

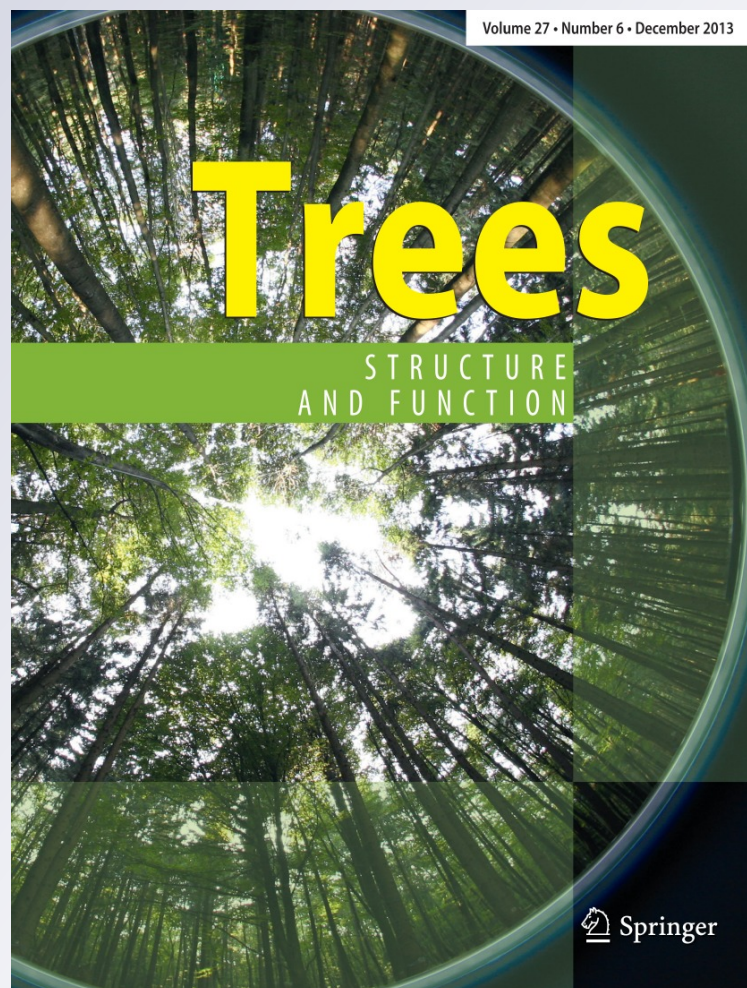
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**Trees**  
Structure and Function

ISSN 0931-1890  
Volume 27  
Number 6

Trees (2013) 27:1559-1569  
DOI 10.1007/s00468-013-0904-y



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# Leaf and stem hydraulic traits in relation to growth, water use and fruit yield in *Prunus avium* L. cultivars

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Received: 17 December 2012 / Revised: 16 June 2013 / Accepted: 2 July 2013 / Published online: 18 July 2013  
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**Abstract** Physio-anatomical traits of rootstock have been considered as determinants of vigor in grafted plants. We evaluated how hydraulic traits of three *Prunus avium* cultivars grown on the same rootstock are related to tree growth and patterns of biomass allocation between vegetative and reproductive parts as well as total water consumption to determine how water, as a limiting resource for agriculture, might be optimized by choosing appropriate cultivars that are at the same time the most successful from the point of view of fruit production. Bing, Lapins and Van cultivars growing under field- and well-irrigated conditions were selected. Leaf and stem hydraulic conductance ( $K_{\text{Leaf}}$  and  $k_S$ ), leaf vulnerability to cavitation, water relations traits, water use and assimilation and growth rates as well as fruit yield were measured. The cultivar with high leaf vulnerability to cavitation and low  $k_S$  and sap flow (Lapins) had low vegetative growth, but larger fruit production compared to the cultivars with higher  $k_S$ , resistance to cavitation and water use (Bing and

Van). As leaf water potential and  $k_S$  were lower and leaves appeared to be embolized in the cultivar that had lower carbon allocation to vegetative organs during the reproductive period (Lapins), we hypothesize that water instead of moving into the leaves is delivered to the fruits, representing the main sink for water transport. It is possible that increases in the dysfunction of the hydraulic system in the most vulnerable cultivars to cavitation during the reproduction stage (Lapins) may represent a signal for enhancing the delivery of water to fruits. This information related to optimization of crop water use in relation to yield can be useful for selecting cultivars with high yield and low water use. This study also shows that physiological traits of the scions substantially affect growth patterns, fruit production and water relation of the plants.

**Keywords** Assimilation rate · Fruit production · Hydraulic efficiency · Sap flow · Sweet cherry · Vulnerability to cavitation

Communicated by M. A. Zwieniecki.

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## Introduction

Gas exchange rate, growth and productivity of plants are largely determined by their hydraulic efficiency (Ryan and Yoder 1997; Sperry 2000; Tyree 2003) as well as by the vulnerability of xylem to cavitation (Tyree and Sperry 1989; Salleo et al. 2000) that affects the water supply to leaves and consequently their water status. Even under conditions of high soil water availability, the xylem's capacity to withstand the tension developed by atmospheric demands may not be enough to avoid the drop of water potential to threshold values at which there is stomatal closure with the concomitant cost of reduced CO<sub>2</sub> uptake. The effects of relative low hydraulic efficiency on tree

growth through changes in leaf water potential and gas exchange have been observed in several tree species (Tyree et al. 1998; Willingen and Pammenter 1998; Nardini and Tyree 1999; Sperry 2000; Meinzer 2002; Atkinson et al. 2003; Solari et al. 2006a, b). Nevertheless, vegetative growth is not only limited by physiological traits or environmental factors. For example, in fruit trees, vegetative growth is strongly affected by competition with reproductive sinks (Forshey and Elfving 1989; Wardlaw 1990), such that seasonal growth of stems, leaves and trunk is reduced as fruit load increases (Miller and Walsh 1988; Blanco et al. 1995; Grossman and DeJong 1995) and the amount of carbohydrates available for vegetative growth is reduced (Grossman and DeJong 1995).

Reproductive sinks can also have a role on leaf water potentials, as water and assimilates are translocated to the flowers and fruits via phloem and xylem. In some tree species, the xylem water inflow to the fruits is greatly reduced when fruits are fully developed and consequently fruit growth is the result of the phloem stream of carbohydrates. This reduction of water movement from the plant to the fruits has been functionally related to xylem dysfunction that decouples fruit water relations from the water status of the parent plant (Bondada et al. 2005; Keller et al. 2006; Dražeta et al. 2001, 2004).

The improvement in fruit production depends on the identification of genetic material and plant characteristics favoring fruit production, as well as selecting cultivars that minimize vegetative growth and maximize carbon allocation to reproduction with high resistance to drought and low water use. Populations and cultivars of the same crop may have different morphological and physiological traits, even when grown under similar environmental conditions, due to genetic differences. In grafted fruit trees, it is generally assumed that the rootstock traits determine the water relations and hydraulic traits and finally the scion vigor (Olien and Lakso 1986; Basile et al. 2003a; Atkinson et al. 2003; Clearwater et al. 2004; Gonçalves et al. 2006; Trifilò et al. 2007). On the other hand, some studies have found that the rootstock genotype affects leaf gas exchange, water relations, hydraulic architecture and fluorescence kinetic, while cultivar genotype affects more the morphological and chemical traits of leaves (Gonçalves et al. 2006, 2007).

*Prunus avium* has been found in archeological sites throughout Europe since the Stone Age and consequently this species has a long history of domestication for fruit production. However to our knowledge, there are no studies evaluating hydraulic traits and water relations in cultivars of *P. avium* grafted on the same rootstock. Our objective was to study stem and leaf hydraulic characteristics, water relations, growth and yield of cultivars of *P. avium* L. grafted on *P. domestica* rootstock growing under similar environmental conditions in the field to

determine (a) if there was variability in these traits between cultivars and (b) which cultivar would be the most successful from the point of view of fruit production. Our hypothesis is that the studied cultivars exhibit different morphological and physiological traits despite growing on the same rootstock, and that the cultivar with low hydraulic efficiency and leaf water potential exhibits low carbon allocation to vegetative organs and relatively low water consumption, but high fruit yield. It is possible that increases in the dysfunction of the hydraulic system in the most vulnerable cultivar to cavitation during the reproduction stage may represent a signal for enhancing the delivery of water to fruits. In this study, we apply advanced physiological techniques to an agricultural system to understand how water, as a limiting resource for agriculture, might be optimized by choosing appropriate cultivars while not reducing yield.

## Materials and methods

### Study site and plant material

The study was conducted between February and March of 2010 in El Porvenir Ranch in Los Antiguos Valley, northwest of Santa Cruz province, Argentina (46°19'S, 71°62'W, 220 m a.s.l.). The climate of this valley is relatively mild compared to the surrounding semiarid areas, which is influenced both by the proximity of the Buenos Aires Lake, the second largest lake in South America, and by air currents from the Pacific Ocean. Mean monthly temperatures range from 2.5 to 14.9 °C and the average annual precipitation is about 192 mm, falling mostly in the fall and winter (April–September) (San Martino and Manavella 2004).

Three sweet cherry cultivars (*P. avium* L.) were selected for the study: Lapins, Bing and Van. These cultivars are the most commonly used for fruit production in Southern Patagonia, representing 28.9, 23.7 and 4.8 % of the cultivars, respectively (Cittadini 2007). For comparative studies, three to six individuals of similar size per cultivar were chosen. The diameter, height and leaf size of each cultivar are shown in Table 1. All the trees were older than 7 years, grown on a rootstock of *P. domestica*, planted as free standing trees (280 trees ha<sup>-1</sup>) and irrigated by gravity (Muñoz 2004). The trees were fertilized and irrigated to ensure non-limited nutrients and adequate soil water availability, and were not pruned during the study.

### Leaf water potential and pressure–volume curves

Leaf water potential ( $\Psi_l$ ) was measured with a pressure chamber (PMS; Corvallis, OR, USA) on three different

**Table 1** Tree diameter and height, leaf size, leaf osmotic potential at zero turgor ( $\pi^0$ ), stomatal conductance ( $g_s$ ), net photosynthesis ( $A$ ) and specific leaf area (SLA) in three *Prunus avium* L. cultivars

	Bing	Lapins	Van
Diameter (cm)	33.8 ± 5.7 <sup>a</sup>	15.2 ± 11.9 <sup>b</sup>	23.0 ± 2.5 <sup>c</sup>
Height (cm)	387.5 ± 4.8	320.0 ± 39.1	382.5 ± 10.3
Leaf size (cm <sup>2</sup> )	66.7 ± 5.9 <sup>a</sup>	51.7 ± 8.5 <sup>ab</sup>	45.1 ± 3.0 <sup>b</sup>
$\pi^0$ (MPa)	−2.24 ± 0.17	−2.71 ± 0.16	−2.58 ± 0.14
$g_s$ (mmol m <sup>−2</sup> s <sup>−1</sup> )	174 ± 39	181 ± 28	123 ± 19
$A$ (μmol m <sup>−2</sup> s <sup>−1</sup> )	13.8 ± 1.4 <sup>a</sup>	14.0 ± 1.4 <sup>a</sup>	10.4 ± 1.1 <sup>b</sup>
SLA (cm <sup>2</sup> g <sup>−1</sup> )	103.57 ± 6.72 <sup>a</sup>	126.72 ± 7.26 <sup>b</sup>	133.12 ± 6.06 <sup>b</sup>

Values are mean ± SE ( $n = 5$ ). Different letters within a column indicate a significant difference ( $P < 0.05$ )

sun-exposed and fully developed leaves per tree ( $n = 3–6$ ). Leaf samples collected prior to dawn (before 0700 h;  $\Psi_{pd}$ ) and midday (1200 h;  $\Psi_{min}$ ) were immediately sealed in plastic bags upon excision and kept in a cooler until balancing pressures were obtained in the laboratory.

Pressure–volume (P–V) curves were determined in fully developed exposed leaves from each cultivar during February 2010. The leaves were cut at the base of the petiole in the field, re-cut immediately under water and the entire leaves covered with black plastic bags with the cut end in water for 2 h until measurements. After each determination of balancing pressure, the leaves were immediately weighed to the nearest 0.001 g, and between readings left to transpire freely on the laboratory bench. After all balancing pressure–weight measurements were obtained, the branches were oven dried at 70 °C to a constant mass and weighed (Tyree and Richter 1981). Pressure readings, fresh mass at each reading, saturated mass and dry mass for each leaf were entered into a pressure–volume relationship analysis program developed by Schulte and Hinckley (1985). The P–V curves were used to calculate leaf osmotic potential at zero turgor ( $\pi^0$ ) and leaf capacitance ( $C_{Leaf}$ ) following Hinckley et al. (1980). The leaf capacitance was calculated as the slope of the relationship between relative water content (RWC) and leaf water potential ( $\Psi_1$ ) and it was multiplied by the saturated mass of water in the leaf and then divided by leaf area. In practice, the ratios of leaf dry weight:leaf area and saturated mass of water:leaf dry weight were determined for each cultivar and used to calculate the leaf area normalized absolute capacitance:

$$C_{Leaf} = \delta RWC / \delta \Psi_1 \times (DW/LA) \times (WW/DW) / M$$

( $C_{Leaf}$  = area normalized leaf capacitance;  $\Psi_1$  = water potential; DW = leaf dry weight (g); LA = leaf area (m<sup>2</sup>); WW = mass of leaf water at 100 % RWC (g);  $M$  = molar mass of H<sub>2</sub>O (g mol<sup>−1</sup>) (Brodribb and Holbrook 2003, 2004).

#### Wood density and saturated water content

Wood density ( $\rho_w$ ) was measured on 14–15 terminal branches from four to five trees per cultivar. After removal of bark and pith,  $\rho$  was calculated as:  $\rho = M/V$ , where  $M$  is the dry mass of the sample (oven dried at 70 °C for 72 h) and  $V$  is the sample volume. Volume was estimated by submerging a fresh sample in a container with distilled water resting on a digital balance with a 0.001 g precision. Saturated water content was determined as the ratio between saturated mass minus dry mass, and dry mass.

#### Leaf hydraulic conductance

Leaf hydraulic conductance  $K_{Leaf}$  was measured at pre-dawn according to Brodribb and Holbrook (2003).

The measurement is based on the analogy between rehydration of desiccated leaves and charging of a capacitor through a resistor as follows:

$$K_{Leaf} = C \ln(\Psi_0 / \Psi_f) / t$$

where  $C$  is leaf capacitance,  $\Psi_0$  is leaf water potential before rehydration and  $\Psi_f$  is leaf water potential after rehydration for  $t$  seconds.

Leaf vulnerability curves of each cultivar were obtained by measuring  $K_{Leaf}$  in leaves rehydrated from a range of initial water potentials ( $\Psi_1$ ). Branches were cut far enough from the leaves in such a way that emboli did not extend into the petioles. Some branches were left to transpire freely on the laboratory bench reaching different water potentials. Then branches were placed in a plastic bag in the dark for approximately 30 min to minimize variations in water potential between leaves. One leaf per branch was harvested to estimate the initial water potential ( $\Psi_1$ ). Another leaf close to the previous one was harvested and rehydrated by submerging the petiole (length: 3–4 cm) in distilled water and then measuring the water potential ( $\Psi_1$ ) after rehydration. Leaf vulnerability curves were plotted as loss of  $K_{Leaf}$  (%) against initial  $\Psi_1$  before rehydration.

### Stem hydraulic conductivity and vessel size

Hydraulic conductivity ( $k_h$ ) was determined on large terminal branches excised before dawn from three to six individuals of each cultivar in February of 2010. A small portion of the branch cut end was then immediately removed by re-cutting under water. The branches were then tightly covered with black plastic bags and transported back to the laboratory. Immediately after arriving at the laboratory, stem segments of about 25-cm long (longer than the longest vessel length (20 cm) determined using the method described by Zimmermann and Jeje (1981)) were rapidly cut under water and attached to a hydraulic conductivity apparatus filled with distilled and degassed water (Tyree and Sperry 1989). The distal end of the stem segment was connected with flexible tubing to graduated micro-pipettes for measuring volumetric water flow. The water flow was generated by a constant hydraulic head of 50 cm. Hydraulic conductivity ( $\text{kg m s}^{-1} \text{MPa}^{-1}$ ) was calculated as  $k_h = Jv/(\Delta P/\Delta X)$ , where  $Jv$  is the flow rate through the branch segment ( $\text{kg s}^{-1}$ ) and  $\Delta P/\Delta X$  is the pressure gradient across the segment ( $\text{MPa m}^{-1}$ ). Specific hydraulic conductivity ( $k_s$ :  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ) was obtained as the ratio of  $k_h$  and the cross-sectional area of the active xylem. After hydraulic conductivity measurements, the segments were perfused with a solution of safranin. After perfusion, thin sections were cut from the middle of the segment, and the stained section was determined using a light microscope.

Fourteen to 15 stem sections from terminal branches of each cultivar were cut and stained with Toluidine-Blue-O to increase visual contrast. Photographs of the cross sections were taken with a camera (TCA-3C Tucsen, China) mounted on a light microscope (Axioplan ZEISS, Germany). Images were then acquired with TSVIEW v 6.1.3.9 Software. The photographs were made at 400 $\times$  to calculate vessel density and dimensions considering two randomly selected fields of view of the xylem tissue. Vessels were measured and counted using SigmaScan Pro v.5.0 software.

### Sap flow

To determine the temporal dynamic of sap flow and daily water use in the three sweet cherry cultivars, heat dissipation sap flow probes were used with heated and reference sensors of 20-mm length (Granier 1985). For probe installation, two holes separated axially by 10 cm were drilled into the sapwood (2-cm depth) and the heated and reference probes were inserted tightly into the holes. All probes were protected from ambient radiation by reflective insulation. Signals from the sap flow probes were collected every 10 s and 10-min means were recorded by a data logger (CR10X; Campbell Scientific Corp., Logan, UT,

USA) equipped with a 32-channel multiplexer (AM416; Campbell Scientific). Sap flux density ( $J_s$ ;  $\text{g cm}^{-2} \text{h}^{-1}$ ) was calculated from the temperature difference between the two probes using an empirical calibration (Granier 1985, 1987) re-validated for trees (Clearwater et al. 1999; McCulloh et al. 2007). The temperature differences were corrected for natural temperature gradients between the probes (Do and Rocheteau 2002). Sap flow values obtained by dividing  $J_s$  per active xylem area (AX) were averaged over 4 days for three individuals per cultivar. The selected trees had an active sapwood area between 89.65 and 185.65  $\text{cm}^2$ . The majority of the water use in these trunks should be captured by the 2-cm probes due the fact that the outermost region of the sapwood is the most water-conductive portion.

### Gas exchange and leaf area index

Assimilation rate ( $A$ ) and stomatal conductance ( $g_s$ ) were measured using a portable photosynthesis system (model LI-6400, LI-COR, Lincoln, NE). Measurements for three trees per cultivar were done on fully developed sun-exposed leaves during mid-morning on sunny days. Photosynthetic photo flux density was held constant at 1,200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  to ensure light saturation, and the  $\text{CO}_2$  partial pressure was set to 400  $\mu\text{mol mol}^{-1}$ .

Twenty new, fully expanded leaves were collected from three to six individuals per cultivar to determine leaf specific area (SLA). The fresh leaf areas were obtained with a TZ5 Panasonic camera and the image analysis was performed using SigmaScan Pro v.5.0 software. Leaves were oven dried at 70 °C until constant weight and the dry mass was determined. Leaf area index (LAI) was estimated with a PAR/LAI Ceptometer (model LP-80, Decagon Devices, Inc.) for each tree per cultivar ( $n = 15$ ). The measurements were made during a cloudy day. To avoid underestimation of LAI, the measurements were done only under tree canopies, 1 m to the east and 1 m to the west from the trunk.

### Tree growth

The stem growth of six trees per cultivar was obtained by periodic readings of dendrometer bands. Dendrometers were manually made and consisted of a stainless steel tape encircling a tree stem, with one end passing through a collar (which was attached to the other end) and connected back to itself with a stainless steel spring, as described by Cattellino et al. (1986). Three months after dendrometer installation (allowing for stem–dendrometer adjustment), a permanent mark was made on the metal band next to the collar. As stem diameter increases, the mark moves away from the collar and the spring is stretched, keeping the dendrometer tight. A digital caliper was used to measure

stem diameter changes with an accuracy of 0.01 mm. Readings were taken approximately every 30 days from August 2010 to August 2011. Before installing the dendrometers, the external cortex was removed to avoid possible errors in measurement due to irregularities on the stem surface. The growth rate was determined from cumulative growth curves plotted with data from percentage stem increments against time. The relative growth rate (RGR) was calculated using the following equation:

$$\text{RGR} = (\ln A_2 - \ln A_1) / (T_2 - T_1)$$

where RGR = relative growth rate;  $T$  = time (days);  $A_1$  = the area of shoot at  $T_1$ ;  $A_2$  = the area of shoot at  $T_2$

#### Fruit production efficiency and quality

Fruit production efficiency was evaluated as fruit yield per leaf area (Yoshida et al. 2006). Fruit number was determined by counting the number of fruits of two branches per tree ( $n = 3\text{--}6$ ) and normalized by leaf area. Five fruits per individual were harvested in January, when the fruits had reached maturity, and determination of fruit quality was made on the same day of harvest at a fruit temperature of 20 °C. Five fruit quality indicators were determined: individual fruit fresh weight (g) using a balance with 0.001 g precision, fruit equatorial diameter (mm) measured with a digital caliper, fruit firmness determined with a custom penetrometer with 0.25-mm tip (modified from Feeny 1970), soluble solid content (SSC) and titratable acidity (TA). Soluble solid content was measured with a digital refractometer (Atago Co. Ltd., Tokyo, Japan) and expressed as °Brix. Titratable acidity was expressed as g malic acid equivalent 100 g<sup>-1</sup> fresh fruit. Five grams of aliquots of fruit juice was titrated up to pH 8.2 with 0.1 N NaOH.

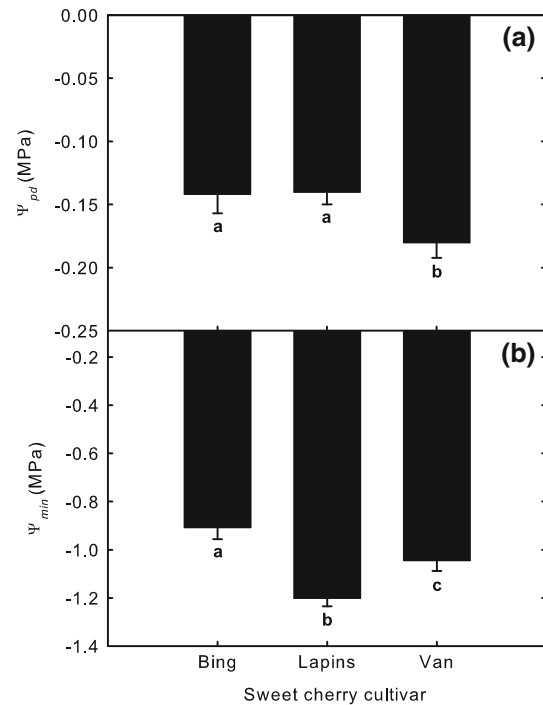
#### Statistical analysis

SPSS 11.5 statistical package (SPSS Inc., Chicago, IL, USA) was used for statistical analysis. All the data of leaf physiological traits within a cultivar were normally distributed (Kolmogorov–Smirnov test). A one-way analysis of variance (ANOVA) was applied to test the data for differences among cultivars. Once it was determined that differences existed among the means, Fisher's LSD test was used to compare the significance within cultivars.

## Results

#### Water relations

All cultivars under well-watered conditions had predawn leaf water potential ( $\Psi_{pd}$ ) higher than  $-0.2$  MPa (Fig. 1a),



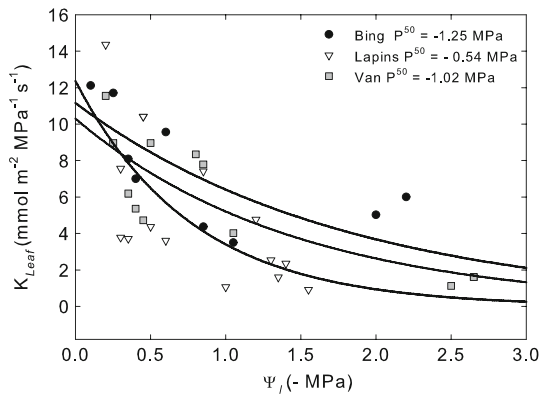
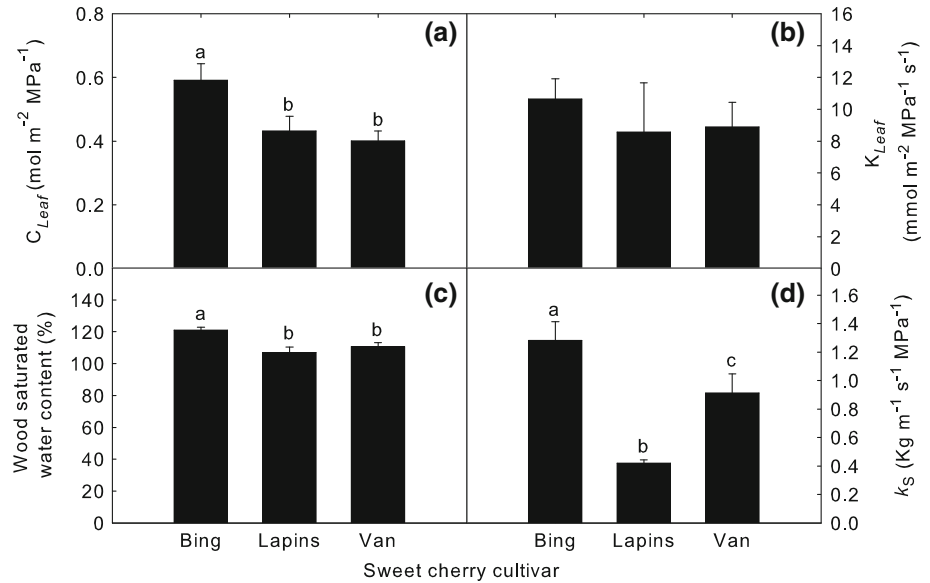
**Fig. 1** **a** Predawn leaf water potential ( $\Psi_{pd}$ ) and **b** minimum leaf water potential ( $\Psi_{min}$ ). Vertical bars indicate mean values ( $\pm$ SE) of three to six trees per cultivar. Different letters between bars indicate significant differences (Fisher's LSD test,  $P < 0.1$  for  $\Psi_{pd}$  and  $P < 0.05$  for  $\Psi_{min}$ )

while minimum leaf water potential ( $\Psi_{min}$ ) reached values between  $-0.9$  MPa and  $-1.2$  MPa (Fig. 1b). Bing had the highest  $\Psi_{min}$  ( $-0.97 \pm 0.07$  MPa), while Lapins was the cultivar with the lowest  $\Psi_{min}$  ( $-1.2 \pm 0.03$  MPa). The maximum leaf water potential gradient ( $\Psi_{pd} - \Psi_{min}$ ) was thus exhibited by Lapins (1.04 MPa). Despite the differences in  $\Psi_{min}$  between cultivars, there were no significant differences in osmotic potentials at the turgor loss point ( $\pi^0$ ) (Table 1) and  $\pi^0$  was significantly more negative than  $\Psi_{min}$  in all cultivars ( $P < 0.05$ ; data not shown).

#### Leaf and stem hydraulic traits

Leaf and stem hydraulic properties differed between cultivars. For example, at leaf level, leaf area-specific hydraulic capacitance ( $C_{Leaf}$ ) varied significantly between cultivars ( $P < 0.05$ ; Fig. 2a), Bing being the cultivar with the highest  $C_{Leaf}$  ( $0.59 \pm 0.05$  mol m<sup>-2</sup> MPa<sup>-1</sup>) and Lapins and Van having similar  $C_{Leaf}$ . On the other hand, there were no significant differences in leaf hydraulic conductance ( $K_{Leaf}$ ) across cultivars (Fig. 2b) and mean  $K_{Leaf}$  was approximately 9 mmol m<sup>-2</sup> s<sup>-1</sup> MPa<sup>-1</sup>. Although  $K_{Leaf}$  did not vary between cultivars, the response curves of  $K_{Leaf}$  to dehydration (vulnerability curves) showed that Lapins was the cultivar with the highest vulnerability to leaf

**Fig. 2** **a** Leaf capacitance ( $C_{\text{Leaf}}$ ), **b** predawn leaf hydraulic conductance ( $K_{\text{Leaf}}$ ), **c** wood saturated water content as percentage of dry weight and **d** stem specific hydraulic conductivity ( $k_S$ ) for three cultivars of *Prunus avium*. Vertical bars indicate mean values ( $\pm$ SE) of three to six trees per cultivar. Different letters between bars indicate significant differences (Fisher's LSD test,  $P < 0.05$ )



**Fig. 3** Leaf vulnerability curves of the three cultivars studied.  $P^{50}$  value indicates leaf water potential ( $\Psi_l$ ) at 50 % of leaf hydraulic conductance ( $K_{\text{Leaf}}$ ) loss. Solid lines are the exponential decay curves fitted to the data (Bing:  $r^2 = 0.52$ ,  $P < 0.05$ ; Lapins:  $r^2 = 0.47$ ;  $P < 0.01$ ; Van:  $r^2 = 0.54$ ;  $P < 0.005$ )

cavitation. In Lapins,  $K_{\text{Leaf}}$  decreased faster with decreasing leaf water potential than the other two cultivars and its water potential at 50 % of conductivity loss ( $P^{50}$ ) was significantly higher ( $-0.54$  MPa) compared to the  $P^{50}$  of Bing ( $-1.25$  MPa) and Van ( $-1.02$  MPa) (Fig. 3).

At stem level, wood saturated water content was lower in Lapins and Van compared to Bing ( $P < 0.05$ ; Fig. 2b). Specific hydraulic conductivity ( $k_S$ ) varied significantly between cultivars ( $P < 0.05$ ; Fig. 2d). Bing was the cultivar with the highest  $k_S$  ( $1.3 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ ), while  $k_S$  was fourfold lower in Lapins than in Bing ( $0.4 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ ). Consistent with the low  $k_S$ , Lapins also exhibited lower vessel size and density than Bing and Van (Fig. 4a, b) and higher wood density than Bing (Fig. 4c).

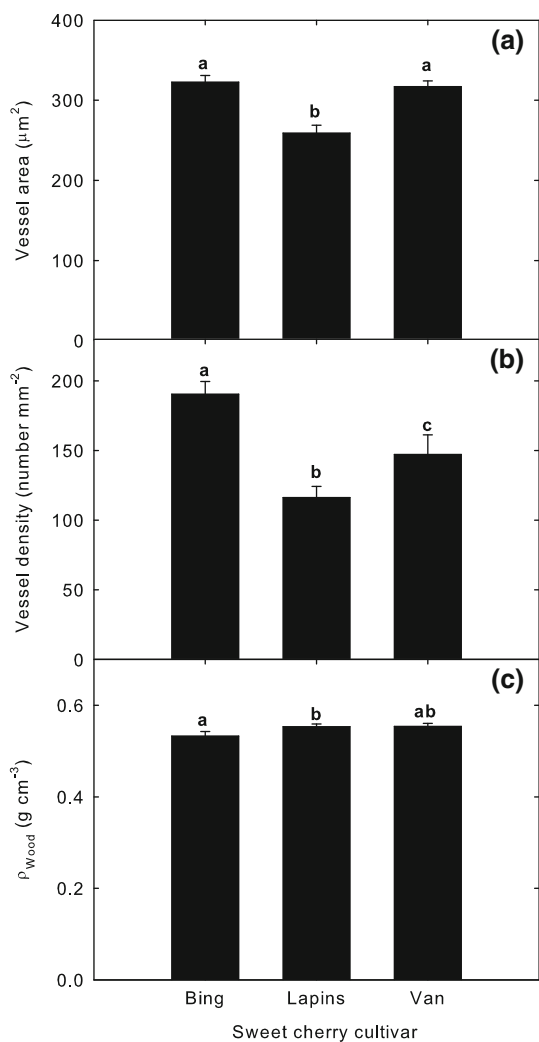
### Sap flow and gas exchange

All cultivars exhibited similar daily pattern of sap flow. Sap flow started at 700–800 h, but a clearly defined maximum value was reached during the afternoon by about 1,700 h (Fig. 5). Differences found in patterns of sap flow between days were consistent with the environmental conditions during the study period (the first 3 days were sunny with higher air saturation deficit (D), while the last day was cloudy with low D). Daily total water use was lower in Lapins ( $17.19 \text{ L d}^{-1}$ ) than in Van ( $23.64 \text{ L d}^{-1}$ ) and in Bing ( $27.94 \text{ L d}^{-1}$ ) (Fig. 5). Although the differences were not significant, water use in Lapins represented 40 and 27 % lower water consumption than in Bing and Van, respectively. Stomatal conductance was similar between cultivars (Table 1). However, Net  $\text{CO}_2$  assimilation ( $A$ ) was significantly lower in Van ( $10.4 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) than in Bing and Lapins (approximately,  $14 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ; Table 1).

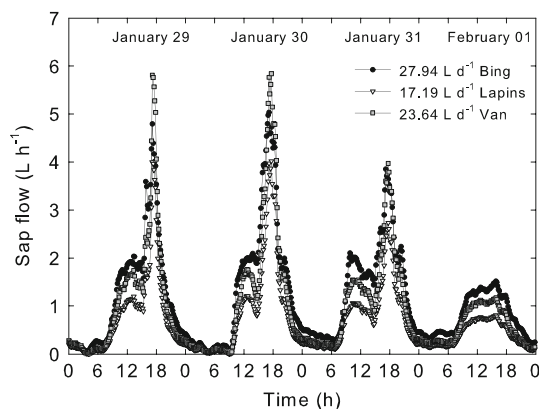
### Tree growth and leaf area index

All the cultivars exhibited active growth during spring and summer (October–January), although they differed in the dates of the beginning and ending of the growth period (Fig. 6). The initial growth in the diameter of the stem occurred in October and the maximum growth rate was observed between December and January. The growth rate started to decrease in February and growth cessation occurred in April in all cultivars. Van tended to have lower growth rates, followed by Lapins and Bing. The increment in stem diameter during the period of the maximum growth ranged between 6.78 % (Van) and 12.35 % (Bing). The relative growth rate (RGR) was significantly higher in Bing

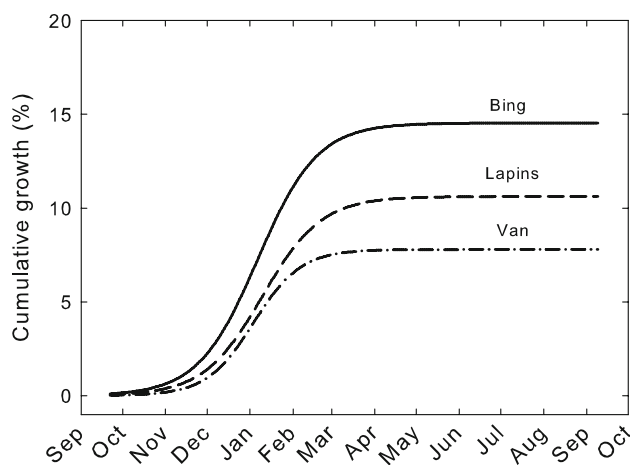




**Fig. 4** a Vessel area, b vessel density and c wood density of terminal branches of three to six trees per cultivar. Bars are means ( $\pm$ SE). Different letters between bars indicate significant differences (Fisher's LSD test,  $P < 0.05$  for (a) and (b) and  $P < 0.1$  for (c))



**Fig. 5** Mean daily pattern of sap flow during the period of maximum growth of three trees per cultivar. Values inside panel indicate the average total water use per tree and per day for each cultivar



**Fig. 6** Stem cumulative growth (%) from August 2010 to August 2011. Each point represents the growth in percentage of the initial area. A sigmoid curve for each cultivar was fitted to the data obtained on four to five trees (Bing:  $r^2 = 0.75$ ;  $P < 0.0001$ ; Lapins:  $r^2 = 0.31$ ;  $P < 0.0001$ , and Van:  $r^2 = 0.39$ ;  $P < 0.0001$ )

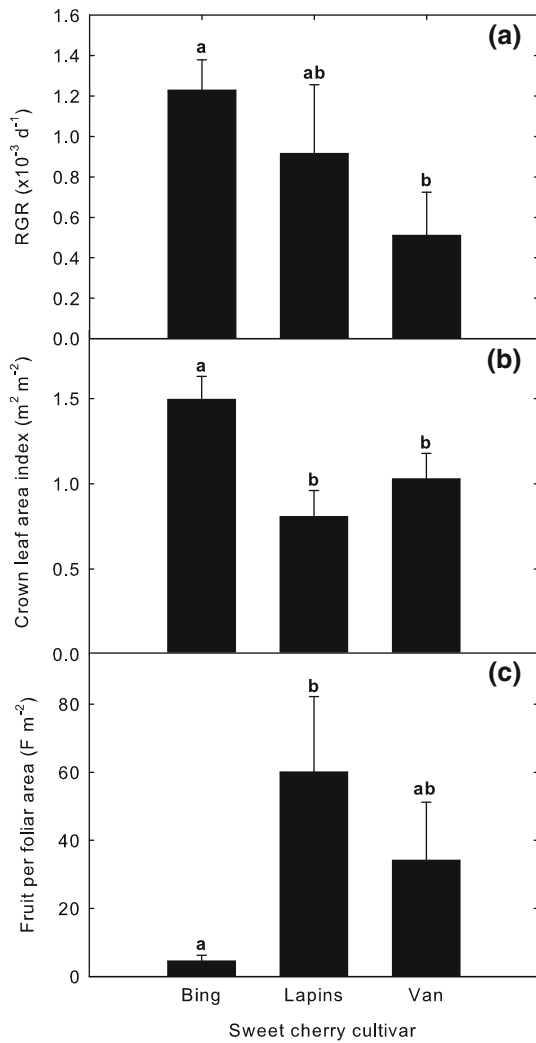
( $1.23 \times 10^{-3} \text{ d}^{-1}$ ) compared to Van ( $0.5 \times 10^{-3} \text{ d}^{-1}$ ), while RGR in Lapins did not show significant differences with Bing and Van (Fig. 7a). Bing also had significantly higher crown leaf area index than Lapins and Van: approximately twofold higher than in the other cultivars (Fig. 7b), but leaves of Bing had the lowest specific leaf area (SLA) between study cultivars (Table 1).

Fruit production efficiency and quality

Fruit production efficiency in relation to leaf area (the amount of fruits per unit leaf surface area) was substantially higher in Lapins than in Bing, while Van did not differ with other cultivars (Fig. 7c). Lapins had 60 fruits per leaf area, while Bing had only 5 fruits per leaf area. Although the number of fruits per leaf area varied between cultivars, fruit quality (size, fresh weight, firmness and titratable acids) was similar except that Lapins had lower soluble solid content than Bing (Table 2;  $P < 0.01$ ).

Discussion

*Prunus avium* cultivars exhibited variability in hydraulic traits at stem and leaf level, growth and fruit productivity despite being grafted on the same rootstock, which may reflect the genetic differences of the scions. On the other hand, results found in this study indicated that a high fruit yield was associated with the cost of reduced vegetative growth resulting in lower water delivery to leaves and more negative leaf water potentials, but without effects on leaf tissue turgor.



**Fig. 7** (a) Relative growth rate (RGR) during the period of maximum growth (December–January), (b) Leaf area index and (c) number of fruits per leaf area. Bars are mean values ( $\pm$ SE) of three to six trees per cultivar. Different letters between bars indicate significant differences (Fisher's LSD test,  $P < 0.1$  for (a) and  $P < 0.05$  for (b) and (c))

**Table 2** Fruit weight, equatorial diameter, fruit firmness, soluble solid content and titratable acids in three *Prunus avium* L. cultivars

	Bing	Lapins	Van
Fruit weight (g)	7.54 $\pm$ 0.26	6.63 $\pm$ 0.57	6.90 $\pm$ 0.49
Equatorial diameter (mm)	24.62 $\pm$ 0.38	24.17 $\pm$ 0.56	24.63 $\pm$ 0.51
Fruit firmness (N)	3.49 $\pm$ 0.30	2.95 $\pm$ 0.15	3.63 $\pm$ 0.57
Soluble solid content (Brix $^\circ$ )	23.68 $\pm$ 0.94 <sup>a</sup>	16.73 $\pm$ 0.70 <sup>b</sup>	20.29 $\pm$ 1.84 <sup>ab</sup>
Titratable acids (%)	0.77 $\pm$ 0.001	0.41 $\pm$ 0.000	0.92 $\pm$ 0.004

Values are mean  $\pm$  SE ( $n = 4-6$ ). Different letters within a column indicate a significant difference ( $P < 0.01$ )

Biomass allocation, fruit production and hydraulic connections of fruits to the plant

It is widely assumed that flowering and fruit set occur at the expense of future tree growth (Snow and Whigham 1989). In fruit trees, fruit sink strength must outweigh that of other plant organs, at least during the initial period of fruit development, thereby allowing photo-assimilate to accumulate preferentially in fruits. In this study, the high number of flowers (1.37 flowers per cm, data not shown) and high fruit production observed in Lapins, compared to Bing and Van, was at the expense of lower crown leaf area index. This suggests that a relatively large part of carbon fixed by photosynthesis in this cultivar was allocated to fruit production instead of vegetative growth. Similar to results obtained for Lapins in this study, in other species of *Prunus* (*P. cerasus*), fruits have priority over other sinks and consequently shoot and leaf growth is reduced (Flore and Layne 1999). While Lapins was able to translocate and partition carbon into reproductive structures in a manner that did not compromise vegetative growth to sustain growth during the current or next season, Bing used the largest part of assimilated carbon to stem growth and leaves production in detriment to the fruit load. Although plant growth and yield are limited both by the supply of and the demand for photo-assimilates (Wardlaw 1990), the higher fruit production (sink of photo-assimilates) with lower source of photo-assimilates (i.e., lower leaf area) observed in Lapins suggests that this cultivar is neither source nor sink limited.

Two mechanisms could protect fruit from environmental stresses experimented by the parent plant: fruit hydraulic isolation (e.g., Düring et al. 1987; Malone and Andrews 2001; Rogiers et al. 2001; Tyerman et al. 2004) or the increase of hydraulic conductance of fruit peduncle allowing the equilibrium between leaf and fruit water potential (Trifilò et al. 2010). Studies suggest various mechanisms that decouple fruits from the water status of the parent plant. Xylem contribution to fruit growth may be minimal and water transport can be made via phloem, suggesting that fruit development could be independent of the water transport from stem to fruit. In apples, for example, the xylem contribution to fruit growth decreases with the development of the fruit, and with the total loss of xylem functionality near fruit harvest (Dražeta et al. 2001, 2004). At the same time, phloem unloading becomes more important for apple fruit cell expansion (Lang 1990) and for *Vitis vinifera* (Choat et al. 2009). In kiwifruit, the xylem becomes dysfunctional at the beginning of the final stage of fruit expansion (Dichio et al. 2003), and fruit transpiration is greatly reduced at the same time (Morandi et al. 2007a). For other *Prunus* species, fruit growth is based on large quantities of water moving from tree to fruit until fruit maturation. For example, in *P. persica*

xylem supports peach growth by 70 % (Morandi et al. 2007b), as a consequence of maintaining the full functionality of xylem until harvest. For *P. avium* cultivars studied here, we do not know if xylem transport is maintained to be active during fruit development and consequently further investigations are needed to assess if substantial water transport remains coupled between leaves and stems with fruits, during fruit growth.

#### Gas exchange, hydraulic architecture and vulnerability to cavitation

Differences in stomatal conductance ( $g_s$ ) and assimilation between cultivars of fruit species have been associated with differences in water transport efficiency (low  $k_S$  and or  $k_L$ , and at leaf level low  $K_{Leaf}$ ) (Basile et al. 2003b; Solari and DeJong 2006); Nevertheless the results of this study did not support totally this finding since  $g_s$  was similar across all cultivars despite differences in  $\Psi_{min}$  and hydraulic traits, such as  $k_S$ ,  $C_{Leaf}$  and leaf  $P^{50}$ . We suggest that leaf gas exchange for *P. avium* cultivars is partially independent of the hydraulic efficiency, contrary, for example, to patterns observed in *Vitis* sp. (Zufferey et al. 2011; Zhang et al. 2012). Under well-irrigated conditions, as it is in this study, it could not be of adaptive significance for stomata to respond to low  $k_S$  such as occurred in Lapins which had three fold less stem hydraulic efficiency than Bing but with similar  $g_s$ . The lack of a relationship both for  $g_s$  and  $A$  with  $k_S$  and with water transport traits at leaf level observed in these cultivars is consistent with other studies that indicate that leaf traits related to gas exchange do not correlate with vulnerability to cavitation (Fichot et al. 2010) or hydraulic efficiency (Macinnis-Ng et al. 2004).

One of the largest differences found between cultivars was in the leaf resistance to hydraulic failure. Leaf vulnerability curves showed that Lapins was twofold more vulnerable to drought-induced cavitation than Bing and Van. Thus, leaves of Lapins lost 79 % of the hydraulic leaf efficiency at their minimum  $\Psi_{min}$ . This high loss of  $K_{Leaf}$  conduced to lower vegetative growth, possibly due to the cost involved in refilling the embolized conduits. Based on the higher leaf vulnerability to cavitation and lower  $\Psi_{min}$  exhibited by Lapins, we hypothesized that this cultivar had the capacity to repair daily embolisms in the leaves, as frequently observed in several species (Bucci et al. 2003; Johnson et al. 2009; Salleo et al. 2009; Secchi and Zwieniecki 2011; Zufferey et al. 2011). This mechanism would allow them to operate close to the hydraulic threshold for catastrophic dysfunction in the early afternoon, but recover on a daily basis. Evidently, this process could have negative consequences on their growth, as refilling of vascular conduits may require a metabolic source of energy, such as sugars stored or supplied by the phloem (Bucci et al. 2003;

Salleo et al. 2009; Secchi and Zwieniecki 2011), resources that otherwise could be used for growth. On the other hand, large loss of leaf hydraulic function in the most vulnerable cultivar may be advantageous to fruit development, as more water can be moved to fruits instead of leaves.

The variability in hydraulic efficiency of the stems was strongly related to xylem vessel anatomical traits in accordance with the Hagen-Poiseuille law, which predicts that the hydraulic efficiency of a vessel increases with the fourth power of its diameter (Tyree and Zimmermann 2002). In this study we found that Bing had the highest  $k_S$  with high density and large vessels, allowing this cultivar to maintain higher sap flow. If vulnerability to cavitation of stems in *P. avium* cultivars is determined by the vessel size, then Bing should be the most vulnerable cultivar to stem cavitation, because these large vessels would necessarily have a very large number of inter-vessel pits, increasing the probability of spread of air from embolized conduits through inter-conduit pits (the 'air-seeding' mechanism) (Tyree and Sperry 1989). In addition and even though stem vulnerability to cavitation was not measured in any of the cultivars in this study, the results of wood density and growth rate suggest also higher vulnerability to cavitation in stems of Bing compared to those of Lapins and Van. This trade-off at stem level between hydraulic efficiency and safety was absent at leaf level across cultivars.

In conclusion, this study indicates that low leaf water potentials, high leaf vulnerability to cavitation and low stem water transport efficiency reduced tree vegetative growth in Lapins, while fruit production was increased. This higher allocation of assimilates to fruits at the expense of allocation of photo-assimilates to vegetative growth helped to minimize total water loss per plant. In addition, our results show that the physiological traits of the scions substantially influence growth patterns, fruit production and water relation characteristics of the plants. This information of the optimization of crop water use in relation to yield can be useful for selecting cultivars with high fruit yield and low water use.

**Acknowledgments** We thank Alicia Jonouk of El Porvenir Ranch for permission to access and use her sweet cherry plantation for this study and for logistic support. This study was partially supported by CyT Chubut, Argentina, CONICET (PIP grant) and ANCYT-FONCYT (PICT grant). This work complies with Argentinean laws.

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