

# Testing a hypothesis of the relationship between productivity and water use efficiency in Patagonian forests with native and exotic species

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## Abstract

The resource use efficiency, the relationship between productivity and the amount of used resources, have been proposed to increase as forests increase their productivity and rate of resource use (Binkley, D., Stape, J.L., Ryan, M.G., 2004. Thinking about efficiency of resource use in forests. For. Ecol. Manage. 1–2, 5–16). To test the generality of this hypothesis, we estimated annual productivity and water use efficiency (WUE) of an exotic Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) plantation and a multi-species native forest in N.W. Patagonia, both growing on the same site. We hypothesized that, within a site, the more productive system (*a priori* the Douglas-fir plantation) has a higher WUE than the less productive system (the native forest), and that within the native forest, the more productive species have higher WUE than the less productive ones. Five taxa were the most conspicuous woody species in the native forest, which was codominated by *Nothofagus antarctica* and *Lomatia hirsuta*. Both studied systems had reached their maximum leaf area index (approximately, 5 and 11 for the native and exotic forests, respectively). Annual productivity was 2.3 times higher in the Douglas-fir plantation than in the native forest, however two native species showed similar values of biomass productivity than the exotic species. The amount of water used by the native system was lower than that used by the Douglas-fir plantation, but not as low as the observed differences in productivity, thus resulting in a higher WUE in the Douglas-fir plantation than in the native forest (1.8 times higher). In addition, WUE was also different among the native species. The lower WUE at the stand level in the case of the native forest probably is due to the presence of retamos and lauras. We concluded that: (1) the more productive system (the Douglas-fir plantation) had a higher WUE than the less productive system (the native mixed forest); (2) within the native mixed forest, the most productive species (*L. hirsuta* and *N. antarctica*) had the highest WUE of all native species. Future research is needed to explain the physiological causes (daily patterns of transpiration and carbon fixation and allocation) of the observed differences in WUE between species and whole systems.

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## 1. Introduction

Forest productivity depends on the supply of resources, the proportion of captured resources, the efficiency of their use, and the allocation of the fixed carbon. Considering the proportion of captured resources, plantation forests are likely to have a greater use of water compared to grasslands and shrublands. A model of forested and grassland catchments showed that the differences in evapotranspiration (EVT) between vegetation systems are larger in areas with annual rainfall higher than

500 mm (Zhang et al., 2001). However, generalizations are difficult because different vegetation types have different limiting factors and controls on EVT (rain interception, leaf area, physiology, volume of explored soil, etc.) (Calder, 1998; Zhang et al., 2001). These factors also produce a high variability of water use even between different forests. In a review of 52 studies of water used by trees, Wullschleger et al. (1998) indicated that almost 90% of the water use data showed that the maximum rates of daily water use by tree were between 10 and 200 kg day<sup>-1</sup>. In general, the magnitude of water used by a tree depends on its size, but also on the degree of coupling between the canopy and the atmosphere, which depends on the relative magnitudes of aerodynamic and canopy conductances (Wullschleger et al., 2000). Thus, water used by each species depends on the interaction between physiological constraints and those imposed by the environment (water, radiation, wind

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speed, etc.). For example, stand-level water used by a conifer stand was similar to that of a broad-leaf forest plot, even when conifers had fourfold higher leaf area indices than the other system (Pataki et al., 2000). For these reasons, the introduction of a new species to a site may or may not produce a change in the amount of water use in comparison with the water used by the native vegetation. The prediction of water use by plantations in comparison to the native vegetation they replace is not straightforward.

As mentioned, productivity also depends on resource use efficiency, the relation between productivity and the amount of used resources. At the scale of forests and years, the efficiency of resource use can change across environmental gradients and silvicultural treatments (Binkley et al., 2004). These authors found evidence supporting the idea that resource use efficiency increases as forests increase the rate of resource use. Some study cases, in which single-species stands were analyzed, have demonstrated that stands with higher resource use also had higher efficiencies (Stape et al., 2004; Gyenge, 2005). In addition, Stape et al. (2004) found that higher water supply was also associated with increased use of light and nitrogen, and also with the simultaneous increase in use efficiency of all three resources. Also, Binkley et al. (2002) proposed the hypothesis that dominant trees have higher resource use efficiency than the other trees of the stand and with the onset of this differentiation in resource use efficiency, the stand-level growth rate decreases.

### 1.1. Productivity, water use and water use efficiency (WUE) in N.W. Patagonia

From 1970, afforestations with exotic conifers mainly with ponderosa pine (*Pinus ponderosa* Dougl. Ex P. & C. Laws) and to a lower extent with Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) in N.W. Patagonia Argentina have been installed in a narrow land area between Andean forests and the Patagonian steppe, characterized by a pronounced seasonality of temperature and precipitation (Schlichter and Laclau, 1998). This area corresponds to the forest-steppe ecotone dominated by forests of the native conifer “ciprés de la cordillera” (*Austrocedrus chilensis* (D. Don) Pic. Ser. Et Bizarri) and/or broad-leaf mixed forests with species such as “ñire” (*Nothofagus antarctica* (G. Forst.) Oerst), “radal” (*Lomatia hirsuta* (Lam.) Diels ex Macbr.), “laura” (*Schinus patagonicus* Phil.), and “retamo” (*Dioctea juncea* (Gillies and Hook.) Miers (Schlichter and Laclau, 1998; Reque et al., 2006). Annual productivity of ponderosa pine plantations greatly exceeds that of grasslands (Schlichter and Laclau, 1998; Laclau, 2003) and ciprés de la cordillera forests (Laclau, 2003). Ponderosa pine plantations in NW Patagonia may use more water, produce more biomass, and have higher WUE than the native vegetation they replace (Schlichter and Laclau, 1998; Gyenge et al., 2002; Laclau, 2003; Gyenge, 2005; Rivero et al., 2006; Licata et al., 2008). On the contrary, the amount of water used by Douglas-fir plantations was not statistically different than that used by the mixed broad-leaf forests they replace (Fernández and Gyenge, 2007). No information is available about productivity of this type of native forest and Douglas-fir

plantations growing in similar areas; therefore, it is not possible to estimate resource use efficiency of these systems based on previous data.

The objective of this study was to test the hypothesis that replacement of native mixed broad-leaf forest by Douglas-fir plantations increases productivity and WUE. To test our hypothesis, two particular objectives were addressed: (1) to estimate Douglas-fir and contiguous native mixed forest annual productivity; and, (2) to estimate WUE of each species and system. This information may contribute to confirm or to refute the general hypothesis that more productive species (plantations with exotic conifers) on a site have higher resource use efficiency than the less productive ones (native vegetation).

## 2. Methods

### 2.1. The study area

The study was carried out in a Douglas-fir forest of 30 ha planted in 1978 that contained a minor component of ponderosa pine (28-year-old at the time of the measurements), and in a contiguous broad-leaf mixed forest (approximately 80-year-old, 2 ha), both located in the basin of El Foyel river, Río Negro province, N.W. Patagonia (41°39'54.3"S; 71°33'11.4"W, 632 m o.s.l.). This site was selected due to the similarity in the climate, slope and soil conditions between both the native and the exotic forest. The soil has a loam-silty loam texture, originated from volcanic ashes, with low density (0.8 g cm<sup>-3</sup>) and 6–8% of organic matter. A clay pan of glacial origin was observed at 60–80 cm depth. Mean annual precipitation was around 1500 mm (Gallopín, 1978, and measurements carried out by the authors).

Species distribution and basal area (ba, m<sup>2</sup>) estimated from diameter at the breast height (dbh, cm) of each species were measured in 6 plots 100 m<sup>2</sup> each and 9 plots 50 m<sup>2</sup> each within the Douglas-fir plantation and the mixed forest, respectively. The minimum size tree included in the sampling was 3 cm of base diameter (bd, measured at 15 cm above soil surface).

Approximately, 11% of the trees in the Douglas-fir forest were ponderosa pines, representing less than 13% in basal area. Tree density (Douglas-firs plus ponderosa pines) was 1421 ± S.D. 117 trees ha<sup>-1</sup> with a total ba of 87.64 ± S.D. 15.18 m<sup>2</sup> ha<sup>-1</sup>. Taking into account only Douglas-firs, plantation density was 1271 ± S.D. 297 trees ha<sup>-1</sup>. Average ba of the Douglas-fir stand was 76.55 ± S.D. 23.66 m<sup>2</sup> ha<sup>-1</sup>, with a maximum of 103.8 m<sup>2</sup> ha<sup>-1</sup> and a minimum of 46.12 m<sup>2</sup> ha<sup>-1</sup>. Mean dbh of the trees was 26.7 ± S.D. 8.7 cm.

In the case of the native mixed forest, the more conspicuous species were ñire, radal and retamo, whose ba represented approximately 80% of the total ba (Fig. 1). On the other hand, in spite that laura was present in almost all plots with a high number of individual trees/shrubs, its contribution to total ba was low (<10%). Mean diameter at breast height was 16 (S.D.: 4.1), 12.1 (S.D.: 3.1), 10.7 (S.D.: 2.1) and 4.6 (S.D. 1.4) cm for ñire, radal, retamo and laura, respectively. Considering all the species, the mean number of individuals per ha was

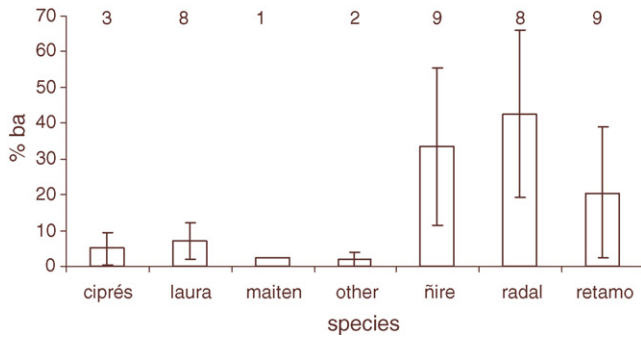


Fig. 1. Percentage (mean and S.D.) of basal area (ba) of each species of the native mixed forest: Ciprés de la cordillera (*Austrocedrus chilensis*), laura (*Schinus patagonicus*), Maiten (*Maytenus boaria*), other species (a group of several species, each represented in a very low proportion within the plots), ñire (*Nothofagus antarctica*), radial (*Lomatia hirsuta*), and retamo (*Diostea juncea*). Numbers at the top of each column indicate the numbers of plots in which each species were present ( $n = 9$  plots).

6618 ± S.D. 3349, with a slightly lower mean basal area than the Douglas-fir plantation (69.6 ± S.D. 19.8 m<sup>2</sup> ha<sup>-1</sup>).

Leaf area index (m<sup>2</sup> m<sup>-2</sup>), estimated from radiation measurements with a light meter (Delta T model SS1-UM-1.05, UK) and assuming an extinction coefficient of 0.5, was 11.6 and 4.99 for the Douglas-fir and the native forests, respectively.

### 2.2. Forest biomass models

Bole volume (VOL, m<sup>3</sup>) of Douglas-fir was estimated from dbh and height ( $H$ , m) data using the equation developed by Rey et al. (2000) for Douglas-fir growing in the study region ( $r^2 = 0.9832$ ;  $\alpha = 0.05$ ):

$$VOL = 0.0241411 + 0.000029134 \times H \times dbh^2 \quad (1)$$

To estimate bole biomass, we multiplied VOL by wood density (0.381 g cm<sup>-3</sup>; Davel et al., 2005).

Biomass stem equations of Laclau (2003) were used for the few ciprés de la cordillera and ponderosa pine trees present in the studied stands.

Equations of aboveground biomass for the rest of the native species were developed from 36 randomly selected trees of the most conspicuous species: 10 trees of ñire and retamo, and 8 trees of radial and laura. The size of those trees covered the range of diameter classes found in the study site. Biomass of each tree was separated in the following compartments: leaves, thin branches (diameter < 5 mm), thick branches (5 > diameter > 50 mm), and bole. These compartments were weighed in the field. After that, subsamples of each sample were oven-dried (96 h, 70 °C) and the resulting dry matter coefficients were used to estimate total dry matter.

In this study, we present the regression equations relating dry weight (in kilograms) of the bole (with bark) with dbh and diameter at the base of the trunk (db, both in cm). Data were transformed when necessary to fulfill the assumptions of normality and homocedasticity.

### 2.3. Annual growth and productivity

Annual growth for each species was estimated from incremental cores taken at breast height ( $n = 5-15$  cores per species) in randomly selected trees. Trees were selected in order to cover the different dbh classes. The last three rings were measured with a caliper and averaged. Regression equations for each species relating average annual bole diameter growth and dbh were performed. We used the diameter distribution and species composition of each plot measured at the beginning of the experiment (winter of 2005) as time 0 for productivity estimation. After that, we added the annual ring growth corresponding to each tree (based on its dbh). Annual productivity for each plot was calculated as the bole biomass difference estimated from initial and final dbh values. The same procedure was performed for the native and the Douglas-fir plots.

Statistical differences in mean annual productivity (average of last 3 years) between species were analyzed with ANOVA. Pairwise multiple comparison procedures (Holm–Sidak method) were performed to detect differences between species ( $\alpha = 0.05$ ).

### 2.4. Water use and water use efficiency

Sapflow density ( $J_s$ ) was measured every 30 s and then averaged every 10 min with a datalogger Campbell CRX 10 and a Campbell AM16/32A multiplexer. Sapflow density was measured using the thermometric method developed by Granier (1985) using 20 mm constant power thermal dissipation probes. Because Douglas-fir and radial trees had a relatively large sapwood depth, we inserted two pairs of probes at the surface (outer part of the xylem, 0–2 cm depth) and at approximately 2–4 cm deep into the sapwood to estimate radial changes in  $J_s$ . A ring of thermal and radiation insulation (Mexpol<sup>®</sup>, 9 mm) was placed around the stem.

Sapflow density was estimated using the formula proposed by Granier (1985):

$$J_s = 0.714 \left( \left( \frac{\Delta T_{\max}}{\Delta T_{\text{act}}} \right) - 1 \right)^{1.231} \quad [\text{ml cm}^{-2} \text{ min}^{-1}]$$

where  $\Delta T_{\max}$  was the maximum temperature difference between thermocouples in each pair (low sapflux density, usually at night), and  $\Delta T_{\text{act}}$  was actual temperature difference between thermocouples.

After that, sapflux per tree was estimated using the following formula:

$$F = J_s SA \quad [\text{ml min}^{-1}]$$

where SA was sapwood area (cm<sup>2</sup>) of the tree. This variable was calculated for each tree from its dbh after determining the relationship dbh:SA from increment cores extracted in five to twelve trees per species. The same relationships were used to estimate sapwood area at the stand level measuring dbh of the trees.

Daily mean stand transpiration ( $T$ , mm day<sup>-1</sup>) was estimated as:

$$T = F_d p_i \text{ BA area}$$

where  $F_d$  was the integral of  $F$  during a day;  $p_i$  was the contribution of each species to the basal area of the plot; BA was basal area and area = 1 ha.

Water use efficiency was estimated as the ratio between mean daily productivity (kg day<sup>-1</sup>) and mean daily water use (l day<sup>-1</sup> or mm day<sup>-1</sup>, at individual tree or forest level, respectively) for each plot of native and Douglas-fir forest. Mean daily productivity was estimated by dividing the annual biomass productivity per 365. Mean daily water use corresponds to the average of water use measured during the growing season (no winter values were considered). In the case of the native forest, water use efficiency was also estimated for each species in each plot.

### 3. Results

#### 3.1. Annual diameter growth and biomass productivity

Parameters of the equations of bole biomass of each native species as a function of db or dbh are shown in Table 1. Mean annual dbh growth varied significantly among species ( $\alpha = 0.001$ , Fig. 2). Diameter growth was similar between Douglas-fir and ponderosa pine (average of 9.4 mm year<sup>-1</sup>,  $P > 0.005$ ,  $n = 15$  and 14 for Douglas-fir and ponderosa pine, respectively). The highest growth rate of the native species was observed in ciprés de la cordillera (6.1 mm year<sup>-1</sup>,  $n = 5$ ), followed by ñire and radial which had similar values (average of both species: 2.9 mm year<sup>-1</sup>,  $\alpha = 0.05$ ,  $n = 10$  trees of each species). Lowest annual diameter growth occurred in retamo and laura (0.2 mm year<sup>-1</sup>,  $n = 10$  and 8, respectively).

Annual stem productivity at the individual plant level (Fig. 3A) varied by an order of magnitude between ñire, radial and Douglas-fir in comparison with the less productive retamo and laura of similar sizes.

A significant higher annual biomass productivity (considering only the boles) was estimated for the Douglas-fir plantation

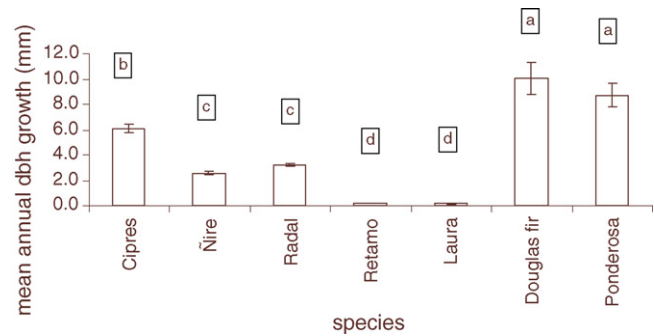


Fig. 2. Mean (S.D.) diameter growth of each species of the native mixed forest: Ciprés de la cordillera (*Austrocedrus chilensis*), laura (*Schinus patagonicus*), ñire (*Nothofagus antarctica*), radial (*Lomatia hirsuta*) and retamo (*Diostea juncea*), and the exotic planted species: Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). Different letters indicate statistical differences between species ( $P < 0.05$ ).

than for the native mixed forest (5479 and 2413 kg of dry stem biomass year<sup>-1</sup>, respectively, Table 2) in spite of the high variability within each. If ponderosa pine productivity is also considered, 700 kg dry stem biomass year<sup>-1</sup> (12% of total productivity) have to be added to the productivity of the Douglas-fir plantation. The difference between the maximum and minimum productivity measured in different plots within each stand was higher in the native forest than in the Douglas-fir plantation (Table 2). This result was due to the different structure (number of individual trees and species composition) of the native forest observed at short distances within a site.

#### 3.2. Water use and water use efficiency

On average, Douglas-fir forest used around 1 mm water day<sup>-1</sup> more than the native mixed forest (Table 2). However, this average was in the range of the maximum and minimum values of water use estimated for each plot of the native forest (Table 2).

In contrast to the large differences found between the productivity of each species at the individual plant level, differences in water use were small among species (Fig. 3B). This resulted in differences in WUE between species being mainly due to differences in productivity and not in water consumption (Fig. 3C).

Considering the whole systems, because productivity of the Douglas-fir plantation was around 2.3 times higher than that of the native forest, but water use differed by only 25%, water use efficiency of the Douglas-fir plantation was 1.8 times higher than in the native system (Table 2, Fig. 4). For individual species, ñire and radial had similar WUE than Douglas-fir (Figs. 3C and 4).

### 4. Discussion

Annual bole productivity of the studied Douglas-fir plantation (28-year-old) growing in N.W. Patagonia (5.5 tonnes ha<sup>-1</sup> year<sup>-1</sup>) was within the range of productivity reported for Douglas-fir forests in N.W. Patagonia (4.7–5.9 tonnes ha<sup>-1</sup> year<sup>-1</sup>; Davel et al., 2007) and N.W. USA

Table 1

Equations of bole biomass (BB, stem dry matter including bark, kg) as a function of diameter at the base of the trunk (cm, db) or diameter at the breast height (cm, dbh) of the most conspicuous species of the native mixed forest: laura (*Schinus patagonicus*), ñire (*Nothofagus antarctica*), radial (*Lomatia hirsuta*), and retamo (*Diostea juncea*)

	Equation	R <sup>2</sup> adj.	n	P
Laura	BB = e <sup>(-0.794+(0.261 × db))</sup>	0.912	8	<0.001
	BB = -8.950 + (2.314 × dbh)	0.938	8	<0.001
Ñire	BB = e <sup>(0.848+(0.140 × db))</sup>	0.754	16	<0.001
	BB = e <sup>(0.263+(0.206 × dbh))</sup>	0.885	10	<0.001
Radal	BB = -31.047 + (4.062 × db)	0.824	8	0.001
	BB = -28.660 + (4.301 × dbh)	0.884	8	<0.001
Retamo	BB = e <sup>(-0.446+(0.236 × db))</sup>	0.921	10	<0.001
	BB = 6.775 + (0.240 × dbh)	0.799	10	<0.001

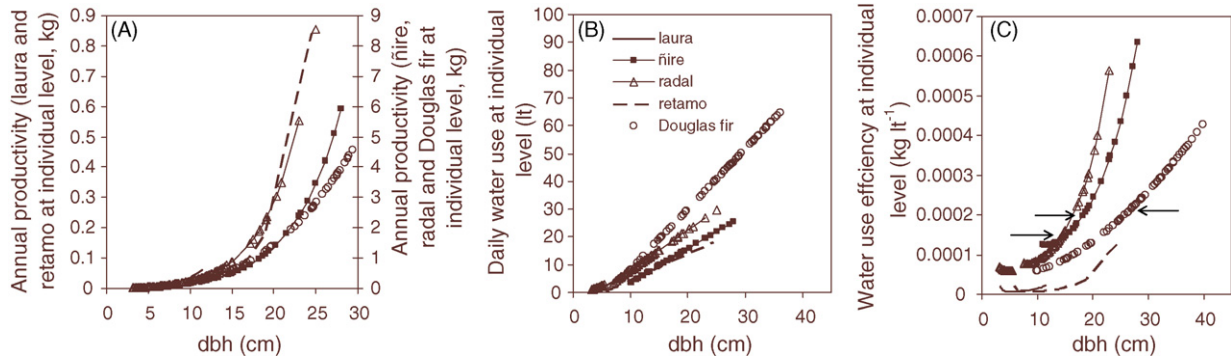


Fig. 3. Mean annual productivity of dry bole with bark, mean daily water use during the growth season and water use efficiency at the plant level, in relation to plant size (dbh), of laura (*Schinus patagonicus*), ñire (*Nothofagus antarctica*), radial (*Lomatia hirsuta*), retamo (*Diostea juncea*), and Douglas-fir (*Pseudotsuga menziesii*). Arrows in C indicate the estimated WUE for mean dbh values of the different species in the studied plots.

(Acker et al., 2002; King et al., 2002; Miller et al., 2004). Mean current productivity of the Patagonian plantation was lower than that of a Douglas-fir forest of similar age (29-year-old, 6.8 tonnes ha<sup>-1</sup> year<sup>-1</sup>) and slightly higher than that of a mature forest (100-year-old, 4.8 tonnes ha<sup>-1</sup> year<sup>-1</sup>) both growing in the H.J. Andrews Experimental Forest Long-term Ecological Research site (Oregon, USA; Acker et al., 2002). Comparing the basal area of the Douglas-fir plantation in N.W. Patagonia (77 m<sup>2</sup> ha<sup>-1</sup>) with that of the mentioned USA forests, the Patagonian plantation developed a higher basal area than both the mature and young Douglas-fir forests (67 and 22.4 m<sup>2</sup> ha<sup>-1</sup>, respectively; Acker et al., 2002). The current relatively low productivity of the Douglas-fir plantation in Patagonia may be explained by the effects of intraspecific competition between trees due to the lack of management (thinning) of the studied plantation. In addition, Acker et al. (2002) also indicated that productivity of Douglas-fir forests could be stabilized at 3–4 tonnes ha<sup>-1</sup> year<sup>-1</sup>, which is higher than the productivity of the native forest in our study. If these values are also valid for Patagonian plantations, productivity of the exotic plantation should be higher than that of the native mixed forests they replace, at least when these have a similar

structure than studied here. Thus, Douglas-fir plantations may be a stronger sink for carbon in N.W. Patagonia compared with native forests.

It is generally accepted that the rate of accumulation of biomass follows linearly the amount of leaf area (Kozłowski and Pallardy, 1997; page 329) until the canopy closes. The mean Leaf Area Index (LAI) for the native mixed forest in our study was similar to the maximum LAI reported for *N. antarctica* dominated forests and shrubs (Schulze et al., 1996). Thus, annual productivity of the native forest in our study may be near its maximum. It is important to note that these forests are characterized by a high variability within stands in short distances but a general similarity between mixed stands dominated by *N. antarctica* within a broad region in N.W. Patagonia (Reque et al., 2006). Therefore, we are confident that the measured productivity value is rather representative for native mixed forests codominated by ñire and radial in areas with annual precipitation of about 1500 mm.

On the other hand, productivity, water use and WUE of the native forest depended on species composition and also on the size of the trees (Fig. 3). This is important to take into account

Table 2  
Mean (±S.D.), maximum and minimum daily water use measured during the growth season, annual productivity of dry bole with bark, and water use efficiency of the Douglas-fir plantation and the native mixed forest in El Foyel Basin, Río Negro, Patagonia Argentina

	Mean	Maximum	Minimum
<b>Water use (mm day<sup>-1</sup>)</b>			
Douglas-fir plantation	5.5 (±1.5)	7.2	3.5
Native mixed forest	4.5 (±1.9)	8.3	2.2
<b>Productivity (kg year<sup>-1</sup>)</b>			
Douglas-fir plantation	5479 (±1382)	7909	2964
Native mixed forest	2413 (±1122)	4759	737
<b>Water use efficiency (kg mm<sup>-1</sup>)</b>			
Douglas-fir plantation	2.67 (±0.27)	3.03	2.29
Native mixed forest	1.50 (±0.52)	1.57	0.92

In the case of productivity, maximum and minimum were the maximum and minimum absolute values of productivity estimated for the plots (n = 6 and 9 to Douglas-fir and native mixed forest).

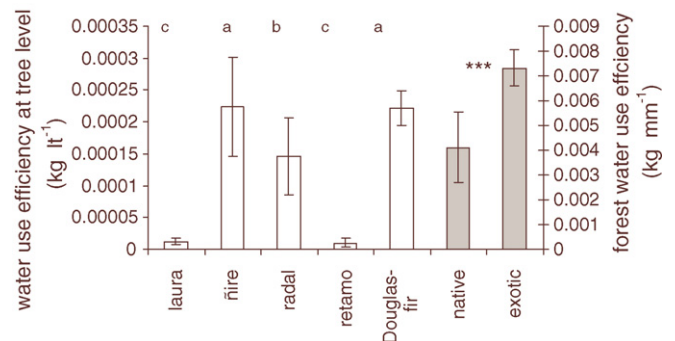


Fig. 4. Mean (S.D.) water use efficiency of the different species at the tree level (kg l<sup>-1</sup>, empty columns) estimated considering size distribution of them within the study plots, and at the forest level (whole systems, kg mm<sup>-1</sup>, solid columns). “Exotic” indicates the Douglas-fir plantation, “Native”: the native mixed forest. Laura (*Schinus patagonicus*), ñire (*Nothofagus antarctica*), radial (*Lomatia hirsuta*), retamo (*Diostea juncea*), and Douglas-fir (*Pseudotsuga menziesii*). Different letters indicate significant differences between individual species (P < 0.05) and asterisks indicate differences between whole systems (P < 0.01).

when different land uses are considered. Differential extraction of some species (for fire-wood, cattle-raising inside the forest, etc.) or size classes may therefore produce changes in productivity, water use and water use efficiency. More research is needed in order to evaluate the impact of different land uses on different processes and services of these forests, such as carbon sequestration, biodiversity conservation and water fluxes regulation, at local and regional scales.

#### 4.1. Relationship between WUE and productivity

The results of our study are consistent with the hypothesis that more productive forest systems also have greater water use efficiency. The Douglas-fir plantation had, on average 2.3 higher productivity and 1.8 times higher WUE than the native forest system it replaces. Maximum WUE estimated for the native forest ( $1.57 \text{ kg mm}^{-1}$ ) was lower than the minimum estimated for the Douglas-fir plots ( $2.29 \text{ kg mm}^{-1}$ ).

Binkley et al. (2004) proposed that the resource use efficiency of a forest is positively related to the magnitude of its resource use. In addition, these authors mentioned that, in the case of *Eucalypts* plantations, more productive sites plantations tended to have higher resource use efficiency than in less productive sites. Thus, more productive plantations, i.e. those growing in better sites, were those which used more resources but also they used them more efficiently. Moreover, within a site, silvicultural treatments (such as fertilization) could enhance productivity if these treatments produce an increase of resource use efficiency.

Two results of our study are notable with respect to the relationship between productivity and water use efficiency: (1) as was previously mentioned, the more productive system as a whole (the Douglas-fir plantation) had a higher WUE than the less productive system (the native mixed forest); (2) within the mixed forest, the more productive species (*ñire* and *radal*) had the highest WUE among the different native species.

A similar trend of a higher WUE by the ponderosa pine plantations compared to the less productive native grasslands has been also observed in a regional study in N.W. Patagonia (Rivero et al., 2006). In addition, within a site and considering only ponderosa pine plantations, more productive stands (those with higher diameter at the same age) had higher water use efficiency (Gyenge, 2005). Moreover, comparing ponderosa pine trees, water use efficiency was similar among trees of similar size, in spite of the differences in stand water use efficiency in which these trees were measured (Gyenge, 2005). The differences arise when different size trees are compared: larger (dominant) pines have higher WUE than smaller ones (suppressed pines) (Gyenge, 2005). These results are in agreement with the hypothesis proposed by Binkley et al. (2002) in relation to differences in resource use efficiency between dominant and suppressed trees. The results presented in this study about increased WUE with tree size (Fig. 3C) also support this hypothesis.

Binkley et al.'s hypothesis (2004) was articulated for species growing over gradients of resource availability and for dominant and suppressed trees. In the particular case of our

study, in which changes in WUE were analyzed, it is possible to add to Binkley et al.'s hypothesis that within a site, at the stand level, more productive systems also have higher resource use efficiency than less productive ones. In addition, within a multiple-species system, more productive species have higher WUE than less productive ones. All these findings support the general idea that species which can exploit and use more resources (within or between sites), exploit them more efficiently than species using less resources. More research is needed to elucidate the causes of these patterns, especially the allocation to root systems.

#### 4.2. Management implications

From a practical point of view, it is important to distinguish between water use and water use efficiency. Fast growing species introduced in N.W. Patagonia showed higher rates of water use than the native species (Gyenge et al., 2002; Rivero et al., 2006; Licata et al., 2008). As was mentioned in Licata et al. (2008), the Andean mountains (cordillera de los Andes) at West Patagonia act as a barrier producing a precipitation gradient from West to East. Water from the Andes provides many environmental and economic services for the rest of Patagonia and for the country. For this reason, an increment in water use by forest plantations could negatively impact superficial or deep-water flux, affecting local or regional economies. However, an increment in WUE could imply an increase in areal productivity without a proportional increase in resource use. In addition, a decrease in tree density (Gyenge, 2005; Licata et al., 2008) or selective harvest (the present study) have the potential to reduce water consumption and also, to increase WUE.

In this study we presented results of biomass productivity, indicating that, at the tree level, some native species (*radal* and *ñire*) could be even more productive than Douglas-fir (Fig. 3A). These results are due to the differences in wood density of native vs. the exotic species ( $0.63$  vs.  $0.38 \text{ kg dm}^{-3}$ , respectively; National Forest Institute of Argentina (IFONA), internal technical reports; Davel et al., 2005). However, if we consider volumetric increments, the exotic species (Douglas-fir) doubled the productivity of the native species, resulting in the measured high growth rates.

Future research is needed in order to understand the underlying genetic–physiological–ecological processes explaining the observed relationship between productivity and water use efficiency in different species and whole systems.

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