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Vigour reduction in girdled peach trees is related to lower midday stem water potentials

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Abstract. Stem or trunk girdling is a technique used in physiological studies and in horticultural practice for interrupting carbon flow through the phloem to other parts of the plant without influencing water flow in the xylem. Trunk girdling in peaches is practiced primarily to stimulate fruit growth but it also tends to decrease shoot vigour for a period of time after girdling. Water flow through the trunk or branches of peach trees is thought to be primarily dependent on the most recently formed ring of xylem and vegetative growth is closely related to stem water potential and stem hydraulic conductance. The aim of the present work was to determine whether vigour reduction due to girdling was correlated with a reduction in midday stem water potential during the period of time between girdling and the subsequent healing of stem tissue. 'Springcrest' peach trees were girdled on two different dates. Fruit yield and size, water sprout growth, proleptic shoot growth and stem water potential were measured. Early and late girdled trees yielded larger fruits and fewer and shorter water sprouts in comparison with control trees. Midday stem water potential declined significantly after girdling and gradually recovered until the time of fruit harvest. These results suggest that the vigour reduction of girdled trees is related to a decrease of midday stem water potential caused by girdling. Early tree girdling increased the reduction in midday stem water potential and shoot growth compared with the later girdling treatment. These results point out that even though girdling only removes bark and phloem tissue it can apparently affect water flow in xylem.

Additional keywords: girdling, peach tree, shoot growth, stem water potential.

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Introduction

Girdling consists in the removal of a ring of bark down to the vascular cambium, which stops the phloem flow of photosynthates to the root and other parts of the plant until the wound heals (Jordan and Habib 1996). Girdling is commonly used in some horticultural tree crops for increasing fruit size and accelerating fruit ripening (Weinburger and Cullinan 1932; Lilleland and Brown 1936; Crane and Campbell 1957; Lewis and McCarty 1973; Winkler *et al*. 1974; Powell and Cash Howell 1985; Fernandez-Escobar *et al*. 1987; Augusti *et al*. 1998; Day and DeJong 1999). Stem girdling is also a technique used in physiological experiments primarily to manipulate source–sink relationships (carbohydrate distribution within plants) and to study phloem–xylem interactions (Fishman *et al*. 2001; Wilson and Gartner 2002; Zwieniecki *et al*. 2004; Salleo *et al*. 2006; Morandi *et al*. 2007; Domec and Pruyn 2008).

Girdling is usually thought to influence only phloem flow and carbon balance (De Schepper and Steppe 2011). It causes an accumulation of carbohydrates and a depletion of mineral elements in the organs above the girdle (Day and DeJong 1990; Jordan and Habib 1996; Di Vaio *et al*. 2001) and a strong limitation of photosynthesis and transpiration has been observed in girdled shoots of different species (Schaffer *et al*. 1987; Roper and Williams 1989; Schechter *et al*. 1994; Di Vaio *et al*. 2001; Iglesias *et al*. 2002; Domec and Pruyn 2008; Wu *et al*. 2008; Sellin *et al*. 2013).

However, in *Prunus persica* (L.) as well as in other tree species, girdling causes a reduction of tree vegetative growth in comparison with control trees (Fernandez-Escobar *et al*. 1987; Day and DeJong 1990; De Villers *et al*. 1990; Di Vaio *et al*. 2001; Wilson and Gartner 2002). Furthermore, the timing of girdling affects shoot growth as well as fruit size (Day and DeJong 1990). Although an increase in fruit growth/size can be explained by greater availability of carbohydrates above a girdle, a decrease in shoot growth in the same part of the tree is more difficult to explain.

Shoot growth in peach has been correlated with cumulative water potential differences during the first half of a growing season (Basile *et al*. 2003). Stem water potential is correlated with stem hydraulic conductance (Tyree and Sperry 1988). Hydraulic conductance is mainly supported by the most external layers of the xylem tissue and in species with ring porous xylem the most recently formed girth growth accounts for a major amount of hydraulic conductance (Ellmore and Ewers 1985; Ameglio *et al.* 2002; Atkinson *et al.* 2003). If hydraulic conductance in trunks of peach trees is mainly dependent on the newly formed ring of xylem in the spring, then trunk girdling should cause a decrease in midday stem water potential for a period after girdling until the girdle heals and xylem development is resumed. Furthermore, girdling earlier in the spring should have a stronger effect on midday stem water potentials than girdling at a later date.

The aim of the present work was to determine whether vigour reduction due to girdling was correlated with a reduction in midday stem water potential during the period of time between girdling and the subsequent healing of stem tissue.

Materials and methods

Plant material

The experiment was conducted in 2010 in an experimental orchard at the University of California Kearney Agricultural Centre, Parlier, CA, USA. Trees used for the experiment were of 'Springcrest' peach grafted on 'Nemaguard' rootstock. All trees were 8 years old, trained to a perpendicular V (DeJong *et al.* 1994) and received normal horticultural care.

Treatments and experimental design

Two girdling treatments (removal of a ring of bark with a 6 mm double-bladed girdling knife) were conducted at the base of the two main scaffolds; the first one (early girdling) was conducted on 31 March; the second one (late girdling) was conducted on 15 April. A randomised block design with five replicates and with single tree plots was used to compare three treatments, namely early girdling, late girdling and an ungirdled control, using 15 trees in all. Midday stem water potential was measured every ~2 weeks on mature leaves that were enclosed in aluminium foiled plastic bags in the morning at least 2 h prior the measurements (McCutchan and Shackel 1992). Measurements were made with a pressure chamber (Soilmoisture Corp, Santa Barbara, CA, USA). From the date of girdling up to harvest, shoot length and number of nodes per shoot were measured on the same days as water potential measurements on three well exposed epicormic shoots (water sprouts) per tree located at breast height. All shoots were tagged on the date of the first girdling treatment, 31 March. Fruit harvest occurred on three dates: 27 May, 1 and 4 June. Harvested fruits were counted and sized into 10 size classes. On 10 June all epicormic shoots on each tree were harvested, weighed and divided into five length classes (0–40, 40–80, 80–120, 120–160 and 160–200 cm).

Statistical analysis

Statistical analyses of the data were performed with SAS statistical software (SAS Institute, Cary, NC, USA). Treatments were analysed by one-way ANOVA with significance level set at 0.05, according to the ANOVA assumptions regarding the normality of distribution (Shapiro and Wilk 1965). Independence (Durbin and Watson 1951) and homogeneity of variance (Levene 1960) were also checked. Means were separated by Tukey's w-procedure at $P = 0.05$. Regressions were performed by Sigmaplot 8.0 (Systat Software Inc., San Jose, CA, USA) and R^2 significance was assessed by ANOVA.

Results

Early and late girdling increased the fruit size in comparison with fruits on control trees (Fig. 1). The total number of harvested fruits per tree was similar across the three treatments (early girdling 138.2 ± 19.25, late girdling 135 ± 14.60, control 129.2 ± 13.45). Early and late girdled trees yielded significantly more fruit in the largest fruit size classes (7, 8 and 9) than control trees whereas control trees yielded significantly more fruits in the smallest fruit size classes (1–5) than girdled trees. There were no significant differences between the two girdling treatments with respect to fruit size. Tree yield was similar in girdling treatments (early girdling 16.1 ± 1.2 kg tree^{-1}, late girdling 16.9 ± 1.4 kg tree^{-1}) but was significantly less in control trees (12.1 ± 1.8 kg tree^{-1}) ($P < 0.05$). A significantly larger percentage of fruits were harvested in the first pick from girdled trees in comparison with control trees (Fig. 2). The opposite occurred in the last pick whereas there were no significant differences in the second pick. Girdled trees had significantly fewer and shorter epicormic shoots than control trees (Fig. 3; Table 1). Early girdled trees had slightly fewer and shorter epicormic shoots than late girdled trees, but the differences were not significant. The number of nodes on tagged epicormic shoots increased over the course of the study but did not significantly vary across treatments (Fig. 4). Shoots of girdled trees tagged before treatments grew less than shoots in control trees (Fig. 5). In particular, in early girdled trees shoots grew significantly less than shoots of late girdled and control trees up to the late girdling treatment date. Later on, until the end of the experiment, shoots of early girdled trees grew significantly less than shoots of control trees and slightly less, though not statistically significant, than shoots of late girdled trees that reached a length intermediate between the other two treatments. Midday stem water potential decreased

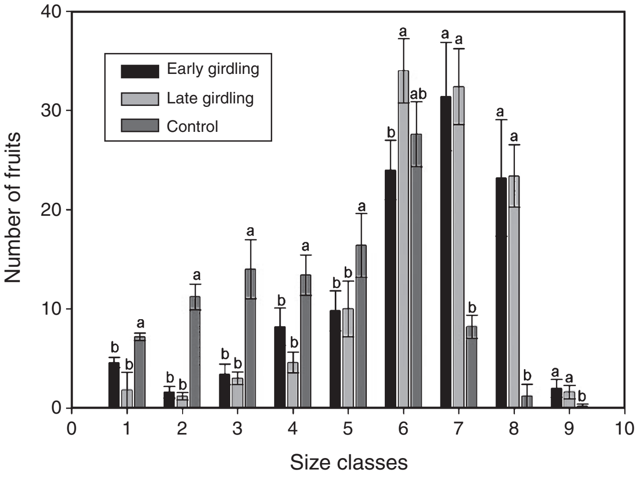

Fig. 1. Fruit size of early girdled, late girdled and control 'Springcrest' peach trees. Each value is the mean of five trees ($n = 5$) ± s.e. Bars with different letters are different at $P < 0.05$ (Tukey's test). Mean fruit fresh weights per each class were: Class 1, 81 g; Class 2, 94 g; Class 3, 100 g; Class 4, 112 g; Class 5, 122 g; Class 6, 140.6 g; Class 7, 160.6 g; Class 8, 186.5 g; Class 9, 210 g.

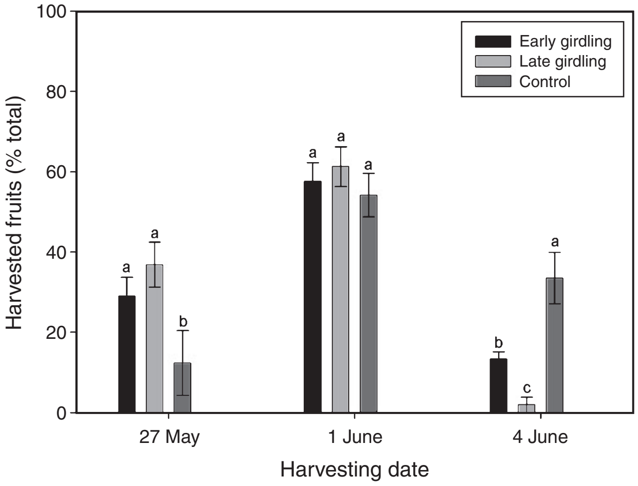

Fig. 2. Percentage of fruit harvested at the three harvesting times in early girdled, late girdled and control 'Springcrest' peach trees. Each bar is the mean of five trees ($n = 5$) ± s.e. Bars with different letters are different at $P < 0.05$ (Tukey's test).

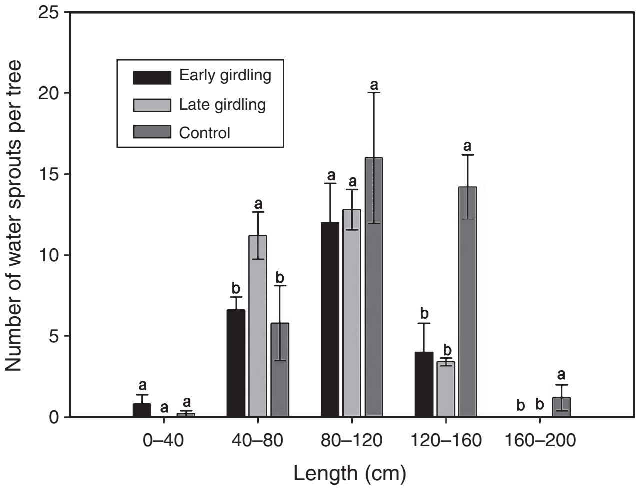

Fig. 3. Epicormic shoot distribution in length classes of early girdled, late girdled and control 'Springcrest' peach trees. Each bar is the mean of five trees ($n = 5$) ± s.e. Bars with different letters are different at $P < 0.05$ (Tukey's test).

Table 1. Epicormic shoot FW per tree and number per tree in early girdled, late girdled and control 'Springcrest' peach trees

Mean of five trees ($n = 5$) ± s.e. Values with different letters are different at $P < 0.05$ (Tukey's test)

	Water sprouts FW (kg)	No of water sprouts/tree
Early girdling	2.5 ± 0.6b	23.4 ± 2.8b
Late girdling	3.2 ± 0.6b	27.4 ± 1.9b
Control	4.9 ± 0.4a	37.4 ± 4.7a

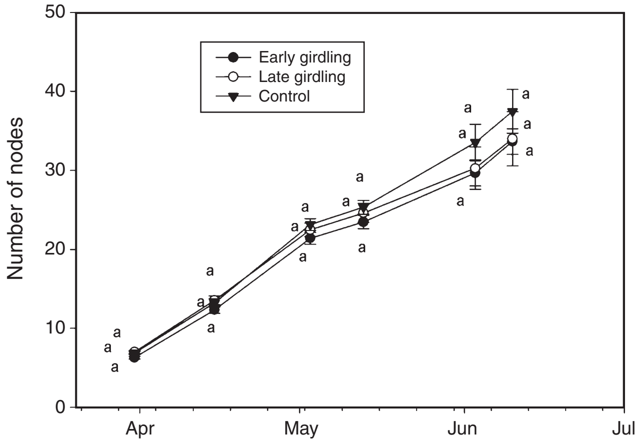

Fig. 4. Number of nodes during shoot growth of selected shoots on early girdled, late girdled and control 'Springcrest' peach trees. Each value is the mean of five trees ($n = 5$) ± s.e. Points with different letters are different at $P < 0.05$ (Tukey's test).

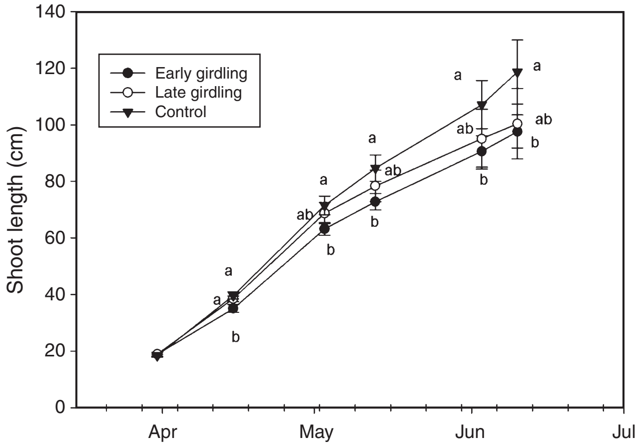

Fig. 5. Shoot elongation of selected epicormic shoots on early girdled, late girdled and control 'Springcrest' peach trees. Each value is the mean of five trees ($n = 5$) ± s.e. Points with different letters are different at $P < 0.05$ (Tukey's test).

as consequence of girdling in both girdling treatments as compared with the control (Fig. 6). In particular, after girdling, early girdled trees had significantly lower stem water potential in comparison with the other two treatments. Late girdling treatment decreased midday stem water potential but the values were intermediate between those of control and early girdled trees. Furthermore, in the two last measurements of the experiment, there was no significant difference in midday stem water potential of late girdled trees and control trees. In both treatments a progressive recovery of stem water potential was observed one month after girdling. Mean lengths of the tagged epicormic shoots on individual trees at the end of the experiment were linearly correlated with the mean stem water potentials measured on the same trees over the experiment period ($R^2 = 0.76$, $P < 0.001$) (Fig. 7).

Discussion

Consistent with numerous previous experiments reported on peach and other horticultural species the girdling treatments

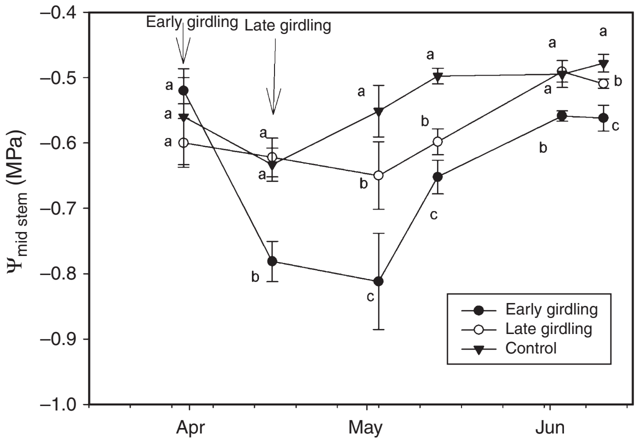

Fig. 6. Midday stem water potentials of early girdled, late girdled and control 'Springcrest' peach trees. Each value is the mean of five trees ($n = 5$) ± s.e. Points with different letters are different at $P < 0.05$ (Tukey's test).

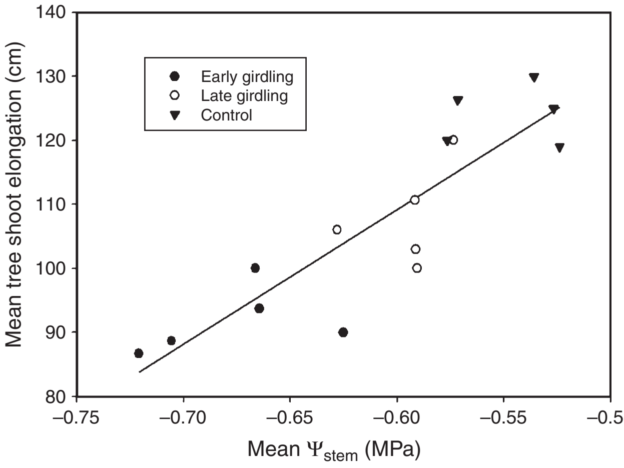

Fig. 7. Relationship between mean midday stem water potential during the experiment (71 days) and mean tagged shoot length in early girdled, late girdled and control 'Springcrest' peach trees. Each value is the mean of the three selected epicormic shoots and three Ψ_{stem} measurements. $R^2 = 0.76$, $P < 0.001$ (ANOVA).

increased fruit size and accelerated fruit ripening (Weinburger and Cullinan 1932; Lilleland and Brown 1936; Crane and Campbell 1957; Lewis and McCarty 1973; Winkler *et al.* 1974; Powell and Cash Howell 1985; Fernandez-Escobar *et al.* 1987; Augusti *et al.* 1998; Day and DeJong 1999).

Contrary to effects on fruit growth, water sprout shoot production and growth were reduced more in girdled trees than control trees, and early girdling was more effective on shoot growth than the late girdling treatment. These results are also consistent with those previously reported on peach and other species (Day and DeJong 1990; Choi *et al.* 2010). Since previous research has also reported increased starch content in leaves, bark and wood subsequent to girdling (Jordan and Habib 1996; Cheng *et al.* 2008; Cimò *et al.* 2013) and the presence of fruits did not limit shoot growth on individual girdled peach shoots (Bussi *et al.* 2009), it is unlikely that shoot growth was limited by fruit competition for carbohydrates in this study.

Contrary to conventional wisdom about girdling primarily interrupting carbohydrate flow in phloem and having minimal influence on water flow in xylem, several recent studies have shown an effect of stem girdling on both xylem and leaf hydraulic conductance with considerable consequences on long-distance water transport. In our experiment (Zwieniecki *et al.* 2000, 2004; Sellin *et al.* 2013), the stem water potential data clearly indicated that early girdling significantly affect water flow in xylem. The midday stem water potential in girdled trees decreased significantly after girdling until fruit harvest. Consistent with previous research with peach, the decreases in midday stem water potential strongly influenced shoot growth (Berman and DeJong 1997; Weibel *et al.* 2003; Solari *et al.* 2006*a*; Solari and DeJong 2006; Tombesi *et al.* 2011, 2012), and in this experiment mean midday stem water potential during the experiment was correlated with shoot growth. Leaf transpiration has been reported to decrease after fruit harvest (Day and DeJong 1990; Wu *et al.* 2008) and this may have also tended to increase stem water potential of shoots after harvest. However, the earlier decreases in stem water potential suggest a cause–effect relationship between the girdling treatments and decreases in midday stem water potential. Midday stem water potential appeared to recover gradually until the time of fruit harvest, presumably because of the wound healing that occurred after girdling and the elimination of fruits at harvest.

Stem or trunk girdling is not generally thought to have significant effects on the upward movement of water in xylem (Noel 1970) but specific experiments indicate that the picture is quite complicated. In experiments with *Populus* spp., *Acer rubrum* and *Acer saccarum*, girdling was found to cause short-term reductions in hydraulic conductance (Zwieniecki *et al.* 2000, 2004; Sellin *et al.* 2013). Zwieniecki *et al.* (2004) attributed xylem conductance reduction caused by girdling in *Acer* spp. to a decrease in xylem ion concentration caused by reduced ion transport between the phloem and xylem. In contrast, Domec and Pruyn (2008) reported less negative stem water potential in girdled *Pinus ponderosa* trees in comparison with control trees. Such stem water potential patterns in *P. ponderosa* and *Populus* spp. have been attributed to reduced leaf transpiration in girdled trees (Domec and Pruyn 2008; Sellin *et al.* 2013). In previous experiments with girdled peach (*P. persica*) trees there were no differences in stomatal conductance between girdled trees and control trees except when measured 15 days after fruit harvest (Day and DeJong 1990). Wu *et al.* (2008) reported that transpiration, stomatal conductance and net photosynthesis rates were correlated with fruit presence above the girdle. Thus, girdled trees suffered gas exchange limitations because of limited sink availability (Paul and Foyer 2001; Wu *et al.* 2008). In horticultural species, fruits are among the largest carbon sinks and can contribute to overcome the gas exchange limitations that, in the experiments reported by Sellin *et al.* (2013) and Domec and Pruyn (2008), apparently caused stomatal closure in girdled trees and consequent increases in stem water potential. When gas exchange is not limited by stomatal closure due to sink limitation, stem water potential is correlated with stem hydraulic conductance that is a function of the conductive portion of xylem tissue (Tyree and Sperry 1988; Solari *et al*. 2006*b*).

Early girdling studies indicated that leaves of trees with diffuse porous xylem structure maintained their turgor after 'notch' girdling but trees with ring porous xylem structure were killed by the same treatment (Richardson 1896). Furthermore, Siminovitch and Briggs (1953) reported that girdling of *Robinia pseudo-acacia* trees (a ring porous species) had little apparent effect on upward water transport if the girdling was done in August or later (after new xylem was well developed) but the tops of trees rapidly showed signs of 'water starvation' if the girdling was done before July. This is consistent with the results of the current study and the concept that, in ring porous species, girdling interrupts the development of early spring xylem in the region of the girdle and results in a period during which xylem water transport cannot keep pace with transpiration and causes decreased midday stem water potentials. In deciduous tree species with ring porous xylem, the outermost part of the xylem tissue is the most conductive and in some species the outermost layer of girth growth accounts for nearly 90% of hydraulic conductance (Ellmore and Ewers 1985). In peach, spring shoot elongation is dependent on cambium reactivation that leads to the formation of conductive xylem tissue (Ameglio *et al*. 2002). Trunk girdling removes a ring of cambium and disrupts the activity of the cambium as well as retard the formation of new xylem (Noel 1970), and the possibility that it can also favour the diffusion of air into mature vessels under high evaporative demand and strong tension in the xylem cannot be totally discounted. Thus, if girdling is conducted in early spring it would coincide with the natural period of maximum girth growth and relative shoot growth. In the present experiment this was associated with a clear reduction in midday stem water potential. A reduction of shoot growth also occurred shortly after girdling and likely was caused by a decreased hydraulic conductance that resulted in reductions in stem water potential during the healing period subsequent to girdling until new xylem tissue developed and hydraulic conductance capacity was restored.

An alternative explanation for the reduction in stem water potential and shoot growth in response to scaffold girdling observed in this experiment is related to a possible transitory effect of girdling on root activity or conductance caused by the blockage of assimilate transport coming from the canopy because of the removal of phloem tissue by the girdling. However, if that was the case, one might expect the pattern of stem water reduction to be more gradual right after girdling, and it would be difficult to explain why girdling at a later date had less effect than girdling earlier in the season. Nevertheless, it is not possible to rule out this hypothesis until further studies of girdling on root growth and activity are conducted.

Both the early and late girdling limited epicormic shoot extension growth but did not appear to influence the shoot plastochron. Thus, shoot internode length was more affected than the number of nodes per shoot. These results are similar to those obtained on scions grafted on dwarfing rootstocks; in comparison with invigorating rootstocks. Dwarfing rootstocks caused the reduction of shoot length but did not reduce the number of shoot nodes (Weibel *et al*. 2003). As in the case of dwarfing rootstocks, in our experiment girdled trees had consistently lower midday stem water potential than control trees (Solari *et al*. 2006*a*).

In conclusion, our results are consistent with the hypothesis that girdling affected not only carbon transport, but also xylem water transport as exemplified by midday stem water potential reductions that occurred until cambium integrity had time to recover and form new xylem tissue. The earlier the tree was girdled, the larger the reduction in midday stem water potential and the stronger the effect on shoot growth.

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