Effect of pruning on branch production and water relations in widely spaced ponderosa pines

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Abstract This study dealt with the effects of pruning on branch and leaf area (F_a) production of ponderosa pines growing in silvopastoral systems in Patagonia. We hypothesized that pruning positively influences the number of branches per whorl and their basal area growth rate, changing F_a production. In addition, we studied some water relations in order to explain potential differences in branch growth rates between treatments. Two mathematical models were developed to estimate branch and total F_a. The averaged diameter at the third year of pruning was, for high-pruned trees 3.1 and 3.6 cm at the bottom and middle of the crown, against 4 and 4.4 cm for low-pruned trees. Pruning did not produce changes in the number of branches per whorl (approximately 7.6 branches per whorl). Water stress may be responsible of this lower branch growth in pruned trees. Water potential, stomatal conductance and transpiration were lower in high- than in low-pruned trees.

Introduction

The presence of tree branches is one of several factors that affect the quality of final wood products. According to Mäkinen and Hein (2006), low stand densities may have negative effects on timber quality. These authors found that one the most pronounced effect of low stand density was the increase in branch diameter, particularly at lower crowns levels. In general, the diameter of the thicker branch in a crown increases with the distance from the apex. Mäkinen and Hein (2006) found that branch diameter of *Picea abies* (L.) Karst. did not differ in the uppermost crown among stand densities, but at the lower portion of the crown (the base of the crown), diameter of the branches was usually lower in trees growing at higher densities. On the other hand, Ishii and Wilson (2001) found that a model of crown structure developed for young trees could be fit to the upper crown of old-growth

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Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Based on these results, one may suppose that the pruning of the lower portion of the crown could result in branch diameter becoming independent of the stand density or age of the tree. However, depending on the ecophysiological capacities of the species, leaf area (F_a) production can increase in response to pruning, increasing also branch diameter in order to maintain an adequate supply of water to the leaves. In this sense, a trend (Gyenge 2005) or a significant higher F_a production (Montagu et al. 2003) were observed in pruned compared to unpruned trees. Based on the relationship between F_a and sapwood area of the branches, the potential increase in F_a growth after pruning could increase branch diameter or the number of branches, which can have important implications on wood quality.

From an ecophysiological point of view, in places without nutrient limitations, the amount of F_a developed in each branch depends on the availability of water (in soil and for the leaves) and solar radiation. The maximum F_a supported by each branch depends on its diameter, which is related to the specific water conductance of the wood ("pipe theory", e.g., Callaway et al. 1994). On the other hand, F_a depends on the amount of solar radiation reaching each branch, which decreases by the interception of the upper branches (Stenberg et al. 1998). For this reason, the effect of tree spacing in F_a distribution along the canopy depends on the shade tolerance of leaves of each species, but also on tree size and age (see Garber and Maguire 2005a). Following a green pruning, some species can increase photosynthesis of the remnant F_a by the increase of stomatal conductance (gs) (Pinkard et al. 1998, Pataki et al. 1998). This can occur if the remnant conducting tissue of the stem (which before the pruning, was conducting water to the pruned branches) can supply water to the remnant foliage. Other species tend to compensate for leaf loss by producing more foliage after pruning (e.g., Montagu et al. 2003). In both cases, an imbalance between green and respiratory organs can lead to significant reduction in growth if the extracted F_a exceeds the compensatory mechanisms. This threshold depends on the interconnection between tracheids or vessels inside the hydroactive xylem (Schulte and Brooks 2003), and the plantation density and/or the degree of canopy closure (Pinkard 2002). For these reasons,

the impact of green pruning on growth depends on the interaction between physiological characteristics of each species and resource availability. In addition, the duration of the impact of pruning depends on the capacity of the tree to reach carbon and water equilibrium between above- and below- ground components of the plant (functional homeostasis, Magnani et al. 2002).

Traditionally, the most important economic activity in semi-arid Patagonia (South Argentina) has been sheep livestock. Presently the sustainability of livestock production systems is threatened by desertification, with its negative effects on pasture quality and quantity. Recently, forest plantations based on fast growing species have been promoted through a subsidy policy in the country. In Patagonia, the exotic ponderosa pine (*Pinus ponderosa* Doug. ex Laws) is the species most commonly planted. In all cases, pine plantations have been designed to produce wood, and thus, have been planted at high densities. However, considering cultural, economic and environmental aspects, silvopastoral systems (SPS) may be an interesting alternative for small and medium land-owners in semiarid Patagonia. For this reason, since 1998 some studies have been carried out in this region to determine the feasibility of SPS using low density ponderosa pine plantations and native grasses (e.g., Fernández et al. 2006). Those studies reported results considering the forage component of the systems but no information is available about pine performance under these conditions.

The primary objective of this study was to test the hypothesis that pruning in pines growing in low density plantations positively influences the number of branches per whorl and their basal area growth rate, increasing branch diameter even in positions closed to the apex compared to unpruned trees. Also, pruned trees would have a higher increment of F_a annual production than unpruned ones. If our hypothesis is correct, then the upper part of the crown of a pruned tree will be different than that of an unpruned tree, and different canopy models have to be developed for different pruning schedules. In addition, we aimed to understand the role of water relations in branch growth rate of low- and high-pruned trees. To test our hypothesis, we used ponderosa pines growing in SPS in N.·W. Patagonia as a study case.

Materials and methods

Study site and experimental treatments

The study site was located in Lemú Cuyén Ranch (40.3°S, 71.1°W, 900 m of altitude) in Neuquén Province, Patagonia, Argentina. The climate of the region is characterized by cold and humid winters, and hot and dry summers. During the period 1978–1999 average annual rainfall was 684 ± 283 mm (with approximately 579 mm in fall-winter and 105 mm in spring–summer). Maximum and minimum annual average temperatures are $17.1°C \pm 0.5$ and $4°C \pm 2.1$, respectively. The soil is a silty clay loam, with 27–40% silt and 20% clay (A. Marcolín, personal communication, 1998).

All measurements were carried out in a plantation of ponderosa pine established in 1985 (approximately 15 years old from plantation at the beginning of the experiment). In a stand of 2 ha with an original density of 500 trees ha^{-1} (500 SPS), ten study plots (40×40 m each) were randomly distributed in winter 1999. This trial was used to investigate several aspects of tree and forage performance in SPS (reported in Fernández et al. 2006), but for the purpose of this study, we only measured trees growing at 500 pines ha^{-1}. Average tree height and diameter at breast height (dbh) at the beginning of this experiment (winter 1999) were 7.77 ± 0.31 m ($\pm$E.E, $n = 163$) and 21 ± 0.61 cm, respectively. At that time, all the trees growing at similar density in a contiguous stand, were pruned at 3 m height. After that, pines of three plots of the silvopastoral system were pruned again to 4.5 m height in winter 2001 and 2003 (Trees #7–14 and #17–20, Table 1). In winter 2004, trees growing in the contiguous stand were pruned to 6.5 m (trees # 1–6, Table 1). Trees pruned at winter 1999 are referred to "low-pruned", whereas those trees pruned at winters 2001 and 2003 are called "high-pruned" trees. A detailed description of

Table 1 Characteristics of the trees used to develop a predictive equation of F_a (m^2) based on dbh (diameter at the breast height, cm) or DLC (diameter at the living crown, cm) and ecophysiological measurements

Tree number	DLC	Dbh	F_a	Year of pruning	Pruning height	Observation
1	22	31.5	84.02	2004	6.5	Contiguous stand
2	15	22.7	24.196	2004	6.5	
3	20.6	31.4	63.071	2004	6.5	
4	16.7	27	51.866	2004	6.5	
5	21.9	33.3	73.362	2004	6.5	
6	21	31.7	60.489	2004	6.5	
7	19.4	29.4	67.38	2003	4.5	SPS stand
8	19.5	28.6	90.716	2003	4.5	
9	19.1	30.8	64.079	2003	4.5	
10	17.5	27.2	49.808	2003	4.5	
11	22.4	32.4	93.157	2003	4.5	
12	22.9	27	69.266	2003	4.5	
13	25.2	32.7	118.07	2001	4.5	
14	15.9	21.2	46.901	2001	4.5	
15	28.7	28.7	140.254	1999	3	
16	27.3	27.3	97.702	1999	3	
17	22.3	28.3	82.856	2001	4.5	SPS stand, high-pruned
18	20	24.8	76.093	2001	4.5	High-pruned
19	19.3	21.6	50.433	2001	4.5	High-pruned
20	24.8	26.4	79.364	2001	4.5	High-pruned
21	26.7	29.1	132.179	1999	3	Low-pruned
22	30.4	30.4	103.909	1999	3	Low-pruned
23	26.7	26.7	120.797	1999	3	Low-pruned
24	25	26.7	109.963	1999	3	Low-pruned

Trees #17–24 were used to estimate branch diameter, leaf annual production, number of branches per whorl, ecophysiological measurements

SPS, silvopastoral system, 500 trees ha^{-1}

these trees is shown in Table 1. Measured trees were randomly selected in each plot.

Leaf area model

The relationship between F_a and the diameter of each branch (DIAM) at 5 cm from the insertion of the branch was estimated for ponderosa pines growing under the situations described in the previous section. During three successive winters (2001–2003), we harvested one randomly selected branch from the top, middle and bottom of tree crowns from the silvopastoral system. One model for each year was developed and compared using F-tests with $\alpha = 0.05$ (Neter and Waserman 1974). 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 F_a. Total surface (A) of the fascicles was estimated using geometric formulae representing the fascicle as six rectangular surfaces with side r and length ℓ (area $= r\ell$), and an external cylinder (area $= 2\pi r\ell$). Combining the formula for six rectangular surfaces plus a cylinder, A of the fascicles was:

$$A = 12.28\pi\ell\left((r1 + r2 + r3)3^{-1}\right)$$

After that, fascicles were oven dried and weighted. Total F_a of each branch was estimated from dry weight of all fascicles and the ratio F_a: dry weight of the sub-sampled fascicles.

In order to develop a simple predictive model of F_a of the entire tree, in winter 2004 we measured the DIAM of all branches, the diameter of the stem at the base of the living crown (DLC) and dbh of several trees growing at silvopastoral system and in a contiguous stand (Trees #1 to #16, Table 1). We also used data from the 8 pines (F_a and DLC) in which we measured annual F_a production (trees #17 to #24, see below). These last trees were not used to build the equation for F_a estimation from DIAM.

Branch diameter and leaf annual production

We measured DIAM of all branches of the same low-pruned (pruned at winter 1999) and high-pruned trees (pruned in winter 2001) during years 2002 ($n = 6$), 2003 and 2004 ($n = 8$). These trees were numbered #17–24 (Table 1). The information was used to determine mean and maximum diameter in each whorl, and the number of branches per whorl. Whorl 1 was the closest to the apex of the tree. Data of successive years were used to estimate basal increments (branch growth rates) and leaf annual production after deducing F_a from branch DIAM with the previously determined leaf area model.

ANOVA tests were used to compare mean diameter and mean maximum diameter of each whorl between high-pruned and low-pruned trees. Also, we analyzed statistical differences using t-tests between high- and low-pruned trees in averaged diameters of branches grouped in three layers in each tree: top (first 3 whorls), bottom (last 4 whorls with green needles) and middle (remnant branches not included in the other two categories). The number of branches per whorl was analyzed using t-tests comparing the top, middle and bottom layers of high- and low-pruned trees at the end of the experiment (year 2004). When necessary, data were transformed to agree with the normality and homocedasticity assumptions of ANOVA.

Ecophysiological measurements

In order to detect if pruning treatment had an effect on tree water relations, some ecophysiological variables were studied at the leaf and tree levels during the driest period of the year 2002 (end of summer, February-March) in the same trees in which we measured branch and leaf annual production. This period was the first dry period after the pruning treatment.

At the leaf level, we measured during February-21-2002, leaf water potential (Ψ, in MPa; at predawn, 10:00, 13:00 and 16:00 h) and stomatal conductance (gs, mol m^{-2} s^{-1}, at 10:00 and 13:00 h) of one-year old needles (three fascicles) located in the north-faced part of the crown (4.5 m height) of four trees of each treatment. Stomatal conductance was measured with a LICOR 6200 system (Infra-red gas analyzer System, Li-Cor Co., USA). After that, Ψ of the same needle was measured with a pressure chamber (PMS Instrument Company, Corvallis, OR, Model 1003). Daily course

of both variables were analyzed by repeated measures ANOVA. In addition, during 3 days of the same dry period (Feb-12, Feb-22, and March-12 of 2002) we measured Ψ at predawn. One way ANOVA was used, after transformation to the reciprocal of each value, to compare predawn Ψ of low- and high-pruned trees within each measurement date.

At the tree level, we measured xylem sapflow density (Js, ml cm^{-2} min^{-1}) using 2 cm-long heated sapflow sensors (Granier 1985) from February to March 2002 and the same period in 2003. This variable was measured in the 8 low- and high-pruned trees in which measured leaf and branch annual production. Two pairs of sensors were installed on the southeast and southwest sides of the trunk of each tree, surrounded with a shield to eliminate bias caused by radiation heating. Measurements were automatically taken every 10 min and stored in a data-logger (IMKO GMBH, Ettlingen, Germany) for further processing. The characteristics of the measured trees are shown in Table 1. The sample unit was each tree (average of the two pairs of sensors). Daily transpiration of each tree was estimated multiplying Js by the sapwood area of each tree, taking into account the decrease of Js in the radius of the trunk according to the formula proposed by Irvine et al. (2002) and validated in Gyenge et al. (2003). This author estimated a decline of sap flux density with sapwood depth with a linear function of sapwood depth: % sap flux density = -0.691 * sapwood depth + 100.99, r^2 adj. = 0.99, $P < 0.01$. Therefore, this relationship was used to extrapolate sap flux density as determined over 0–20 mm sapwood depth to the remainder of the xylem.

Climate data were recorded with an automatic meteorological station located, for security reason, 3 km away from the experimental site, in the same valley. In order to check the assumption that meteorological conditions were similar in both places, we performed simultaneous measurements. The results showed similar meteorological conditions (Licata 2007). Data were collected every 5 min and the 30 min averages were stored in a data logger (Campbell CR10X, Campbell Scientific Inc., Utah, USA). Vapor pressure deficit (VPD, kPa) was estimated from temperature and relative humidity of the air assuming that the leaf has the same temperature as the air (Ewers and Oren 2000).

Results

Leaf area model

The harvested branches had 1–7.5 cm of DIAM. No statistical differences were found between the models developed for each year ($P > 0.05$). The relationship between F_a (m^2) and DIAM (mm) was (parameter $\pm$ S.E., $n = 39$, $P < 0.05$, R^2 adj 0.87, Fig. 1):

$$F_a = 0.0142\,(\pm 0.1268) + 0.001\,(\pm 6.29\text{E}{-}5)\text{DIAM}^2 \tag{1}$$

Using equation 1, we estimated that a difference in pruning height of 1.5 m (3–4.5 m of the crown base height) represented, on average, a 40% in F_a between treatments. On average, F_a was 94 and 55 m^2 in low- and high-pruned trees.

For comparison purposes, the models developed by Callaway et al. (1994) for two populations of ponderosa pine growing in a humid place (mountain, 950 mm annual precipitation) and in a drier site (desert, 450 mm) in native forests in USA are also shown in Fig. 1. Estimations of F_a from the model (1) are similar than those obtained using a model developed for ponderosa pines growing in humid places in USA (Callaway et al. 1994, Fig. 1). In contrast, the model predicts higher F_a in thicker branches (diameter higher than 47 mm, Fig. 1) than the model developed for ponderosa pines growing in desert places (Callaway et al. 1994).
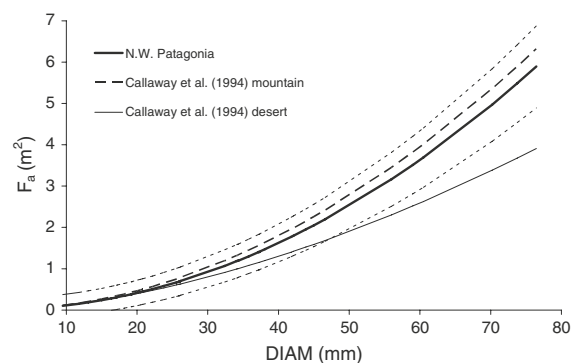

Fig. 1 Relationship between diameter at 5 cm from the insertion of the branch (DIAM, mm) and foliar area (F_a, m^2) of ponderosa pine trees growing at 500 trees ha^{-1} in Patagonia Argentina (mean values and 95% confidence interval (*dotted thin line*), $F_a = a + b$ DIAM^2, $n = 39$, $P < 0.05$, R^2 adj 0.87) and of pines growing in different places in USA (data from Callaway et al. 1994)

When relating diameters of the bole with total F_a of the crown, due to the shape of the bole, a closer relationship was found using DLC (cm) than dbh of the tree (Fig. 2). The model obtained was (parameter ± S.E., $n = 24$, $P < 0.001$, r^2 adj 0.75):

$$F_a = -56.19\,(\pm 16.60) + 6.22\,(\pm 0.74)\text{DLC} \qquad (2)$$

Branch diameter and leaf annual production

Maximum diameters were found from 7th to 12th whorl (Fig. 3). Mean maximum diameter of branches was approximately 5.5 cm (values found in the 6th whorl, Fig. 3). No differences were observed between mean diameter and mean maximum diameter of branches in each whorl comparing trees of the different plots at the beginning of the experiment ($P > 0.05$, Fig. 3 a, b). In following year, significant differences occurred in mean diameter and mean maximum diameter between low- and high-pruned pines in whorl 6 ($P = 0.038$ and 0.0322, respectively) and only in mean diameter at whorl 7 ($P = 0.018$). Surprisingly, in all cases, diameters were higher in low-pruned than in high-pruned trees (data not show). At the end of 2004, low-pruned trees had, comparing the same whorls, higher diameters of branches than high-pruned ones ($P < 0.05$, Fig. 3c, d) in 5th and 7th whorls (mean diameter) and in 2nd and 4th whorls (mean maximum diameter).

In addition, when we grouped the whorls in three layers (top, middle and bottom), mean branch diameter of low-pruned trees at the middle and bottom of
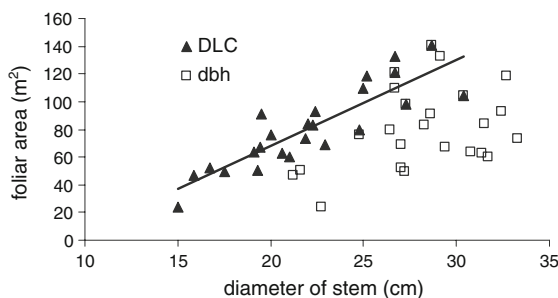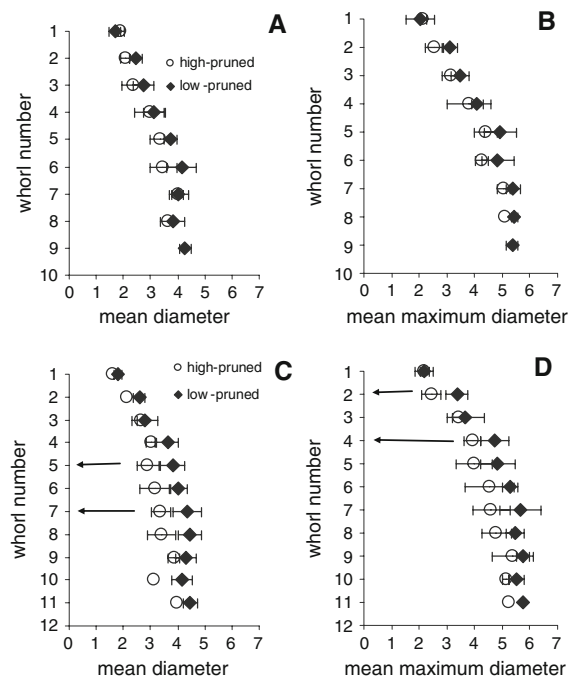

Fig. 3 Branch mean diameter (cm ± SD, **a** and **c**) and branch mean maximum diameter (cm, **b** and **d**) of branches in each whorl (1 = top of the tree) at the beginning (**a** and **b**) and at the end of the study (**c** and **d**) in ponderosa pine trees growing at 500 trees ha^{-1} in Patagonia, Argentina. The values are the average of three trees in **a** and **b**, and four trees in **c** and **d**. The arrows indicate significant differences between treatments ($\alpha = 0.05$). High- and low-pruned referred to pines with 4.5 and 3 m of pruned height (see Table 1)

the canopy was higher than branches of the high-pruned trees at the third year after pruning (Table 2).

In contrast, no differences were found in the average number of branches per whorl between trees and at different heights in the crown (7.6 branches per whorl, Table 3). Maximum and minimum average number of branches per whorl was 8.8 and 6.8, respectively (Table 3). However, the lack of statistical differences could be due to the high variability in the number of branches of high-pruned trees, which presented higher values at the top and middle of their canopy (Table 3).

High-pruned trees showed lower annual basal area increment of branches than low-pruned ones. This explains the lower diameters of branches at the end of the experiment in the high-pruned pines. In this sense, branch basal area increment was 20 against 40 cm^2 year^{-1}, in high- and low-pruned pines, respectively (Fig. 4). The highest branch diameter

Fig. 2 Relationship between leaf area (F_a) of the whole crown and diameter at breast height (dbh, $n = 24$, $P = 0.06$, R^2 adj 0.11) and at the base of the living crown (DLC, $n = 24$, $P < 0.001$, R^2 adj 0.75) in ponderosa pine growing at 500 trees ha^{-1} in Patagonia, Argentina. Adjusted equation: a + b (dbh or DLC)

Table 2 Average of branch mean diameter ($\pm$S.D., cm) and branch mean maximum diameter (cm) of branches situated at the top (first three whorls), bottom (last four whorls) and middle (remnant branches not included in the first two categories) of the ponderosa pine canopy growing at 500 trees ha^{-1} in Patagonia, Argentina

Year	Treatment		No. trees (whorls)	Position in the crown		
				Top First three whorl	Middle	Bottom Last four whorls
2002	High-pruned	Branch mean diameter	3 (8)	2.10 (0.23)a	2.98[a]	3.62 (0.28)a
		Branch maximum diameter		2.61 (0.52)	3.80[a]	4.70 (0.43)
	Low-pruned	Branch mean diameter	3 (9)	2.30 (0.54)a	3.43 (0.43)	4.06 (0.20)a
		Branch maximum diameter		2.87 (0.74)	4.52 (0.59)	5.26 (0.28)
2003	High-pruned	Branch mean diameter	4 (10)	2.25 (0.45)a	3.06 (0.27)a	3.53 (0.40)a
		Branch maximum diameter		2.78 (0.81)	4.08 (0.47)	5.05 (0.37)
	Low-pruned	Branch mean diameter	4 (10)	2.37 (0.51)a	3.78 (0.44)a	4.12 (0.35)a
		Branch maximum diameter		3.00 (0.73)	4.82 (0.67)	5.30 (0.39)
2004	High-pruned	Branch mean diameter	4 (11)	2.12 (0.51)a	3.11 (0.20)a	3.59 (0.40)a
		Branch maximum diameter		2.69 (0.67)	3.96 (0.36)	4.83 (0.38)
	Low-pruned	Branch mean diameter	4 (11)	2.39 (0.54)b	3.96 (0.31)b	4.34 (0.14)b
		Branch maximum diameter		3.08 (0.78)	5.13 (0.43)	5.63 (0.15)

Different letters indicated statistical differences between treatments in each year (*t*-test, $\alpha = 0.05$). High- and low-pruned referred to pines with 4.5 and 3 m of pruned height (see Table 1)

[a] Only 1 whorl

Table 3 Average number of branches ($\pm$SD) situated at the top (first three whorls), bottom (last four whorls) and middle (remnant branches not included in the first two categories) of the ponderosa pine canopy growing at 500 trees ha^{-1} in Patagonia, Argentina measured during 2004

Treatment	Position in the crown		
	Top First three whorl	Middle	Bottom Last four whorl
High-pruned	8.8 (3.8)	7.7 (3.6)	7.8 (0.84)
Low-pruned	7.1 (0.5)	6.8 (0.3)	7.6 (0.85)

High- and low-pruned referred to pines with 4.5 and 3 m of pruned height (see Table 1)

growth rates were observed in the first eight whorls in both treatments.

As in model (1), F_a estimation depends on DIAM, leaf area growth followed the diameter growth patterns of branches. However, there were no significant differences between annual F_a increment between treatments, probably due to the high variability within low-pruned trees (12.7 ± 3.3 and 21.2 ± 7.9 m^2 year^{-1} for high- and low-pruned trees, respectively). When relative annual increment is considered, high-pruned trees produced more leaf area, compared to the initial area they have, than low-

pruned trees. In this regard, a certain degree of compensatory leaf growth was observed.

Ecophysiological measurements

Pre-dawn water potential was measured in three days within one growing season. The first 2 days of measurements were within a period of high VPD values (average of 2.6 k Pa, with maximum values of 4.5 kPa), and low soil water content before the rain event of late February 2002 (Fig. 5). The last day of measurement (in March) was after small rains events typical of early autumn in the studied region. Stomatal conductance and leaf water potential along the day were also measured in one day within the first dry period. Comparing low- and high-pruned trees, the daily pattern of leaf water potential was marginally non-significantly different (Repeated measures ANOVA, $P = 0.057$). However, Tukey HSD test applied for each hour indicated that Ψ at predawn and at 16:00 h (maximum evaporative demand) were lower in high-pruned than in low-pruned pines ($P = 0.006$, Fig. 6). Stomatal conductance was also lower in high-pruned than in low-pruned trees ($P = 0.0004$), and decreased in all trees from 10:00

Fig. 4 Annual basal area increment (cm^2 year^{-1}) of branches during two consecutive growing seasons in ponderosa pine growing at 500 trees ha^{-1} in Patagonia, Argentina. High- and low-pruned referred to pines with 4.5 and 3 m of pruned height (see Table 1)
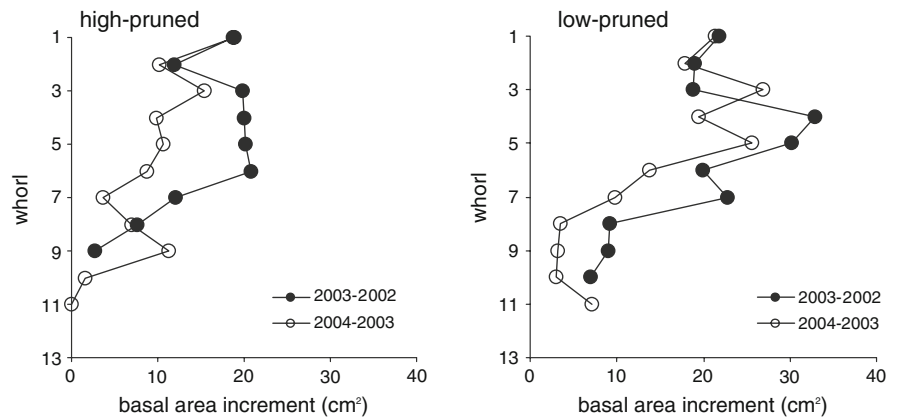
to 13:00 h (Fig. 6) in correlation with the decrease in Ψ (Fig. 7). Stomatal conductance of low-pruned pines at 13:00 h was similar than the gs of high-pruned pines at 10:00 h. Predawn Ψ values during the season were lower in high-pruned trees than in low-pruned trees ($P < 0.05$) during the dry period, and no significant differences were observed in March ($P = 0.338$) when 20 mm of precipitation fell some days before the measurement date.

The amount of water used by each tree (liters day^{-1}) in both years depended positively on F_a (Fig. 8a). High-pruned trees were those with lower F_a (empty symbols in Fig. 8a). However, when daily water use was normalized by F_a (Fig. 8b, liters day^{-1} m^{-2}), trees with lower F_a (high-pruned trees) were those which used relatively more water. Within each year, the relationship between daily water used per m^2 of leaf area and F_a of the tree was described

by the same general formula $y = a + b\, F_a^3$, but with different parameter values ($n = 6$, $P < 0.1$, Fig. 8b).

Maximum water used per unit of F_a, under the measured climatic conditions, was near 0.7 l day^{-1} m^{-2} (Fig. 8b), and this value decreased with total F_a of the trees. The form of the equation indicated a fast saturation response as F_a decreases, which does not allow for a compensation in water use (and maybe in carbon fixation) when some amount of foliar area is removed by pruning.

Discussion

Leaf area model

Estimations of F_a from the model (1) are similar than those obtained using a model developed for

Fig. 5 Daily Precipitation (mm), averaged air temperature (°C) and vapor pressure deficit (VPD, kPa*10 for the scale) of January to March 2002 in ponderosa pine plantation growing at 500 trees ha^{-1} in Patagonia, Argentina. Stars indicate the day in which leaf water potential were measured
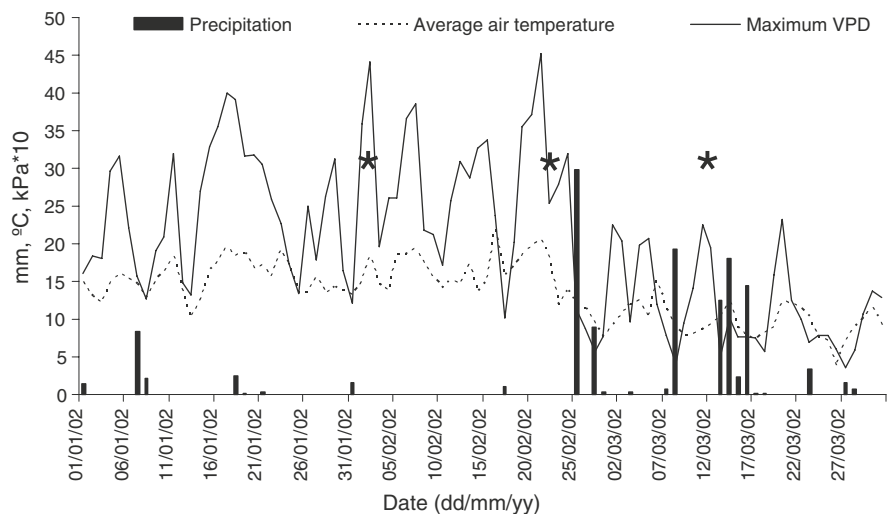
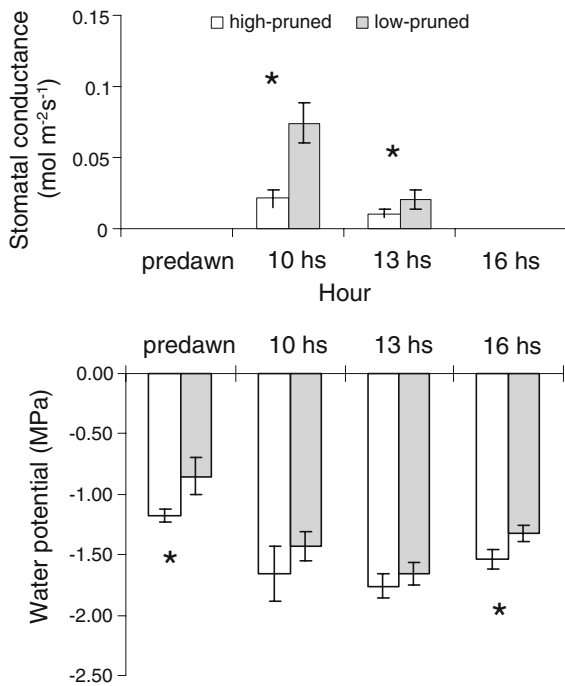**Fig. 6** Daily pattern of stomatal conductance (gs ± SD) and leaf water potential (±SD) at 4 h during one sunny day (Sep-21-2002) in ponderosa pine trees growing at 500 trees ha^{-1} in Patagonia, Argentina. Stars indicate statistical differences between low- and high-pruned trees ($\alpha = 0.05$). High- and low-pruned referred to pines with 4.5 and 3 m of pruned height (see Table 1)
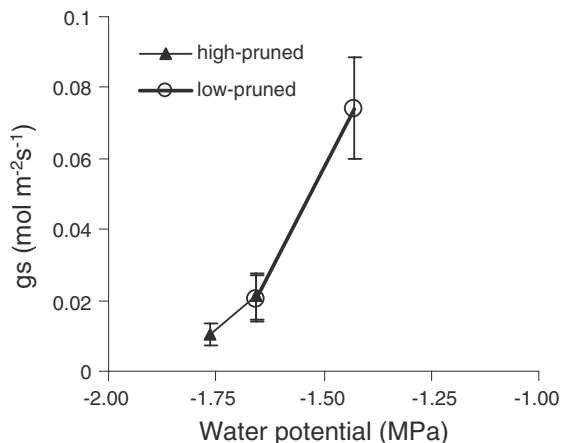

Fig. 7 Relationship between stomatal conductance (gs ± SD) and leaf water potential of low- and high-pruned trees in ponderosa pine growing at 500 trees ha^{-1} in Patagonia, Argentina. High- and low-pruned referred to pines with 4.5 and 3 m of pruned height (see Table 1)

ponderosa pines growing in humid places, but differed with the model developed from ponderosa pines growing in desert places in USA (Callaway et al. 1994). These results suggest that thin branches of ponderosa pine maintain a similar relationship between DIAM and F_a among different environments, and probably, among different ages. However, as drought stress increases, this relationship changes for thick branches (higher than 47 mm) and relatively more sapwood is needed to provide water to the foliage. Considering that in general the upper branches of the pines are the thinnest ones, it is possible that the upper crown of ponderosa pines are similar in different environments and tree ages, as was also found for Douglas-fir (Ishii and Wilson 2001). On the contrary, differences in this relationship in the branches below certain threshold in the crown are expected in trees growing in sites with different water balances. In the particular case of the studied SPS (500 pines ha^{-1}), average diameter of all branches was lower than the threshold diameter value at which the relationship F_a:DIAM changes, whereas maximum diameter of the branches at the middle of the canopy was higher than that DIAM value (Table 2). These observations could give an opportunity to develop a general model for F_a estimation in ponderosa pine, at least restricted to branches with a diameter lower than 4.7 cm.

Model (2) is based on the pipe theory. The pipe model theory emphasizes the importance of the sapwood as conductive tissue, but also the mechanical support function of stems. Kantola and Mäkelä (2004) found that at the tree-level the pipe model ratios were found to be very stable, and this could be independent of site quality, age or crown class in the case of *Picea abies* (L.) Karst. In contrast, Maherali and DeLucia (2001) found that ponderosa pines acclimate to sites with different water balances changing the relationship between F_a and conducting tissue, as was observed in this study compared to data of thick branches of pines growing in desert places. Thus, it is expected that the relationship F_a:DLC changes with site quality in this species. Zhang et al. (2004) found that cultural treatments (fertilization, complete vegetation control) have significant impacts on foliage biomass growth. However, DLC is closely related to current crown status regardless of cultural treatments, and for this reason, is a more robust predictor of the leaf area than dbh, as was found in
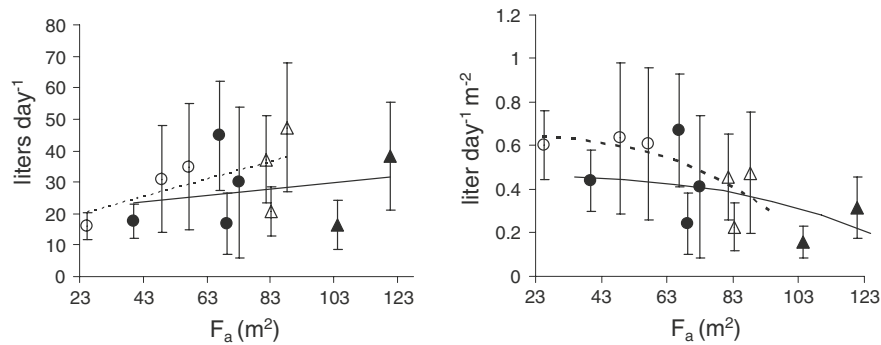
Fig. 8 Water used at individual (liters day^{-1}, ±SD) and normalized by leaf area (liters day^{-1} m^{-2}, F_a) by low- (*circles*) and high- pruned trees (*triangles*) during the driest part of the summer of 2002 (*empty symbols*) and 2003 (*filled symbols*) in

ponderosa pine trees growing at 500 trees ha^{-1} in Patagonia, Argentina. High- and low-pruned referred to pines with 4.5 and 3 m of pruned height (see Table 1)

this study. For management purposes, DLC is easier to measure than crown height or length. A model of F_a based on DLC measurements could be useful in order to develop pruning schedules based on size crown and also, on an ecophysiological basis. For example, several management programs indicate that the pruning must be done at a height in which the stem has a particular diameter, independently of site quality (e.g., Kurtz and Ferruchi 2000). As plant performance (i.e., growth, transpiration, CO_2 assimilation) is related to resource availability, the threshold diameter might be estimated and optimized.

Branch diameter and leaf annual production

The primary objective of this study was to test the hypothesis that pruning in pines growing in low density plantation positively influences the number of branches per whorl, the basal area growth rate of each branch, increasing the branch diameter even in positions closed to the apex. Firstly, green pruning had no effect over the number of branches per whorl (average of 7.7 branches per whorl). This lack of differences in the number of branches per whorl was also observed in a study in that were compared trees growing at different stand densities (Mäkinen and Hein 2006). However, the higher variability in the number of branches per whorl observed in the high-pruned trees at the top and middle of the canopy, suggests an effect of green pruning in our study. More information is needed in order to validate this hypothesis. In addition, we found trends that support the idea that pruning influences vertical distribution

of branch basal area and F_a, but only in the middle and bottom of the crown. Branches situated at the top of the canopy (thinner branches) were similar between trees independently of the treatment. As the size of the thickest branch of the tree determines the log grade, in the case of the studied pines the pruning of branches downward 8th whorl would not increase log quality.

Other studies have shown that the negative relationship between tree density and maximum branch diameter could be explained by the amount of radiation reaching each canopy layer (Stenberg et al. 1998). Below a certain threshold of radiation level, survival of leaves decreases and also, the increment of branch sapwood area does decrease. Accordingly, branch diameter profile may have a peak near the level of maximum lateral extension of the crown (Mäkinen and Hein 2006; Garber and Maguire 2005a). Garber and Maguire (2005a) found that foliage amount (and thus, branch diameter) in lower crown positions is largely influenced by the degree of light attenuation imposed by shoots at higher crown position. In a similar way, trees in a superior social position (tallest trees) have greater maximum branch diameters (Garber and Maguire 2005b). Also, in old growth Douglas-firs, the minimum relative level of photosynthetically active radiation was found in the same height of the crown where a marked decrease of live branch biomass was found (Ishii and Wilson 2001). Based on this knowledge, branches of trees growing in SPS could reach diameters that would decrease log quality. However, successive pruning may solve this problem

even decreasing annual branch diameter growth (see below).

In general, the upper part of the crown is the most important regarding carbon assimilation, and, without pruning treatments, it seems to remain similar in shape and size between older or greater and smaller conifer tree. Several studies have shown that thinning or water availability do not produce changes in the upper part of the canopy. In this regard, Mäkinen and Hein (2006) and Kantola and Mäkelä (2004) found that for the first five whorls or meters down to the crown, branch size of P. abies did not differ between thinning intensities or ages. However, our results indicate that branches at the middle of the crown (whorl 5th and 7th) have a higher diameter growth in low-pruned than in high-pruned pines. Differences in branch diameter at the middle and bottom of the canopy between pruning treatments were also found when whorls were grouped in three main layers, being higher in low-pruned trees. This was an unexpected result. A possible explanation of the decrease in growth can be derived from an ecophysiological point of view. In this regard, hydraulic limitations could be responsible to the decrease in branch growth rate of the high-pruned trees: cavitation of sapwood by air ingression (Ueda and Shibata 2000), root death (Schroth 1999), and/or partial constriction in the base of the branches may limit hydraulic conductance of the tree (Schulte and Brooks 2003) (see below).

Ecophysiological measurements

The negative effect of high pruning on growth points out the low capacity of ponderosa pine to compensate for loss of leaf area. Our data suggest that high-pruned trees experiment more water stress than low-pruned ones, at least during periods of high evaporative demand and low soil water content (see predawn water potential in Fig. 5). Minimum Ψ values reached by leaves of the trees of both treatments agreed with the lower water potential values measured in other studies in N·W. Patagonia (Gyenge et al. 2003), indicating a stomatal regulation of water loss (Grulke and Retzlaff 2001; and see functional homeostasis, Magnani et al. 2002). An increase in stomatal resistance also means a decrease in carbon fixation capacity. In this regard, Grulke and

Retzlaff (2001) demonstrated a stomatal limitation on photosynthesis of ponderosa pine when gs decreased below 0.08 mol m^{-2} s^{-1}. The low gs values of high-pruned trees during the day (Fig. 6) suggest lower photosynthesis rates, which may explain the observed lower growth rates of branches. A similar decrease in growth rate was detected at the stem level (Gyenge 2005). However, in contrast to what was observed in branch growth, in the case of the stem, a decrease in growth rate was only measured the first growing season after pruning and not later. Future research is needed considering the effects of water stress in different periods after pruning and the causes why different tree organs are affected differentially.

Pruning of branches at the bottom of the canopy decreased whole tree transpiration (Fig. 7a) in spite of a certain degree of compensation (higher water used per unit of F_a in high-pruned tress, Fig. 7b). This is a normal response. A linear relationship between water use and F_a was also observed in Pinus radiata D. Don (Teskey and Sheriff 1996) and several Eucalypts species (Hatton et al. 1998). However, the degree of pruned F_a and the decrease in water use were not linearly related, depending this relationship on the degree of compensation. In this regard, full compensation was observed in P. taeda after a 55% of extracted F_a (Pataki et al. 1998), and therefore all trees used similar amounts of water even with such a degree of F_a reduction. In this study, ponderosa pines showed a 10% difference in water use (lower in high-pruned pines) between high- and low-pruned pines differing in 25–40% of F_a. These results suggest a lower compensatory capacity after pruning of ponderosa pine compared to other Pinus species. In this sense, ponderosa pine seems to be very susceptible to pruning, at least, in annual dbh growth (Mowat1947; Gyenge 2005).

Conclusions

In contrast to what was expected at the beginning of the study, pruning treatments applied to ponderosa pines growing in low density plantations did not result in higher branch diameters maybe due to a low hydraulic compensation capacity of the species. Higher water stress was detected in high-pruned pines compared to low-pruned trees, which may

explain the observed differences in branch diameter growth between treatments, as well in stem growth. However, fortunately, differences in branch growth lasted for more years after pruning than differences in stem growth. Future research is needed to elucidate how ponderosa pines respond to pruning in sites with different water balances as well with different stand densities. In addition, further study is needed on the trade-off between losses of stem growth and gains in bole wood quality as a consequence of different amounts of extracted F_a in these plantations characterized by relatively short rotation periods.

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