Relating water use to morphology and environment of Nothofagus from the world's most southern forests
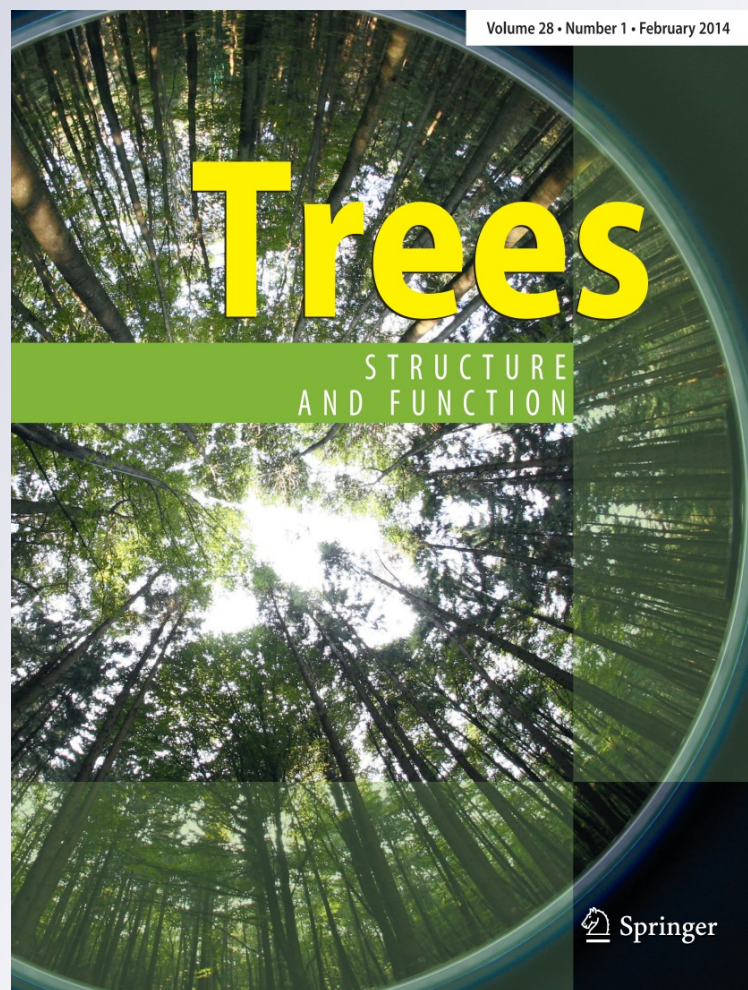
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Relating water use to morphology and environment of *Nothofagus* from the world's most southern forests

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Abstract

Key message **This study is the first to quantify tree water use below 50°S. Tree morphology differs markedly among the two investigated species, reflecting adjustment to different environmental cues.**

Abstract A pronounced environmental gradient dictates the dominance of *Nothofagus* in the foothills on the eastern side of the Andes Mountains in Patagonia, Argentina. Below 50° southern latitude, open forests of *Nothofagus antarctica* (ñire) dominate the landscape towards the Patagonian steppe where annual rainfall is low. With increasing rates of annual rainfall, corresponding with an increase in elevation, closed forests of *N. pumilio* (lenga) replace those of ñire. During a short-term study we assessed differences in stand structure and examined environmental, structural and functional traits related to tree water use of ñire and lenga. Sap velocity reached similar maximum rates (95–100 L m^{-2} sapwood h^{-1}), but whole-tree water use (Q) was significantly lower in ñire (8–13 L day^{-1} tree^{-1}) compared to lenga (20–90 L day^{-1} tree^{-1}) resulting in lower stand transpiration (ñire: 0.51 mm day^{-1}; lenga: 3.42 mm day^{-1}) despite similar tree densities. Related to this, wind speed had a particularly significant impact on Q of ñire, but not lenga. The ratio of leaf area to sapwood area (A_L/A_S) clearly identified ñire to be more structurally proficient at conserving water. While stem diameter (DBH) and crown area (A_C) were well related in both species, only lenga exhibited relationships between variables related to tree allometry and physiology (A_C/Q, DBH/Q). Our results provide the first ecophysiological characterization of the two *Nothofagus* species that define important and widespread ecosystems in southern Patagonia (not only below 50°S), and provide useful data to scale water use of both species from tree to stand.

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Introduction

Nine deciduous and evergreen species in the genus *Nothofagus* grow over a large latitudinal (33–56°S) and altitudinal range (near sea level–2,500 m a.s.l.) in South America to form the most southern forests in the world (Donoso 1996; Veblen et al. 1996). The deciduous *N. antarctica* (G. Foerst.) Oerst. (ñire) and *N. pumilio* (Poepp. et Endl.) (lenga) have the widest geographic range of these species, reflecting their capacity to adapt to varying climate envelopes. In South Patagonia, Argentina, both species form closed or open forests that stretch between the upper (around 960 m a.s.l.) and lower (around 460 m a.s.l.) tree lines along the eastern slopes of the Andes Mountains.

A recent meta-analysis suggests that cool-climate forest biomes, like those dominated by *Nothofagus* in South Patagonia, are among the most vulnerable of the world's forests to climate change (Gonzales et al. 2010). The climate of South Patagonia is characterized by winter rain and prolonged dry periods in summer (Paruelo et al. 1998). A warming trend across Patagonia (Villalba et al. 2003) is consistent with predictions of global climate models for southern South America (e.g. Bates et al. 2008). Isochronal to climate warming, the annual rainfall of the region has decreased (Veblen et al. 2011). Evapotranspiration in the region is accelerated by strong and continuous westerly surface winds (Schneider et al. 2003) that are particularly dry during the vegetative period (Paruelo et al. 1998). Forests dominated by ñire or lenga may diverge in their response to an increasing disparity between a 'drier' wet season and a 'warmer' growth period depending on their morphological and physiological adaptation to the dominant site conditions. Limits to the capacity of *Nothofagus* to endure predicted environmental changes may be particularly pronounced along the eastern slopes of the Andes in South Patagonia where rainfall gradients are naturally steep, decreasing from 8,000 (Patagonian Ice Fields) to <300 mm (Patagonian Steppe) in less than 100 km (Villalba et al. 2003).

Ñire and lenga forests have been broadly described in terms of morphology, biomass allocation and nutrient cycling, including along gradients of altitude (e.g. Barrera et al. 2000; Frangi et al. 2005; Hertel et al. 2008), rainfall (Schulze et al. 1996) and site quality (e.g. Gargaglione et al. 2010). Other studies focussed on the (paleo-)ecology and physiological function of *Nothofagus* spp. dominating the upper (e.g. Stevens and Fox 1991; Daniels and Veblen 2004; Young and León 2007; Fajardo et al. 2011) and lower tree line (Mancini 2009). Most studies have however concentrated on *Nothofagus* forests of northern and central Patagonia, leaving the ecophysiology and related structure–function relationships of ñire and lenga forests below 50°S largely undescribed.

This short-term study describes structure–function relationships for mature, mono-specific, ñire and lenga forests below 50°S. The selected forest types represent at least 70 % of the natural distribution of each species in South Patagonia (Peri 2004). In general, ñire dominates where availability of soil moisture becomes limiting for lenga (Veblen et al. 1996), namely at the transition from the foothill forests to the Patagonian steppe ('xeric tree line', sensu Stevens and Fox 1991). Lenga dominates forests along the foothills, occupying sites of better soil quality and higher rainfall (Peri 2004). In this landscape small differences in geomorphology, particularly elevation, can lead to pronounced differences in the prevailing weather conditions, reflected in the observed distribution of the two tree species. Characteristic differences between the two species have been reported with regard to their specific leaf area (ñire < lenga) and sensitivity of stomata to water limitation, identifying ñire to be more drought tolerant compared to lenga (Peri et al. 2009). Also, Dettmann et al. (2013) showed that across a range of *Nothofagus* species, sapwood of ñire had the smallest vessels and associated hydraulic conductance. These attributes help explain the greater capacity of ñire to survive at the xeric tree line where periodic scarcity of soil moisture is the most limiting factor to tree growth. Given the widespread occurrence of the two forests types in Patagonia, it is surprising how little we know about the effect of environmental drivers on their transpiration. To our knowledge only two studies assess such relations for ñire above 50°S (Fernández et al. 2009; Gyenge et al. 2011) and both found that whole-tree water use (Q) was highly sensitive to atmospheric vapour pressure deficit (D) and increased when soil moisture was not limiting. No reports on such relations are available for lenga.

Our objectives were firstly to quantify Q of ñire and lenga and identify the impact of environmental variables on Q. To accurately estimate Q it was necessary to include an analysis of radial variation of water transport in conducting tissue (i.e. sapwood). Ignoring this variation can lead to over- or underestimation of Q (Gebauer et al. 2008), as has been shown for many species (e.g. Phillips et al. 1996; Wullschleger and King 2000). The existence of a steep gradient of water transport from outer to inner sapwood was reported for *Nothofagus* from New Zealand (Kelliher et al. 1992) and a closely related *Fagus* species (Tateishi et al. 2010), yet the existence of such a gradient is undocumented for any *Nothofagus* species from South America.

Secondly, we assessed how well traits linked to tree architecture (tree diameter, projected crown area) relate to Q at the tree level. Fast and inexpensive measurements of such traits are regularly used to estimate stand transpiration (E) (e.g. Pfautsch et al. 2010, 2011; Barbour and Whitehead 2003 and references therein) and could help determine E of ñire and lenga. This knowledge is of particular importance when attempting to sustain the productivity of these forests under predicted environmental conditions. Thirdly, we assessed if leaf-to-sapwood area ratios (A_L/A_S) of ñire and lenga reflect long-term adaptation to the prevailing climatic conditions during the growing season at each site. We would expect that A_L/A_S is lower in ñire compared to lenga as a consequence of reduced leaf area and not because of increased sapwood area. Hence, A_L/A_S would indeed represent a good index for the relation between potential evaporative demand and water transport capacity (Meinzer et al. 2008). It was shown previously that A_L/A_S declines with increasing evaporative demand (Poyatos et al. 2007) and soil water limitation (Bleby et al. 2009) across a range of biomes, which may also be

applicable to the two species of *Nothofagus* investigated here.

Methods

Study sites

We selected two representative sites in South Patagonia, Santa Cruz Province, Argentina, that contained mono-specific stands of mature *Nothofagus*. Details for tree age is given below. The site dominated by ñire was located 460 m a.s.l. (51°19′01.76″S, 72°11′05.59″W) and has a mean annual temperature (MAT) of 6.5 °C, mean annual pre-cipitation (MAP) of 295 mm and potential evaporation in excess of 1,000 mm year^{-1} (Soto 2004). Soils from this area are classified as Mollisols. The site dominated by lenga forest was located 550 m a.s.l. (51°34′46.90″S, 72°17′11.14″W) where MAT is 4.5 °C, MAP is 645 mm and potential evaporation never exceeds 700 mm year^{-1} (Soto 2004). Lenga forests in South Patagonia typically grow on soils that are described as Sodosols or Inceptisols (Godagnone and Irisarri 1990).

Environmental and stand parameters

Weather stations (Davis Weather Wizard III, Hayward, USA) recorded air temperature (T_{air}), relative humidity (RH), wind speed (u) and irradiance (ε) in a clearing 200 m next to research sites at hourly intervals. D was calculated using T_{air} and RH (Snyder and Shaw 1984):

$$D = \left(0.6108 \times \left(\frac{\exp(17.27 \times T_{air})}{T_{air} + 237.3} \right) \right) \times \left(1 - \frac{RH}{100} \right).$$

(1)

Volumetric soil water content (θ; ML2x, Delta-T, Cambridge, UK) and soil temperature (T_{soil}; SKTS 200, UP GmbH, Cottbus, Germany) were logged at half hourly intervals (Scatter 100, UP GmbH, Cottbus, Germany). Measurement probes were inserted in the topsoil layer (0–8 cm) at the centre of each site where root density is likely to range from 33 (lenga) to around 50 % (ñire; Schulze et al. 1996).

Two 0.25-ha plots were established in each stand. Within these plots, diameters of all trees were measured at breast height (DBH, 1.3 m above ground) to calculate basal area and determine diameter distribution. The height of 15 dominant trees was measured using a clinometer. Two increment cores were extracted from opposite sides of trees at breast height and stained with 1 % methyl orange solution to determine sapwood depth (D_S) as described in Pfautsch et al. (2010, 2012). In total, 24 trees of ñire and 25

trees of lenga were cored to establish the relation of sap-wood area (A_S) to DBH. Bark depth (D_B) was measured at four positions around cored trees using a depth gauge to facilitate estimation of A_S.

Plant area index, canopy cover and leaf area

Plant area index (L_t, m^2 m^{-2}), canopy cover (f_c, dimen-sionless), foliage cover (f_f, dimensionless) and crown porosity (Φ, dimensionless) of stands were evaluated using digital cover photography (DCP) within a 0.1-ha sub-plot of each 0.25-ha plot. Forty digital cover photographs (Ni-kon D90, 50 mm lens, infinity-focus, auto-exposure, JPEG format, 3,216 × 2,136 pixels) were collected during days with homogenous cloud cover.

In brief, first we extracted the blue channel of each photo and classified pixels that were unambiguously either sky or canopy, by identifying two digital numbers (DNl and DNu) at the maximum curvature on the L-shaped curves to the right of the lower maxima and to the left of the upper maxima in the luminance histogram (Macfarlane 2011). The pixels located between DNl and DNu in the histogram are "mixed pixels" and appear around edges between the canopy and the sky. To separate mixed pixels into sky and canopy, we used the dual binary threshold method (Macfarlane 2011). Pixels within gaps smaller than 1 % of the image size in the region previously classified as canopy (DN < DNl) were classified as canopy or sky using a 25 % threshold [i.e. DNl + (DNu−DNl) × 0.25], to minimise loss of small gaps. In the remainder of the image we used a 75 % threshold [i.e. DNl + (DNu−DNl) × 0.75] to minimize the loss of leaves located in bright regions of the image. We then classified gaps less than 1 % of the image size as small gaps and the remainder as large gaps. Crown porosity was calculated as the ratio of small gaps to small gaps plus canopy, and canopy cover was calculated as the ratio of small gaps plus canopy to the whole image. Plant area index was then calculated as detailed in Macfarlane et al. (2007) using a light extinction coefficient of 0.7 (planar leaf surfaces).

Crown area (A_C) of 17 trees per species, including trees sampled to measure water use, were calculated from the radius of each live crown measured in eight azimuth directions, 45° apart. A_C was calculated as the sum of eight triangles:

$$A_C = \sum_{i=1}^{8} \frac{r_i \times r_{i+1} \times \sin(45°)}{2}$$

(2)

where r_1 and r_2 are adjacent radii. Linear regressions of DBH and A_C for individual trees were applied to all trees in each sub-plot to estimate the plot f_c. The ratio of L_t, estimated from photography, to f_c, estimated from crown

area measurements (not f_c from photography) was used to calculate leaf area of individual trees (A_L) according to the following formula:

$$A_L = A_C \times \left(\frac{L_t}{f_c}\right) \qquad (3)$$

where the ratio L_t/f_c was 2.16 for ñire and 2.63 for lenga. Equation 3 is only valid if Φ is independent of tree size. This condition was evaluated by acquiring and analysing photographs taken directly beneath each sample tree ($n = 8$ tree^{-1}). No relationship was found between DBH and Φ for either species (ñire: $r^2 = 0.04$; lenga: $r^2 < 0.01$). Images used for this evaluation were captured using camera settings as described previously. A set of 80 images, representing five complete tree crowns from each species, was manually corrected for woody area using a brush function (size: 50 pixel) of the shareware Image-J. A comparison of corrected vs. uncorrected images revealed that elimination of woody area resulted in an insignificant change of A_L in both species (ñire: $P = 0.34$; lenga: $P = 0.09$). Images were thus processed without correction for woody biomass.

Calculation of stand A_L and A_C used the range of DBH measured in the 0.1-ha sub-plots. For trees smaller than <190 mm DBH for ñire and <240 mm DBH for lenga, we estimated A_C from the ratio of A_C/DBH of the smallest tree measured for that species. The relation of A_L/A_S (commonly expressed in the non-SI unit m^2 cm^{-2}) to DBH was based on data representing the range of DBH of measured trees.

Tree and stand water use

The heat ratio method (HRM) was used to record heat velocity (V_h) at 30-min intervals for the period from 19 November until 2 December 2009. Measurements of heat velocity were transformed into whole-tree water use (as proxy for crown transpiration) following Burgess et al. (2001). One HRM unit (HRM30, ICT International, Armidale, Australia) was installed at DBH on the north-facing side of four trees from each species. Additionally, a fifth tree of each species was equipped with four HRM units at DBH facing north, east, south and west. Installation and sensor design were identical to descriptions provided in Pfautsch et al. (2010). All units were shielded to reduce thermal loading. Selected trees covered 60 % of the naturally occurring variation of DBH. Physical properties of instrumented trees are provided in Table 1a.

Measurement probes contained two thermistors each. Depending on D_S of individual trees, data were recorded at three different sapwood depths by shifting probes into desired positions (ñire: 2, 12.5, 17 mm D_S; lenga: 2, 15, 27.5 mm D_S). Probes recorded data at the outer and inner

depth for 12 days and at the intermediate depth for 2 days that had identical environmental conditions to those prior to shifting. Probes were shifted in sequence to enable cross-validation among data recorded at varying depth, ensuring that changes in magnitude of flow were only related to measurement depth. The ratio of temperature change between both symmetrically aligned thermistor pairs was recorded as V_h and treated independently for each measurement depth to calculate sap flow density (J_S, L m^{-2} sapwood h^{-1}) for each measurement position. Flow densities were then multiplied by the area of the concentric sapwood band that represented each measurement depth, summed for each tree and presented as whole-tree water use (Q, L h^{-1} tree^{-1}). This procedure is described in detail in Pfautsch et al. (2010). Measurements recorded in Tree 4 of ñire were discarded as probes were inadvertently inserted into heartwood. Stand transpiration (E) was estimated by multiplying average J_S of each species with the relevant stand A_S.

At the conclusion of measurements, trees were felled above probe sets, cut surfaces were sealed to prevent non-crown driven water transport and probes were left for 24 h to record zero baseline data. After removal of probe sets, discs (2-cm thick) were cut from each tree that included probe insertion holes. Discs were kept fresh for additional measurements (see below). The planar surface of the remaining stump was used to measure D_S at eight positions to cover circumferential variation of D_S. Sapwood was extracted from each disc, covering the zone of probe installation to determine a 'wound correction factor' (i.e. Burgess et al. 2001). This factor compensates for disruption of water flow around insertion holes of probes. After polishing the vertical plane of these wood samples, circular distortion of xylem vessels was measured using an optical microscope. The wound diameter was 1.9 ± 0.1 mm (mean ± 1 SD) for *N. antarctica* and 2.3 ± 0.2 mm for *N. pumilio*. A block of fresh sapwood was extracted from each disc and its mass and volume (water displacement method) were noted. Sapwood blocks were dried at 90 °C for 3 days and reweighed to calculate sapwood density. Finally, the remaining discs were polished to determine tree age by counting annual rings. Counts indicated that trees were on average 138 years (±21) for nire and 182 years (±15) for lenga.

Statistical analyses

Environmental differences (T_{air}, RH, D, ε, wind speed, soil water content and soil temperature) between sites were evaluated using ANOVA, after homogeneity of variances was tested using Bartlett's Chi-square statistic. Relationships between Q and environmental covariates were explored using a generalised least-squares regression

Table 1 Physical characteristics of trees used for sap flow measurements (a) and assessment of crown architecture (b) of *Nothofagus antarctica* (ñire) and *N. pumilio* (lenga)

Tree no.	N. antarctica				N. pumilio			
	DBH (mm)	D_B (mm)	D_S (mm)	A_S (cm^2)	DBH (mm)	D_B (mm)	D_S (mm)	A_S (cm^2)
(a)								
1	236	23.5 (1.6)	21.0 (1.3)	111.38	411	14.7 (3.0)	54.9 (5.2)	563.47
2	202	22.5 (2.3)	17.8 (3.0)	83.31	332	13.0 (1.5)	44.9 (8.1)	368.30
3	238	22.0 (2.1)	23.6 (5.1)	100.02	232	6.0 (0.8)	33.4 (1.3)	194.92
4	195	23.5 (2.8)	12.7 (5.1)	70.68	556	21.0 (2.5)	46.4 (10.6)	681.54
5					380	10.0 (5.6)	42.8 (5.6)	423.92

Plot number	Tree number	N. antarctica				N. pumilio			
		DBH (mm)	A_C (m^2)	A_L (m^2)	Φ	DBH (mm)	A_C (m^2)	A_L (m^2)	Φ
(b)									
1	1	236	13.74	29.68	0.25	411	41.41	108.91	0.17
	2	202	6.01	12.98	0.28	332	22.19	58.36	0.16
	3	238	13.79	29.79	0.28	232	13.31	35.01	0.10
	4	195	7.01	15.14	0.25	556	66.14	173.95	0.12
	5	210	12.51	27.02	0.35	380	33.46	88.00	0.16
	6	228	11.48	24.80	0.26	384	54.25	142.68	0.22
	7	175	6.71	14.49	0.34	262	20.4	53.65	0.19
	8	189	5.02	10.84	0.21	290	32.23	84.76	0.16
	9	273	15.78	34.08	0.21	513	79.37	208.74	0.15
2	10	195	7.18	15.51	0.34	406	60.35	158.72	0.18
	11	201	12.31	26.59	0.30	293	30.87	81.19	0.21
	12	210	11.55	24.95	0.32	307	29.26	76.95	0.18
	13	214	13.81	29.83	0.28	470	72.31	190.18	0.17
	14	224	10.45	22.57	0.36	335	44.28	116.46	0.13
	15	239	11.06	23.89	0.26	353	37.72	99.20	0.18
	16	251	14.50	31.32	0.35	400	44.88	118.03	0.13
	17	285	13.96	30.15	0.31	360	37.96	99.83	0.20

Trees numbered 1–4 for ñire and 1–5 for lenga in (a) are the same trees as those in (b)

SD is shown in parenthesis

DBH stem diameter at 1.3 m height, D_B bark depth ($n = 6$ tree^{-1}), D_S sapwood depth ($n = 8$ tree^{-1}), A_S sapwood area, A_C projected crown area; estimated parameter using digital crown photography, A_L estimated leaf area, Φ crown porosity (dimensionless)

(GLS). The GLS models included (i) a dummy variable to account for the diurnal cycle of Q in time, (ii) a first-order autoregressive term to account for autocorrelation in the Q-data and (iii) D and u or time-lagged D and u. The model to explore the relation between concurrent Q and environmental coefficients was:

$$Q = \beta_0 + \beta_1 \sin\frac{2\pi t}{N} + \beta_2 D_t + \beta_3 u_t + \varphi Q_{t-1} + \Upsilon_t \quad (4)$$

where β_n represents regression term coefficients, t is time, N is the number of measurements, φ is the autoregressive (AR1) term coefficient and Y is the error term. Linear models were derived between Q and both DBH and A_C of both species. Differences in the relation of A_S to DBH in each species were tested using ANCOVA prior to

establishing species-specific relations. All statistical analyses were computed using AABEL2 (V2.0, Gigawiz Ltd. Co., Tulsa, USA), except the GLS which was executed using the nlme package of R (Pinheiro et al. 2013).

Results

Environmental characteristics

Environmental parameters differed significantly between both research sites during the period of sap flow measurements. Air temperatures and RH at the ñire site were significantly lower compared to the lenga site ($P > 0.001$; Table 2). The amplitude of D was wide at the ñire site,

ranging from 0.2 to 1.7 kPa, and varied from 0.1 to 1.0 at the lenga site. Also average u was significantly faster at the ñire site ($P < 0.001$), being >6 m s^{-1} for almost half of the measurement period and gusts reached 19.5 m s^{-1}. Such high u was never recorded at the lenga site where winds were generally much calmer. As expected for this region, wind never ceased completely at either site. Due to the open stand structure, greater ε_{max} ($P = 0.05$) led on average to higher soil temperatures at the ñire (5.9 °C) compared to the lenga site (4.6 °C). Soil water content was significantly higher in the topsoil layer of ñire compared to lenga, but the overall difference was marginal (ñire: 35.5 %, lenga: 33.8 %; Table 2).

Tree crowns

Crowns of ñire had less foliage than those of lenga. Plant area index was 1.20 m^2 m^{-2} in ñire and 2.47 m^2 m^{-2} in lenga. The standard errors of the means from the two subplots within each stand were 0.04 for ñire and 0.07 for lenga. Crown porosity was also higher in ñire ($\Phi = 0.31$) compared to that of lenga ($\Phi = 0.17$). Crown area was linearly related to DBH in both species (ñire: $A_C = 0.89 \times$ DBH-8.63, $r^2 = 0.61$; lenga: $A_C = 1.95 \times$ DBH-29.51, $r^2 = 0.81$). Average A_C of ñire (11.0 m^2) was a quarter that of lenga (42.4 m^2, Table 1b).

Stand characteristics

Average tree heights were approximately 6 ± 0.3 m and 20 ± 1.4 m for ñire and lenga, respectively. Although stem densities were similar in both stands, the overall smaller DBH of ñire resulted in a considerable smaller basal area (19.4 m^2 ha^{-1}) than that of lenga (59.1 m^2 ha^{-1}) (Table 3). Sapwood density ($\sim$510 kg m^{-3}) and moisture content (47–49 %) were similar in both species (Table 3), and so was bark thickness (ñire: 17 ± 3 mm; lenga: 16 ± 1 mm). Sapwood was consistently narrower in ñire, thus A_S was significantly smaller compared to lenga ($P < 0.001$). While A_S correlated well with DBH of each species (Fig. 1), the resulting trajectories differed significantly ($P < 0.01$). Stand A_S was 4.8 m^2 in ñire representing 24.7 % of the basal area, compared to 24.6 m^2 (41.6 % of basal area) for lenga (Table 3).

Water use

Maximum J_S were consistently recorded in the outer sapwood of both species, reaching an average of 95 ± 28.4 L m^{-2} h^{-1} and 100 ± 32.6 L m^{-2} h^{-1} in ñire and lenga, respectively (Fig. 2). In ñire, J_S declined sharply with depth and did not follow a distinct diurnal course at 12.5 and 17 mm D_s (Fig. 2a). The outer, intermediate and inner sapwood contributed on average 70, 20 and 10 % to Q of ñire. Sap flow density in lenga declined more uniformly with sapwood depth when compared with ñire and showed a pronounced diurnal pattern throughout all measured sapwood depths (Fig. 2b). It is noteworthy that peak J_S in the inner sapwood band of lenga was delayed by several hours. Overall, outer, intermediate and inner sapwood contributed on average 44, 38 and 18 % to Q of lenga.

Peak Q of ñire reached little more than 1 L h^{-1} tree^{-1} at midday (Fig. 3a) with a slight delay to peak ε (Fig. 3b) and daily tree water use ranged from 8 (tree 2) to 13 L day^{-1} tree^{-1} (tree 5). At the same time, peak Q of

Table 2 Environmental characteristics of *Nothofagus antarctica* (ñire) and *N. pumilio* (lenga) research sites

	N. antarctica	*N. pumilio*	*P*
T_{air} (°C)	5.1 (4.0)	6.3 (3.8)	***
RH (%)	36.7 (12.2)	59.7 (11.7)	***
D (kPa)	0.7 (0.3)	0.4 (0.2)	***
ε_{max} (W m^{-2})	1359.0	1112.0	*
u (m s^{-1})	6.2 (3.7)	5.1 (3.2)	***
Soil temperature (°C)	5.9 (1.1)	4.6 (1.0)	***
Soil water content (vol%)	35.5 (2.8)	33.8 (2.0)	***

Parameters shown (T_{air} air temperature, *RH* relative humidity, *D* vapour pressure deficit, ε_{max} maximum irradiance, *u* wind speed) are means of hourly measurements ($n = 287$) recorded during 19–30 November 2009

SD is shown in parentheses

One-way ANOVA was used to test differences in environmental conditions between research sites where * $P \leq 0.05$ and *** $P < 0.001$

**Table 3** Stand characteristics of the *Nothofagus antarctica* (ñire) and *N. pumilio* (lenga) research sites

	N. antarctica	*N. pumilio*
Stems ha^{-1}	512	518
Basal area (m^2 ha^{-1})	19.4	59.1
Mean DBH (mm)	210 (65)	343 (167)
Min/max DBH	102–490	100–1,023
Height of dominant trees (m)	5.8–6.1	19.0–21.0
Mean D_S (mm)	14.2 (6)	41.1 (18)
Stand A_S (m^2 ha^{-1})	4.8	24.6
Stand A_S (%)	24.7	41.6
Sapwood moisture content (%)	46.6	49.2
Sapwood density (kg m^{-3})	507	518

Complete stand inventories were carried out on two 50×50 m quadrats within each forest type

SD is shown in parentheses

D_S sapwood depth, *Stand A_S* proportion of sapwood area relative to basal area
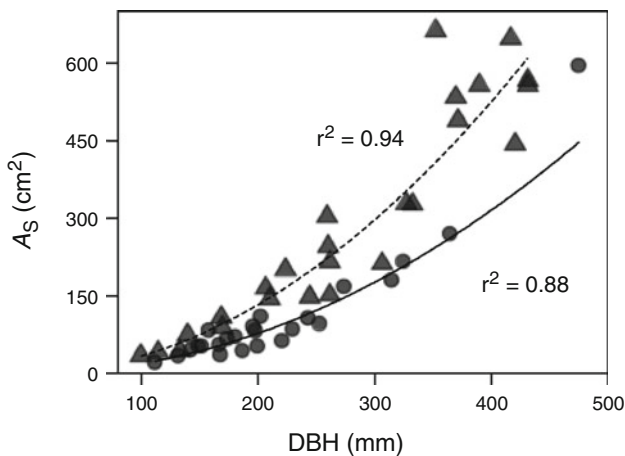
Fig. 1 Relation of DBH to sapwood area (A_S) in *Nothofagus antarctica* (ñire, *circles*, $n = 24$) and *N. pumilio* (lenga, *triangles*; $n = 25$). *Lines* represent power functions (ñire: $A_S = 0.18 \times DBH^{2.02}$; lenga: $A_S = 0.35 \times DBH^{1.98}$). Coefficients of determination are shown

lenga reached more than 8 L h^{-1} tree^{-1} during peak ε (Fig. 3c, d) and daily tree water use ranged from 20 (tree 3) to 90 L day^{-1} tree^{-1} (tree 4). Changes in cloud cover, inferred from abrupt changes in ε, had no measurable effect on Q of either species. Stand transpiration (E) was linearly related to D in both species, although this relation was much more conservative in ñire than in lenga. At 1 kPa of D, E in ñire reached 0.04 mm h^{-1} (Fig. 4a), while E of lenga was nearly ten times that of ñire at similar D (Fig. 4b). This difference in the magnitude of the E vs. D relation is captured in the ten times larger slope of the regression equation (see caption for Fig. 4). Overall, daily rates of E were estimated to be 0.3–0.7 mm day^{-1} in ñire and 1.5–5.0 mm day^{-1} in lenga.

The GLS model yielded a higher coefficient of determination for ñire ($R^2 = 0.79$) compared to that of lenga ($R^2 = 0.64$). The influence of D on Q was significant for both species ($P \leq 0.01$). The influence of u on Q of ñire was significant ($P \leq 0.05$). In contrast, u had no significant effect on Q of lenga. The effect of 1-h lagged covariates, D and u, were tested to account for delayed response between environmental parameters and Q. The output of this 'lagged' model did not increase model strength compared to using concurrent covariates.

Tree allometry and water use

The ratio of leaf-to-sapwood area (A_L/A_S) declined with increasing diameter in both species and was much smaller for ñire than lenga at a comparable diameter range. The ratio dropped from 0.25 to 0.20 m^2 cm^{-2} in ñire and 0.44 to 0.17 m^2 cm^{-2} in lenga (Fig. 5). There was no relation between allometric variables and Q in ñire, whereas lenga
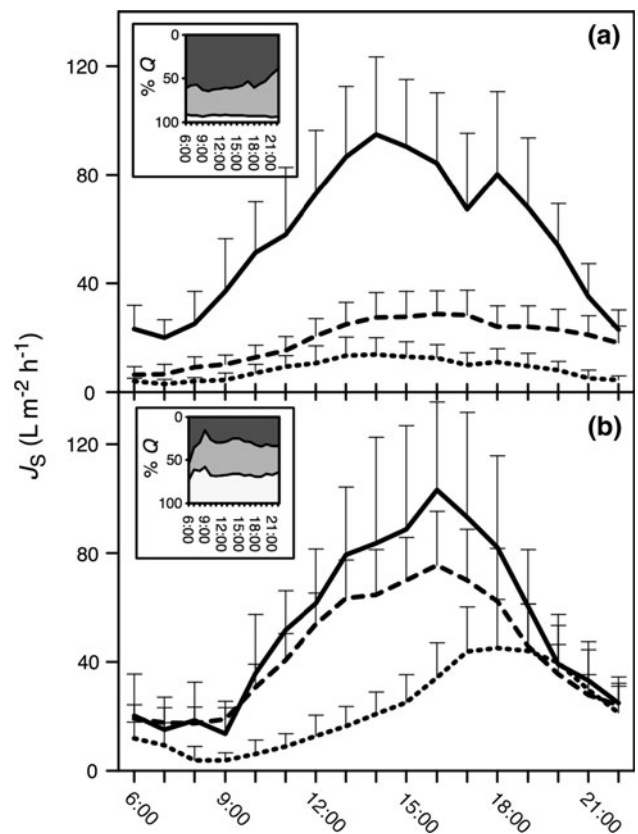

Fig. 2 Diurnal variation of sap flow density (J_S) in the outer (*black line*), mid (*dashed line*) and inner sapwood band (*dotted line*) of *Nothofagus antarctica* (ñire, *panel a*) and *N. pumilio* (lenga, *panel b*). Measurement depths were 2, 12.5 and 17 mm for ñire and 2, 15 and 27.5 mm for lenga. *Insets* show relative contributions of individual sapwood regions (outer = *dark grey shading*, mid = *light grey shading*, inner = *white shading*) to whole-tree water transport (Q). *Error bars* indicate SD

showed a strong and positive linear relation of Q to A_C ($r^2 = 0.99$) and to DBH ($r^2 = 0.98$) (Fig. 6a, b).

Discussion

To our knowledge, this is the first quantitative description of whole-tree water use and stand transpiration for two dominant and widespread *Nothofagus* species of South Patagonia. Combination of this data with structural measurements revealed major differences in structure–function relations of ñire and lenga. Structural characteristics of ñire at the xeric tree line underline the capacity of the species to survive environmental conditions that are characterized by low rainfall, high potential evaporation and strong, continuous winds. Tree allometry is generally and intimately correlated to environmental conditions (e.g. Lines et al. 2012) and our measurements of low tree height, small crown size, high crown porosity, small leaf area, low plant area index and small sapwood area illustrate how ñire maintains some
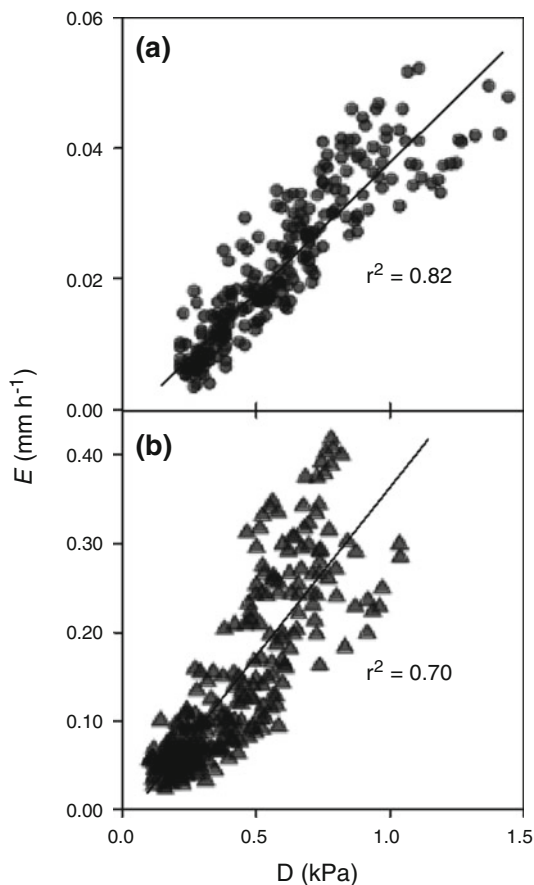
Fig. 3 Diurnal courses for water use (Q) and environmental parameters of *Nothofagus antarctica* (ñire, *panels a, b*) and *N. pumilio* (lenga, *panels c, d*) from 19 to 30 November 2009. *Panels a and c* show average hourly Q (*grey bars* display SD) and volumetric soil moisture content (θ, *dotted line*), while *panels b and d* depict vapour pressure deficit (D, *solid line*) and irradiance (ε, *grey shaded area*)
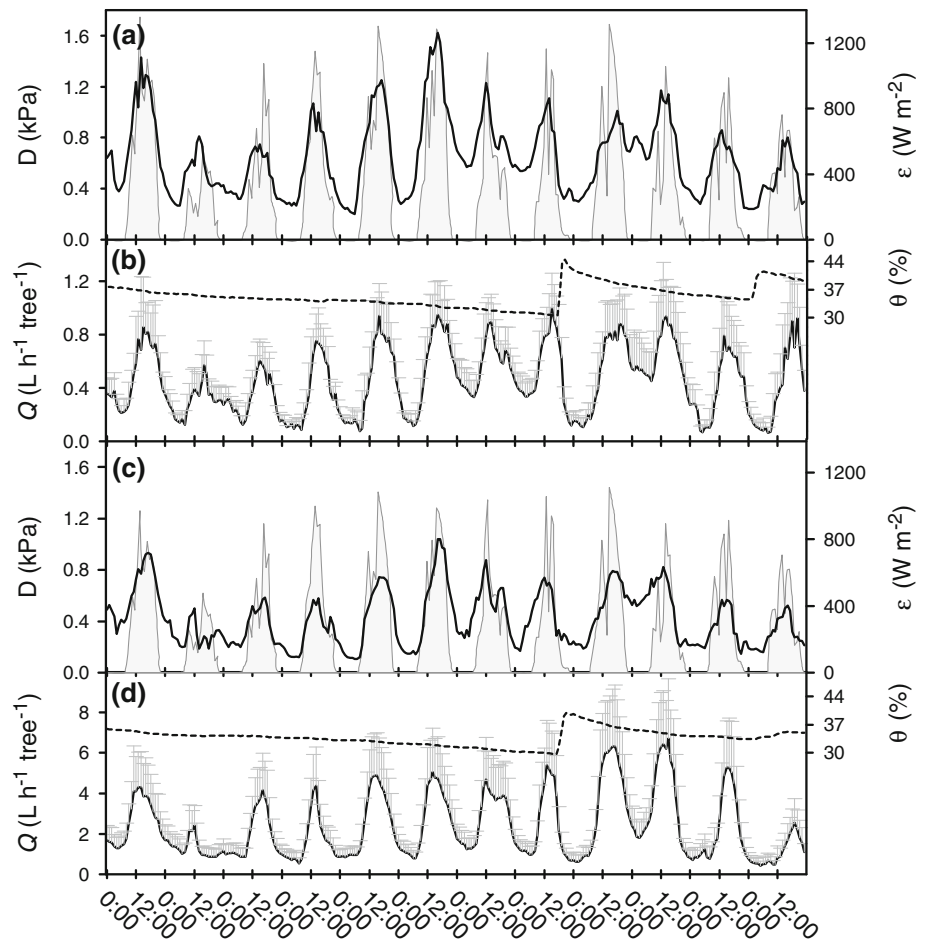
balance between uptake and loss of water under severe environmental conditions. Water use by lenga growing under considerably better site conditions increases with tree and crown size as predicted by universal scaling theory (Enquist 2002). For ñire the narrow range in tree diameters used for sap flow measurements precludes such a conclusion.

We observed a linear increase of E with D for both species. Generally, a linear relation of E and D can be explained as being the result of open stomata allowing opportunistic carbon assimilation when soil water is not limited (Berry et al. 2010), as during our measurement period. However, E of ñire was disproportionally low (one-tenth of lenga) when considering its basal area (one-third of lenga), its A_C (one-quarter of lenga), A_S (one-fifth of lenga) or A_L (one-third of lenga). This indicates that Q, and hence E, of ñire at our research site remained low even during conditions where soil moisture was not limiting. Limitation of E independent of soil moisture was also observed for ñire growing 10° further north (Fernández et al. 2009; Gyenge et al. 2011). Synergetic effects of structural factors listed in the above paragraph (i.e. combination of small crown size and low A_L/A_S) could help explain the disproportionally smaller E of ñire compared to lenga.
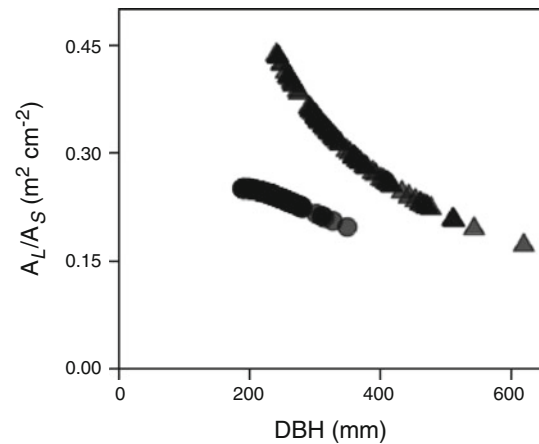
Continuous westerlies are an important driver of ecosystem functioning in Patagonia (e.g. Paruelo et al. 1998; Schneider et al. 2003; Mancini 2009). Wind speed had a significant and positive effect on Q in ñire, but not on lenga. This evidence suggests that these species are receptive to different environmental signals in regulating Q. Previous studies have reported that water availability is the key determinant for survival of tree species at the xeric limit of their distribution (e.g. Novenko et al. 2009; Zhang and Liu 2010) including *Nothofagus* in Patagonia (Mancini 2009; Tonello et al. 2009). However, it seems likely that in southern Patagonia the addition of perpetual, strong winds to already low annual rainfall plays a large role in tree survival as it entails dryness of the atmosphere (Moreno et al. 2009). A positive and nonlinear amplification of wind speed on environmental conditions has recently been identified as necessary to promote stepwise environmental changes in tree line ecotones (Holtmeier and Broll 2010). Hence, limiting E by means of structural and functional adaptations to permanent wind becomes a principal requirement for the survival of open forests dominated by ñire. In addition to generally greater rainfall in lenga forests, their closed canopy structure effectively reduces

Fig. 5 Relation of tree diameter (DBH) to the ratio of leaf area to sapwood area (A_L/A_S) for *Nothofagus antarctica* (ñire, *circles*) and *N. pumilio* (lenga, *triangles*)

Fig. 4 Relation of hourly stand transpiration (E) to vapour pressure deficit (D) for **a** *Nothofagus antarctica* (ñire, *circles*) and **b** *N. pumilio* (lenga, *triangles*); *solid lines* indicate linear functions (**a**: $E_t = 0.039 \times D - 0.002$); **b**: $E_t = 0.385 \times D - 0.021$). Coefficients of determination are shown

penetration of turbulent air and thereby reduces evaporation (Hollinger et al. 1994) and retains soil moisture. Under these environmental conditions stomatal regulation of transpiration in lenga may be low, which could explain the positive linear increase of Q with D when soil water is not limited. Although this relation is also linear and shows an even stronger correlation in ñire compared to lenga, the former species displays an intrinsically more conservative use of water.

We recorded maximum average J_S in the outer region of the sapwood of both species. Absolute maximum J_S was 120 L m^{-2} h^{-1}, a value equal to that reported for ñire growing further north (100–120 L m^{-2} h^{-1}, Fernández et al. 2009). The radial profiles of J_S presented here match reports of declining J_S towards the heartwood for other angiosperms (e.g. Granier et al. 1994; Wullschleger and King 2000; Gebauer et al. 2008; Tateishi et al. 2008). Our investigation of radial variation of J_S for *Nothofagus* clearly highlights that accurate calculation of sap flow-based E depends on a sound understanding of this

variation. This is particularly true, for example, for ñire as the majority of Q (70 %) is concentrated in a narrow band of the outermost sapwood. This is the first report of radial variation of J_S for both *Nothofagus* species and it should encourage future studies of water relations in these forests to include similar assessments.

Sapwood density and maximum J_S were similar for both species. This is contrary to what we expected, as ñire studied here was subjected to lower annual rainfall compared to lenga. Studies have shown that lower annual rainfall, or more broadly aridity, increases the density of sapwood and lowers the water transport capacity in trees (Bucci et al. 2004; Chave et al. 2009). In addition, measurements of anatomical traits of sapwood from four *Nothofagus* species growing in southern Chile showed that ñire had the smallest vessel diameters, lowest hydraulic conductivity and smallest vessel-to-wood ratio (Dettmann et al. 2013). Such features would increase 'hydraulic safety' by maintaining water transport in conducting sapwood under progressively limiting water availability (Sperry et al. 2008). However, sapwood of ñire reported by Dettmann et al. (2013) was 680 kg m^{-3} significantly denser compared to 510 kg m^{-3} measured here. Recent work by Bucci et al. (2012) shows an exceptional plasticity of sapwood density and other traits related to hydraulic functioning within ñire and lenga. Considering these findings in the light of our measurements of Q and maximum J_S for both species of *Nothofagus*, the question arises if wood density is a universal trait that integrates life history and growth as proposed by Enquist (2002). Lower Q of ñire may not necessarily be owed to hydraulic constraints within the conducting sapwood, leading to a decrease in J_S, but it may instead originate from a reduction of A_L/A_S. This interpretation would be in agreement with observations made by Edwards (2006) who showed that individuals of
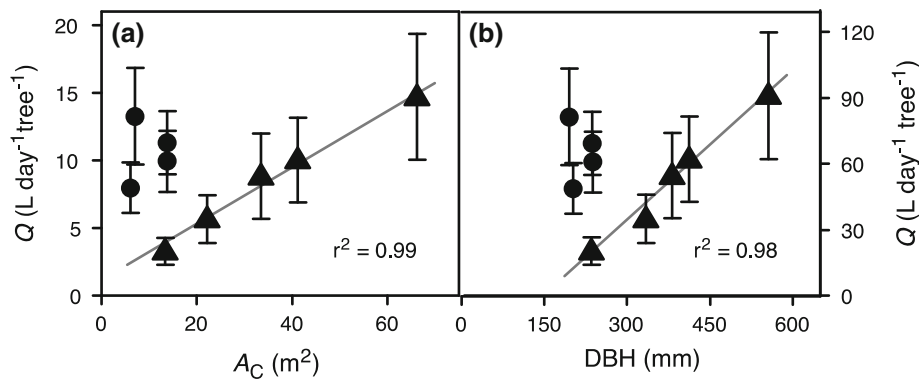
Fig. 6 Relation of projected crown area (A_C, **a**) and tree diameter (DBH, **b**) to water use (Q) of individual *Nothofagus antarctica* (ñire, *circles*, *left y-axes*) and *N. pumilio* (lenga, *triangles*, *right y-axes*) trees. Q of individual trees was averaged for the measurement period of 12 days (19–30 November 2009). *Lines* represent linear fit for lenga only ($Q = 1.32\ A_C + 5.90$; $Q = 0.23\ \mathrm{DBH} - 33.81$). Coefficients of determination are shown. *Error bars* display SD

the genus *Pereskia* growing along a gradient of soil water limitation reduce A_L/A_S rather than increase sapwood density to limit Q.

Lower A_L/A_S for trees with similar DBH in ñire compared to lenga emphasize the importance of long-term morphological adaptation (e.g. smaller A_S at similar DBH) over short-term responses (e.g. reduction of A_L during drought) for deciduous trees. This is in agreement with previous research where A_L/A_S declined under increasing D and decreasing soil water availability (Poyatos et al. 2007; Bleby et al. 2009). Both *Nothofagus* species exhibited A_L/A_S similar to *Pinus* and *Picea* species (DeLucia et al. 2000; Köstner et al. 2002). This places ñire and lenga studied here at the lower end of A_L/A_S for angiosperms (McDowell et al. 2002), but overall their A_L/A_S remain in the range documented for its close relative, European beech ($A_L/A_S = 0.33$; Bartelink 1997). We speculate that A_L/A_S will be small for species towards their distributional limits (i.e. low A_L, high A_S).

Other structural adaptations to increasing water limitation have been reported for *Nothofagus*. For example, the ratio of aboveground/belowground biomass decreases towards the xeric distribution limit of Patagonian *Nothofagus* (Schulze et al. 1996; Hertel et al. 2008; Gargaglione et al. 2010). Such structural adaptations are in accordance with the 'optimal partitioning theory' for available resources (Thornley 1972), predicting that a greater proportion of photosynthates will be directed towards the part of a tree that is responsible for acquiring the most limiting resource. Reduction of leaf and crown area as well as total aboveground biomass with declining soil quality matches other observations along environmental gradients of *Nothofagus* forests in Patagonia (Schulze et al. 1996; Barrera et al. 2000; Hertel et al. 2008). An adaptation to decreasing annual rainfall is also reflected in leaf-level biochemistry of both *Nothofagus* species, evidenced by decreasing abundance of the heavy carbon isotope (^{13}C) in bulk leaf

material with increasing water availability (Peri et al. 2012). Abundance of foliar ^{13}C is commonly linked to intrinsic photosynthetic water use efficiency (WUE) of a plant, and both leaf ^{13}C and WUE increase being low at mesic and high at drier sites (Farquhar and Richards 1984).

Recently, Gyenge et al. (2011) combined measurements of stand structure, tree physiology and environmental parameters to demonstrate how thinning in ñire forests of northwest Patagonia decreased their susceptibility to drought. The applied management strategies resulted in increased soil water availability and higher physiological activity, and thus productivity of the remaining trees. Taking together the wide distribution (Veblen et al. 1996) and socioeconomic importance (Martínez Pastur et al. 2000) of *Nothofagus* forests and predicted climate warming and drying across the region (Villalba et al. 2003; Veblen et al. 2011), there seems an obvious need to develop such strategies also for forests further south. In this respect, our quantitative and qualitative analysis of J_S and Q of ñire and lenga provides a first guideline for land managers to evaluate E of both forest types in southern Patagonia. Certainly, measurements presented here relate to spring conditions only and should be extended to cover more of the vegetative period if an evaluation of annual E is anticipated.

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