Variability of herbaceous productivity along *Nothofagus pumilio* forest-open grassland boundaries in northern Chilean Patagonia

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Abstract In order to develop a general model of aboveground net primary production (ANPP) of herbaceous communities in grazing systems that combine forested and open grasslands in temperate areas, biomass production and a set of biotic and abiotic variables were measured at four adjacent forest and grassland sites in Chile's northern Patagonia for two consecutive growing seasons. At each site, one transect of 80 m long (40 m in open grassland and 40 m in forest) × 10 m wide was established. ANPP was significantly higher in open grasslands but no gradual change in biomass production was observed from inside the forest towards the open grassland. In open grasslands ANPP was spatially uniform but highly variable between years of contrasting weather conditions, whereas in forests it was more spatially heterogeneous and less variable over time. ANPP was highly correlated with cattle consumption. Structural equation models developed for the whole system confirm that ANPP was driven mainly by photosynthetically active radiation (PAR) and available nitrogen. However, we found important differences between forests and the adjacent open grasslands. In forests ANPP was enhanced by positive feedbacks between the amount of transmitted PAR through the canopy and soil nutrient input via cattle dung deposition. In open grasslands nitrogen availability appeared to be the main limiting factor but also

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influenced by weather conditions (dryer or wetter years). The coexistence of forests and grasslands patches, with different susceptibility of ANPP to meteorological and soil nutrient availability, highlights the importance of implementing an integrated silvopastoral system with lenga (*Nothofagus pumilio* [Poepp. & Endl.] Krasser) in northern Patagonia.

Introduction

The Aysén Region in Chile's northern Patagonia has a recent history of colonization (Villagrán et al. 1997; Ortega and Brüning 2004). Since the beginning of the twentieth century, large tracts of deciduous lenga (*Nothofagus pumilio* [Poepp. & Endl.] Krasser) and Antarctic beech (*Nothofagus antarctica* [Forster] Oerst.) have been transformed into open grasslands for livestock grazing with scattered patches of these native forests (Veblen et al. 1996). Two production systems currently coexist in the region, that is, cattle farming and forestry, with different managements and little interaction between them. Forestry use is more recent and has been concentrated almost exclusively in timber and firewood with limited use for grazing. The cattle industry has promoted the expansion of grassland in the lower and middle valley zones to the detriment of forests that have been limited to the upper slope positions. The environmental consequences of these forest fragmentation and land use changes in the region have been intensive soil erosion and loss of native species associated with original ecosystems (Ortega and Brüning 2004; Bizama et al. 2011).

Integrated production systems that combine native trees and open grasslands (silvopastoral systems) might reduce the negative environmental consequences of this separated management practices (Perfecto and Vandermeer 2010). The proper management of a silvopastoral system should maximize productive benefits without compromising long-term continuity of key ecological services associated with the original forests, such as biodiversity conservation, nutrient cycling and carbon sequestration (Mosquera-

Losada et al. 2005; Manning et al. 2006). As novel directions for silvicultural management in *N. pumilio* forests prioritize both ecological and social criteria in timber production (Martínez Pastur et al. 2009), the implementation of silvopastoral systems should be based on reliable scientific knowledge on how trees influence herbaceous vegetation (De Miguel 1999; Mosquera-Losada et al. 2005).

The effect of tree cover on aboveground net primary production (ANPP) of herbaceous communities has been widely studied in semiarid climates (Scholes and Archer 1997; Ovalle et al. 2006; Dohn et al. 2013; De Miguel et al. 2013) and also in temperate climates (Benavides et al. 2009; Le Brocque et al. 2009; Barnes et al. 2011; Rivest et al. 2013). Herbaceous plants response to tree cover depends on forest's structural attributes, such as size, shape, canopy density, or tree species composition (Breshears 2006; Barbier et al. 2008). The forest canopy drastically reduces the photosynthetically active radiation (PAR) that reaches the ground, increases litter accumulation, or enhances the competition for water and soil nutrients leading to a decrease in ANPP (Scholes and Archer 1997; Ludwig et al. 2004; Benavides et al. 2009). In other cases, the net effect of forest on ANPP is positive as compared to open areas due to improved soil physical–chemical conditions (Marañón et al. 2009; Le Brocque et al. 2009), or is neutral (Mordelet and Menaut 1995; Rivest et al. 2013). However, studies with native trees (lenga or Antarctic beech) in northern Patagonia are still limited (Sánchez-Jardón et al. 2010; Bahamonde et al. 2012).

In the valleys of Aysén, herbaceous productivity in the understory of remnant native forests is considerably lower than in open grasslands, but the later are generally subjected to intensification practices such as fertilization (Hepp et al. 1988). However, in extensive grazing systems with null or low fertilization, pasture productivity for grazing has received less attention. A recent study by Sánchez-Jardón et al. (2010) reported maximum ANPP values with intermediate lenga tree cover. Similarly, a positive effect of tree cover on herbaceous productivity has been reported with conifer trees introduced in nearby regions (Fernández et al. 2007). It remains unknown whether the observed influence of trees on pasture productivity is expressed beyond the influence of canopy, for example, does ANPP in open grasslands depend on the distance to a forested area? Is it light availability more important than soil nutrients?

In the transition area between two adjacent ecosystems, such as forests and open grasslands, the abrupt change of some biotic and abiotic variables such as transmitted PAR, litter ground cover, woody debris, and soil nutrient concentration could have significant effects on ANPP (Murcia 1995; Jose et al. 1996; Ries et al. 2004; Breshears 2006), creatingan interactive boundary or the so-called edge effect. Cattle grazing are usually concentrated in the areas where herbaceous production is higher (Casado et al. 1985; De Miguel 1999) which can also affect ANPP due to differential intake (nutrient extraction) and dung deposition (nutrient input) in forest and open grassland (Wiens et al. 1985; McNaughton 1988; Matlack 1994). In addition, patches of adjacent forests and grasslands can interact by transferring materials and nutrients through its boundary (by wind, gravity or dung deposition) which would likely affect the herbaceous productivity (De Miguel et al. 1997; Auerswald et al. 2010; Quinteros et al. 2012). Despite the important implications for herbaceous productivity and nutrient cycling, this interaction has rarely been studied (Gómez-Sal et al. 1992; Ries et al. 2004; Treydte et al. 2010).

We investigated the response of herbaceous productivity to the coexistence of grassland and remnant forest patches within the fragmented landscape. The variability of ANPP was analyzed in extensive cattle's farming that combines both types of patches, in two consecutive growing seasons (2006–2007 and 2007–2008). We hypothesized that ANPP gradually increases from inside the forest towards the open grassland in accordance with the variation of biotic and abiotic variables across the forest-grassland boundary. Thus, the objectives were to assess spatio-temporal variation of ANPP in contact zones between forests and open grasslands and to identify the drivers of herbaceous production. Confirmatory structural equation modelling (SEM) was applied to assess the direct and indirect effects on herbaceous ANPP of a broad set of biotic and abiotic variables, cattle behaviour and intake.

Materials and methods

Study area

The study was conducted in Tamel Aike—Instituto de Investigaciones Agropecuarias (INIA) station in the Simpson Valley (Coyhaique County, Aysén Region, Chile; 45°58′S, 72°08′W, 590 m.a.s.l.). An area of ~50 ha of open grasslands with lenga forest of varying structure (i.e., canopy density, dominant height and the spacing of trees) generally located in the upper slope position was used, which represents a typical grazing system of the Chilean north Patagonia. The area had been subjected to traditional cattle grazing during the summer months for at least 12 years prior to the start of this study. During the two growing seasons (September–March in 2006–2007 and 2007–2008) of study the area was grazed from December to April–May by a stock of approximately 20 cows (with calves) following local recommendations. Dominant herbaceous species in the forest were the natives *Osmorhiza chilensis*, *Acaena ovalifolia*, and *Adenocaulon chilense*, while in the open grasslands prevailed the exotics ones like *Dactylis glomerata*, *Taraxacum officinale* and *Trifolium repens* (for further details on species composition see Sánchez-Jardón et al. 2010).

Long term mean annual temperature recorded at the closest meteorological station (located in Aeródromo Teniente Vidal near the city of Coyhaique) is 8 °C, average maximum temperature in January (warmest month) is 19 °C, and minimum temperature in July (coldest month) is −0.5 °C. Annual precipitation is 994 mm. This type of climate limits the growing season to approximately 6 months, from October to March–April. Differences in temperature and precipitation occurred between the two growing seasons; the second was drier and warmer (mean temperature = 11.9 °C; precipitation = 401 mm) than the first (mean temperature = 10.7 °C; precipitation = 504 mm). Soils are loamy or sand-loamy in texture, with pH ranging between 4.5 and 5.8, derived from volcanic ash (Schlatter 1994) and highly prone to wind erosion (Hepp et al. 1988).

Aboveground herbaceous biomass

Four sites of forests of high canopy density in contact with open treeless grasslands were selected in the study area. All sites faced north and had a gentle slope (<15°). The understory vegetation was predominantly herbaceous and shrubs were scarce. At each site, one transect of 80 m long (40 m in open grassland and 40 m in forest) × 10 m wide was established. Nine 10 × 10 m plots were placed uniformly along each transect (Fig. 1).
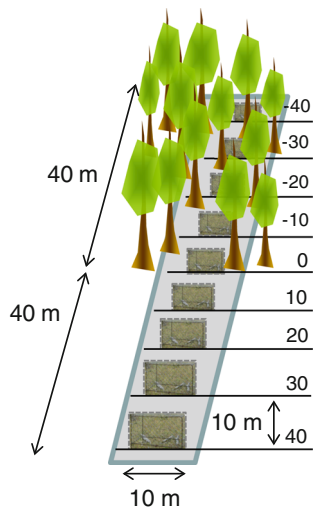
Fig. 1 Diagram showing one of the four adjacent forest and grassland sites selected for analyzing the spatio–temporal variability of herbaceous ANPP

Aboveground herbaceous biomass was harvested every 4–5 weeks during the two growing seasons. Wire enclosure cages (70 × 100 × 50 cm) with a basal area of 0.5 m^2 were placed in each of the nine plots to prevent herbivore intake (i.e., cattle and small- and medium-sized mammals). Herbaceous biomass was cut at ground level inside and outside (in an equivalent 0.5 m^2 area) the cages with an electric shearing handpiece. Cages were relocated in the plot after each sampling date to avoid areas harvested in previous sampling dates, thus fully account for net production (Sala et al. 2000). In the laboratory, samples were oven-dried for 48 h at 60 °C and their dry weight measured. Biomass dry weight values were used to calculate monthly measurements of net primary production (ANPPi) expressed as ANPPi = BIt − BOt-1, where BIt is the biomass inside the cage at a given sampling date and BOt-1 is the biomass outside the cage at the previous sampling date. Similarly, monthly measurements of cattle consumption (intake) were calculated as the difference between the biomass inside and outside the cages at each sampling date (BIt − BOt). At the beginning of the growing season after snow had melted, biomass inside the cage represented the produced biomass (ANPP1 = BI1) and intake was null. Net aboveground primary production and total cattle intake were calculated by adding up monthly values throughout each growing season.

In order to assess the relative importance of legumes in the total herbaceous biomass, a subsample of the biomass harvested in the period of maximum vegetative growth (December–January) was used to determine the relative fraction (% dry weight) of this group. Plant species composition at this period was thought to be the most representative throughout the growing season.

Other variables

A set of biotic and abiotic variables (groundcover, tree cover, photosynthetically active radiation (PAR) transmitted through the canopy, and soil chemistry) were recorded in each plot during the first growing season and the period of maximum vegetative growth (December-January). Groundcover variables (cover of shrubs, herbaceous plants, litter, bare soil, coarse woody debris, and cattle dung) were visually estimated to the nearest 5 % in four circles with a 2.5 m diameter uniformly distributed in each plot. PAR was measured at midday on a sunny summer day in 2007 (January 22–24) with a 0.8 m-long ceptometer (AccuPAR model PAR-80, Decagon Devices Inc., USA). In each plot, 10 readings were taken at one-meter height in four locations (40 readings per plot). Transmitted PAR (%) was calculated as the mean incident PAR compared with a reference measurement in nearby treeless open areas. Reference measurements were recorded every 15 min at a minimum distance of 20 m (mean tree height) from the nearest tree. For this reason transmitted PAR values were maximum (100 %) in all grassland plots.

Soil samples were taken at the beginning of the study (September 2006) after the snow had completely disappeared. Four random soil subsamples at a depth of 0–7 cm from each plot were collected and homogenized. Samples were air-dried and sieved to pass a 2 mm-mesh and then analyzed at the Tamel Aike INIA Laboratory. The pH was determined in a 1:2.5 solution of soil in deionized water. Organic matter (OM) content was calculated (according to Schlesinger 1991) as twice the value of organic carbon (obtained by wet combustion and spectrophotometric reading at 600 nm; Walkley and Black procedure). Total nitrogen (N) was determined by the Kjeldahl method and available N by a potassium chloride extraction according to Sadzawka et al. (2006). The C/N ratio was calculated from total carbon (C) and total N

Table 1 Mean values of aboveground net primary production (ANPP; g m^{-2}) for the four transects (T1, T2, T3, and T4) and the two growing seasons (years) considering (a) forest-grassland plots pooled together (n = 9), and (b) forest or grassland plots separately (n = 4)

	Transects (T)				F(P)	F(P)	F(P)
	T1	T2	T3	T4	T	Year	T × year
(a) All plots							
2006–2007	193.1[b]	220.8[ab]	292.3[ab]	373.9[a]	7.41 (<0.001)	1.5 (0.218)	0.6 (0.647)
2007–2008	127.2[b]	138.8[b]	185.1[ab]	355.3[a]			
(b) Forest plots							
2006–2007	85.9[b]	24.5[c]	229.8[ab]	341.8[a]	21.8 (<0.001)	0.01 (0.910)	3.0 (0.049)
2007–2008	42.0[b]	62.7[b]	145.1[ab]	377.4[a]			
Grassland plots							
2006–2007	307.8	402.3	284.6	417.5	2.7 (0.068)	11.0 (0.003)	1.1 (0.378)
2007–2008	215.8	193.1	222.7	359.3			

Differences between transects and years and their interaction were calculated by two-way ANOVA of log-transformed data; F-values and associated probability (P) are shown. For b, the plot at the contact line between forest and open grassland was excluded from the analyses Different letters indicate significant differences among transects (columns) calculated by Tukey HSD post hoc test

(Schlesinger 1991). Total sulphur (S) was obtained by dry combustion with an Elemental Analyzer (Vario MAX CNS). Extractable phosphorus (P) was estimated in 0.5 M NaHCO$_3$ using the molybdate ascorbic acid method (P-Olsen procedure) and potassium (K) content was determined by an atomic absorption spectrophotometer of an ammonium acetate extraction (Sadzawka et al. 2006).

Data analyses

Mean values of aboveground primary production and cattle intake were first analyzed by two-way ANOVA considering transects and growing seasons as factors. The averaged values were calculated on two spatial scales, that is, the entire transect (forest-grassland plots together) and separate forest and grassland plots. Pair-wise comparisons among transects were calculated by using Tukey Honest Significant Differences (HSD) post hoc tests. Differences among forest and grassland patches were further calculated for each growing season. Similarly, mean values of biotic and abiotic variables, and differences among forest and grassland patches, were further calculated by one-way ANOVA. The relationship among variables was explored by using Pearson correlations. To assess whether there was a spatial autocorrelation of the analyzed variables, further correlations with the transect position (plot number, 1–9) were calculated.

Raw data was log-transformed (+1) prior to analyses to approximate normality. These analyses were performed in R 2.9.2 software (R Core Team 2009).

At the scale of forest-grassland plots (the entire transect) the relationship between biotic and abiotic variables and ANPP was further investigated using structural equation modelling (SEM). Confirmatory SEM tests whether data support an aprioristic model based on a hypothesized causal structure considering direct and indirect effects among variables (Grace 2006). In our model ANPP ultimately depends on the availability of light and available soil nitrogen. Cattle dung, tree litter and legumes would indirectly increase ANPP by increasing soil organic matter (OM) and available N. Unknown or unspecified effects (error variables) on the endogenous variables (all but PAR) were added to the model. In order to evaluate the relative importance of directs and indirect effects of the potential sources of soil nutrient inputs (litter, dung, legumes) on nutrient availability and ANPP, simpler models were further developed for each source and nutrient in forest and grassland plots separately. SEM methods allow to tests entire models as well as individual parameters (variance explained accounted for by other variables, and variance unexplained), therefore it is suited for evaluating the differences between forests and grasslands of both the fitted models and the significant direct and indirect effects. A set of 12 models relating 3 sources × 4

nutrients were constructed with 5 degrees of freedom for both forests and grassland plots (n = 16). Standardized path coefficients were estimated using the maximum likelihood method, according to the small sample size (Finch et al. 1997). Model fitting (the degree of fit between the observed and predicted pattern) was assessed by a χ^2 goodness-of-fit test. Goodness of fit was supplemented by Root Mean Square Error of Approximation (RMSEA), in opposition to χ^2, which is adjusted for sample size (Grace 2006). Either a non-significant χ^2 test or a significant RMSEA indicate that the model fit the data. SEM was carried out using AMOS 18.0.0 software (AMOS Development Corporation, Crawfordville, FL, USA).

Results

### Spatio-temporal variation of ANPP values

Averaged values of ANPP showed significant differences between the four transects but not between the two years analyzed (Table 1a). Considering only the forest plots significant ($P < 0.001$) differences between transects but not between years were also found (Table 1b). Conversely, ANPP values for open grassland plots differed between years but not between transects. In particular, grassland plots in the warmer and drier growing season (2007–2008) exhibited lower ANPP values. Interaction between these two factors was not significant in all cases. Mean monthly values (ANPPi) for the two growing seasons in the four transects are shown in Table 2.

Different spatial trends were observed among the four transects; in two of them (T1 and T2) ANPP was lower in the forest and increased toward the open grassland, whereas in the other two (T3 and T4) ANPP inside the forest was as high as in the open grassland (Fig. 2a). Intake variation across the boundary was similar to that of ANPP (Fig. 2c), in accordance with the high correlation between these two variables in our dataset ($r = 0.93$; $P < 0.001$; n = 72). However, Pearson correlations between ANPP values and distance to the boundary were not significant either inside the forest ($r = 0.17$; $P = 0.519$ and r = 0.14; $P = 0.593$ in the first and second growing season, respectively; n = 16) or in open grasslands ($r = -0.02$: $P = 0.939$ and r = 0.39; $P = 0.131$ in the first and second growing season, respectively; n = 16).

Table 2 Mean monthly values (±SE) of aboveground primary production (ANPP) for two growing seasons in the four transects (n = 4)

	Transect position from forest (−40 m) to grassland (40 m)																	
	−40 m		−30 m		−20 m		−10 m		0 m		10 m		20 m		30 m		40 m	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
2006–2007																		
Oct-06	39.5	12.6	13.7	5.3	21.4	7.3	29.9	11.7	52.5	7.6	85.5	19.9	77.2	16.9	70.9	12.7	72.0	7.7
Nov-06	6.3	6.3	4.0	2.3	31.3	19.1	18.0	12.9	18.1	14.6	10.0	10.0	15.6	15.6	14.8	8.9	7.1	7.1
Dic-06	28.9	6.4	30.7	15.7	33.8	21.4	86.4	52.9	92.7	31.3	78.7	19.8	116.4	45.4	103.3	35.4	108.7	35.5
Ene-07	35.9	25.6	11.9	7.3	63.1	63.1	51.6	35.5	108.4	79.3	143.0	65.4	85.2	53.3	126.7	51.6	64.9	37.6
Feb-07	4.3	4.3	2.6	1.5	78.7	57.4	5.2	5.2	6.8	4.3	25.5	11.5	18.8	8.3	41.0	41.0	60.7	32.3
Mar-07	19.3	7.5	22.9	22.9	29.3	22.5	13.3	8.2	57.6	11.7	18.8	4.7	18.3	13.3	31.9	21.1	16.9	8.1
2007–2008																		
Oct-07	36.0	16.3	30.0	19.7	36.7	15.9	58.6	31.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nov-07	28.4	17.8	129.5	102.1	41.0	26.3	34.5	25.9	150.1	38.2	146.6	59.2	170.5	51.5	110.9	18.8	159.4	58.4
Ene-08	34.8	12.6	14.1	12.1	91.6	89.9	54.2	26.9	28.4	18.2	76.5	30.3	36.3	22.9	78.5	35.2	165.2	56.2
Feb-08	0.0	0.0	6.8	4.0	0.0	0.0	0.0	0.0	10.1	5.9	0.0	0.0	10.0	10.0	0.5	0.5	0.0	0.0
Abr-08	2.4	2.0	5.2	4.0	15.1	15.1	8.1	8.1	7.8	7.8	6.5	3.7	8.8	3.3	5.9	3.8	15.1	8.7
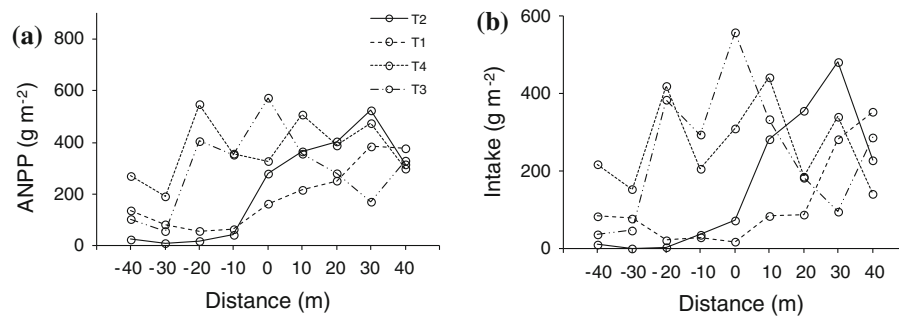
Fig. 2 Herbaceous ANPP values (**a**) and cattle consumption (intake) (**b**) in the nine plots in each of the four selected transects (T1, T2, T3, and T4) in 2006–2007. Distance 0 corresponds to the contact line between forest and open grassland; negative and positive distances refer to forest and grassland, respectively

Factors explaining spatial variation of ANPP

As expected, large differences in transmitted PAR were observed between forests and open grasslands as well as in litter cover (Fig. 3a; Table 3). In contrast, no statistical differences occurred in bare soil cover, coarse woody debris, abundance of dung, or percentage of legumes between forests and grasslands. Forest soil exhibited significant more available N, P and K and C/N ratio than open grasslands (Table 3). In open grasslands none of the variables exhibited significant correlations with position along the transect ($P > 0.05$ for all cases; Fig. 3). In forests, only PAR showed significant correlation with distance to contact line ($r = -0.58$; $P = 0.019$).

SEM analysis for the entire transect (forest-open grassland plots together) showed that PAR and available N both have strong direct effects on herbaceous ANPP (Fig. 4). Other nutrients held in OM seemed to have no relationship with ANPP (Table 4). Soil OM was related to N availability as predicted, but there was no indirect effect of the sources of soil fertility (tree litter, dung or legumes) on ANPP. Also, no positive feedback of ANPP on soil OM via cattle dung deposition was detected at this scale.

In forest the SEM analysis relating soil nutrient sources and nutrients with ANPP indicated that the latter was influenced by the available N and K (Fig. 5). The litter and dung sources for N had contrasting influence on ANPP: the indirect effect of litter was negative (-0.43) whereas dung had positive effects (0.46). K also had an influence on ANPP, apparently via dung (0.36) but not litter or legumes. P and S were not related to ANPP in forests (Table 4). In open grasslands available N had a prominent role in ANPP but it was not related to any of the considered sources of soil nutrients. In particular, dung was not related to any of the nutrients (Table 4), whereas both litter and legumes showed a relationship with P, K and S (negative and positive effect, respectively) but unlinked to ANPP (Fig. 5).

Discussion

The hypothesized gradual response of ANPP along the forest-grassland boundary is not clearly observed in this system. In some transects ANPP tends to increase from the forest edge toward the open grassland, but this is not the general pattern. On the contrary, results indicate that forest-grassland transition areas do not constitute a gradient, but rather two independent units with different spatial and temporal variations of herbaceous ANPP.

The path analysis considering the whole system (forest-open grassland plots together) allows understanding the main interactions between ANPP and biotic and abiotic factors in *N. pumilio* forest patches from northern Chilean Patagonia. In general, results stress the importance of both light and soil nutrients (mainly N) availability as major drivers of ANPP. Both factors are widely recognized as main drivers of plant productivity (Jose et al. 1996; Ludwig et al. 2004; Fernández et al. 2007; Benavides et al. 2009). Organic matter and nutrients like S, P and K do not constitute limiting factors for ANPP probably due to their high availabilities in these soils (Hepp et al. 1988; Table 3). In forests transmitted PAR is highly variable
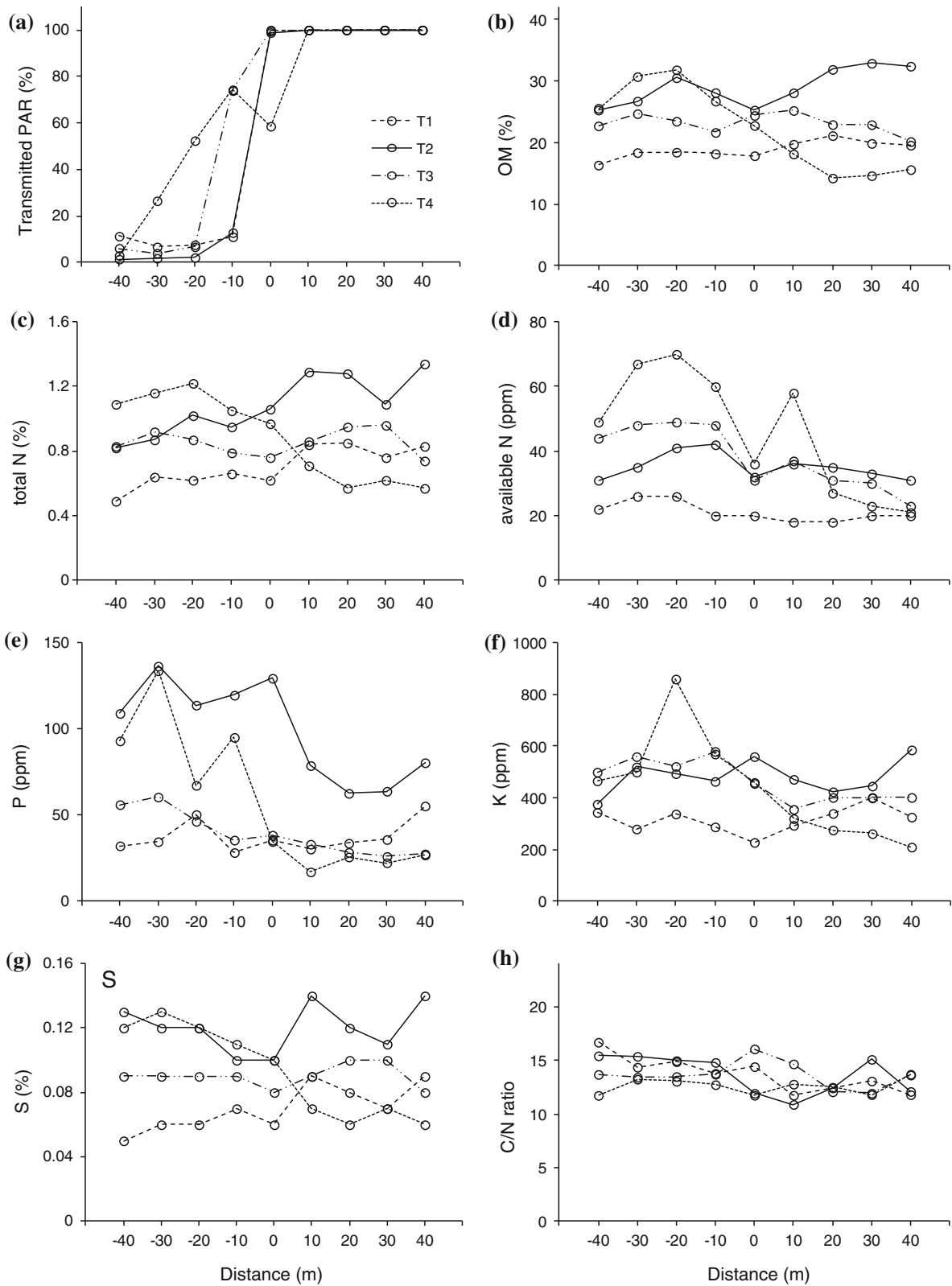
according to forest structure, explaining the variation of ANPP as a function of light-permeability (Breshears 2006; Barbier et al. 2008). While maximum herbaceous production was observed at intermediate tree cover, i.e., low canopy density (∼70 % of transmitted PAR; Sánchez-Jardón et al. 2010), optimal light-permeability can be achieved at high canopy density by changing other structural attributes of the forest stand such as size and shape (Barbier et al. 2008). By contrast open grasslands present maximum transmitted PAR and hence it cannot explain the observed changes in ANPP. The available N is usually a limiting factor of plant growth in non-tropical ecosystems (Schlesinger 1991; Vitousek and Howarth 1991; Attiwill and Adams 1993; Aerts and Chapin 1999). However, open grasslands, which have comparatively lower available N than forests, exhibit higher ANPP values. Also, the two transects with lower tree cover exhibited higher N availability, suggesting that both factors may be influencing herbaceous ANPP in this system. The distinct

influence, however, of light and nutrient availability on these herbaceous communities needs to be further investigated. In addition, the SEM analysis shows that the hypothesized sources of N (dung, litter and legumes) do not affect directly soil OM or available N at this scale.

In open grasslands, the production in the warmer and drier growing season is lower than in the colder and wetter season in open grasslands, probably due to reduced water availability, but this is not observed in forests. Comparing lenga forests with adjacent treeless areas, Promis et al. (2010) detect strong microclimatic differences, especially in daily temperature oscillation (higher in treeless areas), relative air humidity (higher in forests) and wind speed (reduction up to 50 % in forests). The microclimatic modifications seem to indicate that the forest could be acting as a moderating factor of the effects of interannual climatic variation on herbaceous production as has been identified in some Mediterranean silvopastoral systems (De Miguel et al. 2013). The different variation patterns of ANPP in forests and open grasslands suggest the existence of distinct ecological functioning (drivers) of herbaceous production in these two types of patches.

In forests under cattle grazing, soil nitrogen derives from OM inputs from trees (litter and dead trunks), biological fixation of atmospheric N, or through
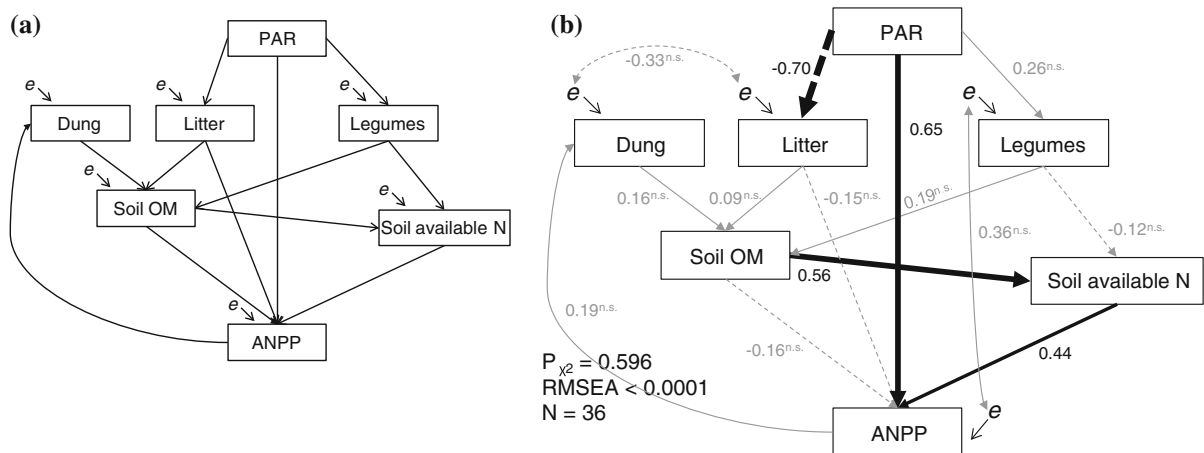
Fig. 4 a Path diagram representing hypothesized causal relationships among transmitted photosynthetically active radiation (PAR), soil organic matter (OM) and available N, sources of soil nutrient and aboveground net primary production (ANPP) of herbaceous communities in a silvopastoral system from northern Chilean Patagonia. The letter *e* represents residual error variables. **b** Model fitting for the entire transect (forest-grassland plots together). *Solid* and *dashed lines* denote positive and negative effects, respectively. The width of the arrows is proportional to the standardized path coefficients. Path coefficients non-significantly different from zero (n.s.; $P > 0.05$) are *light grey*. Fit statistics (*P* value of χ^2 and RMSEA tests) and sample size (N) are also indicated

Table 3 Mean values (±SE) of aboveground primary production (ANPP) and cattle intake for the two growing seasons, and biotic and abiotic variables for the first growing season (2006–2007) in forest and in grassland plots

	Forest plots	Grassland plots
ANPP 2006–2007 (g m^{-2})	170.5 (41.4)b	353.0 (24.6)a
ANPP 2007–2008 (g m^{-2})	156.8 (40.6)	247.7 (26.8)
Intake 2006–2007 (g m^{-2})	127.1 (34.6)b	260.7 (30.8)a
Intake 2007–2008 (g m^{-2})	123.0 (32.7)b	249.3 (32.2)a
Transmitted PAR (%)	18.8 (1.3)b	100 (0)a
Shrub cover (%)	11.9 (1.1)	5.9 (1.5)
Herbs cover (%)	71.7 (0.2)	38.1 (0.6)
Bare soil cover (%)	7.0 (1.3)	6.6 (1.0)
Litter cover (%)	40.3 (0.5)a	6.8 (1.1)b
Woody debris (%)	18.6 (0.7)	13.7 (0.8)
Dung (%)	1.1 (1.7)	1.3 (1.9)
Legumes (%MS)	2.7 (1.4)	4.0 (1.0)
Total N (%)	0.88 (0.23)	0.89 (0.28)
N (ppm)	47.3 (0.6)a	28.8 (0.4)b
S (%)	0.10 (0.27)	0.09 (0.28)
P (ppm)	75.8 (0.5)a	40.5 (0.5)b
K (ppm)	478.9 (24.7)a	357.7 (26.7)b
pH	6.17 (0.02)	6.22 (0.03)
C/N ratio	14.08 (0.09)a	12.7 (0.09)b
OM (%)	24.3 (0.2)	22.5 (0.3)

The plot at the contact line between forest and open grassland was excluded from the analyses. Different letters indicate significant differences between forests and grasslands calculated by one-way ANOVA of log-transformed data (n = 16)

PAR photosynthetically active radiation, OM organic matter

fertilization by dung (Schlesinger 1991; Williams and Haynes 1995; Bardgett et al. 1998; McGregor and Brown 2010). Litter in the forests under study is very abundant and it negatively affects herbaceous ANPP, as usually reported in forested areas of the temperate world (Facelli and Pickett 1991; Scholes and Archer 1997; Xiong and Nilsson 1999). Also, litter is not correlated with any of the analyzed soil nutrients (total N, K, P, and S), and negatively correlated with available N. During the early stages of litter decomposition high soil N supply is necessary for the microbial activity (St. Luce et al. 2011), especially if litter have high lignin content and C/N ratio. Lenga litter have relatively low N content (8–10 mg g^{-1}), high lignin: N ratio (41.7), and low nitrification rates

(Caldentey et al. 2001, Decker and Boerner 2006), suggesting a reduction of available N due to immobilization of N by litter. Moreover, microorganisms can immobilize mineral N or release it into the soil solution, as low N concentration in soil solution limits microbial growth (Henriksen and Breland 1999). Besides, N_2 fixation by legumes is held to represent only a minor contribution to N supply in temperate terrestrial ecosystems (Vitousek and Howarth 1991; Aerts and Chapin 1999).

Our results indicate that in forests the main source of soil fertility (especially available N) is provided by dung (Fig. 5b). As a consequence ANPP in forests is explained by a positive feedback mechanism that involves the transmitted PAR through the canopy, cattle behaviour, and soil nutrient input. In our case, transmitted PAR, ANPP, animal intake and dung input are variables with high positive correlations in forests. In more dense forest light is the limiting factor for herbaceous production and it increase as the canopy become more open. Animal behaviour is influenced by the spatial distribution of grassland productivity (Casado et al. 1985; McNaughton et al. 1989) which could explain the close relationship between ANPP and animal intake. The presence of cattle increases soil fertility through their excrements (McNaughton et al. 1989; Gómez-Sal et al. 1992; De Miguel 1999; Ryrie and Prentice 2011). Largest accumulation of dung is related to high organic phosphate and C (Williams and Haynes 1995), K and S (Badía et al. 2008; McGregor and Brown 2010) and available N (with the participation of microorganisms), with positive effects on ANPP.

In open grasslands ANPP is not limited by light but it shows strong differences depending on meteorological conditions indicating that ANPP is likely limited by water availability (i.e., lower precipitation and higher temperature). Besides, ANPP do not show significant correlations with any of the analyzed nutrients (S, P and K), except available N. Neither litter, nor legumes, nor dung (although its abundance is of the same order of magnitude than in forest) seem to be direct sources for available N. Unlike forests, available N in grasslands is not correlated with total N, which suggests that there is a certain immobilization of this nutrient in the soil (equal amount of total N but less available N). The more extreme conditions for soil microbial activity in grasslands (higher apparent density, higher temperature range, lower humidity,

Table 4 Pearson correlation coefficients between aboveground primary production (ANPP), cattle intake and biotic and abiotic variables recorded in the first year of study (2006–2007) considering (a) forest-grassland plots pooled together (n = 36), (b) forest and (c) grasslands plots separately (n = 16)

	ANPP	PAR	Intake	Dung	Legumes	Litter	Total N	N	S	P	K	pH	OM
(a) All plots													
PAR	**0.806**												
Intake	**0.944**	**0.680**											
Dung	**0.366**	0.225	**0.391**										
Legumes	**0.381**	0.257	**0.399**	0.078									
Litter	**−0.534**	**−0.615**	**−0.494**	**−0.372**	**−0.270**								
Total N	0.139	0.084	0.186	0.288	0.237	**−0.358**							
N	0.033	−0.249	0.144	0.206	0.050	0.280	**0.541**						
S	−0.081	−0.129	−0.028	0.205	0.174	−0.227	**0.890**	**0.546**					
P	**−0.434**	**−0.464**	**−0.392**	0.156	0.046	0.155	**0.627**	**0.463**	**0.722**				
K	−0.005	−0.189	0.083	0.293	0.253	0.065	**0.726**	**0.732**	**0.640**	**0.615**			
pH	0.328	0.266	0.293	0.276	−0.294	−0.034	−0.023	0.163	−0.055	−0.200	0.013		
OM	−0.088	−0.138	−0.004	0.234	0.208	−0.154	**0.903**	**0.599**	**0.838**	**0.732**	**0.788**	−0.256	
C/N ratio	**−0.480**	**−0.455**	**−0.420**	−0.215	−0.100	**0.461**	**−0.416**	−0.041	−0.290	0.095	−0.061	**−0.534**	−0.002
(b) Forest plots													
PAR	**0.727**												
Intake	**0.975**	**0.693**											
Dung	**0.678**	**0.660**	**0.610**										
Legumes	0.462	0.257	0.439	0.292									
Litter	**−0.647**	**−0.542**	**−0.560**	**−0.744**	−0.279								
Total N	0.244	0.189	0.218	**0.626**	−0.132	−0.377							
N	**0.511**	0.423	0.484	**0.757**	0.166	**−0.589**	**0.883**						
S	<0.01	−0.023	−0.051	0.472	−0.133	−0.192	**0.891**	**0.748**					
P	−0.340	−0.230	−0.352	0.225	−0.448	−0.021	**0.709**	**0.513**	**0.816**				
K	0.400	0.391	0.336	**0.586**	0.096	−0.484	**0.775**	**0.886**	**0.667**	0.411			
pH	**0.560**	**0.572**	0.477	0.485	0.040	−0.407	0.196	0.311	0.179	−0.029	0.250		
OM	0.016	0.074	−0.004	0.495	−0.205	−0.211	**0.946**	**0.816**	**0.908**	**0.823**	**0.762**	0.015	
C/N ratio	**−0.614**	−0.312	**−0.595**	**−0.615**	−0.243	**0.554**	**−0.646**	**−0.659**	**−0.473**	−0.120	**−0.443**	**−0.527**	**−0.380**
(c) Grassland plots													
PAR	NA												
Intake	**0.898**	NA											
Dung	0.174	NA	0.249										

and lower C/N ratio) would reduce N mineralization (Jackson et al. 1990; Attiwill and Adams 1993; Belsky and Blumenthal 1997) to a greater extent than in forests. Nevertheless, open grasslands achieve higher ANPP than forests, in spite of their lower amount of available N. It is possible that in these grasslands of relatively recent creation and without apparent restitution of the nutrients extracted by cattle, their production is maintained at the expense of the fertility inherited from the original forest soil. Processes involved in ANPP are possibly more complex in grasslands than in forests, comprising a larger set of variables than those analyzed in this study. Grasslands herbaceous production response could involve soil nutrient contents and mineralization process, as well as meteorological circumstances and microclimatic differences, related either to the absence of trees (e.g., soil moisture, temperature, desiccating action of the wind) or to higher stocking (e.g., trampling increases soil compaction).

Conclusions and management directions

The existence of forest patches and adjoining open grasslands seems to not determine gradual variations in ANPP conditioned by fluxes through their boundaries. Each type of patch possesses particular characteristics related to their different structure and function. Open grasslands and forests constitute a physiognomic and a functional concept. In forests the canopy structure determines the ecological functioning of the understory vegetation. Forests are capable to buffer ANPP interannual variations and, sometimes, to maintain ANPP values as high as those in adjoining open grasslands. The integrated discussion of our results allows us to propose the hypothesis of a positive feedback between PAR-ANPP-cattle grazing where grazing intensity is associated to ANPP values. The effect of animal intake would promote fertilization via their excrements. On the contrary, ANPP in open grasslands is highly variable year to year and their soil fertility inherited from the original forests does not seem to limit herbaceous production but to be held-up by a lower organic matter mineralization rate.

The results are of interest for the implementation in the region of silvopastoral systems with native trees. In fragmented landscapes, forest patches with

Table 4 continued

	ANPP	PAR	Intake	Dung	Legumes	Litter	Total N	N	S	P	K	pH	OM
Legumes	0.025	NA	0.196	0.127									
Litter	−0.028	NA	−0.029	−0.406	**−0.559**								
Total N	−0.070	NA	0.139	−0.009	**0.742**	**−0.618**							
N	0.398	NA	**0.530**	−0.373	0.151	0.201	0.350						
S	0.006	NA	0.191	−0.083	**0.830**	**−0.553**	**0.924**	0.364					
P	0.130	NA	0.253	0.273	**0.850**	**−0.767**	**0.831**	0.042	**0.864**				
K	−0.017	NA	0.242	0.129	**0.604**	−0.456	**0.857**	0.370	**0.729**	**0.657**			
pH	0.106	NA	0.021	−0.022	−0.307	0.453	**−0.533**	0.109	**−0.570**	**−0.581**	**−0.349**		
OM	−0.010	NA	0.225	0.082	**0.568**	**−0.576**	**0.940**	0.382	**0.838**	**0.771**	**0.853**	**−0.621**	
C/N ratio	0.330	NA	0.335	0.192	−0.428	0.154	−0.201	0.095	−0.228	−0.101	−0.068	−0.254	0.124

Data was log-transformed prior to analysis. For b and c the plot at the contact line between forest and open grassland was excluded from the analysis. Significant coefficients (P < 0.05) are highlighted in bold

PAR photosynthetically active radiation transmitted through the canopy, OM organic matter, NA not available (PAR is 100 % in treeless areas)

Fig. 5 a Path diagram representing hypothesized causal relationships among sources of soil nutrient (litter, dung, and legumes), nutrients pool (available N, P and K and total S) and aboveground net primary production (ANPP) of herbaceous communities. Models were fitted separately for forests (**b**) and open grasslands (**c**). *Solid* and *dashed lines* denote positive and negative effects, respectively. Residual error variables on the observed variables are not shown for simplicity. The width of the arrows is proportional to the standardized path coefficients. Path coefficients non-significantly different from zero (n.s.; $P > 0.05$) are light grey. Fit statistics (P value of χ^2 and RMSEA tests) are also indicated ($n = 16$)

an optimal light-permeability (either by a low canopy density or by an appropriate size and shape) constitute valuable resources for cattle grazing. Forests represent fertility patches that complement spatially and temporally the productivity of open grasslands.

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