Control of scion vigour by kiwifruit rootstocks is correlated with spring root pressure phenology


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Abstract

Root pressure was measured continuously over spring in eight clonal kiwifruit rootstocks selected from seven Actinidia species (A. chrysantha, A. delicosa, A. eriantha, A. hemsleyana, A. kolomikta, A. macrosperma, A. polygama), using pressure transducers and miniature compression fittings. Rootstocks that promoted scion vigour developed root pressures up to 0.15 MPa before or during scion budburst, whereas those that reduced scion vigour developed root pressure up to 0.05 MPa only after scion shoot expansion. When several seasons were compared, the date of onset of root pressure and the magnitude of pressure achieved were consistent for each rootstock. Root pressure was first recorded between late July and early September in vigour-promoting rootstocks, while scion budburst and initial shoot growth were in late August and early September. Vigour-reducing rootstocks did not develop significant root pressure until October. The date of onset was similar for the grafted rootstock and ungrafted plant of the same clone, but was not clearly related to the timing of shoot growth by the ungrafted plant. In the grafted plants the leaf and xylem water potentials of the scion were more negative, midday turgor was 0.3–0.5 MPa lower, and wilting was sometimes observed in developing shoots growing on low-vigour rootstocks, indicating that water stress was contributing to reductions in growth. Leaf turgor was correlated with average root pressure but not pressure measured during the day, suggesting that root pressure was not supporting transpiration during peak flows and was, instead, indicative of higher root hydraulic conductance. The rapid temporal rise in root pressure observed each spring in the various rootstocks was not accompanied by changes in xylem sap solute potential, but when rootstock clones were compared those that developed higher root pressures had higher sap solute potentials. Xylem sap solute potential varied between rootstocks from −0.07 MPa to −0.15 MPa, while root pressures measured at the same time varied between 0.0 MPa and 0.09 MPa, suggesting that an osmotic mechanism could account for the observed root pressure. Differences in phenology between the rootstocks and scion appeared to account for the rootstock effects on shoot growth, and changes in root pressure provided a useful indication of seasonal changes in root hydraulic properties and solute transport behaviour.

Key words: Actinidia, Actinidia chinensis, Actinidia delicosa, Actinidia hemsleyana, Actinidia kolomikta, Actinida macrosperma, Actinida polygama, kiwifruit, phenology, root pressure, rootstock, scion vigour, water relations.

Introduction

Rootstocks are used for the control of vigour and fruit quality in many horticultural crops (Webster, 1995). Despite their economic importance, the mechanism for scion vigour control by rootstocks is poorly understood. Previously, the effects of experimental kiwifruit (Actinidia species) rootstocks on scion shoot growth (Clearwater et al., 2006) and vine hydraulic architecture (Clearwater et al., 2004) have been described. Rootstock ‘vigour’ was defined according to the leaf area index produced by the scion, which was itself a function of the proportion of shoots that grew rapidly without self terminating (Clearwater et al., 2006). Rootstocks that reduced scion vigour were found to exert an effect on shoot growth during the earliest period of shoot development in spring, starting immediately after budburst. Low-vigour rootstocks reduced shoot growth and increased the proportion of shoots that terminated

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(abortion of the shoot apex) and stopped growth early in the season (Clearwater et al., 2006). Vine hydraulic conductance and canopy physiology were measured later in the season and did not provide a direct explanation for the effects of rootstock on growth (Clearwater et al., 2004). In this study, the properties of the roots and their effects on shoot physiology during the important spring period when the first cluster of leaves emerged from the bud were measured.

The development of root pressure, defined as positive xylem pressure that arises in the roots (Kramer and Boyer, 1995), is a noticeable feature of kiwifruit vines in spring (Davison, 1990). Root pressure usually rises before budburst and results in copious ‘bleeding’ (exudation) from the xylem if pruning cuts are made during this time. Exudation from a cut stem can occur for many days with no apparent negative effects for the vine. Spring root pressure has often been used to collect sap for compositional analysis and the diagnosis of nutritional disorders (Ferguson et al., 1983; Clark et al., 1986). Wang et al. (1994a, b) proposed that the capacity for root pressure or water supply in spring might be associated with Actinidia rootstock effects on levels of floral abortion by the scion. Although it is not widely recognized, root pressure occurs in kiwifruit throughout the summer (not only before budburst), but only develops at night during humid weather when night-time transpiration is prevented (kiwifruit stomata do not close completely at night, resulting in significant night-time transpiration if the humidity does not rise to saturation; Green et al., 1989). Observations of root pressure have been made for centuries in a wide variety of other plant species, with the most parsimonious explanation that it is an osmotic process resulting from the accumulation of apoplastic solutes in the xylem of the roots (Kramer and Boyer, 1995).

Preliminary observations of exudation and root pressure for this study suggested that there were differences in the timing and magnitude of root pressure between the rootstocks. A method for reliably monitoring xylem pressure was therefore developed, and root pressure and shoot water relations monitored over the 2-month period between budburst and flowering. These observations relate to our earlier studies of shoot growth and vine hydraulic conductance, and their significance for rootstock effects in other perennial fruit crops is discussed.

**Materials and methods**

**Plant material**

The rootstock trial used for this study has been described previously (Clearwater et al., 2004, 2006). Briefly, shoots from eight rootstock clones encompassing a range of Actinidia species and growth forms were taken in 1995 and rooted in a nursery. A. humslwyanam Dunn ‘Kaimai’ (formerly known as ‘TR2’) is a registered rootstock cultivar known to promote flowering and vigour in green kiwifruit (Wang et al., 1994b). A. deliciosa (A. Chev.) C.F. Liang et A.R. Ferguson var. deliciosa ‘Hayward’ is the common green kiwifruit, grown internationally. The other six clones, of unknown potential as rootstocks, were selected from five species held in the Actinidia germplasm collection at the HortResearch Te Puke Research Orchard, New Zealand. The species were A. eriantha Benth., A. macrosperrna C.F. Liang, A. chrysantha Merr., A. polygama (Sieb. et Zucc.) Maxim., and A. kolomikta (Maxim. et Rupr.) Maxim. Hereafter each clonal selection will be referred to by its species name. Two clones from A. kolomikta were used; these are referred to with the suffixes ‘k’ and ‘s’. All of the clones, except A. kolomikta, grow as vigorous, deciduous vines when grown ungrafted at the Te Puke site. A. kolomikta is a deciduous species from colder continental climates in north-east Asia, that grows slowly and is difficult to grow to maturity 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, 1999). Grafted plants were planted in 1997 at the Te Puke site and the scions trained on to a pergola structure and managed according to normal commercial practice, except that no growth regulators were used to promote bud burst.

Measurements of the dates of onset of root pressure and budburst of ungrafted plants were made on the mature parent vines from which the original rootstock cutting material was taken. All of these vines (except the A. kolomikta parents) were grown on t-bar structures in germplasm repository blocks, with only one individual of each clone available. These vines were managed with a less-intensive fertilizer and pruning regime than the rootstock trial. Ungrafted A. kolomikta plants were only available as small plants less than 1 m high, growing in a nursery area. All the parent plants were growing within 500 m of the rootstock trial.

The climate at the Te Puke Research Orchard, in the Bay of Plenty, New Zealand, can be described as mild temperate, with average daily minimum and maximum temperatures varying from approximately 13 °C and 24 °C in summer to 5 °C and 13 °C in winter. Average annual rainfall is approximately 1700 mm, with a relatively even distribution throughout the year. Soils at the research site are deep and free draining, significant soil moisture deficits are uncommon, particularly during the spring when this study was conducted. Mild radiation frosts are occasional in winter and spring but are not usually severe enough to result in freezing of the soil or the stems of the kiwifruit vines (freezing was not observed during this study).

**Root pressure**

Root pressure was measured relative to atmospheric pressure using low-cost temperature-compensated pressure transducers (Sensym SDX100G2, Honeywell), calibrated against another pressure transducer (100 PSI gauge, Gems, Basingstoke, UK) and connected to a datalogger and multiplexer (CR10X and AM416, Campbell Scientific, Utah). A 3.5 mm hole was drilled through the bark below the graft union to a depth of 10–15 mm into the xylem of the rootstock stem. The hole was immediately flushed of debris with clean water and a custom-made compression fitting sealed into the hole. The compression fitting (Fig. 1A), made from a 16-gauge disposable hypodermic needle, was a modification of a design presented by Edwards and Jarvis (1981) that allowed the sealing of transducers to the xylem even when xylem sap was exuding rapidly. After the compression fitting was sealed into the newly drilled hole, a 3-way luer stopcock was pushed onto the hub of the fitting, and then the port of the pressure transducer was pushed onto one port of the stopcock (Fig. 1B). Before connection, the port of the pressure transducer was filled with silicone oil, and the compression fitting hub and luer stopcock filled with water. The extra port of the stopcock was used to release any back pressure generated by pushing the fittings together, and made it possible to check for
The ungrafted rootstock parent vines, and for three individual grafted plants of each rootstock in the rootstock trial. Budburst was monitored by marking four dormant canes and counting the number of ‘burst’ buds (the budburst stage, defined as an emerging bud with the first appearance of green tissue; Brundell, 1975) on each cane at weekly intervals. Exudation, an indication of the development of root pressure, was monitored by piercing the stem surface with an 18-gauge hypodermic needle. Pushing the needle through the bark until it struck the sapwood resulted in a drop of exudation fluid after the needle was removed, if root pressure was present. Tests were made as soon after dawn as possible, before significant transpiration from the bark or any developing shoots had begun.

**Scion shoot water relations**

Leaf (Ψ_l), xylem (Ψ_x), and solute (Ψ_s) potentials were measured on scion shoots during fine sunny weather after shoot emergence in the springs of 2003 and 2004. Potentials were measured at dawn (from 06.00 h) and 13.00 h on 30 September 2003, on three plants of each of five of the rootstock treatments. A pressure chamber was used to record the water potentials of at least two non-transpiring (Ψ_l) and two transpiring (Ψ_x) leaves per plant from mid-canopy positions. Non-transpiring leaves were covered with aluminium foil the previous evening. A second set of transpiring leaves was cut into pieces and immediately frozen in liquid nitrogen inside 5 ml disposable syringes, thawed on a later date, and the osmolality of the leaf sap measured with a vapour pressure osmometer (Vapro 5520, Wescor, Utah). Ψ_s was calculated from osmolality based on the Van’t Hoff relation (Nobel, 1999). Leaf turgor (Ψ_t) was calculated as the difference between Ψ_l and Ψ_s, (ignoring the contribution of leaf xylem sap solute potential; Boyer, 1995). Similar measurements were made on 27 September and 15 October 2004, except that repeated measurements of Ψ_l, Ψ_x, and Ψ_s were made at intervals during the day on three plants of two of the rootstock treatments (A. hemsleyana and A. kolomikta ‘k’, chosen to represent the extremes of early and late development of root pressure).

**Xylem sap solute potential**

The xylem sap solute potential of the grafted plants was measured on four dates (29 August, 5 September, 19 September, and 18 October) during the spring of 2003 for comparison with root pressures measured during the same period. Sap was collected as root pressure-driven exudate, hence samples were only obtained from rootstocks (up to six plants per treatment) that had developed positive root pressure. During the night (when transpiration rates were low and root pressure maximal), a 1 mm hole was drilled into the xylem of the rootstock stem, within 100 mm of the soil surface. A new 16-gauge disposable hypodermic needle was gently pushed into the hole, causing sap to drip from the needle hub. Approximately 0.2 ml (10 drops) of exudate was allowed to drop from the hub (to flush out contaminants from the drilling process) before the barrel of a new 1 ml tuberculin syringe was pushed onto the hub and left to fill with sap. Once the syringe was full it was removed from the needle and the plunger inserted and used to push the sap into a 1.5 ml Eppendorf tube, and the sample frozen immediately in liquid nitrogen. The osmolality of the samples was measured later using the vapour pressure osmometer and Ψ_s calculated as described above.

To summarize, root pressure was monitored in grafted plants using pressure transducers in the spring of 2001 and 2003. The timing of first exudation and budburst (rootstock phenology) was monitored in grafted and ungrafted plants in the spring of 2002 and 2003, xylem exudates for solute potential determination were collected from the grafted plants in 2003, and scion shoot water relations were measured in the spring of 2003 and 2004.
Results

Temporal changes in root pressure

Measurements of xylem pressure using pressure transducers showed clear differences between rootstocks in the magnitude and timing of onset of root pressure in spring (Fig. 2). The earliest rootstock to develop pressure, *A. hemsleyana*, was already exuding sap when the transducers were installed. Root pressure rose steadily in this rootstock from approximately 18 August, around the time when minimum soil temperatures were observed. Sustained positive pressure was measured in the *A. macrosperma* rootstock from 20 August, with daily maximum average pressure rapidly rising to over 0.10 MPa. This rootstock consistently developed the highest xylem pressures observed, peaking at approximately 0.15 MPa. The *A. delicosa* rootstock developed positive pressure on 31 August, 5 d after the point of 50% budburst of the scion.

Fig. 2. Time-course of soil temperature (A) and root pressure relative to atmospheric pressure (B–F) for five *Actinidia* rootstocks, measured in 2003 (solid lines, average of three plants per rootstock) and 2001 (dotted lines, 1 plant per rootstock). The vigour imparted to the scion by each rootstock is given in parentheses (based on shoot growth and leaf area; Clearwater et al., 2006). Arrows indicate the approximate date of 50% budburst of the scion on 26 August 2003 (rootstock had no effect on the date of budburst).
on 26 August. The *A. eriantha* and *A. chrysantha* rootstocks (measurements made on single plants in 2003, data not shown) also developed positive pressure around 28 August. By contrast, the *A. polygama* and *A. kolomikta* ‘k’ rootstocks did not develop positive pressure above 0.02 MPa until 1 October (Fig. 2).

The date of onset of pressure was consistent between years for each rootstock. Comparing the measurements in 2001 and 2003 suggests that the rise in root pressure for the *A. hemsleyana*, *A. macrosperma*, and *A. delicosa* rootstocks occurs around a similar calendar date for each rootstock in each year (Fig. 2). Soil temperature records were also similar for the two years (Fig. 2). The 2001 measurements did not continue long enough to record positive pressures in the *A. polygama* and *A. kolomikta* ‘k’ rootstocks.

All rootstocks showed a decline in average root pressure and an increase in diurnal fluctuations in pressure after approximately 17 September (Fig. 2). This period clearly coincided with the later stages of budburst and the probable onset of transpiration from the newly expanded leaves of the scion. Prior to this date, the rootstocks that had already developed positive pressure showed small daily peaks in pressure that coincided with maximum air temperature and VPD around midday (Fig. 3). Pressure fluctuations were out of phase with soil temperature, which peaked later in the day (not shown in Fig. 3). During this period evaporation from the bark and buds appeared minimal, and peaks in pressure may have been caused by temperature-driven fluctuations in stem and sap volume. Transducers open to the atmosphere did not show similar diurnal fluctuations in pressure. After day 17 September the opposite diurnal pattern was observed, with root pressure highest at dawn and decreasing to a minimum around midday at the time of maximum air temperature and VPD (Fig. 3). The change in phase and increase in amplitude of pressure fluctuations indicated that transpiration from the expanding shoots had begun, with water loss by transpiration causing a daytime decrease in xylem pressure. Anomalies in this pattern (days without a daytime decrease in pressure) correspond with rain-fall and low VPD (e.g. around 12 October, Fig. 2, rainfall data not shown). It is not known whether the minimum pressures achieved over the period when transpiration was occurring were representative of actual xylem pressure as it is possible that the water in the compression fittings or xylem access hole cavitated below pressures of −0.1 MPa.

**Rootstock phenology**

The timing of onset of exudation of the grafted rootstocks was related to the timing of exudation observed from the ungrafted parent plant, although the parent plant was consistently later than the grafted plants by 5–20 d (Fig. 4). However, the approximate date of mid-budburst of the parent plant was not clearly related to the date of onset of exudation of either the grafted or parent plant. The *A. hemsleyana* rootstock developed root pressure earlier than the other rootstocks, but shoots of the ungrafted parent plant were among the last to break bud. The date of onset

![Fig. 3](image-url). Example of a 5 d time-course of root pressure (line and dots), air temperature (line only), and air vapour pressure deficit (VPD, dots only) for a single *Actinidia macrosperma* rootstock during budburst (A) and after shoot expansion (B) during the spring of 2003. Once root pressure had developed, it fluctuated with the same phase and period in all rootstocks (Fig. 2).

![Fig. 4](image-url). Timelines for root pressure development of grafted *Actinidia* rootstocks (solid line) and their respective ungrafted parent plants (dashed lines) in 2003. For these data root pressure was detected as the presence or absence of exudation after the xylem was punctured with a needle. Dots indicate the approximate date of 50% budburst of the other rootstocks, but shoots of the ungrafted parent plant were among the last to break bud. The date of onset...
of first exudation for grafted rootstocks (detected using the needle test) was generally earlier than the date of onset of measured positive root pressure (measured using pressure transducers) for the same plants (compare Figs 2, 3). The needle test was effective for detecting low positive pressures, but gave variable results compared with continuous monitoring when weather conditions favoured transpiration.

**Scion shoot water relations**

Scion shoots growing on rootstocks with lower root pressure had lower daytime leaf turgor and more negative xylem and leaf water potentials during the period of rapid spring shoot growth (Fig. 5). There were no differences between rootstocks in shoot water relations when pressure chamber and leaf sap osmolality measurements were made at dawn, but by 13.00 h turgor, xylem and leaf water potentials were significantly less in low root pressure rootstocks (A. polygama and A. kolomikta ‘k’) compared with high root pressure stocks (Fig. 5). The difference between leaf and xylem water potentials was least with the lowest root pressure rootstock (A. kolomikta ‘k’), suggesting the leaf transpiration rate was lowest (or leaf hydraulic conductance highest) with this rootstock. At 13.00 h turgor and xylem water potentials of leaves on the high root pressure A. macrosperrna, A. hemsleyana, and A. deliciosa stocks were similar to dawn values, suggesting an adequate supply of water to the expanding leaves (Fig. 5).

The pattern of signs of water stress on a rootstock with low root pressure was confirmed when the A. hemsleyana and A. kolomikta ‘k’ rootstocks were compared in more detail a year later on 27 September (Fig. 6). Turgor was lower and xylem and leaf water potentials were usually more negative with the A. kolomikta ‘k’ rootstock, particularly in the mid-afternoon when transpiration was highest. By 15 October, after further shoot development, the A. hemsleyana rootstock continued to maintain relatively high leaf turgor and water potentials, whereas those for A. kolomikta ‘k’ decreased more during the day. On this date leaf turgor at midday was close to zero for the A. kolomikta ‘k’ rootstock (Fig. 6), and wilting of some leaves was observed.

Afternoon leaf turgor during spring growth was not correlated with root pressure recorded on the same afternoon (Fig. 7A), but was correlated with the average root pressure recorded over the five previous days (Fig. 7B). Therefore, shoot water status during transpiration was not related the level of xylem pressure maintained by the rootstock while transpiration was occurring, but was related to an average measure of pressure that is dominated by the maximum pressures achieved at night.

**Xylem solute potential**

The rise in xylem pressure associated with the onset of spring root pressure for each rootstock was not associated with a corresponding decrease in xylem sap solute potential (shown for the A. deliciosa stock only; Fig. 8). Sap solute potential was relatively constant for all the rootstocks over the period that xylem pressure increased and then fluctuated with the onset of vine transpiration. However, when comparing rootstocks, xylem pressure was correlated with sap solute potential, with rootstocks that developed higher root pressures having more negative xylem sap solute potentials (Fig. 9). For all rootstocks, root pressure was 0.06–0.08 MPa lower than the corresponding potential maximum osmotic pressure, as indicated by xylem sap solute potential (Fig. 9).

**Discussion**

This study shows that the effect of these Actinidia rootstocks on scion vigour is correlated with the spring root

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Fig. 5. Leaf ($\Psi_l$), xylem ($\Psi_x$) solute ($\Psi_s$), and turgor ($\Psi_p$) potentials for A. chinensis scion leaves growing on five Actinidia rootstocks at dawn (A) and 13.00 h (B) on 30 September 2003. At dawn, $\Psi_l$, and $\Psi_s$ were the same and there were no significant differences between rootstocks for any variable (ANOVA, $P > 0.05$). At 13.00 h there were significant differences between rootstocks for $\Psi_p$, $\Psi_x$, and $\Psi_s$ (ANOVA, $P < 0.05$). Error bars indicate Fisher’s Least Significant Differences for each parameter ($P < 0.05$, $n=3$ plants per rootstock); A. polygama and A. kolomikta (low vigour) were different from the other three rootstocks (high vigour, see Fig. 2 for explanation of vigour classes), but there were no differences within these two groups.
pressure phenology of each rootstock. High vigour rootstocks (*A. hemsleyana*, *A. macrosperma*, and *A. deliciosa*) developed high root pressure before or during scion budburst and the scion shoots were not water-stressed during spring growth. *A. eriantha* and *A. chrysantha*, examined in less detail, also developed root pressure during scion budburst and were classified as higher vigour rootstocks by Clearwater *et al.* (2006). Low vigour rootstocks (*A. polygama* and *A. kolomikta ‘k’*) developed root pressure after scion budburst and their scion shoots exhibited signs of water stress (more negative midday water potentials and low turgor). It is therefore likely that the effect on scion vigour was the result of a rootstock effect on scion water relations early in the growing season. Based on observations of root anatomy, Wang *et al.* (1994a) hypothesized that rootstock effects on *Actinidia* floral abortion were associated with root pressure and water availability from the roots in spring. Instead, an association was found between water supply and shoot vegetative growth which was not correlated with floral effects (discussed further below). A similar conclusion has been reached recently by another research group concerning the mechanism of vigour reduction by a peach rootstock (Basile *et al.*, 2003; Solari *et al.*, 2006). For this

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**Fig. 6.** Time-courses for xylem (\(\Psi_x\)), leaf (\(\Psi_l\)), solute (\(\Psi_s\)), and turgor (\(\Psi_p\)) potentials of leaves from the *Actinidia chinensis* scion growing on *A. hemsleyana* (high vigour, high root pressure) and *A. kolomikta ‘k’* (low vigour, low root pressure) rootstocks on 27 September and 15 October 2004 (\(n=3\) plants, 2 leaves per plant, ±1SE).
Actinidia system it is now relevant to ask what the role of root pressure might be for these plants, and what significance these results have for the understanding of rootstock effects in other horticultural crops.

The widely accepted view is that root pressure is an osmotic pressure resulting from the accumulation of solutes in the xylem of the roots, and that it is of minor functional significance (Kramer and Boyer, 1995). Root pressure has been shown to remove air emboli from xylem vessels of wild grapevines prior to leaf expansion in spring (Sperry et al., 1987). Given similarities in growth form and xylem anatomy, a similar refilling mechanism probably operates in kiwifruit (Clearwater and Clark, 2003). The roots of Actinidia and some other plant species are considered unusual because the cortex and endodermis, with intact suberin lamellae, are retained during secondary thickening (Lemon and Considine, 1993; Wang et al., 1994a). Casparian bands and suberin lamellae within endodermal cells act as barriers to the apoplastic movement of ions from the stele and therefore have an important role in the development of root pressure (Steudle and Peterson, 1998). The propensity with which Actinidia species develop root pressure may therefore be functionally linked to their unusual root anatomy. In the context of this study, the best explanation for the role of root pressure is that the onset of positive root pressure in spring was an indication of physiological activity in the roots, and the capacity (hydraulic conductance) of the roots to supply water to the shoots. Positive root pressure may also have enhanced stem hydraulic conductance through removal of air emboli (Sperry et al., 1987; Fisher et al., 1997). Increasingly negative daytime xylem pressures after budburst indicated that root pressure cannot

**Fig. 7.** Correlations between leaf turgor ($\Psi_L$) of the scion, measured on the afternoon of 30 September 2003 (Fig. 5) and root pressure recorded the same afternoon (left) or averaged over the five preceding days (right), for five Actinidia rootstocks ($n=3$, ±1SE).

**Fig. 8.** Xylem sap solute potential ($\Psi_s$) for the Actinidia deliciosa rootstock, measured during the spring rise in root pressure of 2003 ($n=1$ on the first sampling date when only one plant was exuding, $n=6$ on the later dates, ±1 SE).

**Fig. 9.** The relationship between xylem sap solute potential ($\Psi_s$) and root pressure measured on the same night that sap samples were collected (average pressure between midnight and 06.00 h), for five Actinidia rootstocks during the spring of 2003. Each point represents the average for a rootstock on a particular date (1 date for A. kolomikta ‘k’, four dates for the other rootstocks, $n=1$–6 plants per date). The dotted line indicates the 1:1 line where root pressure equals $\Psi_s$. 

support significant transpirational flow (Fig. 2). Daytime root pressure was not correlated with shoot water status and root pressure was not ‘lifting’ water to the shoots during transpiration (Fig. 7A). However, average (including nocturnal maximum) root pressure during this period was correlated with shoot water status, suggesting that root hydraulic conductance and transpiration rates were higher in plants that had higher nocturnal root pressures (Fig. 7B). Similarly, the complete lack of root pressure (day or night) in the low vigour rootstocks during shoot expansion was probably indicative of low root hydraulic conductance over the same period.

Whole plant hydraulic conductance measurements for these rootstock and scion combinations has previously been reported and, paradoxically, it was found that the low vigour rootstocks had higher whole-plant leaf-specific hydraulic conductance (conductance per unit leaf area) than high vigour rootstocks (Clearwater et al., 2004). However, those measurements were taken in November, after significant shoot expansion and after the date that root pressure was developed by the low-vigour rootstocks. A potential explanation is that the delayed onset of root activity (observed in this study), after leaf area has already been restricted by shoot termination, resulted in the higher ratio of root conductance to leaf area observed for the remainder of the season with the low-vigour rootstocks (Clearwater et al., 2004).

A similar scenario could apply to other horticultural crops for which attempts have been made to relate the effects of low vigour rootstocks to hydraulic conductance and water status. Basile et al. (2003) found that reduced growth on low vigour peach rootstock was related to low stem water potentials, and that the effects of rootstock on growth reduced as the season progressed. In studies of apple rootstock effects, water relations measurements have usually been made after shoot expansion when water potential measurements are more convenient (e.g. using a pressure chamber on mature leaves), leaf area is maximal, rates of transpiration are high, and sap flow measurements are possible (heat-based sap-flow measurements are inaccurate when sap velocity is very low; Olien and Lakso, 1986; Higgs and Jones, 1990; Cohen and Naor, 2002). The applicability of a phenology-based mechanism for rootstock effects on scion vigour depends on the shoot growth pattern of each crop. Shoot growth and termination commence before flowering in *Actinidia*; if leaf area is low and a large crop is set, the vine may have low vegetative vigour for the rest of the season. In many other crops, including apple, flowering precedes significant shoot growth. This mechanism may not explain the well-known dwarfing effect of the M9 series of apple rootstocks, but the results for kiwifruit (this study) and peach (Basile et al., 2003; Solari et al., 2006) suggest that temporal changes in root properties and spring water status effects should be considered.

What is happening in the roots during the period that root pressure first develops? The increase in root pressure may have been indicative of a change in the physiology of existing fine roots or the development of new roots. Root pressure is known to be responsive to the supply of mineral salts, particularly nitrates (Kramer and Boyer, 1995; Ewers et al., 2001), and exudation from kiwifruit vines increases when an excess of fertilizer is applied (CJ Clark, personal communication). The phenology of root growth for these *Actinidia* rootstocks is not known, although regular sampling of fine roots over the spring period did not suggest a flush of root growth coincident with the rise in pressure (data not shown). Detailed studies of root growth of the *A. deliciosa* rootstock have previously failed to detect a discrete growth flush in spring (Buwalda and Hutton, 1988; Reid et al., 1993; Reid and Bowden, 1995). In this study, the rise in root pressure for an individual genotype did not correspond with any clear change in xylem sap osmolarity (assuming stem-collected samples are representative of root sap osmolarity), indicating that either a simple osmotic mechanism did not apply (Enns et al., 2000; Pickard, 2003), or that a change in root solute permeability (the reflection coefficient) may have been more important than a change in solute concentration (Steudle, 2000). The solute potential of the external soil solution was unknown, but provided it was above \(-0.06\) MPa to \(-0.08\) MPa then the measured sap solute potentials were high enough for the observed pressures to be explained by an osmotic mechanism (Fig. 9). Differences in root pressure between genotypes were correlated with differences in sap osmotic mechanism, suggesting that differences in solute transport behaviour contributed to differences between rootstocks.

This study does not demonstrate a direct causal link between water supply to the shoots and spring growth, although it is well known that in many plant species even moderate water stress can cause immediate reductions in shoot growth (Kramer and Boyer, 1995). Solari et al. (2006) manipulated peach stem water potential directly and concluded that there was a causal link between rootstock effects on water status and shoot extension growth. The shoot water potentials and turgor of the low root pressure kiwifruit plants recovered at night when transpiration was low. There were no differences in osmotic potential of hydrated shoots at dawn, suggesting that osmotic adjustment had not occurred. Shoot growth and termination may have been directly affected by reduced daytime turgor and changes in water potential gradients, or indirectly affected by changes in the carbon balance of developing shoots. Imposition of water stress on kiwifruit by drying soil causes reduced leaf area and stomatal conductance (Miller et al., 1998), both of which may reduce photosynthesis and therefore delay the transition from reliance on stored reserves to autotrophic shoot growth (Greer et al., 2003).
From these results the possibility that the higher scion vigour of the early root pressure plants is the result of earlier, more extensive mobilization of carbohydrates or minerals stored or absorbed by the roots cannot be excluded. However, flower numbers per shoot of the _Actinidia chinenis_ scion were not reduced by the low-vigour rootstocks (Clearwater et al., 2004), even though kiwifruit flower development is known to be sensitive to carbohydrate reserve availability in spring (Grant and Ryugo, 1982; Snelgar et al., 1992). Wang et al. (1994b) identified rootstocks (including the _A. hemsleyana_ clone used in this study) that reduced floral abortion during early shoot growth of commercial green kiwifruit scion (_A. delicosa_ var. _deliciosa_ ‘Hayward’), but effects on flowering in their study were not associated with differences in scion vegetative growth. The effects of rootstocks on _Actinidia_ scion vigour in spring may therefore be independent of effects on flowering. Supply of minerals from the roots may also be unimportant for initial shoot growth of kiwifruit, because _15N_-labelled nitrogen applied to the soil before budburst is not detected in expanding _A. delicosa_ shoots until 3–4 weeks after shoot growth commences (Ledgard and Smith, 1992; Clark and Ledgard, 1993), later than the time that shoot growth was reduced by low-vigour rootstocks in this study. Both observations suggest that the availability of carbohydrates and minerals from the roots are not the cause of early differences in scion shoot growth between rootstocks. It is proposed that reduced water availability in spring causes a reduction in growth on low-vigour rootstocks, followed by associated effects on carbohydrate and mineral availability to the expanding shoots.

The timing of root pressure development of grafted rootstocks was similar to that of the ungrafted parent plants, although budburst usually began 10–20 d later in the ungrafted plant. Robust comparisons are difficult because only one parent plant was available for each genotype, they were growing in a different location, and they received less intensive management than the rootstock trial. However, root pressure timing was not clearly related to the timing of shoot growth of the parent plant. The phenology of shoot growth therefore does not appear to be a useful indication of root phenology when screening potential rootstock cultivars. The temporal mismatch between shoot and root activity may be related to differences between the maritime climate of New Zealand where this study was conducted and that of continental east Asia where the plants were originally sourced.

Differences in phenology between the roots and shoots appear to be responsible for some of the effects of these _Actinidia_ rootstocks on shoot vigour. A similar mechanism could be important for rootstock–scion combinations used in other crop species, although the importance of a discrete seasonal change in root properties may not be obvious in crops that do not develop root pressure in spring. Further research is needed to understand how root physiology changes over the period that root pressure develops, to understand the interactions between root and shoot phenology, and to exploit these interactions in the selection of new rootstock cultivars.

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References


