

Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina

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Abstract. Both ecosystem carbon gain and nutrient availability are largely constrained by the magnitude and seasonality of precipitation in arid and semi-arid ecosystems. We investigated the role of precipitation on ecosystem processes along an International Geosphere Biosphere Programme (IGBP) transect in temperate South America. The transect consists of a contiguous precipitation gradient in the southern region of Argentinean Patagonia (44–45° S), from 100 mm to 800 mm mean annual precipitation (MAP) and vegetation ranging from desert scrub to closed canopy forest. Gravimetric soil water content tracked changes in seasonal and annual precipitation, with a linear increase in soil water content with increasing MAP. Above-ground net primary production (ANPP) increased linearly along the gradient of precipitation ($\text{ANPP} = -31.2 + 0.52 \text{ MAP}$, $r^2 = 0.84$, $p = 0.028$), supporting the relationship that carbon assimilation is largely controlled by available water in these sites, and was in general agreement with regional models of ANPP and rainfall. However, inorganic soil nitrogen was also highly linearly correlated with both MAP ($[\text{N}] = 0.19 \text{ MAP} - 32$, $r^2 = 0.96$, $p = 0.003$) and ANPP ($\text{ANPP} = 2.6 [\text{N}_{\text{inorganic}}] + 59.4$, $r^2 = 0.79$, $p = 0.042$), suggesting a direct control of precipitation on nitrogen turnover and an interaction with nitrogen availability in controlling carbon gain. The asynchrony of precipitation and changes in dominant vegetation may play important roles in determining the carbon-nitrogen interactions along this rainfall gradient.

Keywords: Ammonium; Biogeochemistry; IGBP; Nitrate; Primary production; Rainfall; South America; Temperate ecosystem.

Nomenclature: Correa (1971); Dimitri (1972).

Abbreviations: ANPP = Above-ground net primary production, IGBP = International Geosphere Biosphere Programme; MAP = Mean annual precipitation.

Introduction

The use of natural gradients, which vary systematically in climate or other variables, is an invaluable tool for understanding mechanisms of abiotic control on ecosystem processes (Jenny 1980; Vitousek & Matson 1991). A number of gradient studies have been carried out looking at the effect of climatic variables on ecosystem processes, including the effects of temperature and precipitation on biogeochemical cycles (e.g. Pastor & Post 1986; Amundson et al. 1989; Burke et al. 1991; Epstein et al. 1996; Raich et al. 1997; Chadwick et al. 1999; Austin 2002). The value of gradient studies stems from the ability to examine variation in a single factor while maintaining many of the other environmental variables as constant as possible. The challenge is to find clean gradients where confounding factors do not affect the interpretation of patterns in ecosystem processes. An initiative of the International Geosphere-Biosphere Programme (IGBP) identified a set of naturally-occurring transects of climate and vegetation around the globe with the objective of understanding large-scale controls on ecosystem processes. These IGBP transects represent an array of regional-scale gradients on all continents that vary in major environmental variables (Koch et al. 1995).

In the Patagonian region of South America, from 40 to 55° S, there is a strong east-west precipitation gradient, with a shift in vegetation in less than 150 km from xeric desert shrubland to grass-shrub steppe, leading to a low stature tree cover and finally closed canopy forest (Walter 1994). This rainfall gradient, identified as an IGBP transect, provides the opportunity to examine a wide range of ecosystems occurring in close proximity, with changes in dominant life form, annual precipitation, but with little change in elevation or soil origin. Additionally, this gradient offers the opportunity to examine nitrogen cycling along a gradient that has experienced little human-derived nitrogen deposition from industrial sources (Holland et al. 1999).

Global change research attempts to understand the

impact of human activities at the global scale. Nevertheless, understanding of global scale ecological principles is hindered by the strong geographical bias in ecosystem studies. For example, much of the theory of biogeochemistry in temperate ecosystems has come from studies in the northern hemisphere (e.g. Vitousek & Reiners 1975; Gorham et al. 1979; Aber et al. 1991; Burke et al. 1991; Likens & Bormann 1995); it is not clear whether the understanding derived from those studies is applicable to southern-hemisphere ecosystems. As an illustration, a recent studies in temperate Chile and Argentina demonstrated that the dominant loss of nitrogen in these undisturbed old-growth forests was predominantly via an organic nitrogen pathway instead of the inorganic path characteristic of other studies, most of which were located in areas close to pollution sources (Hedin et al. 1995; Perakis & Hedin 2002).

Our objective in this study was to describe the pattern of primary production and nutrient availability along a southern-hemisphere precipitation gradient and to attempt to identify how climate and vegetation interact to ultimately regulate carbon and nitrogen cycling. Our hypothesis was that while water availability may be the primary control on carbon gain in these ecosystems, the indirect effects of precipitation on changes in nitrogen turnover and life form would additionally impact ecosystem functioning.

Site description

The combination of the influence of topography and consistent climatic patterns generate a gradient of decreasing rainfall from the Andean mountain range to the Argentinean coast. Westerly winds from the Pacific Ocean are predominant during the entire year. The fact that very few land masses occur at these latitudes (40 - 60° S) allow these winds to gather extensive force as they move across an almost unbroken expanse of ocean (Strahler & Strahler 1983). The subpolar low-pressure system is more pronounced in winter months, resulting

in higher rainfall at this time of year (Prohaska 1976). The second component determining weather patterns in the Patagonian region is the almost true north-south distribution of the Andean mountain range. The Andes impede the movement of the humid air masses coming from the Pacific ocean, and orographic lifting on the western (Chilean) side of the mountains results in very high rainfall, exceeding 6000 mm in some areas. As these air masses descend on the eastern side of the Andes, temperatures increase and the air becomes drier (due to adiabatic warming), resulting in an exponential decrease in precipitation with distance from the peak of the Andean range (Jobbágy et al. 1995). Thus, the combination of the westerly wind patterns with the north-south orientation of the Andean mountain chain determines the steep east-west gradient in mean annual precipitation (MAP) (Walter & Box 1983).

We located a transect that we divided into five distinct vegetation zones, following an order of increasing MAP (Table 1) and representing important ecosystems in the Patagonian region. These ecosystems can be seen as representing a contiguous gradient of response to changing precipitation (Bertiller et al. 1995; León et al. 1998). The location of the ecotones between vegetation types may vary with a number of interacting factors, including fire frequency and exogenous disturbances (Veblen & Markgraf 1988; Veblen et al. 1992; Aguiar & Sala 1998). We selected sites with the minimum amount of disturbance and land-use impact possible, although light to intermediate grazing had or was occurring in the grassland/shrubland sites. The forested sites, to our knowledge, had never been harvested for timber. Previous work at these sites include a study on rooting depth and water use by Schulze et al. (1996), who found that above-ground biomass varied by an order of magnitude (150 g.m⁻² to 3408 g.m⁻²) from the driest to the wettest site, and belowground biomass followed that increase (330 g.m⁻² to 1484 g.m⁻²) (Fig. 1). Coupled with this change in biomass was a decrease in bare soil, which was maximum at the 125 mm desert scrub site (72%) and decreased in the wooded sites, which had complete canopy cover. The differential re-

Table 1. Site location and characteristics. Location and altitude determined with global positioning system unit (Garmin®), mean annual precipitation estimated using the relationship developed by Jobbágy et al. (1995). Distance of transect calculated as km from driest site.

Site description	Latitude (S)	Longitude (W)	Precipitation (mm)	Elevation(m a.s.l.)	Distance (km)
1. <i>Nassauvia</i> desert scrub	45°26.95'	69°49.97'	125	349	0
2. <i>Mulinum-Stipa</i> shrub-steppe	45°24.64'	70°17.57'	170	474	37.5
3. <i>Festuca</i> grassland	44°52.65'	71°19.53'	290	998	119
4. <i>Nothofagus antarctica</i> woodland	44°51.33'	71°34.82'	520	872	139
5. <i>Nothofagus pumilio</i> forest	44°51.33'	71°43.26'	770	875	150

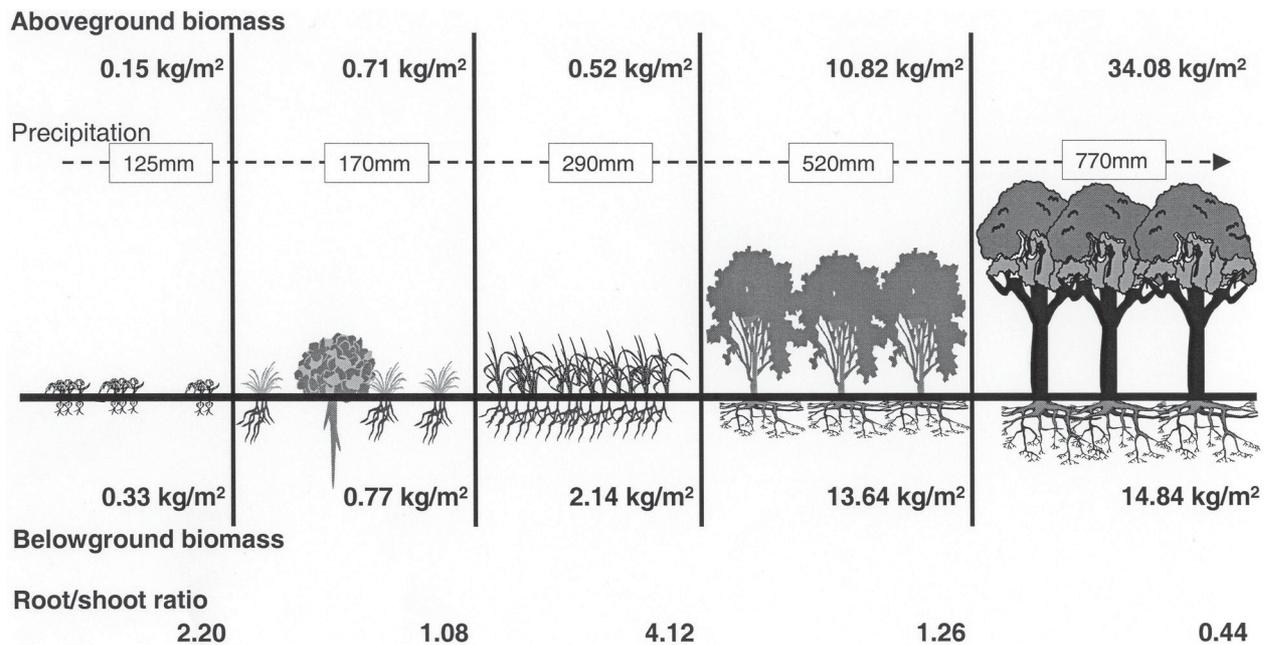


Fig. 1. Representation of life form, above- and below-ground biomass, and root/shoot ratio along precipitation gradient in Patagonia, Argentina (45° S) (data from Schulze et al. 1996). Mean annual precipitation (MAP) estimated from algorithm developed by Jobbágy et al. (1995).

sponse of above and below-ground biomass to changing precipitation resulted in a shift in the root-shoot ratio, with a maximum below-ground allocation in the grassland site and a minimum in the wettest forest site (Fig 1., Schulze et al. 1996).

Because of the remote nature of the sites, long-term climatic data for all sites were unavailable. A study by Jobbágy et al. (1995) estimated rainfall in this region based on distance from the Andean continental divide and longitude, and successfully explained 90% of the spatial variability in precipitation in this region. Using the algorithm developed by Jobbágy et al. (1995) and detailed meteorological data available for one of the sites, we assigned values of mean annual precipitation as 125 mm, 170 mm, 290 mm, 520 mm and 770 mm. Following is a general description of the vegetation of the sites:

Site 1 Nassauvia glomerulosa desert-scrub (125 mm MAP)

This site is located in the Central District of the Patagonian phytogeographic province (Soriano 1956), which is characterized by low annual precipitation and very low plant cover (less than 50%). Extensive bare soil areas are interrupted by individuals of the dominant dwarf shrub species *Nassauvia glomerulosa* and *Chuquiraga avellanadae*, interspersed with small patches of bunch grasses, primarily *Poa ligularis* (Bertiller & Bisigato 1998; León et al. 1998). Soil texture is very coarse with abundant pebbles.

Site 2 Mulinum spinosum-Stipa speciosa shrub-steppe (170 mm MAP)

The shrub-grass steppe of the Occidental district of Patagonia (Soriano 1956) is characterized by its near equal distribution of shrubs and grass life forms. The dominant grasses are perennial C₃ tussock or bunch grasses (*Stipa speciosa*, *S. humilis* and *Poa ligularis*) and interspersed in the bare soil matrix are three dominant shrub species (*Adesmia campestris*, *Senecio filaginoides* and *Mulinum spinosum*). These species account for over 90% of the biomass of the shrub-grass steppe and represent two distinct strategies for resource capture and use (Soriano & Sala 1983; Sala et al. 1989). Grasses have a shallow root system and absorb water predominantly from the upper layers of the soil. In contrast, shrubs have deep roots and absorb most of the water from deep soil layers. Patterns in resource acquisition are associated with phenological patterns. Most shrub species are deciduous with sharp transitions between phases whereas grasses maintain green leaves during the entire year.

Site 3 Festuca pallescens grassland (290 mm MAP)

This site is representative of the sub-Andean district of the phytogeographic province of Patagonia (León et al. 1998). A higher plant cover than the shrub-grass steppe and a change in life-form composition characterizes this vegetation type. The largest physiognomic difference is the dominance of grass species and

the small contribution of shrubs that are quite abundant in the previous two sites. *Festuca palllescens* is the dominant grass species, it is a perennial tussock grass and is accompanied by other grass species such as *Hordeum comosum*, *Bromus* spp. and *Poa* spp. (Bertiller et al. 1995). The dominant shrub is *Mulinum spinosum*, which tends to increase in cover in areas that are overgrazed (Aguiar et al. 1996), but at a much lower density than in the 170 mm site.

Site 4 *Nothofagus antarctica* forest (520 mm MAP)

Nothofagus antarctica is the widest ranging *Nothofagus* species in South America, found from 36° 30' to 56° S, and from sea level to 2000 m a.s.l. (Veblen et al. 1996). *N. antarctica* has both a shrub and tree growth form, depending on the soil characteristics and water availability. It commonly occurs adjacent to stands of *Nothofagus pumilio* (see following site description) but typically on drier or less favourable soils, and forms extensive woodlands in contact with grassland steppe vegetation. However, it also can colonize sites with poorly drained soils, leading some authors to suggest the possibility that the *Nothofagus* distribution may be related to adaptation for low nitrogen availability in soil (Armesto et al. 1992). Effective vegetative reproduction gives *N. antarctica* some competitive advantage in areas that experience periodic disturbances such as fire or wind storms (Burns 1993).

Site 5 *Nothofagus pumilio* forest (770 mm MAP)

Nothofagus pumilio is found throughout a large portion of temperate South America in both Argentina and Chile from 35° 35' to 55° S in both the Andean mountain range and in the coastal cordillera of Chile. In general, these forests have very low diversity of woody species. Pure monospecific stands of *N. pumilio* occur primarily in the region of the North Patagonian and Magellanic rain forests south of 43° 20' S (Veblen et al. 1996). Further north, *Nothofagus pumilio* also forms dense monospecific stands but exclusively at higher elevations (Veblen et al. 1992). Old growth stands include trees aged at over 300 years (Rebertus & Veblen 1993), but disturbances from wind and fire often limit the upper age of stands.

Methods

Above-ground net primary production

The methods chosen to evaluate ANPP measurements were determined by the dominant life form in the site; all sites represent production in 1998. There was no possibility of using the same methodology in all sites due to the differences in carbon turnover in woody vs. herbaceous dominated ecosystems (Sala & Austin 2000). Accordingly, we used different estimation methods for the forest and grassland-shrubland sites. For the 125 mm and 290 mm sites (shrubland and grassland), we harvested 10 randomly-located 1-m² plots (5 m × 20 cm) at peak biomass (January 1999), which included the above-ground biomass of all shrub, grass and herbaceous species. On return to the laboratory, samples were stored in a freezer (−4 °C) until they were separated into categories of green, senesced and dead biomass. Sorted samples were oven dried (70 °C) for 48 h and weighed. All green biomass harvested in January 1999 was considered to represent primary production for the previous year (1998). In the 170 mm site (shrub-grass steppe) we harvested grass and herbaceous species in a similar manner (20 m × 1 m plots) but shrub production was assessed using an algorithm developed specifically for this site (Fernández et al. 1991). We harvested a subsample of green biomass (20 cm × 25 cm) for 20 individuals of each of the principal shrub species (*Mulinum spinosum*, *Senecio filganioides*, and *Adesmia campestris*) and estimated total shrub production based on an empirically-derived relationship between the subsample of green biomass, the geometry of the shrubs and their relative density in the ecosystem (Fernández et al. 1991; Jobbágy & Sala 2000).

In the two forest sites (520 mm and 770 mm), we evaluated ANPP for the non-woody increment (leaf and small branch) using litter fall during the year as an estimate of above-ground production (Whittaker & Marks 1975; Sala & Austin 2000). We randomly located 20 circular 40 cm diameter litter traps in a 50 m × 50 m grid at each site, with periodic collections throughout the year. For all forest litter, samples were transported to the laboratory, dried in a 70 °C oven, separated into leaf, fine branch and reproductive components, dried and weighed. The sum of the entire year's litter fall (Jan-Dec 1998) was the estimate of production for 1998. In all cases, ANPP was scaled to g dry mass m⁻².yr⁻¹.

Water availability and soil inorganic nitrogen

Soil samples were collected at three time points during the year (early, peak and end of growing season),

using a stratified random design to locate transects for sampling. We chose five 25-m transects in a north-south orientation and took five samples at 5-m intervals along this transect. Soil samples consisted of the top 0-5 cm of mineral soil and were taken using a PVC tube. We stored soil samples in an ice chest until they were processed, always within 48 h of sampling. When processed, we sieved fresh soils through a 2-mm mesh and made a composite sample of the samples of each transect using the same mass of sieved soil from each sample (25 g each for a total of 125 g per sample). A subsample of 10 g of soil was extracted for determination of inorganic nitrogen (NH_4^+ and NO_3^-) in 50 ml 2N KCl. We kept soil samples cold until return to the laboratory where we filtered extracts as soon as possible. In the laboratory, we placed a subsample in a drying oven at 105 °C for 48 hours for determination of gravimetric soil water content. We corrected soil nitrogen concentrations for soil water content (Robertson et al. 1999).

Soil extracts were analysed using an Alpkem® autoanalyzer (O-I Corporation, College Station, Texas, USA), which is a colorimetric analysis of inorganic nitrogen in liquid extracts. The detection limit from the manufacturer is 0.09 ppm for NO_3^- and 0.15 ppm for NH_4^+ , although due to some adjustments in the specifications of the autoanalyzer, the working limits of detection in this laboratory are 0.03 ppm for NO_3^- and 0.12 ppm for NH_4^+ (Tagliacruz pers. comm.).

Leaf nitrogen of dominant species was measured by sampling sun leaves of 5 individuals of dominant overstorey vegetation. The leaves of each individual were considered a sample. Samples were ground to pass through a 40 µm mesh and % C and % N content were determined using a Carlo-Erba® NA 1500 elemental analyzer.

Statistical analyses

Mean gravimetric soil water content and soil inorganic N ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and total inorganic N) were calculated on an annual basis using a weighted mean of the number of days between sampling points, with linear interpolation of the two measurements. Differences between seasons in inorganic nitrogen and soil water were tested using a one-way ANOVA and a significance level of 5%. Analysis of data trends with MAP were completed using the regression module of Statistica® software, with a significance level of 5% used in all cases.

Results

Water availability

Mean soil water content correlated linearly with mean annual precipitation (Fig. 2):

$$\% \text{ Soil H}_2\text{O} = 0.001 \cdot \text{MAP} - 0.091; r^2 = 0.94, p = 0.007; (1)$$

variation in precipitation translated to changes in soil water availability. Additionally, the variance in soil water content across seasons was largest in the driest site, and declined with increasing MAP, as the coefficient of variation in soil water during 1998 decreased with increasing rainfall (Fig. 2). While the coefficient of variation in precipitation between years is known to be largest in drier sites (Noy-Meir 1973; Knapp & Smith 2001), it appears that seasonal variation in soil water content is also most pronounced in drier sites, and decreases with increasing rainfall.

Above-ground net primary production (ANPP)

ANPP increased along the gradient of precipitation, with minimum values of 16 $\text{gm}^{-2}\cdot\text{yr}^{-1}$ in the *Nassauvia* desert scrub (125 mm) to a maximum in the wooded *Nothofagus* site (520 mm MAP) of 339 $\text{m}^2\cdot\text{yr}^{-1}$. Across all sites, we observed a linear increase in production with precipitation (Fig. 3), with

$$\text{ANPP} = -31.8 + 0.52 \text{ MAP}; r^2 = 0.84, p = 0.028. (2)$$

ANPP was linearly correlated with total biomass (biomass data from Schulze et al. 1996), with

$$\text{ANPP} = 0.006 \text{ BIOMASS} + 63.5; r^2 = 0.77, p = 0.05. (3)$$

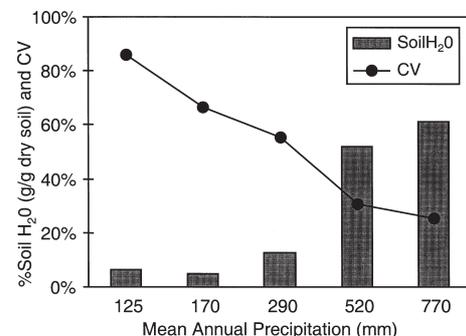


Fig. 2. Gravimetric soil water measurements (0-5 cm layer) for 1998 in relation to mean annual precipitation of site. Bars represent mean annual values of soil water and the line represents the coefficient of variation (%) at each site for 1998.

Table 2. Categories of ANPP ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) for 1998 along the precipitation gradient in Patagonia. For grasses and shrubs, values represent means of green biomass harvested in January 1999 (see Methods for detailed explanation) and for wooded sites, values are means for litterfall during 1998.

	Mean Annual Precipitation of site				
	125 mm	170 mm	290 mm	520 mm	770 mm
Grass	2.68 ± 0.24	21.30 ± 1.55	54.57 ± 5.59		
Shrub	13.24 ± 1.66	42.87 ± 0	24.24 ± 10.61		
Leaf (tree)				284.91 ± 17.71	274.37 ± 13.40
Branches (tree)				53.96 ± 5.20	40.44 ± 3.70
Total	15.92 ± 1.64	64.18 ± 1.55	78.82 ± 9.35	338.37 ± 21.05	314.81 ± 12.39

The contribution of different life forms to total ANPP changed with the precipitation of site (Table 2). Shrub production as a proportion of total site production was greatest at the 125-mm site (83%), while grass production was greatest at the 290 mm site (69%). The two wettest sites had near equal proportion of production of fine branches and twigs (15%), such that leaves dominated the litter fall at these sites.

Soil and foliar nitrogen

Inorganic soil nitrogen concentrations ($\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$) varied across the precipitation gradient (Fig. 4, Table 3) and total inorganic nitrogen and ammonium were significantly linearly related to mean annual precipitation (Fig. 4) where

$$N_{\text{inorganic}} = 0.19 \text{ MAP} - 32; r^2 = 0.96, p = 0.003; \quad (4)$$

$$\text{NH}_4^+ = 0.17 \text{ MAP} - 30; r^2 = 0.96, p = 0.003. \quad (5)$$

In contrast, soil NO_3^- was unrelated to precipitation, highest at the 290 mm *Festuca* grassland site in all seasons (Table 3). Total inorganic nitrogen also predicted ANPP, with

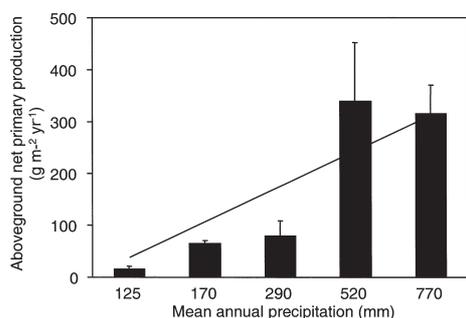


Fig. 3. ANPP versus MAP for 1998. Bars represent mean values for site, with error bars (+/- sd) to show intrasite variability. The regression fitted through the mean ANPP at each site was $\text{ANPP} = -31.2 + 0.52(\text{MAP})$, $r^2 = 0.84$, $p = 0.028$. Values for ANPP at the wettest sites do not include large woody increment. Methods for calculating ANPP were site specific (see Methods for detailed explanation).

$$\text{ANPP} = 2.6[N_{\text{inorganic}}] + 59.4; r^2 = 0.79, p = 0.042. \quad (6)$$

There was seasonal variation in nitrogen concentrations, particularly for NH_4^+ (Table 3), although across-season variation in inorganic nitrogen values did not coincide with variation in soil water content (Fig 2). Values for soil NH_4^+ were maximum in the dry sites in April (beginning of wet season) but in the wetter sites, in the December sampling date (end of growing season). The opposite pattern was observed for soil NO_3^- , with

Table 3. Gravimetric soil water content and inorganic nitrogen concentrations at different dates during 1998. Values represent mean of five transects (\pm se) for each site. The seasons represented are fall (April) early spring (October) and peak growing season in summer (December). Letters represent significant differences between seasons in a single row (site) at $p < 0.05$.

Site rainfall (mm.yr ⁻¹)	Soil water content (%g/g dry soil)		
	April	October	December
125	12.61 ± 0.38 ^a	2.57 ± 0.13 ^b	2.20 ± 0.12 ^a
170	8.16 ± 0.78 ^a	3.93 ± 0.47 ^b	1.66 ± 0.08 ^c
290	16.72 ± 4.46 ^a	15.15 ± 1.58 ^a	4.02 ± 0.20 ^b
520	47.97 ± 6.75 ^a	54.47 ± 4.82 ^a	30.85 ± 1.35 ^b
770	48.36 ± 10.52 ^a	81.82 ± 13.32 ^b	49.50 ± 2.62 ^a
	Extractable ammonium ($\text{NH}_4\text{-N}$ $\mu\text{g/g}$ dry soil)		
	April	October	December
125	2.35 ± 0.31 ^a	1.08 ± 0.35 ^b	1.29 ± 0.16 ^{ab}
170	2.51 ± 0.43	1.91 ± 0.74	1.41 ± 0.44
290	4.34 ± 0.39 ^a	7.14 ± 0.93 ^{ab}	9.42 ± 1.38 ^b
520	41.82 ± 8.06	61.81 ± 3.84	57.34 ± 4.29
770	66.94 ± 2.65 ^a	129.84 ± 12.18 ^b	138.45 ± 13.75 ^b
	Extractable nitrate ($\text{NO}_3\text{-N}$ $\mu\text{g/g}$ dry soil)		
	April	October	December
125	0.11 ± 0.01 ^a	0.14 ± 0.03 ^a	0.22 ± 0.04 ^b
170	0.45 ± 0.12 ^{ab}	0.20 ± 0.06 ^b	0.67 ± 0.05 ^a
290	1.54 ± 0.22	2.21 ± 0.24	1.29 ± 0.32
520	0.90 ± 0.60	0.40 ± 0.06	0.55 ± 0.11
770	0.16 ± 0.05	0.10 ± 0.02	0.06 ± 0.03
	NH_4/NO_3 ratios		
	April	October	December
125	22.2 ± 1.7 ^a	10.4 ± 5.5 ^{ab}	6.7 ± 1.6 ^b
170	7.7 ± 2.7	9.4 ± 2.7	2.4 ± 0.9
290	3.1 ± 0.5 ^a	3.3 ± 0.4 ^a	8.9 ± 2.5 ^b
520	131.9 ± 39.4	166.6 ± 23.0	132.9 ± 38.5
770	552.9 ± 123	1690.8 ± 615.3	2444.9 ± 844.6

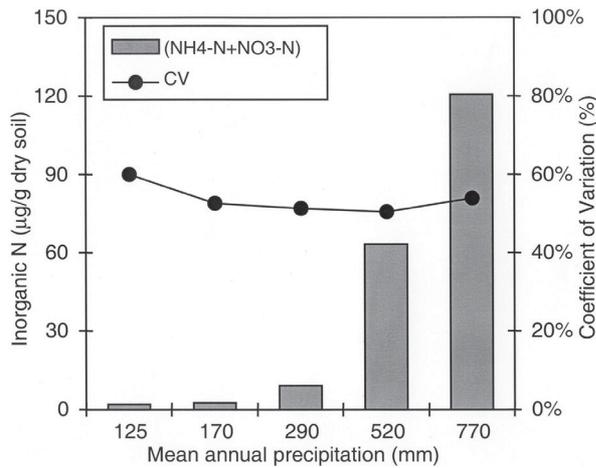


Fig. 4. Soil inorganic nitrogen concentrations ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) for 1998 in relation to mean annual precipitation. Bars represent mean annual values for April, October and December and line represents the coefficient of variation (%) during the year.

maximum values in dry sites in December and maximum values in wetter sites in April (but did not vary significantly). Soil NH_4/NO_3 ratios increased markedly with increasing site precipitation (Table 3), but varied significantly among seasons only in the driest sites, with minimum values observed in the December sampling date. The proportion of inorganic nitrogen in the form of nitrate was thus maximum in the driest sites and declined with increasing rainfall.

Concentrations of N in dominant plant species also varied with precipitation (Table 4), with an increase in %N and a decrease in C:N ratio with increasing rainfall, where

$$\%N = 0.0008 \text{ MAP} + 0.87, r^2 = 0.32, p = 0.001; \quad (7)$$

$$\text{C:N} = -0.03 \text{ MAP} + 56, r^2 = 0.30, p = 0.002. \quad (8)$$

The variance explained by precipitation of site was

Table 4. Leaf nitrogen concentrations and C:N ratios of dominant vegetation along the Patagonian precipitation gradient. Values are means for species at that site ($n = 5$) \pm se.

Species	MAP (mm)	Life form	Leaves	
			%N	C:N
<i>Nassauvia glomerulosa</i>	125	shrub	0.67	69
<i>Mulinum spinosum</i>	170	shrub	1.00	49
<i>Stipa speciosa</i>	170	grass	1.06	44
<i>Festuca pallescens</i>	290	grass	1.27	36
<i>Nothofagus antarctica</i>	520	tree	1.64	32
<i>Nothofagus pumilio</i>	770	tree	1.24	38

lower than for the regressions of soil water content and inorganic nitrogen, possibly due to the influence of life form on nitrogen allocation patterns.

Discussion

Water availability is one of the important abiotic controls on ecosystem processes, affecting carbon and nutrient cycles both directly through carbon fixation, mineralization, and uptake as well as controlling inputs and outputs of nutrients (Noy-Meir 1973, 1979/1980). Regional scale analyses have shown that water availability directly affects net primary production (Lieth 1975; Sala et al. 1988) and decomposition (Meentemeyer 1978; Austin & Vitousek 2000). The direct effect of water availability on net primary production is observed in our study with a linear increase in ANPP with increasing rainfall, suggesting that primary production in these sites is limited, at least in part, by water availability (Fig. 3). However, linked with changes in precipitation are the marked changes in inorganic nitrogen concentrations in the soil (Fig. 4) and nitrogen concentration in dominant vegetation (Table 4). The covariance of water and soil nutrient concentrations along this gradient suggests that these variables may both contribute to the pattern of increase in carbon gain observed in these ecosystems (Burke et al. 1997), and that variation in ANPP may be due to the combination in changes in site fertility and available water.

Comparison with other studies of net primary production in similar ecosystems of the northern hemisphere (Table 5) suggests that ANPP values for this transect are similar to values observed in the same range of precipitation for grasslands (Sala et al. 1988). However, drier sites were overestimated when using a model developed across a broader range of precipitation (Knapp & Smith 2001). One of the primary differences between the precipitation gradient in the central United States

Table 5. Comparison of actual ANPP values with those generated by an algorithm developed for ANPP grassland ecosystems in the Central Great Plains of the United States (Sala et al. 1988), and for North American ecosystems (Knapp & Smith 2001).

Site	ANPP ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)		
	Measured	Sala et al. (1988)	Knapp et al. (2001)
1. <i>Nassauvia</i> desert scrub	16	41	122
2. <i>Mulinum-Stipa</i> shrub-steppe	64	68	138
3. <i>Festuca</i> grassland	79	140	183
4. <i>Nothofagus antarctica</i> woodland	339	278	268
5. <i>Nothofagus pumilio</i> forest	315	428	360

where these models were developed and that in Patagonia is seasonality of rainfall. Maximum precipitation occurs in winter in the Patagonian systems (Walter & Box 1983), whereas convective storms during summer are predominant in the central United States (Sala & Lauenroth 1982). This asynchrony in precipitation and temperature regime could contribute to the differences in ANPP observed in Patagonian sites with respect to northern hemisphere ecosystems of similar precipitation. Low water availability during the middle or end of the growing season may result in water stress, which would not occur in systems where high temperature and water availability coincide. Thus, the effective growing season may be shorter in these sites of predominantly winter rainfall, and similar mean annual temperature, and result in lower ANPP, particularly in the low precipitation sites.

An alternative explanation is of a statistical and ecological nature. The slope of the regression models such as those used to account for regional ANPP patterns based on precipitation vary as a function of the range of precipitation. Expanding the range of conditions to include forest ecosystems with much higher precipitation than those observed in this study necessarily reduces the slope of the ANPP-precipitation model and increases the y-intercept. The response of ANPP with precipitation over a broad range of precipitation is curvilinear (Lieth 1975; Austin 2002) with a saturation threshold that depends on temperature. Consequently, broader models that include forest ecosystems tend to overestimate production of the ecosystem in the driest conditions.

A characteristic of the Patagonian transect is that a pronounced change in both precipitation and dominant vegetation occurs over a very short distance (150 km), whereas changes in other environmental variables are relatively small. The decrease in water stress on carbon fixation is coupled to increasing competition for light as biomass increases. Larger and taller species outcompete smaller and shorter species by shading them (Fig. 1). Plant characteristics that provide an ecological advantage at the wet end of the gradient would be an increase in structural component of the vegetation with increasing allocation to secondary growth and increase in maximum height. Thus, the life-form shift results from the dry extremes of entirely shrub species, with characteristics that allow them to withstand conditions of variable precipitation both seasonally and inter-annually (Fig. 2, Jobbágy et al. 1995), to increasingly herbaceous life forms as variation in precipitation input declines. At the same time, the increase in primary production results in increased plant cover and biomass, to the point where light becomes limiting and a higher allocation to woody biomass represents a competitive advan-

tage at limiting light conditions (Fig. 1, Table 2, Schulze et al. 1996). The effect of life form on ecosystem functioning across the gradient would be higher maintenance respiration in woody life forms due to increased above-ground allocation as light availability becomes limiting as water stress is reduced. The trade-off for fast growing photosynthetic tissue versus a higher allocation to woody structural tissue could have negative feedbacks on nutrient cycling, with a larger proportion of recalcitrant litter contributing to the soil organic pool in these wetter sites (Table 2). A study on a precipitation gradient of forested sites north of this transect in Patagonia demonstrated that within a single tree species (*Austrocedrus chilensis*), plants had the highest N conservation in sites of 1000 mm MAP, with drier sites showing lower estimates of soil N retention, and higher potential soil N mineralization (Buamscha et al. 1998).

The asynchrony of rainfall and temperature resulted in the accumulation of nitrate in the soils in the driest sites (Table 4). While total inorganic nitrogen concentrations in the soil increased (Fig. 4, Table 3); $\text{NH}_4/\text{NO}_3^-$ ratios also increased by up to 3 orders of magnitude with increasing rainfall (Table 3). This resulted in a much higher percentage of available nitrogen in the drier sites in the form of NO_3^- which is highly mobile in most soils (Paul & Clark 1996) and is quickly taken up by the vegetation when water stress is not excessive. The presence of NO_3^- in the soil in these dry sites suggests an excess in the production of nitrogen relative to the demand by the vegetation, possibly due to the differential effects of water stress on plants versus soil microorganisms (Austin 2002). The availability of N may limit carbon gain in these sites in moments when water availability is adequate (winter months). Overall, N limitation may be higher than in sites where soil microbial activity and plant uptake are occurring simultaneously.

The coincident changes in both water and nitrogen availability suggest that carbon-nitrogen interactions are an important component determining ANPP along this gradient of precipitation. There are direct effects of water availability on carbon fixation but also on nitrogen turnover. A study of *Pinus taeda* in Texas showed a higher correlation of LAI (leaf area index) with soil N concentration than with precipitation (Hebert & Jack 1998), suggesting that N availability may be as important as rainfall in regulating carbon gain. Relative increases in carbon gain exceed relative changes in soil inorganic N, suggesting that nitrogen limitation may become increasingly important in wetter sites in spite of higher overall soil N concentrations. The carbon-nitrogen interactions that determine the relative demand for available water and nutrients appear to be an important component determining ecosystem functioning along this precipitation gradient.

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