

Short- and long-term responses to seasonal drought in ponderosa pines growing at different plantation densities in Patagonia, South America

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Abstract Trees drought responses could be developed in the short- or in the long-term, aiming at sustaining carbon fixation and water use efficiency (WUE). The objective of this study was to examine short- and long-term adjustments occurring in different size *Pinus ponderosa* Dougl. ex P. & C. Laws trees in response to seasonal drought when they are growing under different competition level. The following variables were studied: branch and stem hydraulic conductivity, canopy and stomatal conductance (g_c , g_s), transpiration (E), photosynthesis (A_{\max}), wood $\delta^{13}\text{C}$ (as a proxy of intrinsic WUE), leaf to sapwood area ratio ($A_L:A_s$) and growth in the biggest (B) and the smallest (S) trees of high (H) and low (L) density stands. $A_L:A_s$ was positively correlated with tree size and negatively correlated with competition level, increasing leaf hydraulic conductance in H trees. Accordingly, higher g_c and E per unit A_L were found in H than in L trees when soil water availability was high, but decreased abruptly during dry periods. B trees maintained stable g_c and E values even during the summer drought. The functional adjustments observed in H trees allow them to maintain their hydraulic integrity (no apparent k_s losses), but their stem and leaf growth were

severely affected by drought events. i WUE was similar between all tree groups in a wet season, whereas it significantly decreased in SH trees in a dry season suggesting that when radiation and water are co-limiting gas exchange, functional adjustments not only affect absolute growth, but also WUE.

Keywords Hydraulic conductance · Leaf to sapwood area ratio · Water use efficiency · Intraspecific competition

Introduction

The maintenance of gas exchange depends on short-term physiological and long-term structural mechanisms that allow plants to optimize carbon gain per water loss. In the short term, stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) regulates transpiration (E , 1 day^{-1}) while in the long term, the adjustment in the leaf area to sapwood area ratio ($A_L:A_s$, $\text{m}^2 \text{ cm}^{-2}$) ensures the capacity of the hydraulic pathway to feed the leaves with water. Both mechanisms minimize cavitation and at the same time maximize the photosynthetic surface area. The hydraulic model based on Darcy's law described by Whitehead and Jarvis (1981) and Whitehead et al. (1984), taking into account the considerations developed in McDowell et al. (2002, 2006), introduces a theoretical basis of the homeostatic relationship between structural parameters ($A_L:A_s$) and the soil to leaf water potential gradient ($\Delta\psi = \psi_s - \psi_l$, MPa) as follows:

$$\frac{A_L}{A_s} = \frac{ks\Delta\psi}{h\eta gcD} \quad (1)$$

where D is atmospheric vapor pressure deficit (as was mentioned in McDowell et al. 2002, a net radiation term should be added for poorly coupled canopies, kPa), g_c is

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canopy conductance to water vapor ($\text{mol m}^{-2} \text{s}^{-1}$), k_s is the sapwood permeability of the hydraulic pathway ($\text{mmol s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$), η is water viscosity at a given temperature (Pa s) and h is height (m).

Several studies, some of them about ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws), have dealt with homeostatic mechanisms developed by plants growing under different environmental constraints (Magnani et al. 2002; Maherali and DeLucia 2001) and stand densities (Simonin et al. 2006; McDowell et al. 2006), as well comparing plants with different height and age (Ryan et al. 2000; Fischer et al. 2002; McDowell et al. 2002; Simonin et al. 2006). In particular, McDowell et al. (2006) found that stand $A_L:A_s$ ratio in *P. ponderosa* decreased with basal area, and they hypothesized that this long-term structural change is an homeostatic response to decreased water availability (due to intra-specific competition increase) that maximizes whole-tree carbon uptake and water-use efficiency. Within a stand, $A_L:A_s$ ratio varied between different size trees. In open *P. ponderosa* stands, $A_L:A_s$ ratio was higher in the smallest (and probably younger) trees (Fischer et al. 2002), whereas in dense stands, the opposite trend was observed (Simonin et al. 2006).

The relationship between photosynthesis and stomatal conductance was, however, invariant with basal area, and absolute values of both were elevated at lower basal areas (McDowell et al. 2006). Intrinsic water use efficiency (δWUE), estimated from ^{13}C discrimination, was higher in trees growing at lower basal areas (McDowell et al. 2006). However, other studies have demonstrated that water use efficiency patterns of ponderosa pine in response to management and resource availability are variable, showing a negative, positive or no relationship with the basal area of the stand, resource availability and the time period after thinning (Warren et al. 2001; Skov et al. 2004; McDowell et al. 2003, 2006).

The objective of this study was to examine what kind, if any, of short- and long-term adjustments do occur in different size even-aged young *P. ponderosa* trees in response to seasonal drought when they are growing in plantation conditions under very different intra-specific competition levels. In addition, the consequences of those changes in δWUE were analyzed. This information could be valuable to develop management strategies for relatively short-rotation plantations based on this species aiming to increase their adaptability to drought conditions. Based on the available background information, we hypothesized that trees growing at high-density plantation and the smallest trees of the stand, (1) have a lower $A_L:A_s$ ratio and therefore (Eq. 1), (2) those trees have lower k_s and/or higher gc , compared to trees growing in low-density plantations and the biggest trees of the stand. We also expected that those short- and long-term responses of trees

growing under high-competition level are not enough to reach similar growth during drought periods than open-stand (or biggest) trees.

Materials and methods

Study site

The study was carried out in a *P. ponderosa* plantation stand installed in Patagonia, South America, where this species is grown in quite-short rotation periods (around 40 years). The stand was located within La Veranada ranch ($41^\circ 13' 53''\text{S}$, $71^\circ 11' 40''\text{W}$), 10 km away from San Carlos de Bariloche city (Río Negro Province, Argentina). The climate in the region has cold, humid winters and hot, dry summers (with approximately 80 % of the annual precipitation falling from April to September as rain and snow). Climatic data recorded approx. 20 km away from the study site (INTA EEA Bariloche, $41^\circ 07' 43''\text{S}$, $71^\circ 15' 06''\text{W}$, series 1981–2006) indicate a mean annual precipitation of 835 mm, and an average annual temperature of 8.4 °C (5.3 and 11.5 °C for the cold and warm season, respectively).

Two experimental plots with different intra-specific competition levels were installed within the 6 ha ponderosa pine plantation. The trees were 25 years at the beginning of the study (winter 2007). The different competition levels were established based on basal area (BA) and number of trees per unit area, and named “low” and “high” density (519 and 2 500 trees ha^{-1} respectively; Table 1). The different tree densities were the result of different initial plantation densities and not due to thinning or differential mortality. This situation provided an opportunity to measure the long-term acclimation capacity of this species to high competition levels under Patagonian conditions. Ten trees were selected in each plot (density treatment), which

Table 1 Characteristics of the low- and high-density ponderosa pine plots and average characteristics of the biggest (*B*) and smallest (*S*) trees of each plantation density plot (\pm SD) at the beginning of the study in Arroyo del Medio site, Patagonia, Argentina

	Low density	High density
Tree density (trees ha^{-1})	519	2 500
Basal area ($\text{m}^2 \text{ha}^{-1}$)	38.13	79.70
Diameter at breast height (cm) ^a	<i>B</i> 34.7 (± 2.8) <i>a</i> <i>S</i> 24.8 (± 3.4) <i>b</i>	<i>B</i> 24.6 (± 3.2) <i>b</i> <i>S</i> 13.8 (± 2.7) <i>c</i>
Height (m)	11.84 (± 0.84)	13.25 (± 1.15)
Leaf area (A_L , m^2) ^a	83.7 (± 31.9) <i>a</i>	26.8 (± 24.7) <i>b</i>
Leaf area index (LAI)	4.7	6.5
Relative density	6.89	17.76

^a ANOVA, different letters mean statistical differences between treatments, $P < 0.01$

were the biggest and the smallest (based on stem diameter, B and S , respectively) trees of each plot (5 individuals in each size range and density treatment). Trees had similar age and their different size was the result of differential annual growth rate, being higher in B than S (Fernández et al. 2012). The trees in the low density plot had a diameter at breast height (dbh) around 10 cm higher (152 %) and A_L 57 m² higher (312 %) than in the trees in the high density plot (Table 1). Relative density, estimated as the basal area divided by the square root of the quadratic mean stand dbh (Curtis 1982) of the high density plot was more than twice as high as in the low density plot (Table 1). However, maximum height was similar between plots, indicating a similar site quality (Table 1).

Intensive growth and ecophysiological measurements were carried out during three consecutive growing seasons (beginning of spring in October to beginning of autumn in April), from 2007–2008 to 2009–2010. Climatic data (air temperature and humidity, wind velocity, solar radiation, precipitation) were measured every 30 s and averaged every 10 min with a HOBO[®] weather station in an open site located 100 m from the forest plantation. Vapor pressure deficit (VPD) was estimated as the difference between saturated and measured vapor pressure at ambient air temperature from the weather station.

Soil type was sandy loam with 6 % clay, 35 % silt and 59 % sand. Maximum soil depth reached approximately 80 cm, determined by the presence of a clay pan. Field capacity (FC or soil water potential of -0.03 MPa) was estimated at the Soil Laboratory of INTA Agricultural Experimental Station of Bariloche (National Institute for Agricultural Technology, Argentina).

Inter-annual sampling

Every winter, starting at the beginning of the study, winter 2007, dbh, diameter at the base of the living crown (DBLC, diameter of the internode below the first branch with green leaves) and height were measured in the 10 selected trees to estimate the annual increase in basal area (cm² year⁻¹), stem volume (m³ year⁻¹, estimated from dbh and height using the equation of Andenmaten et al. (1995) and leaf area (A_L , m² year⁻¹).

Particular equations to estimate A_L were developed for each density treatment using branch diameter at 5 cm from the insertion and DBLC as independent variables. We harvested one randomly selected branch from the top, middle and bottom of five trees in each stand density. Two orthogonal diameters at 5 cm from the branch insertion were measured. All leaves of the branches were collected and oven dried to constant weight. Previously, 20 fascicles from each branch were randomly selected and measured to estimate leaf area. Total surface of the fascicles was

Table 2 Equations (ax^b) to estimate foliar area (A_L , m²) from branch basal diameter (mm) and diameter at the base of the living crown (DBLC, cm)

	a (\pm SE)	b (\pm SE)	R^2 adj.	P
Branch	0.00029 (0.0005)	2.284 (0.395)	0.73	<0.001
DBLC high density plot trees	0.009 (0.013)	2.849 (0.452)	0.92	<0.001
DBLC low density plot trees	0.153 (0.303)	1.927 (0.592)	0.57	<0.01

estimated using geometric formulae representing the fascicle as six rectangular surfaces and an external cylinder. After that fascicles were oven dried and weighted. Total A_L of each branch was estimated from dry weight of all fascicles and the ratio A_L : dry weight of the sub-sampled fascicles. In order to develop a simple predictive model of A_L of the whole tree, we measured the diameter of all branches and the diameter of the stem at the base of the living crown (DBLC) of six trees growing at each stand density (see more details in Gyenge et al. 2009). At the branch level, no difference was found between models developed for trees growing at the different stand densities. However, branches with living leaves attained higher diameters in low than in high stand density trees (maximum values of 9.1 and 6.4 cm, respectively). At the tree level, a higher variability between trees in the DBLC: A_L ratio was observed in the low than in the high density plot (Table 2).

Specific conductivity of the wood ring produced during each growing season (k_{sw}) was measured as in Spicer and Gartner (1998) and Fernández et al. (2010). The method consisted of a double-ended pressure chamber into which wood samples are introduced with a modified pressure sleeve to seal samples sides allowing only a longitudinal flow. A longitudinal section of the stem including the complete ring produced during the last growing season was extracted and preserve in pure water. In the laboratory, a subsample was recut under water with the following dimensions: length: 5 cm (in the direction of the tracheids), width: the whole ring (including both, early- and latewood).

An integrated value of intrinsic water use efficiency (ϵ , WUE) was estimated from $\delta^{13}C$ of wood rings (both late- and early wood) corresponding to season 2007–2008 (a dry season, see below) and 2009–2010 (a wet season). $\delta^{13}C$ was analyzed using an isotope ratio mass spectrometer (Finnigan MAT Delta S, USA) following the methodology of Hoefs and Schidlowski (1967) and Panarello (1987) in the Institute of Geochronology and Isotopic Geology (Instituto de Geocronología y Geología Isotópica, INGEIS, CONICET—University of Buenos Aires, Argentina).

The instantaneous intrinsic water use efficiency (WUE) was estimated as the ratio between photosynthesis at light saturation (A_{\max} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) measured with a LICOR-6400 portable photosynthesis system (LI-COR, Lincoln, USA) with a 6400-02B LED light source. Measurements were done in 37 fascicles (3 needles each) from different branches of the sun exposed portion of the canopy. After that, each needle was measured with a calliper and its surface area estimated following Gyenge et al. (2009).

An estimation of the solar radiation intercepted by each selected tree was made by installing two solar radiation sensors (HOBO® Pendant Temperature/Light Data Logger) per tree, one on a branch of the second whorl from the apex and one on the lowest whorl having green leaves of each tree. Each radiation sensor was attached to a north-oriented branch of the selected whorl, at about 15 cm from the branch (to avoid leaf shading) with a hand-made device. The inclination of each sensor was adjusted using a bubble level. In the case of the lower branch, the sensor was installed on the oldest cohort of green leaves. Total solar radiation reaching the sensors was automatically recorded during periods of at least two whole sunny days in each tree. Eight trees per plantation density treatment were measured. Solar radiation in each sensor was normalized as a relative value of the radiation reaching the meteorological station in the open area next to the trees. At the end of the measurements, all sensors were calibrated against the radiation sensor of the meteorological station (used as the control, open area sensor) in order to correct, if necessary, any systematic bias. An average relative radiation value for each position/tree was obtained from the data of two sunny days.

Within-season sampling

Gravimetric soil water content was estimated from wet and dry weight of soil samples taken periodically (every 15–30 days) from October (spring) to April (autumn) every 20 cm from the soil surface down to the maximum soil depth.

Pre-dawn (ψ_{pd} , MPa) and midday (ψ_{md}) water potential were measured one or two times per month (see Fig. 4 for dates) in one previous-year fascicle of 4–5 pines during the different seasons with a Scholander-type pressure chamber (PMS Instruments, Corvallis, USA). We used scaffolding to reach leaves growing in full sunlight conditions (approximately at 5–8 m height in the low and in the high density plot, respectively).

Sap flow density (J_s , $\text{ml cm}^{-2} \text{min}^{-1}$) was measured with the heat dissipation method developed by Granier (1985) every 30 s and averaged and recorded every 10 min with a Campbell CR10X datalogger and a Campbell

AM16/32A multiplexer. In brief, we measured sapflow density in the outer portion of the xylem of the different size trees (5 B and 5 S per plantation density), as well as the changes in sapflow due to radial position within the xylem. This last variable was measured in two of the five trees of each group (size \times tree density), using sensors 2 cm long installed deeply in the stem. The portion of the stem containing the sapflow sensors was covered by a thermal and radiation insulator (Mexpol®, 9 mm) in order to avoid a thermal gradient effect on the stem. Daily transpiration (E , litres day^{-1}) of each tree was estimated using the sapwood area (A_s), and taking into account the reduction in sapflow density in the deeper portion of the sapwood during the season. Radial J_s linearly decreased from the outer to the inner portion of the sapwood as described in Gyenge et al. (2003) and other studies in USA cited therein. Sapwood area (A_s) was estimated from cores taken from trees growing at different densities inside the plantation. Wood cores indicated no heartwood area development; therefore, all xylem at dbh was considered conductive.

Canopy conductance (g_c , mm s^{-1}) was estimated according to Monteith and Unsworth (1990) (see Eq. 2 Appendix 1 of this paper). After that, g_c was related to VPD to estimate the sensitivity of stomata to VPD, as in Oren et al. (1999) (Eq. 3 Appendix 1).

The extent of native embolism in branch xylem was estimated by measuring the specific conductivity (k_s , $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$) and the volume fraction of water in the xylem (V_w) at the beginning and during the driest period of seasons 2007–2008 and 2008–2009 (Eqs. 4, 5, Appendix 1).

At the tree level, whole tree plant liquid phase hydraulic conductance (Kh , $\text{ml min}^{-1} \text{MPa}^{-1}$) was estimated from transpiration and water potential (Eq. 6 Appendix 1). After that, whole plant leaf specific hydraulic conductance (K_L , $\text{ml min}^{-1} \text{MPa}^{-1} \text{m}^{-2}$) was estimated dividing Kh by the leaf area of each tree.

We applied one-way ANOVA to compare growth at the end of the season and ecophysiological parameters between groups of trees (grouped by size range or density). We checked for ANOVA assumptions in each case. Within each year, we applied Kruskal–Wallis one-way ANOVA on Ranks and Tukey's tests for post hoc comparisons to compare A_L annual change. Mathematical models were compared with F test (Neter and Wasserman 1974).

Results

Inter-annual sampling

The first two seasons (2007–2008 and 2008–2009) had much higher mean VPD values than the 2009–2010 season

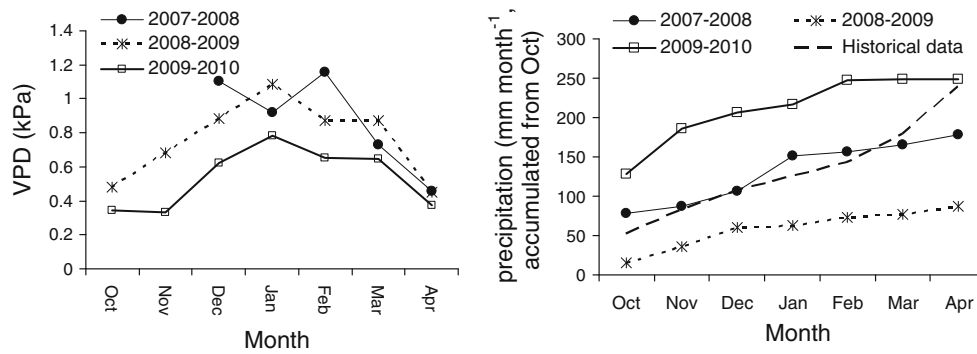


Fig. 1 Average monthly vapor pressure deficit (VPD *left*) and accumulated precipitation (*right*) from October to April (growing season period) in La Veranada ranch (41°13'53"S, 71°11'40"W).

Historical data from Bariloche city (from 1981 to 2006) located 10 km away from the study site (Río Negro Province, Argentina)

(average values from December to April: 0.9 ± 0.3 , 0.8 ± 0.2 and 0.6 ± 0.1 kPa, respectively; Fig. 1). Cumulative precipitation, considering the growing season period, of the first two seasons was similar or lower than the historical mean (923, 411 and 932 mm, respectively), with the higher values observed during season 2009–2010 (1 482 mm). In 2007–2008, precipitation level was mostly similar to the mean historical level, but with lower than the average precipitation observed in April (early autumn; Fig. 1).

hand, maximum tree height was similar between plots throughout the three seasons (data not shown) and therefore volumetric increase followed the abovementioned dbh growth trends.

At the beginning of the study, biggest trees in each plot had a dbh around 10 cm higher than in the smaller trees, being the size of smallest trees of the low density plot similar than the biggest trees of the high density plot (Table 1, $P < 0.01$). Thereafter, differences in mean dbh of the trees increased every year due to the higher annual dbh growth rates of the trees in the low density plot (around 10 mm year^{-1}) in comparison to the trees in the high density plot (around 3.5 mm year^{-1} , Table 3). On the other

The A_L annual change in the low density plot was positive, while negative changes (net leaf mortality) were observed in the trees growing in the high density plot during the first two dry seasons (Table 3). At the beginning of the study, A_L followed a similar ranking to that observed in dbh, with average values of 111 and $56 \text{ m}^2 \text{ tree}^{-1}$ for the biggest and the smallest trees of the low density plot, and 46 and $8 \text{ m}^2 \text{ tree}^{-1}$ for the biggest and the smallest trees of the high density plot. A_L increased around 8 and $1 \text{ m}^2 \text{ year}^{-1}$ in the low density plot trees and the biggest trees of the high density plot, respectively, whereas A_L decreased at a rate of $0.3 \text{ m}^2 \text{ year}^{-1}$ in the smallest trees of the high density plot (Table 3). As A_L was estimated from an equation with DBLC as independent variable (Table 2), a negative change in A_L is due to the mortality of the bottom

Table 3 Mean annual diameter growth ($\text{mm year}^{-1} \pm \text{SD}$) and leaf area growth (A_L , $\text{m}^2 \text{ year}^{-1} \pm \text{SD}$) and leaf area:sapwood area ratio ($A_L:A_s$, $\text{m}^2 \text{ cm}^{-2}$) of biggest (B) and smallest (S) ponderosa pines growing at low (L) and high (H) density plantation

	BL	SL	BH	SH
Annual diameter growth				
2007/2008	12.6 (± 1.1) a	7.2 (± 1.6) b	4.1 (± 1.3) c	1.7 (± 0.4) d
2008/2009	12.2 (± 2.0) a	7.4 (± 1.0) b	5.3 (± 1.4) c	2.2 (± 1.0) d
2009/2010	12.5 (± 0.5) a	8.2 (± 0.7) ab	5.6 (± 0.7) b	1.5 (± 0.5) c
Average	12.4 (± 0.2)	7.6 (± 0.5)	5 (± 0.8)	1.8 (± 0.4)
Annual leaf area growth				
2007/2008	11.5 (± 4.0) a	4.6 (± 1.6) ab	4.1 (± 6.7) ab	0.4 (± 0.4) b
2008/2009	10.7 (± 3.6) a	5.8 (± 0.6) ab	-8.3 (± 12.2) b	-1.0 (± 1.4) b
2009/2010	11.3 (± 1.3) a	6.2 (± 1.6) ab	6.9 (± 10.4) ab	-0.4 (± 0.8) b
Average	11.1 (± 0.4)	5.5 (± 0.9)	0.9 (± 8.1)	-0.3 (± 0.7)
$A_L:A_s$ ratio				
2007/2008	0.122 (± 0.011) a	0.115 (± 0.006) a	0.098 (± 0.025) a	0.049 (± 0.007) b
2008/2009	0.123 (± 0.011) a	0.118 (± 0.004) a	0.078 (± 0.026) b	0.042 (± 0.014) c
2009/2010	0.125 (± 0.011) a	0.121 (± 0.006) a	0.085 (± 0.021) b	0.039 (± 0.014) c
Average	0.123 (± 0.001)	0.118 (± 0.003)	0.087 (± 0.010)	0.043 (± 0.006)

Different letters indicate statistical differences between treatments within each season

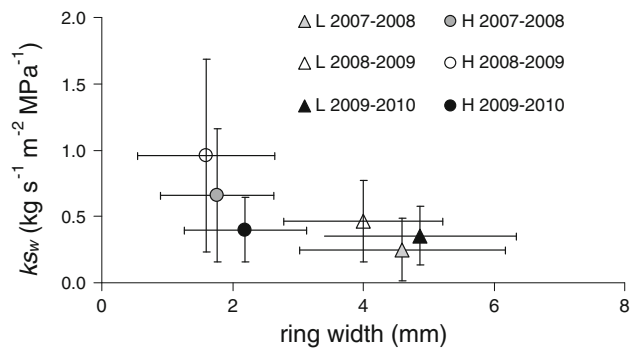


Fig. 2 Specific hydraulic conductivity (k_{sw}) in relation to the ring width produced during each growing season of ponderosa pines growing in low (L) and high (H) density plantation

of the crown during the period between two consecutive measurements, shortening the crown total length and displacing the DBLC to an upper (and thinner) position within the stem.

When comparing treatments within each season, the $A_L:A_s$ ratio was similar between trees of the low density plot, being higher than the high density trees in the last two seasons (Table 3). Moreover, smallest trees of the high density plot showed a lower $A_L:A_s$ ratio than the other treatments during the last two seasons.

Despite the fact that the specific conductivity of the ring produced during each growing season (k_{sw}) was similar between density and size range of trees within each year, it is important to note that the trees with the lowest annual growth rate (smallest trees of the high density plot) showed the maximum k_{sw} , particularly during the driest seasons (Fig. 2). The season 2009–2010 was more humid than the former two (Fig. 1), probably allowing a higher growth rate of the suppressed trees, which was correlated with a lower k_{sw} , similar to that observed in the other treatments trees (Fig. 2).

Mean $\delta^{13}C$ of ring wood during season 2009–2010 (a humid season) was similar between all trees. However, mean $\delta^{13}C$ was significantly more negative in the smallest

trees of the high density plot ($-26.9\text{‰} \pm 0.8$) compared to the biggest trees of the low density plot ($-24.2\text{‰} \pm 0.8$) during the 2007–2008 season (dry season). The relationship A_{max} versus g_s was similar in pine needles growing at both plantation densities (Fig. 3). For this reason, intrinsic WUE pattern was also similar for both plantation densities, showing maximum values when g_s was around $0.05\text{ mol m}^{-2}\text{ s}^{-1}$, and decreasing at higher or lower g_s values (Fig. 3).

The amount of radiation reaching the top of the canopies, as a proportion of the solar radiation in the open field, was similar between the biggest trees of both plantation densities and the smallest trees of the low density plot (from 0.91 to 0.72) and higher than the radiation reaching the smallest trees of the high density plot (0.43 ± 0.18). No statistical difference was found comparing the proportion of radiation at the base of the canopy of all measured trees, with a mean value of 0.11.

Within-season sampling

Within each season, and during the three studied seasons, soil water content decreased from field capacity (FC) to values as low as 6 % DW following similar patterns in all soil layers and in both density treatments (Fig. 4). However, between-season comparison showed that the minimum soil water content was reached approximately 2 months later in the humid season (in February, middle summer 2009–2010) as compared to the previous drier seasons (beginning of January, Fig. 4).

Plant pre-dawn water potential (ψ_{pd}) was in general lower in trees at the high than at the low density plots, particularly during the two driest seasons (Fig. 4). In the humid season 2009–2010, ψ_{pd} was similar in both density plots. Minimum ψ_{pd} of trees at the high density plot during the driest periods was about -1.9 MPa whereas it was -1.4 MPa in the low density plot (Figs. 4, 5). On the other hand, ψ_{md} was similar in both density plots and all studied seasons (isohydric behaviour), reaching mean minimum

Fig. 3 Relationship between photosynthesis at light saturation (A_{max} left) and instantaneous water use efficiency (WUE, $A_{max}:g_s$ ratio, $\mu\text{mol CO}_2\text{ mol}^{-1}\text{ H}_2\text{O}$ right) with stomatal conductance (g_s , $\text{mol m}^{-2}\text{ s}^{-1}$) of *P. ponderosa* needles growing in high (H) and low (L) density plots

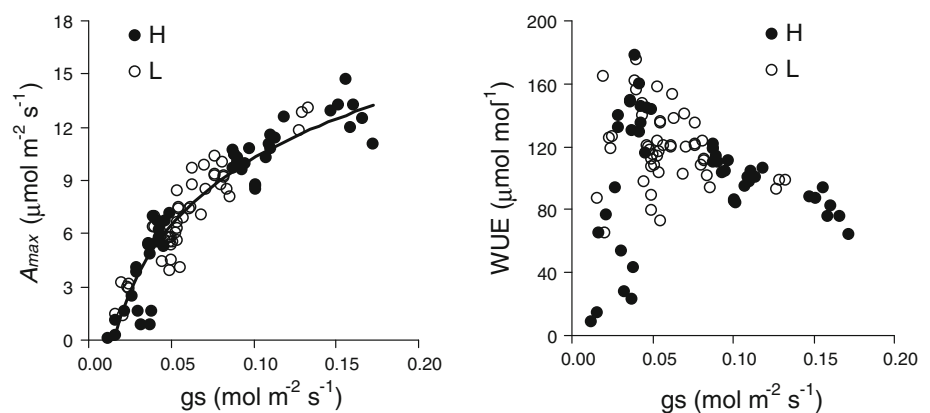


Fig. 4 Seasonal dynamic of soil water content (% dry weight *left*) and pre-dawn water potential (MPa *right*) of ponderosa pines growing at two plantation densities (*high* and *low*, *H* and *L*, respectively) during three consecutive growing seasons. Asterisks indicate dates at which significant differences were observed between pre-dawn water potential of *H* and *L* trees (** $P < 0.05$; *** $P < 0.01$). *FC* soil field capacity

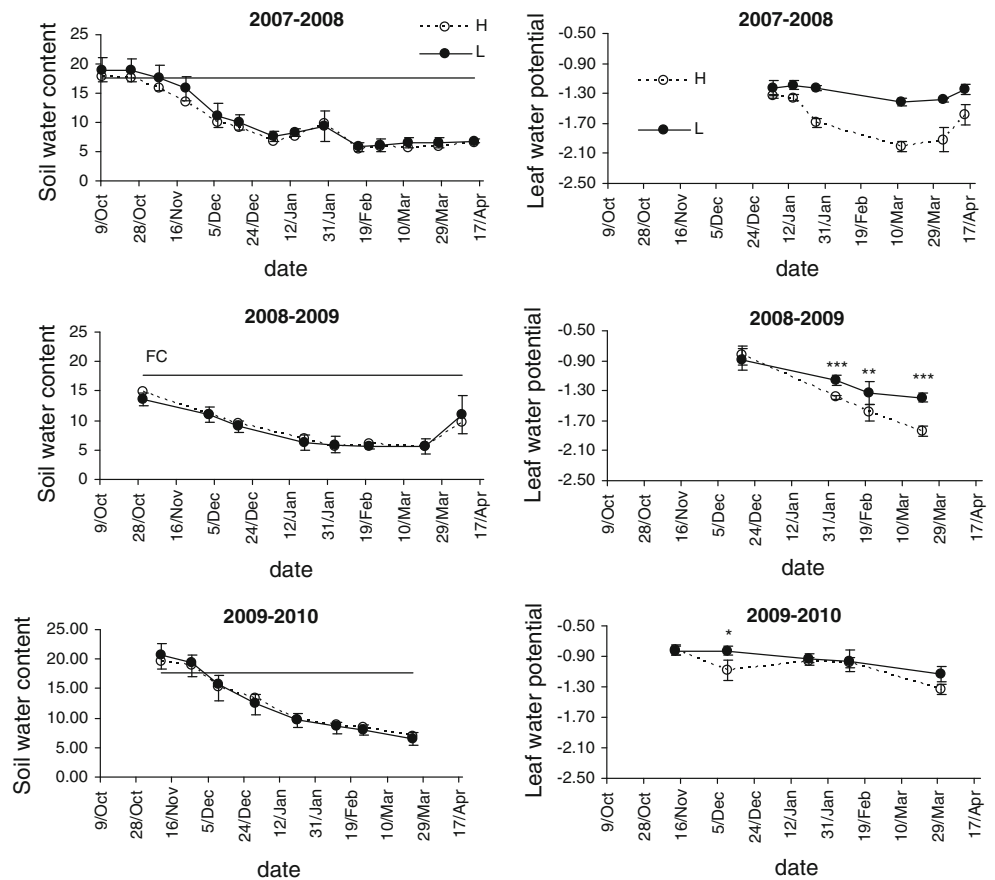
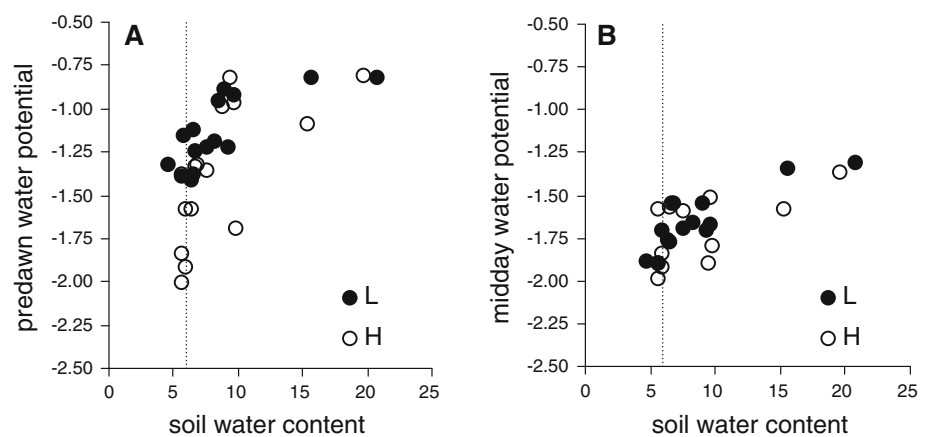


Fig. 5 Relationship between pre-dawn (a) and midday (b) water potential (MPa) of *P. ponderosa* leaves with soil water content (% dry weight) during three consecutive growing seasons. The trees were growing at two plantation densities (*high* and *low*, *H* and *L*, respectively). Vertical dashed line indicates 6 %DW of soil water content, the minimum value observed in the study site



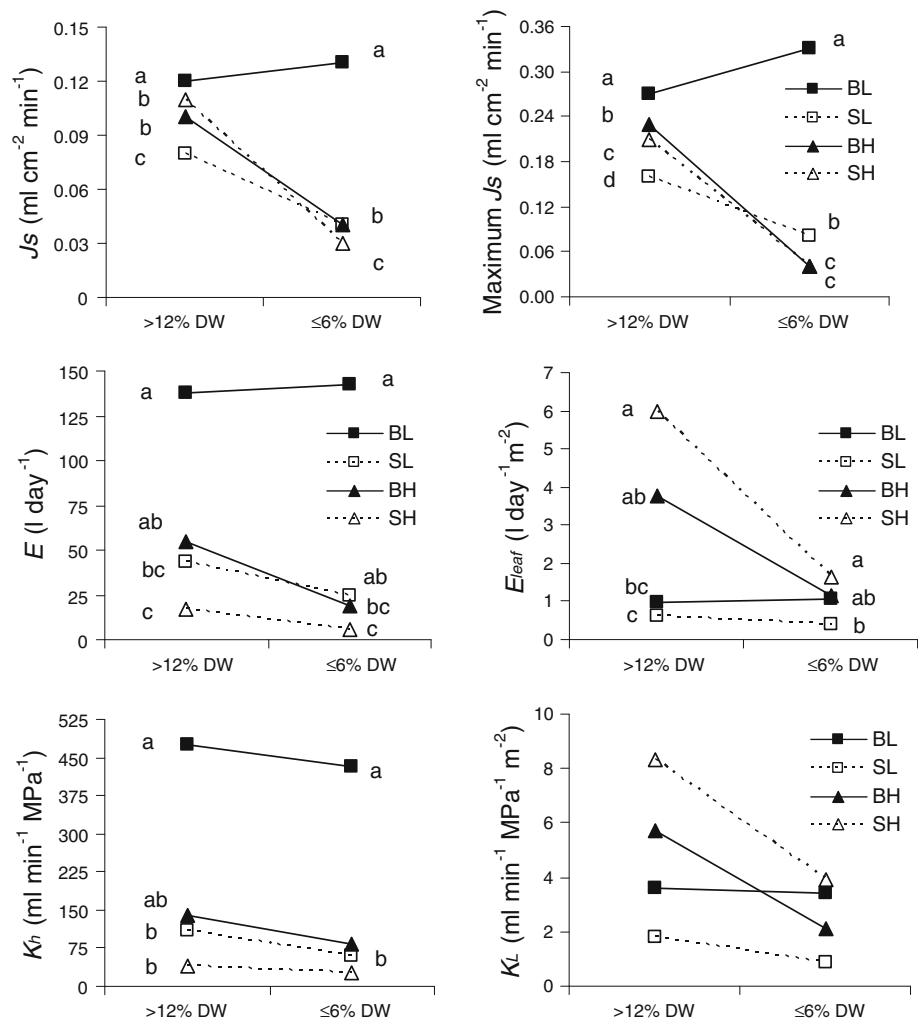
values around -1.7 MPa, with absolute minimum values of -2 MPa (Fig. 5).

Predawn water potential decreased abruptly below -1.0 MPa when soil water content of the entire profile was close to 8 % DW (Fig. 5). However, at soil water content lower than 8 % DW, the trees growing in the high density plot reached lower ψ_{pd} values than trees at low competition level in spite of the similarity in soil water content.

To understand the short-term responses to water deficit, sapflow density (J_s) analysis, as well as that related to

variables derived from it (E and g_c), was concentrated on days with high atmospheric demand and different values of soil water content (different ψ_{pd}). In general, only the biggest trees of the low density plot could maintain relatively stable water relations when soil water content decreased to minimum values in comparison with the smallest trees in the same plot and all trees in the high density plot (Fig. 6). Comparing the magnitude of mean J_s and maximum diurnal J_s (from 2 to 7 p.m.) between trees, these variables were higher in the biggest trees of the low

Fig. 6 Average (daily) and maximum (from 2 to 7 p.m.) sapflow density (J_s , $\text{ml cm}^{-2} \text{s}^{-1}$), mean daily transpiration per tree (E , l day^{-1}) and per leaf unit area (E_{leaf} , $\text{l day}^{-1} \text{m}^{-2}$), whole tree plant liquid-phase hydraulic conductance (K_h , $\text{ml min}^{-1} \text{MPa}^{-1}$), leaf-specific hydraulic conductance (K_L , $\text{ml min}^{-1} \text{MPa}^{-1} \text{m}^{-2}$) of biggest (B) and smallest (S) *P. ponderosa* trees growing in low (L) and high density (H) plots during two periods with contrasting soil water availability. Different letters indicate significant differences between treatments within each period



density plantation than all the other trees. In addition, trees at the high density plot and smallest trees of the low density plot reduced their J_s and maximum diurnal J_s around 66 % as the soil profile dried (Fig. 6). Moreover, maximum J_s showed similar values to average J_s in high density plot trees during the driest period, indicating the strong resistance they experienced in the soil-to-leaf hydraulic pathway.

Daily water use of trees (transpiration, E) during the humid period followed the same trend as the average size (stem diameter) whereas E normalized by A_L (E_{leaf}) followed the opposite pattern (Fig. 6). As was described for J_s , the highest reduction in E observed during periods with low soil water content was observed in the high density plot trees (about 65 %), followed by the smallest trees in the low density plot (reduced by about 44 % compared to humid periods), whereas the biggest trees in the same plot showed no reduction at all in E despite the seasonal water shortage (Fig. 6).

The magnitude of gc and its relationship with VPD were different depending on the tree size, the plantation density

and the soil water content. In this regard, the highest values of gc at VPD = 1 kPa (parameter b of Eq. 3, Appendix 1) during the humid period was observed in the high density plot trees (note that gc is a leaf-area normalized variable, Table 4). In contrast, during the dry periods, the biggest trees of the low density plantation showed a slightly higher b than that observed in the same treatment but in the previous humid period, whereas all other tree groups showed a marked decrease in b (Table 4). The highest relative decrease was observed in the trees of the high density plot (Table 4). As was expected based on the literature (e.g. Oren et al. 1999), the sensitivity of the stomata to VPD (m) was positively correlated with b .

Despite the reduction in soil water availability during the growing season (Fig. 4), branch k_s and V_w were relatively constant in both plantation density treatments, with no difference between them ($P > 0.05$ for each date). The average k_s of all branches was $1.758 \pm 0.506 \text{ kg m}^{-1} \text{MPa}^{-1} \text{ s}^{-1}$. On the other hand, we did not find a clear relationship between k_s and V_w if all data are pooled together (data not shown). Only in one date (October 2008),

Table 4 Average diurnal canopy conductance (g_c , from 8 a.m. to 9 p.m., mm s^{-1} , and below, in $\text{mol m}^{-2} \text{s}^{-1}$); reference g_c (b , mm s^{-1}) and stomatal sensitivity to VPD (m , $\text{mm s}^{-1} \ln(\text{kPa})^{-1}$) of biggest (B) and smallest (S) ponderosa pine trees growing in low (L) and high density (H) plantations during two periods with contrasting soil water availability

	Tree social status and plantation density			
	BL	SL	BH	SH
Soil water content >12 % DW				
Average g_c				
mm s^{-1}	0.81 (± 0.35)	0.51 (± 0.23)	3.00 (± 1.40)	4.47 (± 2.03)
$\text{mol m}^{-2} \text{s}^{-1}$	0.032 (± 0.014)	0.020 (± 0.009)	0.120 (± 0.056)	0.179 (± 0.081)
b	1.169 (± 0.009) d	0.652 (± 0.004) c	4.116 (± 0.023) b	6.415 (± 0.051) a
m	-0.921 (± 0.019) d	-0.531 (± 0.009) c	-3.278 (± 0.054) b	-5.395 (± 0.114) a
Soil water content ≤ 6 % DW				
Average g_c				
mm s^{-1}	0.60 (± 0.37)	0.18 (± 0.10)	0.32 (± 0.19)	0.50 (± 0.27)
$\text{mol m}^{-2} \text{s}^{-1}$	0.024 (± 0.015)	0.007 (± 0.004)	0.013 (± 0.008)	0.020 (± 0.011)
b	1.395 (± 0.025) a	0.335 (± 0.006) d	0.567 (± 0.016) c	0.933 (± 0.018) b
m	-0.879 (± 0.033) a	-0.220 (± 0.007) d	-0.404 (± 0.020) c	-0.623 (± 0.022) b

Different letters indicate significant differences between treatments within each period

the V_w was lower in the low than in high density plot trees (0.57 ± 0.01 vs. 0.48 ± 0.02 , respectively; $P = 0.025$) despite soil water content was near field capacity in both plots (Fig. 4). During the growing season, mean V_w ranged from 0.42 to 0.58.

Whole tree plant liquid phase hydraulic conductance (K_h) was higher in the biggest trees of the low density plot compared to all other tree groups (Fig. 6). However, the patterns are different if K_L is analyzed. During the humid part of the season, trees in the high density plot presented higher (but non-significantly) K_L than low density plot trees, whereas in the driest part of the season, only the biggest trees of the low density plot maintained K_L values similar to those of the humid period. The other trees showed a decrease in K_L to values of about 50 % of their original K_L . However, despite the relative decrease, K_L of high density plot trees was still similar to that of the biggest trees in the low density plot (Fig. 6).

Discussion

The results of this study showed that ponderosa pines growing at very different plantation densities present both short- and long-term responses to water shortage which depend on the general competition level (tree density) and the relative size of the tree within the stand. In this regard, different water relations (and growth) were observed comparing the smallest trees in the low density plot and biggest trees of the high density plot, which were very similar in size at the beginning of the study, but differed in their intraspecific competition level. The observed responses are discussed below, trying to understand their impact on tree growth and water use efficiency.

Short-term responses: stomatal control of water potential and hydraulic integrity

Based on ψ_{pd} measurements, it is clear that the trees in the high density plot experienced higher levels of drought stress than trees in the lower density plot, particularly during dry seasons (Figs. 4, 5), despite the fact that the soil water content was similar in both plots (considering the upper 80 cm of soil, above the clay pan). However, similar leaf water potential values were observed at midday (around -2 MPa) for all tree sizes and plantation densities. This is in agreement with the well-described isohydric behaviour of ponderosa pine (Piñol and Sala 2000; Magnani et al. 2002; Gyenge et al. 2003; Skov et al. 2004; Simonin et al. 2006), which implies strict stomatal control of leaf water potential and transpiration.

The different pre-dawn potential values of trees growing at different densities during the dry periods, as well as the different hydraulic conductance of trees (see below), determined differential stomatal responses to evaporative demand (g_c patterns), as well as in J_s and E . Only the biggest trees of the low density plot were able to maintain high water use and whole tree-hydraulic conductance throughout the growing season, even during the driest part of each season and the driest season itself. The limitation in gas exchange experienced by the trees in the high density and the smallest trees in the low density plot could lead to a negative carbon balance in those trees supporting the hypothesis of a decrease in their carbon reserves which could affect the present season growth (Ogle and Pacala 2009) as well as the initial growth in the next growing season (resilience after drought).

In agreement with the initial hypothesis about g_c , this variable was higher in trees at the high density in

comparison with trees at low density plot. However, this could be maintained only during a short period within the early growing season, characterized by high soil water availability. At that time, E_{leaf} and K_L were also highest in those high density plot trees. It appears that those trees have the strategy of using available resources as much as possible during the short time period when they are available (high spender strategy). In contrast, trees growing under lower competition levels (low density plot trees) exhibited a comparatively more conservative use of water, with low—but stable over time— gc values. This very different gc behavior may lead to different carbon fixation and growth patterns over time. Indeed, stem growth lasted longer in the biggest trees of the low density plot than in all other trees (Fernández et al. 2012).

On the other hand, the abovementioned short-term mechanisms were extremely efficient in preventing a dramatic decrease in branch V_w and k_s in response to soil dehydration. The same maintenance of hydraulic integrity is also expected for stem wood, as was suggested by Piñol and Sala (2000) comparing different species.

Long-term responses: allometric changes

Changes in $A_L:A_s$ ratio have been reported for ponderosa pine contrasting in size (e.g. Simonin et al. 2006), stand basal area (e.g. McDowell et al. 2006) and soil water availability (e.g. Callaway et al. 1994; Piñol and Sala 2000, Maherali and DeLucia 2001). The present study also showed this kind of quite long-term response to water balance in young even-aged trees growing in a common site but with very different competition levels. In this regard, a significant lower $A_L:A_s$ ratio was always observed in the smallest trees of the high density plot compared to all other trees, whereas the biggest trees of the same plots began to differentiate from those of the low density plot after a very dry season. As a whole, the main differences were observed between different stand density plots, with no size-dependent differences in the low density plot where water stress was not so marked. Those differences in $A_L:A_s$ ratio were due to both differential stem and leaf area growth rates (and mortality in the case of leaves) in the different density treatments.

As stated before, the more dramatic changes in $A_L:A_s$ ratio were observed in the smallest trees of the high density stand, and it would be important to determine the adaptive meaning of those whole-tree changes, i.e. whether the leaf area reduction (for a particular sapwood area) could lead to an advantage due to an increase in leaf specific hydraulic conductance of the tree, or whether it is simply the result of carbon imbalance with no positive income at all (i.e. Ogle and Pacala 2009). The suppression phenomenon driven by changes in the water balance of the tree responds not only

to the conditions of soil water availability but also the reduction of radiation reaching the crown. Therefore, the observed plastic changes, which may occur as an adaptive change in other contexts, may in turn favor a positive feedback leading to a faster plant dieback in the case of our study.

In contrast to the observed changes in the $A_L:A_s$ ratio, the A_L : diameter of the branches relationship appears to be a conservative ratio. In this regard, a similar A_L per unit branch area was estimated for branches (with diameter lower than 50 mm) of ponderosa pine trees growing in very different sites: another wetter site in NW Patagonia (Gyenge et al. 2009) and desert or humid sites in USA (Callaway et al. 1994). It seems that the leaf area adjustment is not at the branch level but at the stem level, with the ratio A_L : diameter at the base of the living crown (or dbh) being the plastic trait in this species.

In contrast to the results describing plastic responses of wood permeability (k_s) to site water balance in ponderosa pine (Maherali and DeLucia 2001), in the present study stem k_s was very conservative, with a trend of increased k_s in slow-growing trees of the high density plot. That k_s increase was, however, difficult to explain based on the wood anatomical analysis of those trees (Fernández et al. 2012). It seems that different threshold values of plant water balance trigger different plastic responses (leaf area vs. wood permeability) in the plant. Anatomical studies of the wood support these findings, indicating that the proportion of earlywood and latewood, as well as tracheid dimensions, were similar among different size trees growing at different plantation density (Fernández et al. 2012).

The higher gc values in trees of high than low density plot when soil water was relatively high may be explained, at least in part, by the observed changes in the $A_L:A_s$ ratio. In addition, ring wood k_s of some of the smallest trees at high density plot was also higher in all other trees, also contributing to an increase in leaf specific hydraulic conductance of the tree. Estimations of K_L (Fig. 6) are in agreement with this hypothesis, i.e. trees at high density plot showed the maximum values compared to trees at low density plot. However, it is important to note that Kh did not follow the same pattern, and at the whole tree level (and not per unit leaf area) the biggest trees at the low density plot were those with the highest capacity of moving water from the soil to the leaves throughout the growing season. If we consider the average of humid and dry periods, Kh was higher in the biggest trees of both treatments, followed by the smallest trees of the low density stand and finally, the smallest trees of the high density plot. These results allow us to understand the position of dominance over available water resources of largest trees of each stand.

Consequences of ecophysiological responses on water use efficiency and growth

The similar $\delta^{13}\text{C}$ between trees during the 2009–2010 season suggests that the observed changes in the smallest trees of the high density plot are sufficient enough to compensate for the decreased radiation availability for those trees, at least when no water availability is also limiting (wet season). Moreover, the differences in $i\text{WUE}$ during the dry year agreed with the positive relationship between $i\text{WUE}$ (estimated from ^{13}C) and growth described by Cregg et al. (2000). What could be the cause of such a decrease in $i\text{WUE}$ observed in water-stressed trees? Since the general relationship between $A_{\text{max}}:g_s$ was similar between trees growing at both plantation densities, but WUE changes at different g_s (Fig. 3), there are two possible causes of the observed differences: (1) the C used to build the wood ring in each treatment was fixed in different periods within the growing season (different C allocation patterns), or (2) even if the C is fixed in the same period and allocated to the same compartment (ring wood), g_c differences lead to differences in $i\text{WUE}$. Regarding the first possibility (1), several studies have highlighted the importance of carbon allocation patterns, including the dynamics of carbon reserves (e.g. Michelot et al. 2011), and internal C fractionation (e.g. Li and Zhu 2011) to be considered in order to interpret $\delta^{13}\text{C}$ results. Taking this into account, it is difficult to assign the apparent higher $i\text{WUE}$ observed in the drought year (ring 2007–2008) in less stressed trees (biggest trees of the low density plot) as compared to high-stressed ones (smallest trees of the high density plot) to a different behavior in response to the drought itself. On the other hand, considering g_c dynamics, it appears that g_s values of biggest trees of the low density plot were always around the g_s that optimizes $i\text{WUE}$ (around $0.03 \text{ mol m}^{-2} \text{ s}^{-1}$, see Fig. 3), whereas trees in the high density plot varied from very high to very low g_c values (0.18 to $0.01 \text{ mol m}^{-2} \text{ s}^{-1}$), resulting in lower $i\text{WUE}$. Differences between years can be explained by differences in soil water dynamics and VPD affecting g_c dynamics in each treatment. In this regard, this study has shown that the sensitivity of g_c to VPD depended on the treatment (through differences in maximum g_c) and soil water content. In addition, another factor must be added to WUE analysis: the amount of radiation reaching each tree. Canopy conductance patterns tell us about water vapor exchange dynamics, which are correlated to carbon dynamics if radiation availability is the same in all treatments. However, smallest trees of the high density plot received less radiation than all other trees (around 45 % of radiation in the canopy top), decreasing carbon fixation capacity for a given g_s value. This could also contribute to the ^{13}C -estimated low $i\text{WUE}$, at least in season 2007–2008.

Despite WUE maintenance, at least in the humid season, growth rates were significantly lower in the high density than in low density plot trees, possibly due to the reduction in tree leaf area. Therefore, the measured responses to seasonal drought were sufficient for $i\text{WUE}$ but not for absolute carbon gain maintenance in high density compared to low density plot trees. It is interesting to note the similarity of size between the biggest trees in the high density and the smallest trees in the low density plot at the beginning of the study, indicating that they had similar mean growth rates until that time. However, the first measurement season (2007–2008) was particularly dry compared to the historical mean, and the response of those trees began to diverge from then on. Finally, the higher g_c and K_L values of high density plot trees during the first part of the season (when available water was high) were not enough to develop stem and leaf growth rates similar to trees growing at low density plot.

From the management point of view, our results indicate that *P. ponderosa* trees growing in low density plantations—for standard values of Patagonian plantations—go through severe drought events with no severe impact on their water relations, particularly in the biggest trees of the stand, leading to quite stable annual leaf and stem growth rates. On the contrary, severe drought events have a marked impact on water relations (but hydraulic integrity of the tree is maintained), stem growth and leaf area (through leaf mortality), and probably non-structural carbon reserves, of trees growing under high competition level. This suggests that growth resilience of these trees would be lower compared to trees growing in low-density stands, making drought effects long-lasting. Further research is needed focused on resilience patterns and intra-specific competition thresholds that determine the observed responses to drought.

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Appendix 1

Canopy conductance

Canopy conductance (g_c , mm s^{-1}) was estimated according to Monteith and Unsworth (1990) as:

$$g_c = \frac{\gamma(T)\lambda(T)E}{C_p\rho(T)\Delta W} \quad (2)$$

where $\gamma(T)$ is the psychrometric constant (as a function of temperature T , kPa K^{-1}), $\lambda(T)$ is the latent heat of

vaporization of water (J kg^{-1}), E is transpiration expressed on A_L basis ($\text{kg m}^{-2}\text{s}^{-1}$), C_p is the specific heat of air, $\rho(T)$ is the density of the air (kg m^{-3}), and ΔW is the leaf-to-air vapor pressure difference (or gradient, kPa), assuming that leaf temperature was the same as air temperature.

Sensitivity of stomata to VPD

It was estimated following Oren et al. (1999) as:

$$gc = -m \ln(\text{VPD}) + b \quad (3)$$

where m is the stomatal sensitivity to VPD ($\text{mm s}^{-1} \ln(\text{kPa})^{-1}$) and b the reference gc at $\text{VPD} = 1 \text{ kPa}$ (mm s^{-1}). Parameters were estimated using least squares regression analysis. No lag time between sap flux data and VPD was observed, as was also reported in Fischer et al. (2002).

Specific conductivity of branch wood

Specific conductivity (k_s , $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$) is a measure of the hydraulic efficiency of a unit of xylem and is defined by Darcy's law as:

$$k_s = \frac{Ql}{A_s \Delta P} \quad (4)$$

where Q is the volume flow rate (m^3s^{-1}), l is the length of the segment (m), and ΔP is the pressure difference between the two ends of the segment (MPa). All conductivity calculations were corrected to 20°C to account for changes in fluid viscosity with temperature (Spicer and Gartner 1998). To determine k_s of branch wood, single branches (0.5–1 m long) from five trees growing at each density plot were excised in the afternoon (maximum VPD—maximum loss of k_s), sprayed with water and wrapped in plastic bags to avoid desiccation and the possibility of further k_s reduction by dehydration. In the laboratory, a segment from the middle of the branch was cut under water to avoid new embolisms and attached to the end of a transparent plastic hose. A 1-ml graduated pipette was attached to the other end of the hose, located 1 m above the branch sample. Volume flow rate was measured by timing the movement of the meniscus across 0.1 ml graduations. Repeated measurements on the same sample showed that direction of flow did not affect results.

Volume fraction of water in the xylem of the branch

Volume fraction of water (V_w) was determined in 4–5 cm long barked twig segments as:

$$V_w = \frac{W_f - W_d}{\rho_w W_f} \quad (5)$$

where W_f and W_d are the fresh and dry weight of segments, V_f is fresh volume (estimated from the length and the

average diameter of both ends), ρ_w is the density of water. Dry weight was determined after oven-drying the samples at 80°C for 48 h (see Borghetti et al. 1998). Sample weight was measured to the nearest 0.1 mg.

Whole tree plant liquid phase hydraulic conductance

Whole tree plant liquid phase hydraulic conductance (Kh , $\text{ml min}^{-1} \text{MPa}^{-1}$) was estimated as:

$$Kh = \frac{E}{\psi_{\text{soil}} - \psi_{\text{md}}} \quad (6)$$

where ψ_{soil} is the soil water potential (estimated from ψ_{pd}) and E is the average transpiration estimated from 14:00 to 19:00 h taking into account the radial sapflow decrease (Gyenge et al. 2003). Calculation of Kh was limited to those dates in which water potential was measured.

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