still have been limited by the hydraulic capacity of their roots. The low *K* g plant value for *A. kolomikta* (Table 4) illustrates this potential limitation, with hydraulic capacity reduced relative to crown projected-area. Cohen and Naor (2002) also found that *K* g was lower in apple trees with dwarfing rootstocks. In both examples, plant size and leaf area per plant were reduced in low-vigour plants, but they had a high potential evaporative demand and occupied more space relative to their hydraulic capacity. The cause of low root conductance and open crown structure with the *A. kolomikta* rootstock is not known, but it is possible that the phenology of this rootstock contrasts more strongly with that of the scion than the other rootstocks. *A. kolomikta* is naturally distributed in more northern latitudes and higher altitudes in north-east Asia than the scion and other rootstocks (Liang, 1983). Ongoing measurements are now testing whether shoot growth in spring is limited by root function and plant water status.

The vigour of the *A. macrosperma* and *A. hemsleyana* stocks was associated with faster scion shoot and leaf development in spring and a higher proportion of non-terminating extension shoots. The resulting high leaf area was supported by high hydraulic conductance (*K* plant). Huber values were low and *K* s,plant values were high, indicating roots and stem with high hydraulic conductance and high sap flux relative to stem diameter. *K* l,plant was reduced in these stocks, but because of the high LAI the proportion of self-shaded leaves was probably higher, and *K* s,plant was equivalent or higher than the low-vigour rootstocks. Compared with other species, *K* l,plant for these vines are comparable with those for annual crops and some other temperate deciduous woody plants (Tsuda and Tyree, 1997, 2000), and high compared with some temperate evergreen trees (Phillips *et al*., 2002). There were also consistent differences between the two high-vigour stocks. Scions on *A. hemsleyana* had a higher LAI than on *A. macrosperma*, and overall plant size and *K* were higher. Final leaf area and crown size was lower with the *A. macrosperma* stock, but shoot growth in spring was still relatively rapid. Fast initial canopy development, but a reduction in overall vigour, is of practical interest because of the expense of controlling summer vegetative growth in commercial *Actinidia* orchards. However, overall hydraulic conductance on a leaf area or crown area basis was similar with the two vigorous *Actinidia* stocks, indicating that with vigorous rootstock–scion combinations leaf area development was well co-ordinated with root and stem hydraulic capacity.

There were no clear differences in leaf photosynthetic capacity between rootstocks during midsummer, although there were clear reductions in SLA and the rate of leaf expansion during spring in the low-vigour stocks. The similarity in photosynthetic capacity between stocks shows that changes in leaf properties on their own are unlikely to provide a direct explanation for rootstock effects in kiwifruit. Primarily because of higher *g* s, the rate of ambient photosynthesis by sunlit leaves was higher with both the low-vigour stocks. This result contrasts with some of the effects of rootstocks on photosynthesis in other fruit crops. In citrus, root conductance and leaf gas exchange by rootstock seedlings were positively correlated with the vigour imparted to the scion (Syvertsen and Graham, 1985). In apple it has been suggested that some of the effect of dwarfing rootstocks is through hydraulic effects on water transport and, ultimately, the rate of photosynthesis (Cohen and Naor, 2002). In this study the rate of
photosynthesis of sunlit leaves was lower in the high-vigour rootstocks, but whole-plant carbon gain was probably higher because of the higher LAI and crown area.

Conclusion
Partitioning of hydraulic resistance between the roots, stems, and leaves of grafted *Actinidia* plants showed that the largest resistances (lowest conductance) to flow were found in the roots and leaves. As there were no significant differences in $K_{i,soil-stem}$ of the upper stems and leaves, overall differences in hydraulic architecture between the grafted plants were dominated by the effect of the rootstocks. The differences in stomatal conductance of the scion reflected differences in hydraulic architecture between rootstock. The differences in the hydraulic architecture of these plants did indicate, however, that the observed rootstock effects are at least linked to changes in crown structure and biomass partitioning to the roots.

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References


