Grassland productivity and diversity on a tree cover gradient in *Nothofagus pumilio* in NW Patagonia

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ABSTRACT

Extensive areas of primary forests of lenga (*Nothofagus pumilio* (Poepp et Endl.) Krasser) have been transformed into grasslands over the past few decades. In Chile's Aysén region, grazing in remnant forests is common practice but there is little empirical evidence of tree-understorey interactions therein. In an attempt to establish a scientific basis for silvopastoral implementation, the relationship between lenga cover and grassland productivity, quality and species richness was examined. Tree cover was quantified in 14 (20×20 m) sites where aboveground herbaceous biomass was evaluated monthly throughout two growing seasons. Herbage quality and plant species richness were measured once at the peak of biomass production in the second year. We discuss radiation transmitted through the canopy and water supply as drivers of the tree-understorey relationship. Changes in herbaceous species composition and richness with varying tree cover are described. Despite interannual differences, scattered trees or medium-density forests allow higher productivity than open areas, as well as an acceptable nutritive value and preservation of native species. Although further studies are required, our results suggest that presence of lenga trees within grazing areas can be an advantageous alternative in terms of biodiversity and productivity, to traditional grazing systems in open grasslands.

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1. Introduction

In western Patagonia, native forests have undergone a dramatic ecological transformation since the colonization of the early 1900s. In Chile's Aysén region, colonists used fire to transform extensive areas of native forest into the existing seminatural grasslands (Veblen et al., 1996). Non-native herbaceous species were introduced following the fires and now are widely naturalized in the area. Over the last few decades traditional extensive grazing with cattle and sheep has constituted the major socio-economic activity in this region (Delgado and Bachmann, 2008).

In the transition zone between evergreen forests and the steppe, lenga (*Nothofagus pumilio* [Poepp. et Endl.] Krasse) forest is by far the dominant one. This is a broad-leaf deciduous species with the largest distribution area in Chilean Patagonia and in Northwestern Argentina (Donoso, 1993). It is the most profitable firewood and timber species in Patagonia (Martínez Pastur et al., 2000), and exploitation has been very intensive in recent years.

Antagonism between forestry and grazing has given rise to a fragmented landscape, with remnant patches of native forests at the top of the hills and grasslands in the valleys. The former are grazed along with the latter, albeit at a lower stocking rate. Moreover, the above mentioned fires and grazing have severely increased soil erosion and nutrient leaching (Veblen et al., 1996; Alauzis et al., 2004). Land managers are becoming increasingly interested in improving soil quality and conserving landscapes. One alternative to the existing grazing practices could involve integrating forestry and livestock grazing, through implementation of silvopastoral systems.

Silvopastoral systems can be defined as complex management systems integrating trees, grasslands and animals in a common area (Nair, 1993). Tree cover modifies several physical processes such as intensity and length of solar radiation, interception of precipitation, wind exposure, water availability and nutrient cycling (Sibbald, 1999; Ovalle et al., 2006). Interaction among these processes can have important consequences for productivity, biodiversity and environmental services (Palma et al., 2007). Moreover, trees create crucial wildlife habitats, which enable survival and growth of specialist species that could not otherwise occur, and provide ecological continuity at landscape scale (Breshears, 2006), enhancing

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the agronomic values and plant species richness of degraded lands (Manning et al., 2006). A number of studies confirms that both biodiversity and production goals can be addressed if some tree cover is maintained in grazing systems (Tscharntke et al., 2005; Le Brocque et al., 2009). In the Mediterranean basin, where silvopastoralism is an ancient practice, this fact has been well described (de Miguel, 1999). Similar influences have been found in the silvopastoral management systems of Mediterranean Chile (Ovalle et al., 1990; Ovalle et al., 2006) and Australia (Le Brocque et al., 2009).

The negative effect of trees on the understorey may result from shading, rainfall interception, litter accumulation, root competition or a combination of these factors (Scholes and Archer, 1997). The positive effects, involving fertilization and amelioration of environmental conditions, have been broadly demonstrated in savannah-like ecosystems all over the world and in different types of silvopastoral systems presenting different densities or tree distributions (Nair, 1993; Mosquera-Losada et al., 2005). However the intensity of the sheltering effect can vary, depending upon the vegetation and climatic conditions of the area (Callaway and Walker, 1997).

Herbage quality can be influenced by the presence of trees (Treydte et al., 2008) and it is generally recognized that losses of pasture production are accompanied by an increase in quality. Plant species diversity can also be enhanced in complex silvopastoral systems, in comparison to treeless grasslands (Vandermeer et al., 1998). Without the sheltering effect, the survival of some species would be hindered, thus affecting species richness.

Few silvopastoral initiatives have been developed either in Argentine or Chilean Patagonia, and little information is available on the effects of tree cover on productivity and structure of grasslands. Some studies have been conducted with exotic trees, with positive effects generally reported (Fernández et al., 2007). A recent study involving *Nothofagus antartica* (G. Forster) Oersted in southern Patagonia (Schmidt et al., unpublished results) revealed a positive effect of tree cover on pasture productivity.

The present study aims to quantify the effects of lenga tree cover on grassland productivity and quality, as well as on plant species composition and richness. By examining the effects of tree cover on the understorey, we address the following questions: (1) Do trees increase herbage productivity relative to treeless pastures? (2) If so, at what tree cover value productivity is maximized? (3) How does tree cover affect herbage quality and maintenance of native plant species?

2. Material and methods

2.1. Study field and experimental layout

The study was located on a moderately altered lenga forest located at Tamel Aike – Institute of Agricultural Research (INIA) station in the Simpson Valley (Coyhaique County, Aysén region, Chile; 45°58′S, 72°08′W, 590 m.a.s.l.; Fig. 1). The climate is cold-temperate with strong winds and higher precipitation in spring and autumn. Temperature and precipitation data were obtained from the closest meteorological station at the Teniente Vidal Aerodrome, near the city of Coyhaique. Long-term (20-year series) average annual temperature is 8 °C, mean maximum temperature in January (hottest month) is 19 °C and minimum temperature in July (coldest month) is −0.5 °C. Average annual precipitation is 994 mm; the hottest months (January–March) have the lowest rainfall. This climate restricts the length of the growing season to approximately six months, from October to March–April. During the experiment, differences occurred between the two growing seasons, the first (2006–2007) was wetter and cooler than the second (2007–2008) (Fig. 2).
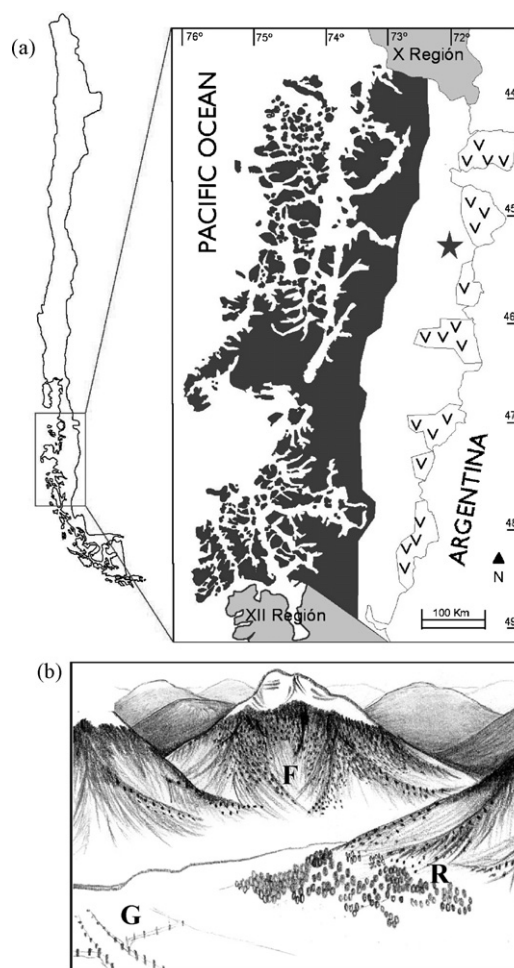
Fig. 1. Location map of the Aysén region (a), showing the distribution of lenga (unshaded area) between evergreen forests (shaded area) and steppes (∨). The star corresponds to location of the study field at Tamel Aike. Modified from Quintanilla (1989). Schematic view of a typical Chilean Patagonian valley after extensive human-set fires (b), where primary forests remain at higher (less accessible) altitudes (F) and seminatural, cultivated grasslands are found at lower altitudes (G), where remnant fragments of native forests can also be found (R).

The Tamel Aike experimental station covers 200 ha and is used for agronomic research. For the purpose of simulating a grazing production system in Chilean Patagonia, one 50 ha sector (comprising grasslands and lenga woodlands) was delimited and grazed from December to April–May by a stock of approximately 20 cows (with calves). Fifteen sites (20 × 20 m) within a range of tree cover (from open grassland to dense forest) were distributed in this sector. One open grassland site was found to be unsuitable and excluded after the first year. At each site, photosynthetically active radiation (PAR) was measured at midday on a sunny summer day in 2007 (January 8–10) and 2008 (January 21-23), using a 0.8 m length ceptometer (AccuPAR model PAR-80, Decagon Devices INC., USA). Although light transmitted through the canopy changes seasonally in deciduous forests, summer measurement maximizes differences between sites. Transmitted PAR (%) was calculated at each site as the mean incident PAR compared to PAR recorded in an open area. One hundred readings were taken along two diagonal transects at each site (200 records per site) in 2007 and following a quadrangular grid (100 records per site) in 2008. Reference measures in nearby open areas were recorded every 15 min, at a minimum distance of 20 m from the closest tree. A high correlation between transmitted PAR in 2007 and 2008 (Pearson $r = 0.99$) indicated that no significant difference existed between years or measuring methods. In addition,
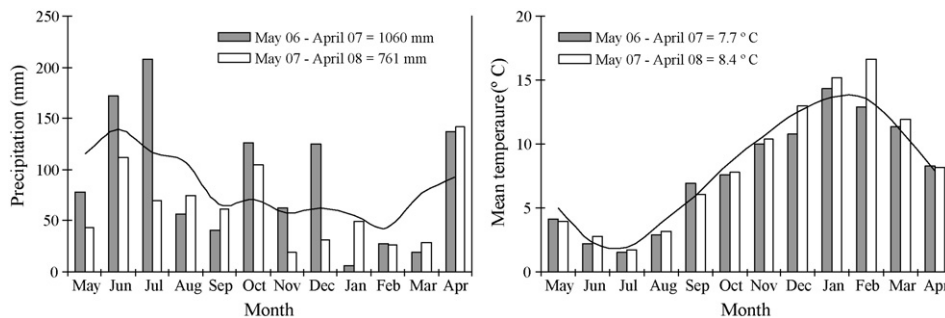
Fig. 2. Monthly precipitation and mean temperature during two growing seasons (2006–2007 and 2007–2008). Lines show long-term (1980–2006) averages. The growing season for grasslands usually lasts from October to March–April.

tree cover in the 14 sites was measured in January 2007 by digital hemispherical photography (processed by the freeware Gap Light Analyser; Frazer et al., 1999). This variable was closely correlated with transmitted PAR in both years ($r = -0.96$ and -0.97, respectively). In the present study, transmitted PAR was used as the single indicator of tree cover, although the results of the analyses did not differ when using data from hemispherical photographs.

2.2. Plant measurements

The aboveground biomass was harvested every 4–5 weeks during two growing seasons. Grassland productivity was determined with the use of wire exclosure cages ($70 \times 100 \times 50$ cm), which prevent grazing by herbivores (i.e. cattle and small- and medium-sized mammals). A varying number of cages (2, 3 or 4) was located at each site and distributed according to the proportion of tree cover and open areas within the site. Forty cages were used in the 14 sites. Aboveground herbaceous biomass was cut at ground level inside and outside the cages, using an electric shearing handpiece. Samples were oven-dried for 48 h at 60 °C and their dry matter (DM) were measured. After each sampling date, the cages were placed in a different position inside the site in order to avoid previously harvested areas.

Herbage quality was determined at the peak of biomass production of the second year (January 2008) using 1 mm sieved oven-dried aboveground biomass samples from each of the 14 sites. Samples were sent for analysis to the Bromatology lab of Remehue–INIA. Content of water-soluble carbohydrates (WSC) was determined with the Anthrone method and by reading the absorbance at 620 mm, following Thomas (1977). Nitrogen content was determined with the Kjeldhal method, and crude protein (CP) was obtained through multiplication of nitrogen concentration by a factor of 6.25 (AOAC, 1970). Fibres were assessed by means of the acid detergent method (ADF) following Van Soest (1963). Analyses were also conducted on samples of green leaves from the non-native species *Dactylis glomerata* L. and *Trifolium repens* L. which were dominant in the study field.

Plant species occurrence was also recorded in January 2008, by determining their presence in 10 quadrats (50×50 cm) regularly distributed at each site. Taxonomic determination follows Correa (1969-1999). Species richness was calculated as the total count of herbaceous and woody species, and native species percentage as the relative proportion of these to the total number of species.

2.3. Data analysis

Biomass (g DM m^{-2}) at a given sampling time was calculated as DM(in) − DM(out), where DM is the dry matter inside and outside cages, respectively, at consecutive sampling times t_n for DM(in) and t_{n-1} for DM(out). Grassland productivity derived

from the addition of partial measures of biomass from October to March–April.

Four cover classes were established according to the values of transmitted PAR: open areas (0% tree cover, 100% transmittance), scattered trees (>0–40% tree cover, >40–100% transmittance), medium-density forests (>40–80% tree cover, >20–40% transmittance) and dense forests (>80% tree cover, >0–20% transmittance). These groups were used for illustrating rough differences in understorey productivity (Two-way ANOVA: cover classes × years).

The remaining analyses were performed with the transmitted PAR values from the 14 sites as a continuous variable. We quantified trends in agronomic and diversity variables across the tree cover gradient using regression analyses. Data from each year were fitted to linear or second order polynomial models. The latter were considered to better fit the relationship only when the linear function was not significant (*F* test) and the quadratic term in the polynomial model (*t* test) was significant ($P < 0.01$).

3. Results

In all tree cover classes aboveground biomass reached a constant level in January, after ~130 days from the start of each growing season (Fig. 3). Productivity in the first growing season was nearly twice as high as in the second one (ANOVA $F = 17.6$, $P < 0.001$). Compared with open areas, grassland productivity was greater at intermediate covers (ANOVA $F = 4.3$, $P = 0.03$) although this difference between cover classes was less notable in the drier year than in the wetter one (ANOVA $F = 14.7$, $P = 0.001$).

Second order polynomial relationships were found between grassland productivity and transmitted PAR in both growing seasons (Fig. 4). Differences between growing seasons were higher at the intermediate than at the extreme values of transmitted PAR. According to the fitted models, the maximum values of productivity were attained at 50% and 70% of transmitted PAR, in the wetter (2006–2007) and drier (2007–2008) years, respectively.

Herbage quality varied linearly with transmitted PAR (Fig. 5); negative relationships with increasing transmitted PAR were found for CP and ADF, and positive ones for WSC. A similar pattern was observed in complete samples and in green leaves of *D. glomerata* and *T. repens*, except for CP in leaves of *D. glomerata*. In all cases, transmitted PAR explains more variation in leaves of *D. glomerata* and *T. repens* than in complete samples.

Thirty-eight species were found in all 14 sites at the peak of biomass of the second growing season (Table 1). All shrub species were native, as well as half of the herbaceous ones. Many species are ubiquitous through the tree cover gradient, being the most common *D. glomerata*, *T. repens* and *Taraxacum officinale*. Some native species are distinctive of either the dense forests (e.g. *Blechnum penna-marina*, *Geum magellanicum*, *Vicia nigricans*, *Viola magellanica*) or the open grasslands (e.g. *Anemone multifida*, *Silene magallanica*, *Festuca* sp. and *Luzula racemosa*).
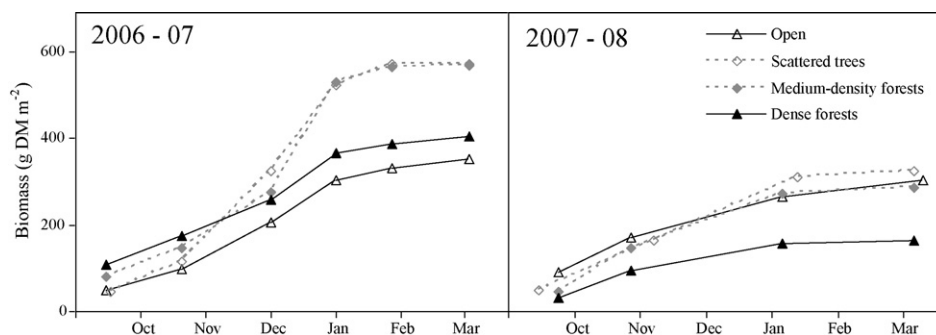
Fig. 3. Accumulation curves of the aboveground herbaceous biomass along the two growing seasons of study. The 14 sites were grouped into four tree cover classes (0%, >0–40%, >40–80% and >80% of tree cover). Oct: October, Nov: November, Dec: December, Jan: January, Feb: February, Mar: March.
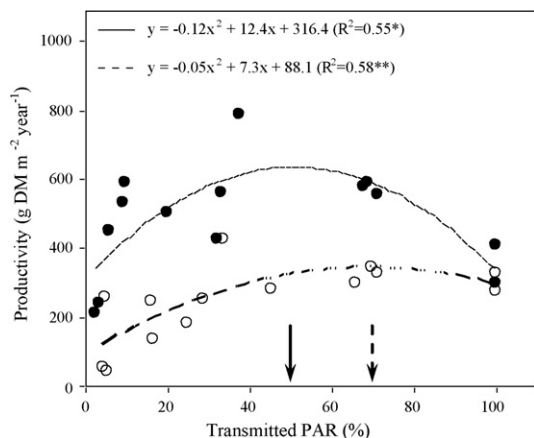

Fig. 4. Second order polynomial models between transmitted PAR and grassland productivity, during seasons 2006–2007 (full dots, continuous line) and 2007–2008 (empty dots, dashed line). Productivity refers to biomass accumulated up during the growing season (October to March–April). Arrows indicate transmitted PAR values at which predicted maximum values occur in the first (continuous line) and second (dashed line) growing seasons. Significance levels: *$P < 0.05$; **$P < 0.01$. Coefficients of determination (R^2) are given for each significant function.

No significant relationship was found between species richness and transmitted PAR (Fig. 6). In some of the densest forests, however, few species occurred. On the other hand, the percentage of native species fell linearly with a decrease in tree cover.

4. Discussion

According to our results, aboveground herbaceous productivity in open areas is comparatively lower than in woodlands. Previous evidence of greater productivity with increased tree cover has been reported in savannahs (McPherson, 1997; Scholes and Archer, 1997) and savannah-like ecosystems (Ovalle et al., 2006; Moreno, 2008). In our case, grassland productivity decreases under dense forest thus the relationship is a second order polynomial. Similar results were observed in shrub-grass rangelands from North America (Dodd et al., 1972; Pieper, 1990). Although the specific mechanisms responsible for short-term responses are not investigated here, our results suggest that competition for water or light offset the general positive effect of the tree canopy. Intra-seasonal and year-to-year variation of the tree effect may support this idea. A fast increase in biomass at intermediate covers reveals a positive
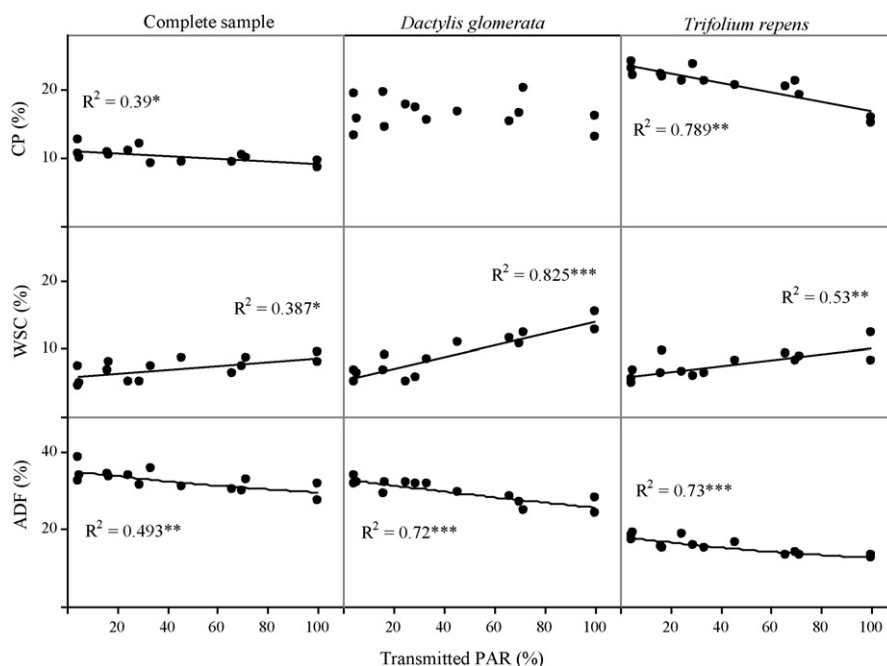
Fig. 5. Linear relationship between transmitted PAR and herbage quality parameters: crude protein (CP), water-soluble carbohydrates (WSC) and acid detergent fibres (ADF), evaluated at the biomass peak (January 2008). Parameters are expressed as a percentage of dry matter (%, g g^{-1}). Significance levels: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Coefficients of determination (R^2) are given for each significant function.

Table 1
List of species occurrence across the tree cover classes. Asterisks denote shrub life form. Status: n = native, according to Marticorena and Quezada (1985).

Species	Family	Status	Open areas	Scattered trees	Medium-density	Dense forests
Acaena ovalifolia Ruiz et Pav.	Rosaceae	n	+		+	+
Acaena pinnatifida Ruiz et Pav.	Rosaceae	n	+	+	+	+
Adenocaulon chilense Less.	Compositae	n		+	+	+
Anemone multifida Poir.	Ranunculaceae	n	+	+		
Arrhenatherum elatius (L.) P.Beauv.	Gramineae		+			
Berberis serratodentata Lechler *	Berberidaceae	n				+
Blechnum penna-marina (Poir.) Kuhn	Blechnaceae	n			+	+
Bromus stamineus Desv.	Gramineae	n	+	+	+	+
Cerastium arvense L.	Caryophyllaceae		+	+	+	+
Cerastium glomeratum Thuill.	Caryophyllaceae			+	+	
Chusquea cuelou E. Desv. *	Gramineae	n	+			+
Codonorchis lessoni (Brongn.) Lindl.	Orchidaceae	n			+	+
Crepis capillaris (L.)Wallr.	Compositae		+	+		
Dactylis glomerata L.	Gramineae		+	+	+	+
Elymus spp.	Gramineae	n	+	+		+
Festuca spp.	Gramineae	n	+	+		
Fragaria chiloensis (L.) Duch.	Rosaceae	n	+	+		+
Galium aparine L.	Rubiaceae					+
Geranium sessiliflorum Cav.	Geraniaceae	n	+	+	+	+
Geum magellanicum Pers.	Rosaceae	n			+	+
Hipochaeris radicata L.	Compositae		+	+	+	+
Holcus lanatus L.	Gramineae		+	+	+	+
Luzula racemosa Desv.	Juncaceae	n	+			
Maytenus disticha (Hook, f.) Urban *	Celastraceae	n				+
Myosotis stricta Link ex Roem.Schult.	Boraginaceae		+			
Nothofagus pumilio (End. Poepp.) Krasser *†	Fagaceae	n			+	+
Osmorhiza chilensis H. et A.	Umbeliferae	n		+	+	+
Plantago lanceolata L.	Plantaginaceae		+	+		
Poa pratensis L.	Gramineae		+	+	+	+
Ribes magellanicum Poir. *	Saxifragaceae	n				+
Rumex acetosella L.	Polygonaceae		+	+	+	+
Silene magallanica (Desr.) Bocquet	Caryophyllaceae	n	+			
Stellaria media (L.) Vill.	Caryophyllaceae				+	+
Taraxacum officinale Weber	Compositae		+	+	+	+
Trifolium repens L.	Papilionaceae		+	+	+	+
Veronica serpyllifolia L.	Scrophulariaceae			+	+	
Vicia nigricans Hook, et Am.	Papilionaceae	n			+	+
Viola maculata Cav.	Violaceae	n			+	+

† Shrub under 1 m in height.

net effect of trees during the early season. A lower biomass production after the peak of biomass (January) may be associated to a decrease in rainfall and soil water availability during the summer. In addition, lenga, as a deciduous species, reaches its peak of cover canopy by January thus limiting understorey light availability. However, seasonal water shortage limiting herbage growth occurs in woodlands as well as in open areas. Belowground processes may be important too, although no evidence of competition has been found so far in nearby silvopastoral systems with exotic tree species (Fernández et al., 2007). Lenga has a relatively shallow rooting system and belowground interactions with the herbaceous vegetation would be possible (Schulze et al., 1996). Furthermore, lenga canopy changes along the growing season and its relationship with herbage growth seasonality is a very motivating basis for further studies.

Grassland productivity is maximized at intermediate tree covers, but according to the polynomial models described here, in the wetter year, maximum value occurs at a higher tree cover (50% of transmitted PAR) than in the drier one (70% of transmitted PAR). This opposes to the general idea that trees enhance understorey growth particularly in drier sites (Joffre and Rambal, 1993). However, many comparative studies refer to environments where water is limiting but not much information exists in temperate biomes.

The spatial heterogeneity created by woody vegetation affects plant communities. Although the number of species found in dense forests is slightly lower than in the rest of the sites, most of them are native. Moreover, percentage of native species decreases linearly with decreasing tree cover. In fact, non-native species are rare in primary lenga forests. In an undisturbed lenga forest in Argentina, Damascos and Rapoport (2002) found only two exotic species in a total of 26.

The influence of trees on herbage nutritional quality confirms that crude protein is usually higher in shaded plants (Neel et al., 2008) while water-soluble carbohydrates increase with radiation (Samarakoon et al., 1990) and generally no effect is reported on digestibility (Peri et al., 2007). Only crude protein in *D. glomerata* showed no increment with tree cover, although Peri et al. (2007) did report it in a silvopastoral system with *Pinus radiata* in New Zealand. The linear relationships found between herbage quality parameters and transmitted PAR support the hypothesis that pastures in woodlands have a higher nutritive value than in treeless areas, despite a loss of water-soluble carbohydrates which might compromise the intake by herbivores (Fraser et al., 2009). However, a combination of shaded and unshaded pastures may provide cattle with a better combination of nutrients (Ludwig et al., 2008).

Our results suggest that native trees from Northwestern Patagonia can increase grassland productivity, at intermediate tree covers, while at the same time allow a relatively high herbage nutritive value and species richness to be maintained, including a high proportion of native species. However there is a need of further research in the area, comprising more years' measurements and considering the specific mechanisms involved on the tree-understorey relationship.
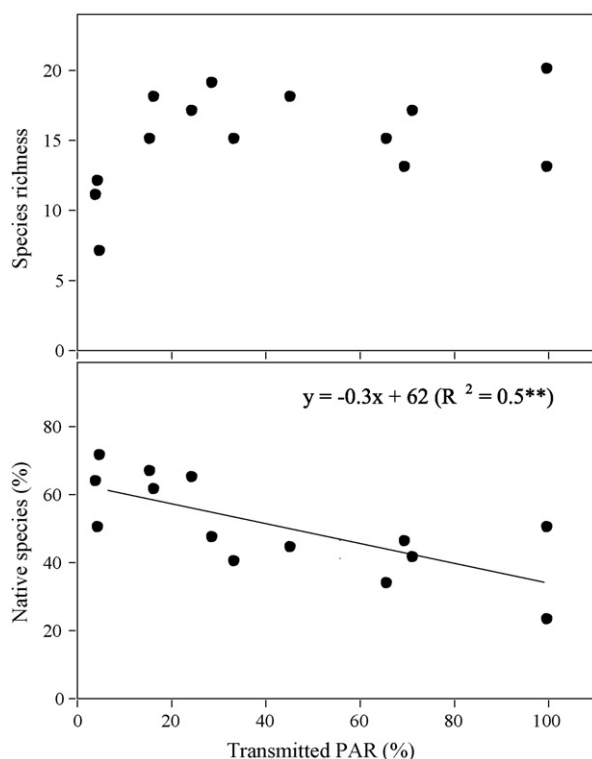
Fig. 6. Relationship between transmitted PAR and total number of species and percentage of natives, surveyed in the 14 study sites. Significance level ([**]$P < 0.01$) and coefficient of determination (R^2) are given for the significant function.

Acknowledgements

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