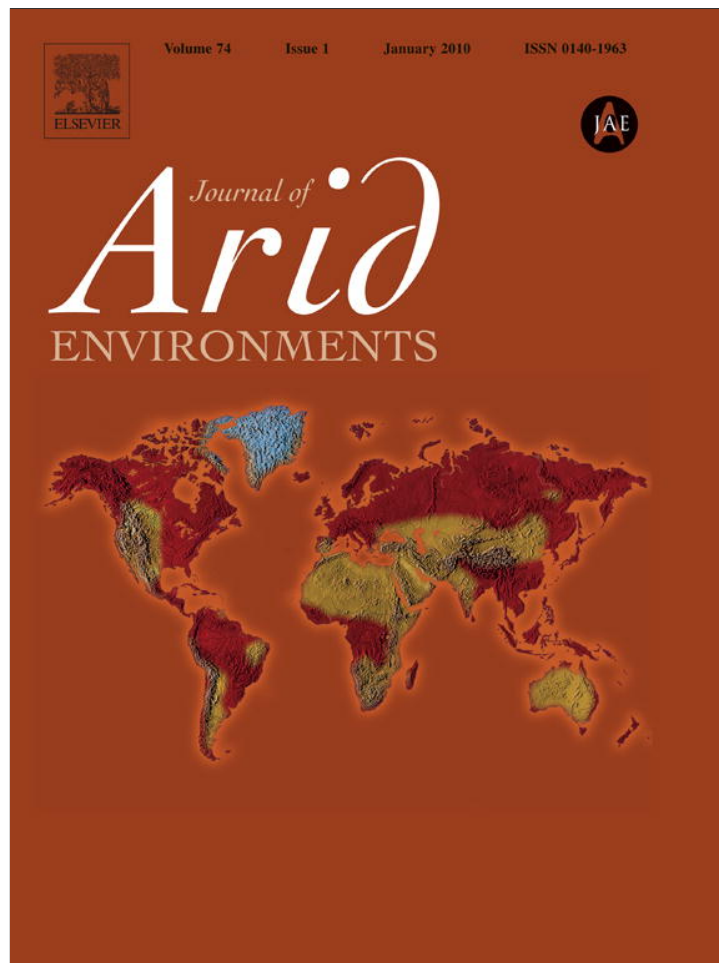


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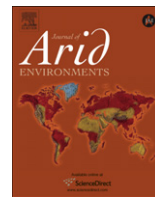
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Biomass, carbon and nutrient storage for dominant grasses of cold temperate steppe grasslands in southern Patagonia, Argentina

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ABSTRACT

We hypothesized that different dominant grasses species display contrasting nutrient accumulation, allocation and conservation strategies. Also, we expect a distinctive pattern of carbon and biomass partitioning according to plant sizes. The aim was to quantify the amount of biomass, carbon and nutrients in both above- and belowground components for four dominant grasses in grasslands steppe. We analyzed biomass, carbon and nutrients (N, P, K, Ca, Mg and S) of each dominant grass species corresponding to different sizes and separated in components (green and senesced leaves, pseudostem, and fine and coarse roots). Total biomass accumulation for individual grass plants was affected by plant size and species and ranged from 15.4 to 684 g dry matter plant⁻¹. The biomass root/shoot ratio ranged from 0.28 to 3.40. Total nutrient concentration generally graded in all species the following order: green leaves > fine roots > pseudostem > coarse roots > senesced leaves. Storage of any particular nutrient varied depending mainly on species. Mean nutrient resorption efficiency varied according to the growing season and specie being maximum for K and minimum for Mg. The equations developed for individual grass plants could be used to assist quantitative predictions of biomass, carbon and nutrient accumulation per hectare.

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1. Introduction

The Magellanic Patagonian steppe (southern Patagonia, Argentina) is a cold semiarid environment characterized by strong winds and high evaporation rates that cover 3 million hectares where grasses and shrubs are the dominated plant functional types with contrasting root systems. In this ecosystem *Stipa chrysophylla* Desvaux, in Gay and *Festuca pallescens* (St. Ives) Parodi are dominant tussock species commonly associated with cool season *Poa duseunii* Hack. and *Carex andina* Phil. short-grasses (Roig et al., 1985). The main activity in this environment is extensive sheep production in large paddocks (2000–5000 ha) on a year-round basis, with stoking rates ranged from 0.13 to 0.75 head ha⁻¹ yr⁻¹ (Cibils and Coughenour, 2001).

Most of the actual knowledge about the environmental factors that affect net primary production at regional level derives from the importance of mean annual precipitation, radiation and temperature (Jobbágy and Sala, 2000). However, data on biomass and

nutrient accumulation in both above- and belowground components of plant functional types are essential for evaluating the impacts of grazing on bioelement recycling and long-term effects on the mineral balance that affect the net primary production of grasslands. The nutrient concentration in plants is affected by nutrient availability in soil through the rate of litter decomposition and inherent physiological plant adaptations (Fitter, 1998). The main physiological plant traits are nutrient retention in long-lived components, nutrient resorption from senescing tissues and the allocation of nutrients in plant components (Bertiller et al., 2005). Resorption is a strategy of plants to conserve nutrients (Killingbeck, 1996). This becomes important in arid ecosystems which are characterized by the lack of water and nutrient availability where plants showed a high capability for reducing nutrient losses to dominate these sites (Mazzarino et al., 1998).

The differential concentration and allocation of nutrients in plant components may be a response to differences in biomass accumulation and biological functions between tissues such as photosynthesis and nutrient uptake (Taiz and Zeiger, 2006). Most of the nutrient cycling researches in grassland ecosystems have been focussed on aboveground pools (Bertiller et al., 2005; Jobbágy and Sala, 2000). However, net primary production, nutrient concentration and fine roots turnover rates of belowground components in grassland systems can equal or even exceed those

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from aboveground pools (Mokany et al., 2006). Therefore, research of belowground pools is necessary to quantify nutrient sequestration in the underground structures. In addition, there is an initial lag phase as plant size increase after defoliation, followed by a period of nearly constant linear growth and then an asymptotic phase where leaf area exceeds optimal values (Duru and Ducrocq, 2000; Robson et al., 1988). This accumulation process decreased the photosynthetic capacity of the individual leaves and its nutrient concentration as leaf area increased (Peri et al., 2003; Woledge and Pearse, 1985).

Furthermore, recently there has been an increasing interest of research related to improve the understanding of carbon (C) sequestration mainly under Article 3.4 of the Kyoto Protocol of the United Nations Framework Convention on Climate Change where countries can count this sequestration as a contribution to reduce greenhouse gas emission (IPCC, 2001). However, in Patagonia there is a lack of knowledge in C fixation particularly for grassland ecosystems.

We hypothesized that different dominant grasses species in grassland steppe display contrasting nutrient accumulation, allocation and conservation strategies. Also, we expect a distinctive pattern of factors controlling C and biomass partitioning according to plant sizes. Therefore, the aim was to quantify the amount of biomass, carbon and nutrients in both above- and belowground components for four dominant grasses grown in grassland steppe ecosystems of southern Patagonia.

2. Materials and methods

2.1. Study areas

Four undisturbed study areas of 50 km² (10 × 5 km) were selected in the Magellanic steppe in Santa Cruz province, southern

Patagonia, Argentina (Fig. 1). These were: 1. Grass steppe with vegetation dominated by *Stipa chrysophylla* (50–60%) associated with *Nassauvia ulicina*, *Poa dusenii*, *Carex andina* (centre of study area located at 51° 13' 09"S, 69° 13' 22"W). 2. Grass riparian-type meadows located in a river floodplain with vegetation dominated by *Festuca pallescens* (60–70%) associated with *Juncus balticus*, *Hordeum pubiflorum*, *Carex macloviana* and *Azorella trifurcata* (51° 24' 33"S, 70° 28' 06"W). 3. Grass steppe with short vegetation dominated by *Poa dusenii* (30–40%) associated with *Festuca gracillima*, *Carex andina*, *Nardophyllum bryoides* and *Rytidosperma virescens* (50°5' 23"S, 71° 00' 46"W). 4. Grass steppe with short vegetation dominated by *Carex andina* (25–30%) associated with *Festuca pallescens*, *Azorella monantha*, *Poa dusenii*, and *Rytidosperma virescens* (50° 54' 20"S, 71° 51' 10"W).

Climate is cold temperate and subhumid with a mean annual temperature of 6.5–7.5 °C, a long-term annual rainfall of 200–400 mm evenly distributed throughout the year. Severe and frequent windstorms occur in spring and summer, with wind-speeds over 120 km h⁻¹. Soils were coarse textured classified as Molisols. Thirty bulked soil sample cores from the four study areas 0–30 cm in depth, corresponding to main root distribution, were taken at random to refer with nutrients accumulation in plants (Table 1). The samples were air dried and ground to pass a 2-mm sieve. The pH of soil samples was determined with an electronic meter immersed in a 1:5 mixture of soil and water. The percentage of clay, silt and sand in each sample were determined using a Malvern Mastersizer 2600 laser particle size analyzer (Malvern Instruments Ltd, Worcestershire, UK). Soil organic carbon (C) analysis was carried out by using the traditional wet digestion method, soil nitrogen (N) concentration by the semi-micro Kjeldahl method, and available soil phosphorus (P) was analysed by the Truog P method (Sparks, 1996). Major cations (Mg, K, Ca) were

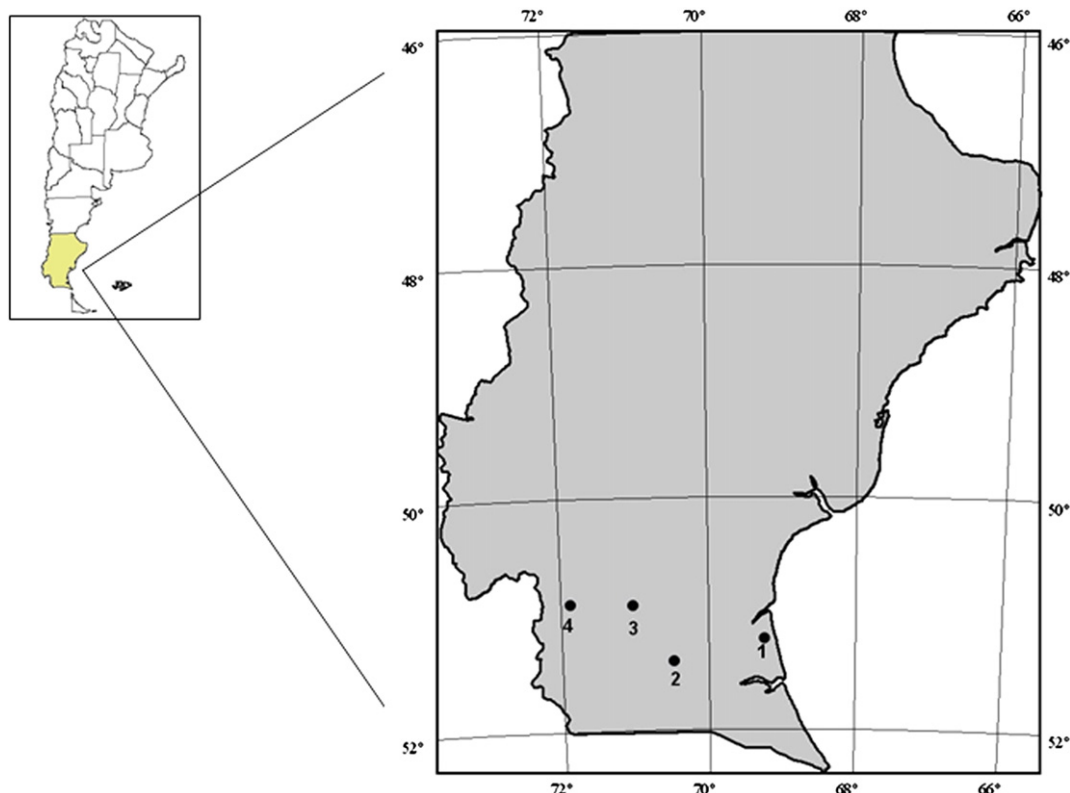


Fig. 1. Location of the study areas of 50 km² within the Magellanic steppe in Santa Cruz province, southern Patagonia, Argentina. 1. Grass steppe with vegetation dominated by *Stipa chrysophylla*. 2. Grass riparian-type meadows located in a river floodplain with vegetation dominated by *Festuca pallescens*. 3. Grass steppe with short vegetation dominated by *Poa dusenii*. 4. Grass steppe with short vegetation dominated by *Carex andina*.

Table 1

Soil properties in sampled sites of *Festuca pallescens*, *Stipa chrysophylla*, *Poa duseinii* and *Carex andina* communities at a depth of 0–0.30 m in the Magellanic steppe.

Sites	<i>Festuca pallescens</i>	<i>Stipa chrysophylla</i>	<i>Poa duseinii</i>	<i>Carex andina</i>
% Clay	13.2	22.0	6.0	10.0
% Silt	46.9	11.5	25.6	47.3
% Sand	39.9	66.5	68.4	42.7
pH	7.1	6.2	5.6	5.3
N total (%)	0.7	0.1	0.4	0.7
C organic (%)	7.2	2.7	3.1	3.8
P Truog (mg kg ⁻¹)	81.4	41.5	42.0	37.0
K (cmol(+) kg ⁻¹)	0.7	2.8	1.3	0.5
Mg (cmol(+) kg ⁻¹)	14.8	5.2	3.2	2.1
Ca (cmol(+) kg ⁻¹)	35.7	18.7	28.8	13.4
C/N	9.3	12.5	6.6	5.3

measured using standard analytical techniques with an Atomic Absorption Spectrophotometer.

2.2. Species-specific sampling and biomass determination

Three plots (replicates) of 0.5 × 5 m were randomly located at each study area. Within each plot, nine individuals of each dominant grass species corresponding to different sizes were randomly selected. This gives a total of 108 sampled plants (4 species × 9 sizes × 3 plots). Then, the individuals were classified in different size classes to test for “the size effect” on plant biomass, carbon and nutrient concentration, and nutrient allocation in plant components. Height and two orthogonal diameters of each plant at the top of the canopy were measured. *F. pallescens* plants size ranged from 28 ± 1.5 (small) to 780 ± 21 mm in height (big) and from 26 ± 1.4 to 340 ± 16 mm in diameter. *S. chrysophylla* plants size varied from 24 ± 1.3 (small) to 550 ± 18 mm in height (big) and from 38 ± 1.5 to 550 ± 27 mm in diameter. The size of *P. duseinii* plants ranged from 20 ± 0.7 (small) to 350 ± 9 mm in height (big) and from 19 ± 0.3 to 170 ± 2 mm in diameter. *C. andina* plants size ranged from 15 ± 0.9 (small) to 250 ± 11 mm in height (big) and from 16 ± 1.2 to 174 ± 18 mm diameter.

Each plant was harvested during the spring growth period (November–December) corresponding to the vegetative growth peak and summer (January–February). Then, plants were separated into the following components: green leaves; senesced leaves; pseudostem and roots classified as fine (diameter <0.2 mm) and coarse (0.2–1.1 mm) roots for biomass calculations and nutrient analysis. All components from each sampled plant were weighed fresh. Roots from individual plants were excavated to maximum rooting depth for all size classes in circular plots centred on the base of selected plants (up to 0.6 m for *F. pallescens*, 0.4 m for *S. chrysophylla*, 0.35 m for *P. duseinii*, 0.30 m for *C. andina*). These roots were sorted in diameter class and weighed in fresh. Sub samples were taken for oven drying to estimate biomass.

Leaf area (LA) of each individual grass species size was determined by scanning the total harvested leaves per plant. The leaves were spread randomly over a transparent sheet and then scanned using a flat-bed scanner. The leaf area was determined using image analysis software (DT-Scan, Delta-T Ltd., Cambridge, UK). LA has been widely used as a key plant parameter of grass size related to different processes such as growth rate, photosynthesis and nutrient uptake (Duru and Ducrocq, 2000; Peri et al., 2003; Woledge and Pearce, 1985). *F. pallescens* plants size ranged from 0.05 (small) to 4.42 m² (big) in LA, *S. chrysophylla* plants size varied from 0.01 (small) to 1.85 m² (big), *P. duseinii* plants ranged from 0.008 (small) to 0.05 m² (big), and *C. andina* plants from 0.007 (small) to 0.063 m² (big).

2.3. Chemical sample analysis

Samples of components from the nine size classes of each studied species were collected during spring (water non-limiting) and summer (water stress period), then dried in a forced draft oven at 65 °C to constant weight and ground in a mill containing 1 mm stainless steel screen for nutrient analysis. Nitrogen (N) content was determined using the semi-micro Kjeldahl technique (Sparks, 1996). Phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulphur (S) concentrations were determined with a plasma emission spectrometer (Shimadzu ICPS-1000 III) following the methodology proposed in Johnson and Ulrich (1959). Organic carbon content was quantified with an LECO CR-12 elemental analyser (Wang and Anderson, 1998).

2.4. Data and statistical analysis

Nutrient accumulation of plants was estimated by multiplying mean nutrient concentrations from chemical analysis and the mass of each biomass component (dry weight measurements). Total biomass, carbon and nutrient accumulation functions were fitted using non-linear regression analysis. Different sigmoid functions (Chapman-Richard, Logistic, Weibull, Gompertz, Hill and Schumacher) were compared to fit total biomass, carbon and nutrients accumulation against leaf area. The coefficient of determination (R^2) and standard errors of the estimates (ESE) of total biomass, carbon and nutrient accumulation were used to quantify the accuracy of the functions. The logistic function (Eq. (1)) with three parameters fitted the data better than others sigmoidal functions for total biomass, carbon and nutrient accumulation. The parameters and statistics for each species are given in Appendix 1

$$Y = \frac{a}{1 + (x/b)^c} \quad (1)$$

Where Y = biomass, carbon and nutrient of individual plants (kg); x = total leaf area (m² plant⁻¹); a , b , and c are the parameters estimated.

Nutrient resorption efficiency was calculated following the method proposed by Killingbeck (1996) and widely used for grassland (Bertiller et al., 2005). This was calculated for the four studied species and two growing season (spring and summer) based on the nutrient concentration in green leaves minus nutrient concentration in senesced leaves divided by nutrient concentration in green leaves, the quantity multiplied by 100.

Comparisons of main factors for each species were carried out by two-way analyses of variance (ANOVA) with the F -test. Significantly different averages were separated with standard error of means (SEM) to evaluate least significant differences (LSD). This analysis was carried out to detect potential interactions between a plant species variable (such as nutrient concentration) and the main factors (size classes and season). All tests were evaluated at $p < 0.05$. Statistical analyses was carried out by using the Genstat statistical package (Genstat 5 – v.1997).

3. Results

3.1. Carbon and nutrient concentration

Carbon and nutrient concentrations varied ($p < 0.05$) according to tissue components in all species studied (Tables 2–5). Carbon concentration was higher in coarse roots and green leaves. In all species, N, K, P and S were more concentrated ($p < 0.01$) in leaves,

Table 2
Season and plant size variation in mean carbon and nutrient concentration of *Festuca palllescens* components (data expressed as a percentage of dry matter) grown in a steppe in southern Patagonia.

	Green leaves	Senesced leaves	Pseudostem	Fine roots	Coarse roots
C	%	%	%	%	%
<i>Growing season</i>					
Spring	41.00 b	38.40 a	36.95 b	39.25 b	40.60 b
Summer	42.32 a	39.25 a	41.94 a	42.68 a	43.43 a
<i>Plant size</i>					
Small	41.01 b	38.35 a	38.25 b	40.05 b	41.05 b
Big	42.35 a	39.30 a	40.64 a	41.88 a	42.98 a
<i>Interaction</i>	ns	ns	ns	ns	ns
N					
<i>Growing season</i>					
Spring	2.044 a	0.547 a	0.962 a	0.747 a	0.640 a
Summer	0.969 b	0.422 b	0.411 b	0.539 b	0.436 b
<i>Plant size</i>					
Small	1.700 a	0.495 a	0.868 a	0.719 a	0.576 a
Big	1.314 b	0.474 b	0.505 b	0.567 b	0.501 b
<i>Interaction</i>	ns	*	ns	*	ns
P					
<i>Growing season</i>					
Spring	0.203 a	0.051 a	0.071 a	0.115 a	0.111 a
Summer	0.148 b	0.036 b	0.052 b	0.096 b	0.066 b
<i>Plant size</i>					
Small	0.190 a	0.048 a	0.065 a	0.110 a	0.094 a
Big	0.161 a	0.039 b	0.057 a	0.102 a	0.083 b
<i>Interaction</i>	ns	ns	ns	ns	ns
K					
<i>Growing season</i>					
Spring	1.832 a	0.233 a	0.528 a	0.366 a	0.356 a
Summer	0.958 b	0.189 b	0.370 b	0.288 b	0.262 b
<i>Plant size</i>					
Small	1.461 a	0.201 a	0.473 a	0.341 a	0.326 a
Big	1.330 a	0.221 a	0.425 b	0.314 a	0.292 b
<i>Interaction</i>	ns	ns	ns	ns	ns
Mg					
<i>Growing season</i>					
Spring	0.111 a	0.087 a	0.151 a	0.323 a	0.208 a
Summer	0.081 b	0.081 a	0.101 b	0.211 b	0.139 b
<i>Plant size</i>					
Small	0.098 a	0.085 a	0.144 a	0.299 a	0.198 a
Big	0.095 a	0.084 a	0.108 b	0.235 b	0.150 b
<i>Interaction</i>	ns	ns	ns	*	*
S					
<i>Growing season</i>					
Spring	0.140 a	0.075 a	0.061 a	0.139 a	0.088 a
Summer	0.071 b	0.049 b	0.034 b	0.062 b	0.061 b
<i>Plant size</i>					
Small	0.128 a	0.074 a	0.054 a	0.103 a	0.081 a
Big	0.083 b	0.050 b	0.040 b	0.098 a	0.067 b
<i>Interaction</i>	ns	ns	*	ns	ns
Ca					
<i>Growing season</i>					
Spring	0.260 b	0.230 a	0.270 b	0.780 b	0.506 b
Summer	0.294 a	0.247 a	0.325 a	0.964 a	0.636 a
<i>Plant size</i>					
Small	0.265 b	0.235 a	0.245 b	0.815 b	0.555 b
Big	0.289 a	0.242 a	0.350 a	0.930 a	0.587 a
<i>Interaction</i>	ns	ns	ns	ns	ns

Different lower-case letters indicate significant ($p < 0.05$) differences between levels of each factor (growing season and plant size). Interaction effect between plant size and growing season is indicated as ns = non-significative, * = $p < 0.05$.

while Mg and Ca were more concentrated ($p < 0.05$) in roots. Total nutrient concentration generally graded in all species the following order: green leaves > fine roots > pseudostem > coarse roots > senesced leaves.

Table 3
Season and plant size variation in mean carbon and nutrient concentration of *Stipa chrysophylla* components (data expressed as a percentage of dry matter) grown in a steppe in southern Patagonia.

	Green leaves	Senesced leaves	Pseudostem	Fine roots	Coarse roots
C	%	%	%	%	%
<i>Growing season</i>					
Spring	42.78 b	40.32 a	40.20 b	40.12 b	40.73 b
Summer	44.56 a	41.45 a	42.49 a	43.70 a	44.70 a
<i>Plant size</i>					
Small	42.51 b	39.97 a	40.28 b	41.20 a	40.88 b
Big	44.83 a	41.80 a	42.42 a	42.62 a	44.56 a
<i>Interaction</i>	ns	ns	ns	ns	ns
N					
<i>Growing season</i>					
Spring	1.721 a	0.618 a	1.184 a	0.794 a	0.695 a
Summer	0.815 b	0.458 b	0.554 b	0.517 b	0.555 b
<i>Plant size</i>					
Small	1.368 a	0.543 a	1.035 a	0.736 a	0.686 a
Big	1.168 b	0.533 a	0.702 b	0.575 b	0.564 a
<i>Interaction</i>	ns	*	ns	*	ns
P					
<i>Growing season</i>					
Spring	0.147 a	0.026 a	0.051 a	0.094 a	0.065 a
Summer	0.073 b	0.018 b	0.043 a	0.083 b	0.045 b
<i>Plant size</i>					
Small	0.119 a	0.023 a	0.047 a	0.092 a	0.055 a
Big	0.101 a	0.021 a	0.046 a	0.086 b	0.056 a
<i>Interaction</i>	ns	ns	ns	ns	ns
K					
<i>Growing season</i>					
Spring	0.755 a	0.247 a	0.404 a	0.638 a	0.322 a
Summer	0.546 b	0.128 b	0.228 b	0.350 b	0.247 b
<i>Plant size</i>					
Small	0.681 a	0.196 a	0.339 a	0.529 a	0.300 a
Big	0.620 a	0.179 a	0.293 b	0.459 a	0.268 a
<i>Interaction</i>	ns	ns	ns	ns	ns
Mg					
<i>Growing season</i>					
Spring	0.143 a	0.080 a	0.129 a	0.090 a	0.200 a
Summer	0.070 b	0.059 b	0.098 b	0.079 b	0.104 b
<i>Plant size</i>					
Small	0.132 a	0.074 a	0.118 a	0.087 a	0.175 a
Big	0.081 b	0.065 a	0.109 a	0.083 a	0.134 a
<i>Interaction</i>	ns	ns	ns	*	*
S					
<i>Growing season</i>					
Spring	0.099 a	0.057 a	0.069 a	0.084 a	0.070 a
Summer	0.055 b	0.032 b	0.057 a	0.051 b	0.056 b
<i>Plant size</i>					
Small	0.087 a	0.052 a	0.068 a	0.073 a	0.067 a
Big	0.068 b	0.036 b	0.057 a	0.062 a	0.059 b
<i>Interaction</i>	ns	ns	*	ns	ns
Ca					
<i>Growing season</i>					
Spring	0.255 b	0.205 b	0.267 b	0.226 b	0.173 b
Summer	0.299 a	0.240 a	0.378 a	0.441 a	0.311 a
<i>Plant size</i>					
Small	0.262 a	0.210 a	0.277 b	0.272 b	0.224 a
Big	0.291 a	0.235 a	0.367 a	0.395 a	0.259 a
<i>Interaction</i>	ns	ns	ns	ns	ns

Different lower-case letters indicate significant ($p < 0.05$) differences between levels of each factor (growing season and plant size). Interaction effect between plant size and growing season is indicated as ns = non-significative, * = $p < 0.05$.

Nutrient concentration in some components also changed according to different species. For example, N concentration was higher in green leaves and fine roots of *C. andina* plants (Table 5), and in green leaves and pseudostem of *S. chrysophylla* (Table 3). The

Table 4

Season and plant size variation in mean carbon and nutrient concentration of *Poa duseunii* components (data expressed as a percentage of dry matter) grown in a steppe in southern Patagonia.

	Green leaves	Senesced leaves	Pseudostem	Fine roots	Coarse roots
C	%	%	%	%	%
<i>Growing season</i>					
Spring	41.87 b	39.07 a	40.41 b	41.97 b	43.38 b
Summer	44.72 a	41.85 a	42.32 a	44.50 a	46.79 a
<i>Plant size</i>					
Small	42.27 a	39.52 a	40.75 a	42.45 a	44.76 a
Big	44.32 a	41.40 a	41.98 a	44.03 a	45.41 a
<i>Interaction</i>	ns	ns	ns	ns	ns
N					
<i>Growing season</i>					
Spring	2.010 a	0.499 a	0.854 a	0.765 a	0.496 a
Summer	1.015 b	0.447 b	0.531 b	0.596 b	0.400 b
<i>Plant size</i>					
Small	1.742 a	0.475 a	0.729 a	0.751 a	0.479 a
Big	1.283 b	0.471 a	0.656 a	0.610 b	0.417 a
<i>Interaction</i>	ns	*	ns	*	ns
P					
<i>Growing season</i>					
Spring	0.241 a	0.062 a	0.125 a	0.092 a	0.075 a
Summer	0.121 b	0.032 b	0.072 b	0.070 b	0.042 b
<i>Plant size</i>					
Small	0.186 a	0.051 a	0.109 a	0.083 a	0.061 a
Big	0.176 a	0.044 a	0.088 b	0.079 a	0.056 a
<i>Interaction</i>	ns	ns	ns	ns	ns
K					
<i>Growing season</i>					
Spring	1.254 a	0.235 a	0.873 a	0.410 a	0.378 a
Summer	0.768 b	0.069 b	0.463 b	0.241 b	0.244 b
<i>Plant size</i>					
Small	1.098 a	0.182 a	0.724 a	0.347 a	0.332 a
Big	0.925 a	0.122 a	0.611 b	0.303 a	0.290 b
<i>Interaction</i>	ns	ns	ns	ns	ns
Mg					
<i>Growing season</i>					
Spring	0.102 a	0.082 a	0.101 a	0.131 a	0.082 a
Summer	0.072 b	0.062 b	0.067 b	0.106 b	0.038 b
<i>Plant size</i>					
Small	0.093 a	0.079 a	0.087 a	0.129 a	0.066 a
Big	0.081 a	0.065 a	0.081 a	0.107 b	0.054 a
<i>Interaction</i>	ns	ns	ns	*	*
S					
<i>Growing season</i>					
Spring	0.103 a	0.043 a	0.057 a	0.093 a	0.063 a
Summer	0.068 b	0.028 b	0.045 b	0.069 b	0.038 b
<i>Plant size</i>					
Small	0.095 a	0.036 a	0.053 a	0.083 a	0.057 a
Big	0.077 b	0.035 a	0.050 a	0.079 a	0.044 b
<i>Interaction</i>	ns	ns	*	ns	ns
Ca					
<i>Growing season</i>					
Spring	0.226 b	0.205 b	0.270 b	0.332 b	0.235 b
Summer	0.301 a	0.250 a	0.348 a	0.490 a	0.432 a
<i>Plant size</i>					
Small	0.225 b	0.200 b	0.276 b	0.335 b	0.265 b
Big	0.303 a	0.255 a	0.342 a	0.487 a	0.402 a
<i>Interaction</i>	ns	ns	ns	ns	ns

Different lower-case letters indicate significant ($p < 0.05$) differences between levels of each factor (growing season and plant size). Interaction effect between plant size and growing season is indicated as ns = non-significant, * = $p < 0.05$.

concentration of P was higher in green leaves, fine roots and coarse roots of *F. pallescens* (Table 2), and K was lower in senesced leaves, pseudostem and coarse roots of *S. chrysophylla* (Table 3). While concentrations of Ca and S were higher in all components (except

Table 5

Season and plant size variation in mean carbon and nutrient concentration of *Carex andina* components (data expressed as a percentage of dry matter) grown in a steppe in southern Patagonia.

	Green leaves	Senesced leaves	Pseudostem	Fine roots	Coarse roots
C	%	%	%	%	%
<i>Growing season</i>					
Spring	42.67 b	39.67 b	42.42 a	40.69 b	43.20 a
Summer	45.43 a	41.80 a	43.38 a	42.45 a	44.75 a
<i>Plant size</i>					
Small	43.45 a	40.60 a	42.47 a	41.07 a	43.45 a
Big	44.65 a	40.87 a	43.33 a	42.06 a	44.50 a
<i>Interaction</i>	ns	ns	ns	ns	ns
N					
<i>Growing season</i>					
Spring	2.233 a	0.530 a	0.951 a	0.838 a	0.487 a
Summer	1.122 b	0.451 b	0.542 b	0.734 b	0.440 a
<i>Plant size</i>					
Small	1.919 a	0.494 a	0.887 a	0.807 a	0.477 a
Big	1.436 b	0.486 a	0.606 b	0.765 a	0.451 a
<i>Interaction</i>	ns	*	ns	*	ns
P					
<i>Growing season</i>					
Spring	0.155 a	0.054 a	0.101 a	0.108 a	0.073 a
Summer	0.124 a	0.037 b	0.045 b	0.086 b	0.049 b
<i>Plant size</i>					
Small	0.148 a	0.047 a	0.079 a	0.099 a	0.064 a
Big	0.131 a	0.043 a	0.067 b	0.094 a	0.058 a
<i>Interaction</i>	ns	ns	ns	ns	ns
K					
<i>Growing season</i>					
Spring	1.229 a	0.171 a	0.814 a	0.339 a	0.219 a
Summer	0.845 b	0.133 a	0.456 b	0.254 b	0.159 b
<i>Plant size</i>					
Small	1.059 a	0.157 a	0.727 a	0.313 a	0.203 a
Big	1.015 a	0.148 a	0.543 b	0.280 a	0.175 a
<i>Interaction</i>	ns	ns	ns	ns	ns
Mg					
<i>Growing season</i>					
Spring	0.097 a	0.083 a	0.103 a	0.108 a	0.040 a
Summer	0.090 b	0.079 a	0.097 b	0.098 b	0.026 b
<i>Plant size</i>					
Small	0.095 a	0.082 a	0.102 a	0.106 a	0.032 a
Big	0.093 a	0.080 a	0.098 a	0.100 a	0.034 a
<i>Interaction</i>	ns	ns	ns	*	*
S					
<i>Growing season</i>					
Spring	0.121 a	0.058 a	0.055 a	0.081 a	0.052 a
Summer	0.074 b	0.041 b	0.044 b	0.070 b	0.041 b
<i>Plant size</i>					
Small	0.118 a	0.052 a	0.053 a	0.077 a	0.048 a
Big	0.084 b	0.047 a	0.046 a	0.073 a	0.045 a
<i>Interaction</i>	ns	ns	*	ns	ns
Ca					
<i>Growing season</i>					
Spring	0.224 b	0.180 a	0.248 b	0.286 a	0.118 b
Summer	0.305 a	0.210 a	0.345 a	0.340 a	0.353 a
<i>Plant size</i>					
Small	0.215 b	0.165 a	0.284 a	0.311 a	0.292 b
Big	0.314 a	0.225 a	0.308 a	0.315 a	0.179 a
<i>Interaction</i>	ns	ns	ns	ns	ns

Different lower-case letters indicate significant ($p < 0.05$) differences between levels of each factor (growing season and plant size). Interaction effect between plant size and growing season is indicated as ns = non-significant, * = $p < 0.05$.

pseudostem) of *F. pallescens* (Table 2), Mg was higher in senesced leaves of *C. andina* (Table 5). Plants of *F. pallescens* had the highest mean total nutrient concentration (9.3%) and *S. chrysophylla* presented the lowest value (7.4%). Carbon concentration in all

components was lower in *F. pallescens* compared with other species.

In general, nutrient and carbon concentration varied according to the growing season and plant size (Tables 2–5). In all components and species, plants grown during spring had higher N, P, K, S and Mg concentration than plants grown during summer. In contrast, Ca and carbon were more concentrated in summer.

Similarly, nutrient concentration in the majority of tissues components showed higher values in small plants, except Ca and carbon where the higher concentration values were found in big plants.

3.2. Nutrient resorption efficiency

Mean nutrient resorption efficiency varied according to the growing season and species (Fig. 2). Mean N-resorption efficiency was lower ($p < 0.05$) in *S. chrysophylla* compared with other species in both season. While *S. chrysophylla* showed the highest ($p < 0.05$) P-resorption efficiency value in spring, *C. andina* had the lowest ($p < 0.05$) values in both season. In spring, mean K-resorption efficiency was lower ($p < 0.05$) and mean Mg-resorption efficiency was higher ($p < 0.05$) in *S. chrysophylla* compared with other species. Mean Ca- and S-resorption efficiency was higher in

C. andina and *P. dusenii* during summer, respectively compared with other species.

Mean nutrient resorption efficiency was significantly higher in spring than in summer only for N ($p = 0.001$) and Mg ($p = 0.038$). In contrast, there were no differences in mean nutrient resorption efficiency between plant sizes (data not shown).

Also, the nutrient resorption efficiency showed a different magnitude response depending on a particular nutrient. For example, the maximum value of mean nutrient resorption efficiency was obtained for K (grand mean of 81.1%) and the minimum for Mg (15.7%) with intermediate values of 17.5% for Ca, 46.9% for S, 62.2% for N and 73.3% for P.

3.3. Biomass and above- and belowground biomass ratio

The fitted logistic function successfully represented the relationship between total mean biomass and leaf area (Appendix 1). The total mean biomass accumulated by grass species ranged from 15.4 g dry matter (DM) plant⁻¹ at 0.06 m² leaf area to 684 g DM plant⁻¹ at 4.4 m² leaf area for big plants of *C. andina* and *F. pallescens*, respectively (Appendix 2). The biomass distribution in components depended on plant size and species. While coarse roots of *C. andina* was the main component as leaf area increased (from 59.5% of total biomass at 0.009 m² leaf area to 31.2% at 0.06 m² leaf area), the biomass distributed in senesced leaves was the main component for the other species (e.g. from 8.2% of total biomass at 0.01 m² leaf area to 42.7% at 1.8 m² leaf area for *S. chrysophylla*) (Appendix 2). The green leaves component varied from 0.18 g plant⁻¹ at 0.009 m² leaf area for *C. andina* to 116 g plant⁻¹ at 4.4 m² leaf area for *F. pallescens*.

The proportions of belowground components also depended on plant size and species (Fig. 3). For all species, the biomass root/shoot ratio decreased as plant size increased. This root/shoot ratio decreased from 3.4 at 0.009 m² leaf area to 1.5 at 0.06 m² leaf area for *C. andina*, and from 1.4 at 0.01 m² leaf area to a steady-state asymptote of 0.3 beyond 0.37 m² of leaf area for *S. chrysophylla* (Fig. 3). Thus, while roots biomass was greater for all grass species with small size, the aboveground biomass of bigger plants (maximum leaf area) represented nearly 70, 78, 63 and 43% of the total biomass for *F. pallescens*, *S. chrysophylla*, *P. dusenii* and *C. andina*, respectively.

3.4. Total carbon and nutrient accumulation

The total carbon sequestered ranged from 0.5 g C plant⁻¹ at 0.009 m² leaf area for *C. andina* to 275 g C plant⁻¹ at 4.4 m² LA for *F. pallescens* (Fig. 4). *S. chrysophylla* sequestered more carbon than *F. pallescens* from 0.8 to 1.85 m² LA, and *P. dusenii* more than *C. andina* plants throughout the LA range. Total accumulation of N, P, K, Ca, Mg and S for all grass species are presented in Fig. 5. Total nutrient accumulation as leaf increase followed the order: *F. pallescens* (11.5 g plant⁻¹) > *S. chrysophylla* (5.5 g plant⁻¹) > *P. dusenii* (0.37 g plant⁻¹) > *C. andina* (0.23 g plant⁻¹). Storage of any particular nutrient varied depending mainly on the species (Fig. 5). In *F. pallescens* plants, nutrient storage was in the order N > K > Ca > Mg > P > S, while *S. chrysophylla* stored more S (0.22 g S plant⁻¹) than P (0.20 g P plant⁻¹) at 1.85 m² LA. For *P. dusenii* and *C. andina* plants this order of nutrient storage changed: N > K > Ca > P > Mg > S. Also, there were differences in nutrient storage according to plant size of different species. For example, at a plant size of 1 m² leaf area, while *F. pallescens* plants accumulated a mean value of 1.66 g N plant⁻¹, 1.13 g K plant⁻¹, 0.96 g Ca plant⁻¹, 0.36 g Mg plant⁻¹, 0.21 g P plant⁻¹ and 0.18 g S

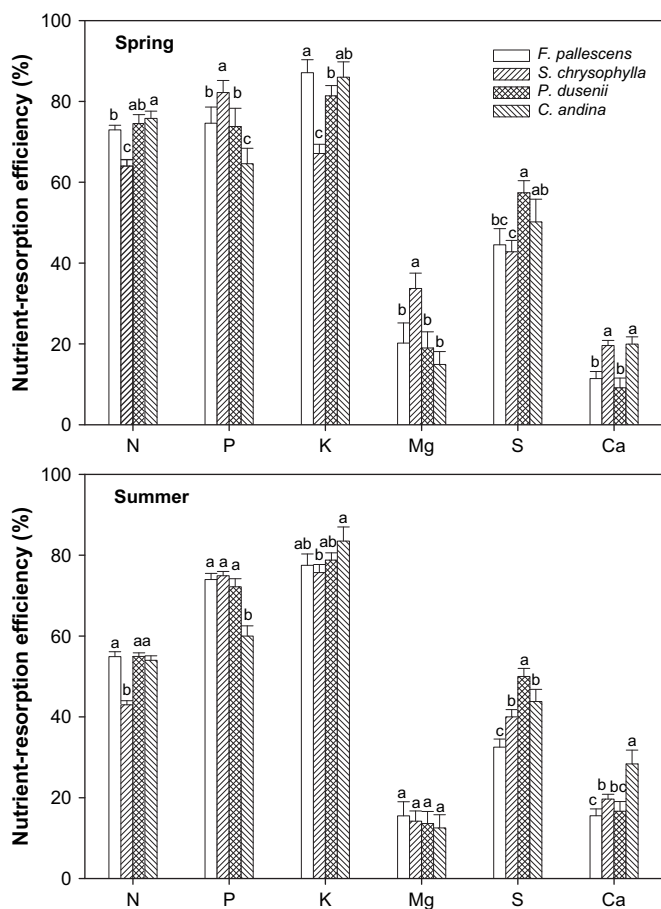


Fig. 2. Nutrient-resorption efficiency of four individual grass species (*Festuca pallescens*, *Stipa chrysophylla*, *Poa dusenii* and *Carex andina*) during spring (water non-limiting) and summer (water stress period) growing season in the Magellanic steppe of southern Patagonia, Argentina. Bars represent mean nutrient-resorption efficiency values ± 1 standard error, $n = 27$. Different lower-case letters indicate significant ($p < 0.05$) differences between species.

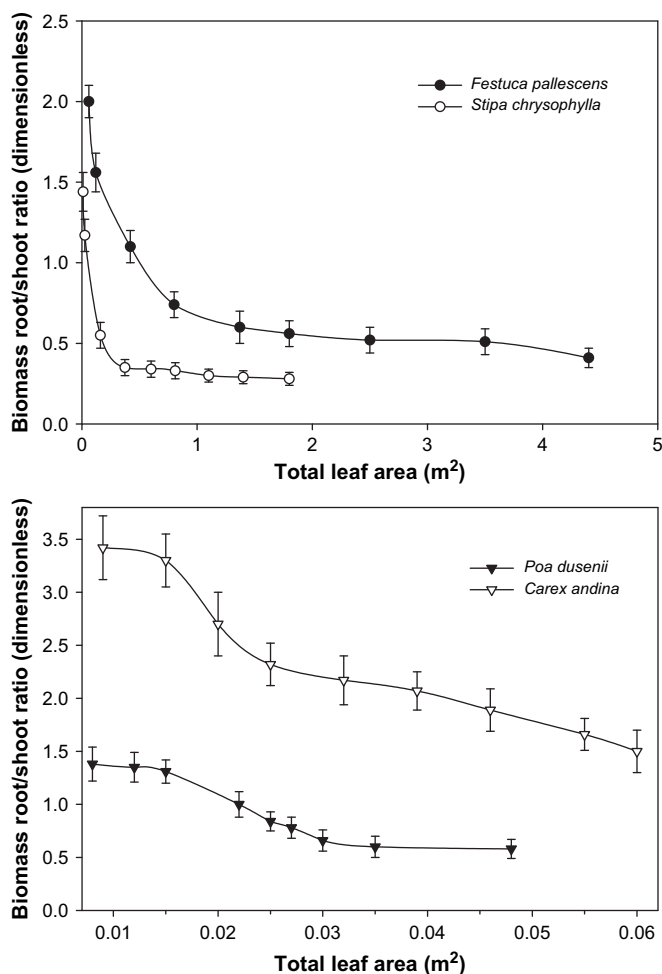


Fig. 3. Biomass root/shoot ratio against plant size of four individual grass species (*Festuca pallescens*, *Stipa chrysophylla*, *Poa dusenii* and *Carex andina*) grown in the Magellanic steppe of southern Patagonia, Argentina. Points represent the mean biomass root/shoot ratio ± 1 standard error, $n = 3$.

plant⁻¹, *S. chrysophylla* plants stored 1.64 g N plant⁻¹, 0.79 g K plant⁻¹, 0.57 g Ca plant⁻¹, 0.21 g Mg plant⁻¹, 0.13 g P plant⁻¹ and 0.14 g S plant⁻¹.

3.5. Carbon and nutrient allocation in plant components

Significant differences ($p < 0.05$) were found in carbon and nutrient distribution (expressed as percent of total nutrient quantity per plant) between components (Appendix 3). For example, plants allocated more N, P and K mainly in green leaves (ranged from 23.0 to 41.7%, 17.7 to 49.7% and 25.8 to 51.3%, respectively), more Mg, S and Ca in fine roots (ranged from 6.5 to 66.0%, 8.4 to 55.8% and 9.7 to 68.3%, respectively), and more carbon in coarse roots (ranged from 14.5 to 60.5%).

Carbon and nutrients allocation varied significantly according to species (Appendix 3). For example, while *F. pallescens* plants allocated more carbon (mean of 29.2%), Mg (43.3%), S (34.5%) and Ca (45.3%) in fine roots, *P. dusenii* plants allocated more N (mean of 34.1%) and *S. chrysophylla* more P (37.4%) in green leaves.

Also, carbon and nutrient allocation varied according to and the plant size (Appendix 3). In general, big plants allocated more carbon and nutrients in green and senesced leaves than

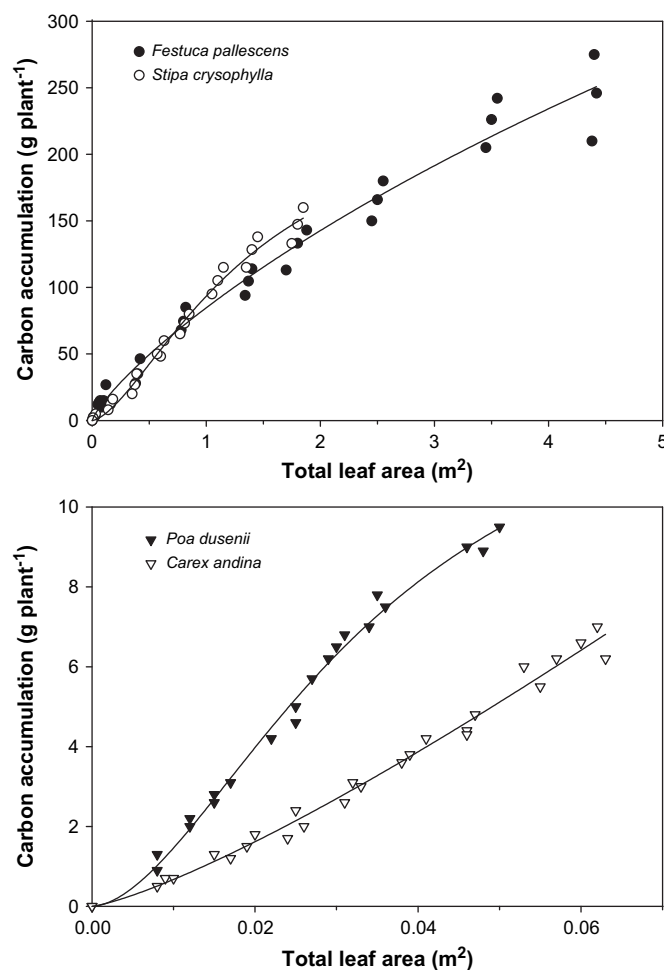


Fig. 4. Total carbon accumulation against plant size of four individual grass species (*Festuca pallescens*, *Stipa chrysophylla*, *Poa dusenii* and *Carex andina*) grown in the Magellanic steppe of southern Patagonia, Argentina. The parameters and statistics of each fitted function are given in Appendix 1.

small plants. The opposite occurred for pseudostem (except *C. andina*), fine and coarse roots components where small plants had higher values of nutrient and carbon. For example, while small *C. andina* plants allocated 60.5% of carbon in coarse roots, big plants only allocated 32.2%. In contrast, small *S. chrysophylla* plants allocated less N in green leaves compared with big plants (26.9 vs. 41.7%).

4. Discussion

Total biomass accumulation for individual grass plants found in this work was affected by plant size and species (Appendix 2). This was empirically derived using a non-linear regression. Total biomass accumulated for big *F. pallescens* plants was forty five times greater than *C. andina* plants. The biomass distribution in components depended on plant size and species. For example, while coarse roots of *C. andina* was the main component as leaf area increased, senesced leaves was the main component for the other species (Appendix 2). This is consistent with Mokany et al. (2006) who reported that biomass allocation is affected by plant size. Also, biomass root/shoot ratio of individual grass plants decreased with increasing size (Fig. 3). It is possible that these species has more root biomass to ensure establishment at early growth phases to

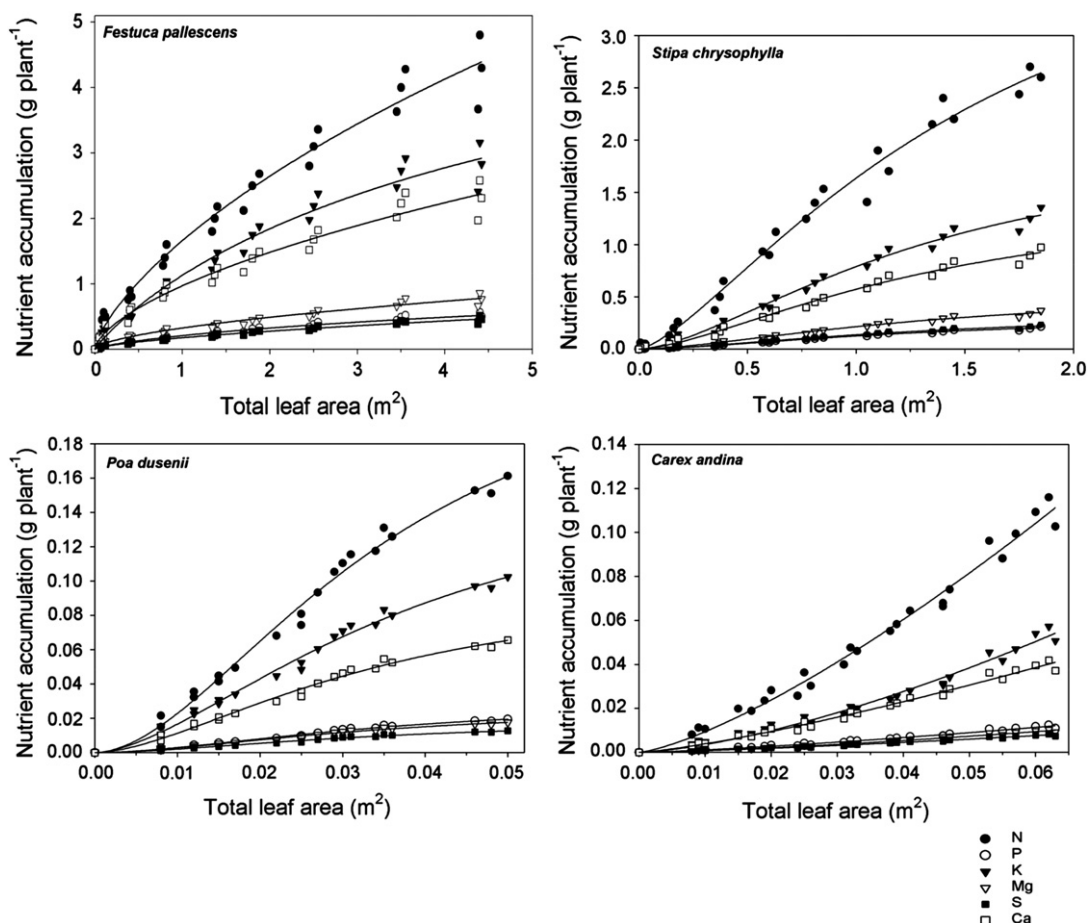


Fig. 5. Nutrient accumulation against plant size of four individual grass species (*Festuca pallescens*, *Stipa chrysophylla*, *Poa duseii* and *Carex andina*) grown in the Magellanic steppe of southern Patagonia, Argentina. The parameters and statistics of each fitted function are given in Appendix 1.

improve water and nutrient uptake. Specially, the primary production allocated belowground for *C. andina* was greater than that allocated aboveground across all plant sizes. The belowground biomass data was lower than the values reported by Reeder and Schuman (2002) for short-grass steppe with a root/shoot ratio of 4.0 for un-grazed grasslands and for a *F. pallescens* grassland (root/shoot ratio of 4.12) reported by Austin and Sala (2002) in drier sites in Patagonia compared with our study areas in the Magellanic Patagonian steppe. This trend is supported by Mokany et al. (2006) who indicated that the root/shoot ratios become lower as moisture availability increases.

In general, nutrient concentrations founded in this work were in the range from those presented for similar specie in Patagonia (Carrera et al., 2000; Mazzarino et al., 1998; Rodríguez et al., 2007). Concentrations of N and P in green leaves of perennial grasses were similar to those reported by Bertiller et al. (2005) for other grass and shrub species in north Patagonia (0.9–2.8% N and 1.2–2.4% P). Roots were one of the components that concentrated more P, mainly in *F. pallescens* plants. P has an influence on root system growth and plays a role for the strategy establishment and nutrients uptake (Lambers et al., 1998). There was a difference in carbon and total nutrient concentration between components. The nutrient concentration in the fine roots component found in this work was higher than those reported by Jackson et al. (1997) for temperate grasslands. The higher nutrient concentration in fine roots than in coarse roots was consistent with Rodríguez et al.

(2007) who reported higher N concentration in fine roots of perennial grasses. N and P concentration of senesced leaves found in the present work were higher than those reported by Mazzarino et al. (1998) for *F. pallescens* and *P. ligularis* (N 0.2–0.3%; P 0.05–0.09%) in Patagonia showing probably stronger mechanisms of nutrient conservation. Also, there was a difference in the order of total nutrient concentration between components according to grass species. Carrera et al. (2000) showed that the N concentration in green leaves changed between grass species during late autumn. Carbon concentration in all components was lower in *F. pallescens* compared with other species. This contrast with Mazzarino et al. (1998) who reported slightly lower C concentration values for green leaves of *F. pallescens* compared with *S. speciosa* and *P. ligularis*. These differences could be due to a differential increment in cell wall components (e.g. carbonated structures) in plant tissues of different species (Lambers et al., 1998). In general, nutrient and carbon concentration varied according to the growing season and plant size (Tables 2–5). Similarly, Carrera et al. (2000) reported that green leaves of perennial grasses in the Patagonian Monte varied markedly between late spring (December) and late autumn (June) and Austin and Sala (2002) reported an increase in N concentration with mean annual precipitation in dominant plants in Patagonia. In contrast, Bertiller et al. (2006) reported that while N and P concentrations in green leaves of 19 species in Patagonia were not significantly correlated to a regional humidity gradient, P concentration in senesced leaves

increased with humidity. However, Ca and carbon were more concentrated in summer. This information is also consistent with Lambers et al. (1998), who reported that plants have greater concentrations of N, P and K when growth conditions becomes more favourable.

Resorption is a strategy of plants to conserve nutrients. Mean nutrient resorption efficiency found in this work varied according to the species (Fig. 2) being, for example, the mean N-resorption efficiency higher in *C. andina* and lower in *S. chrysophylla*, and the mean S-resorption efficiency higher in *P. dusenii*. This contrast with Bertiller et al. (2005) who reported that there were no differences in N- and P-resorption efficiency among perennial grass species across an aridity gradient in north Patagonia. Mean nutrient resorption efficiency was lower during the drought period of summer mainly for N and Mg, showing that it may be associated with lower nutrient availability for plants during the dry season. This is consistent with Killingbeck (2004) who described a conceptual model for determinants of realized resorption where low water availability is a parameter that decrease nutrient resorption in leaves. Bertiller et al. (2006) reported that P-resorption efficiency decreased with humidity for 19 species in Patagonia and Carrera et al. (2000) showed that for three grass species (*Stipa tenuis*, *Poa ligularis* and *Stipa speciosa*) N-resorption efficiency was higher in June compared with December in the Patagonian Monte. Maximum value of mean nutrient resorption efficiency was obtained for K and minimum for Mg. The high nutrient resorption efficiency of the perennial grasses studied may be related to their short leaf lifespan. While N, P and K have consistently been reported to be absorbed in high quantities, Mg and Ca have been found in small quantities or accreted into senesced leaves (Killingbeck, 2004). The mean N-resorption efficiency obtained (62.2%) in the present work was slightly lower and P-resorption efficiency (73.3%) was similar to those founded by Bertiller et al. (2005) for perennial grasses in north Patagonia. However, these values of resorption efficiency suggested that the grass plants studied had in general a strong mechanism of nutrient conservation related to poor nutrient litter, low nutrient mineralization and/or low N availability in soil (Lambers et al., 1998).

Carbon and nutrients accumulation of individual plants was affected by grass species and size. The individual total carbon and nutrient accumulation functions were empirically derived and summarised into easily transferable coefficients using a non-linear regression. Carbon and nutrient accumulation of individual *F. pallescens* plants at any size was greater compared to other species. *F. pallescens* plants had larger crowns with more biomass of photosynthetic green leaves, and consequently had faster growth rates which may demand more nutrients. This response was mainly due to differences in biomass accumulation rates and to differences in tissue nutrient concentration. The carbon sequestered of each species was located mainly belowground in roots (Appendix 3). This is consistent with Hungate et al. (1997) who reported that up to 98% of C sequestration in grassland ecosystems occurred belowground and with Reeder and Schuman (2002) who reported that the 80–90% of plant C short-grass steppe was stored roots in the central Great Plains of USA. Storage of any particular nutrient varied depending mainly on species (Fig. 5). However, N was the mineral element that grass plants required in greatest amounts because it serves as a constituent of many plant cell components such as amino acids and nucleic acids (Taiz and Zeiger, 2006).

We conclude that biomass accumulation and partitioning in components, carbon and nutrient concentration and accumulation was strongly affected by grass species and plant size.

Quantification of roots biomass was important to improving our understanding of carbon cycles and storage in grassland ecosystems. Also, data from chemical composition of senesced leaves and nutrient resorption efficiency found in the present study may provide information for decomposition, nutrient cycling and soil nutrient availability. The logistic functions developed for individual grass plants provides a valuable tool for understanding and could be used to develop quantitative predictions of carbon and nutrient accumulation per hectare. However, futures studies may include the effect of grazing because it may change the nutrient balance of the grassland, due to changes in biomass partitioning, nutrients uptake, return of nutrients from litter and nutrient export.

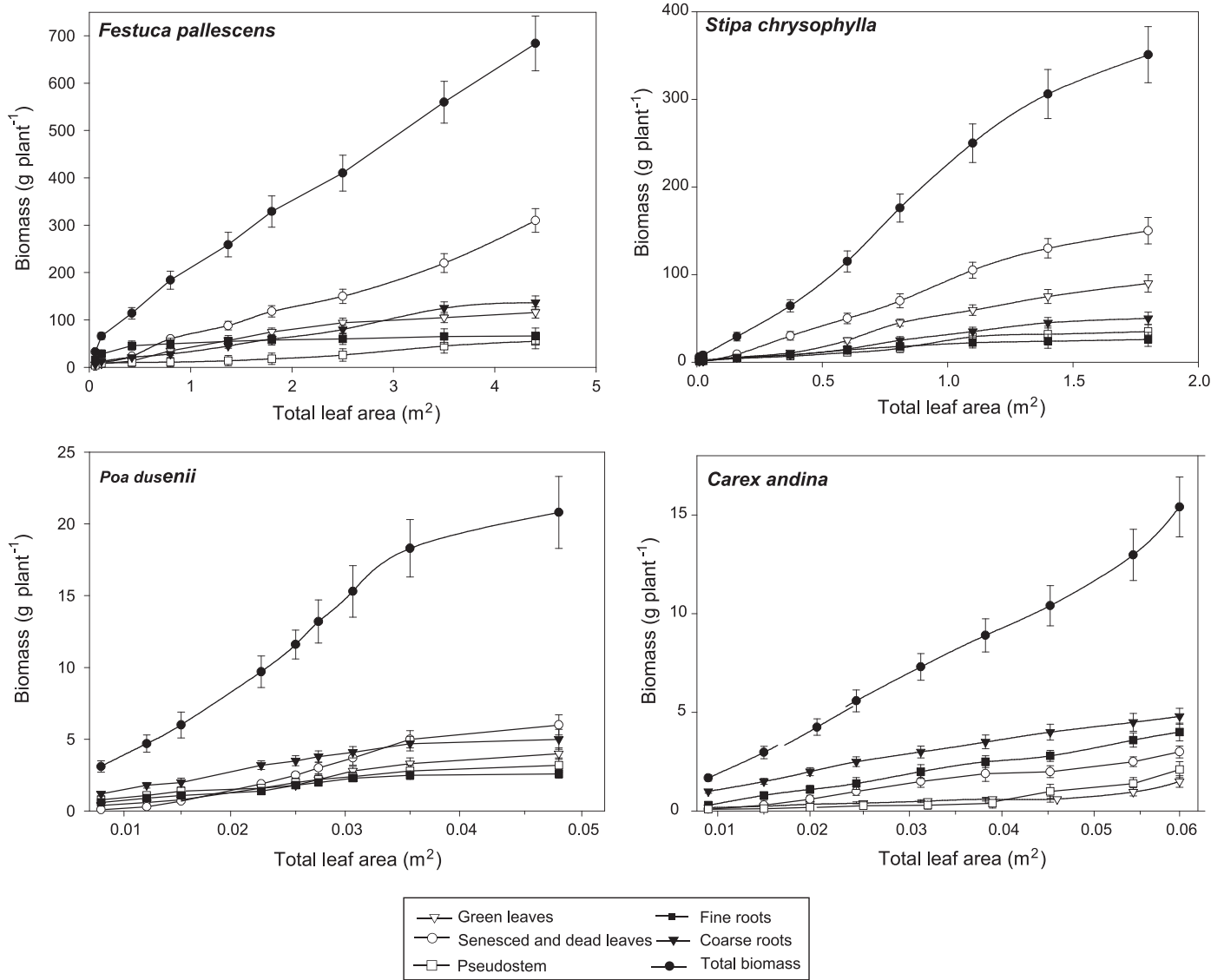
Appendix 1

Parameters and statistics (coefficient of determination R^2 and standard errors of the estimates ESE) of the logistic function (Eq. (1)) for the total biomass, carbon and nutrients accumulation of *Festuca pallescens*, *Stipa chrysophylla*, *Poa dusenii* and *Carex andina*.

		a	b	c	R ²	ESE
Biomass	<i>Festuca</i>	3935.691	35.250	-0.8092	0.98	32.56
	<i>Stipa</i>	594.421	1.3969	-1.5516	0.95	13.29
	<i>Poa</i>	33.939	0.0348	-1.7550	0.99	0.60
	<i>Carex</i>	556.111	1.0011	-1.2731	0.97	0.59
C	<i>Festuca</i>	1588.227	34.939	-0.8095	0.99	13.20
	<i>Stipa</i>	250.298	1.3969	-1.5516	0.98	5.59
	<i>Poa</i>	14.488	0.0348	-1.7550	0.96	0.25
	<i>Carex</i>	237.174	1.0011	-1.2731	0.97	0.26
N	<i>Festuca</i>	29.5826	49.4155	-0.7233	0.99	0.24
	<i>Stipa</i>	4.7449	1.5774	-1.4145	0.96	0.12
	<i>Poa</i>	0.2484	0.0356	-1.8022	0.98	0.005
	<i>Carex</i>	4.4711	0.9851	-1.3409	0.94	0.004
P	<i>Festuca</i>	2.1944	22.0662	-0.7287	0.95	0.03
	<i>Stipa</i>	0.3231	1.3177	-1.5998	0.92	0.08
	<i>Poa</i>	0.0307	0.0363	-1.7330	0.99	0.001
	<i>Carex</i>	0.3051	1.2825	-1.0518	0.91	0.002
K	<i>Festuca</i>	6.5920	5.6889	-0.9053	0.92	0.17
	<i>Stipa</i>	2.0548	1.3430	-1.5992	0.99	0.05
	<i>Poa</i>	0.1680	0.0382	-1.5447	0.97	0.003
	<i>Carex</i>	1.8844	1.2913	-1.1450	0.64	0.002
Ca	<i>Festuca</i>	27.7004	180.216	-0.6381	0.98	0.14
	<i>Stipa</i>	1.5118	1.3761	-1.5447	0.97	0.04
	<i>Poa</i>	0.1001	0.0343	-1.6727	0.96	0.002
	<i>Carex</i>	1.5983	1.0520	-1.2918	0.99	0.001
S	<i>Festuca</i>	2.0752	20.1038	-0.7892	0.93	0.02
	<i>Stipa</i>	0.3609	1.3613	-1.5738	0.94	0.01
	<i>Poa</i>	0.0195	0.0346	-1.7153	0.92	0.0004
	<i>Carex</i>	0.2757	1.0056	-1.1932	0.93	0.0003
Mg	<i>Festuca</i>	3.7841	25.4583	-0.6952	0.94	0.08
	<i>Stipa</i>	0.5662	1.3631	-1.5830	0.95	0.01
	<i>Poa</i>	0.0269	0.0346	-1.7504	0.96	0.001
	<i>Carex</i>	0.2942	1.0334	-1.1451	0.93	0.0004

Appendix 2

Total mean biomass accumulation and biomass distribution in plant components against plant size of four individual grass species (*Festuca pallescens*, *Stipa chrysophylla*, *Poa dusenii* and *Carex andina*) grown in the Magellanic steppe of southern Patagonia, Argentina. Points represent the mean biomass ± 1 standard error, $n = 3$.



Appendix 3

Grassland species, season and plant size variation in mean carbon and nutrients allocation in components (data expressed as

percent of total nutrient quantity per plant) of individual plants grown in a steppe in southern Patagonia.

Different lower-case letters indicate significant ($p < 0.05$) differences between plant sizes of each specie's component.

	Plant Size	Green Leaves	Senesced leaves	Pseudostem	Fine roots	Coarse roots
Carbon						
<i>Festuca pallescens</i>	Small	15.4 a	5.7 b	11.7 a	48.5 a	18.7 a
	Big	17.6 a	43.8 a	7.9 b	9.9 b	20.8 a
<i>Stipa chrysophylla</i>	Small	17.0 b	7.9 b	16.1 a	34.2 a	24.8 a
	Big	26.7 a	41.6 a	9.8 b	7.4 b	14.5 b
<i>Poa dusenii</i>	Small	12.9 a	3.0 b	24.6 a	19.3 a	40.2 a
	Big	19.5 a	27.4 a	14.9 b	12.7 a	25.5 b
<i>Carex andina</i>	Small	10.9 a	5.6 b	5.9 b	17.1 a	60.5 a
	Big	10.1 a	18.6 a	13.7 a	25.4 a	32.2 b
N						
<i>Festuca pallescens</i>	Small	30.4 a	3.9 a	11.1 a	41.5 a	13.1 a
	Big	36.5 a	31.3 b	7.9 b	8.9 b	15.4 a
<i>Stipa chrysophylla</i>	Small	26.9 a	5.7 a	18.4 a	29.1 a	19.9 a
	Big	41.7 b	29.5 b	11.1 a	6.2 b	11.5 a
<i>Poa dusenii</i>	Small	28.1 a	2.2 a	25.7 a	19.0 a	25.0 a
	Big	40.1 b	18.7 b	14.7 b	11.7 a	14.8 b
<i>Carex andina</i>	Small	26.8 a	4.4 a	6.6 a	21.0 a	41.2 a
	Big	23.0 a	13.5 b	14.3 b	28.8 a	20.4 b
P						
<i>Festuca pallescens</i>	Small	25.6 b	2.6 b	7.1 a	49.4 a	15.3 a
	Big	36.2 a	24.2 a	5.9 a	12.4 b	21.3 a
<i>Stipa chrysophylla</i>	Small	25.1 b	2.5 b	10.7 a	42.8 a	18.9 a
	Big	49.7 a	16.6 a	8.3 a	11.6 b	13.8 a
<i>Poa dusenii</i>	Small	26.3 b	1.7 b	28.7 a	17.6 a	25.7 a
	Big	39.6 a	15.4 a	17.3 b	11.5 a	16.2 a
<i>Carex andina</i>	Small	19.7 a	3.5 b	5.8 b	22.9 b	48.1 a
	Big	17.7 a	11.5 a	13.0 a	32.9 a	24.9 b
K						
<i>Festuca pallescens</i>	Small	42.8 a	2.6 b	11.0 a	32.1 a	11.5 a
	Big	51.3 a	20.7 a	7.8 a	6.8 b	13.4 a
<i>Stipa chrysophylla</i>	Small	25.8 b	3.7 b	12.5 a	41.1 a	16.9 a
	Big	46.9 a	22.6 a	8.9 a	10.3 b	11.3 a
<i>Poa dusenii</i>	Small	27.1 b	1.0 b	34.9 a	12.7 a	24.3 a
	Big	43.2 a	9.5 a	22.3 b	8.8 a	16.2 a
<i>Carex andina</i>	Small	33.8 a	2.8 a	11.8 b	16.5 a	35.1 a
	Big	28.1 a	8.4 a	24.7 a	22.0 a	16.8 b
Mg						
<i>Festuca pallescens</i>	Small	7.4 a	2.6 b	7.8 a	66.0 a	16.2 b
	Big	13.0 a	30.4 a	8.1 a	20.6 b	27.9 a
<i>Stipa chrysophylla</i>	Small	16.2 b	5.3 b	17.2 a	26.9 a	34.4 a
	Big	28.4 a	30.9 a	11.8 a	6.5 b	22.4 b
<i>Poa dusenii</i>	Small	13.8 a	2.9 b	26.7 a	28.1 a	28.5 a
	Big	21.0 a	26.1 a	16.2 b	18.5 b	18.2 b
<i>Carex andina</i>	Small	17.1 a	8.2 b	10.1 a	31.2 a	33.4 a
	Big	12.1 a	20.9 a	18.0 a	35.4 a	13.6 b
S						
<i>Festuca pallescens</i>	Small	18.1 a	4.3 b	6.5 a	55.8 a	15.3 a
	Big	24.0 a	37.8 a	5.1 a	13.2 b	19.9 a
<i>Stipa chrysophylla</i>	Small	19.4 b	5.5 b	15.9 a	35.4 a	23.8 a
	Big	33.6 a	32.0 a	10.7 a	8.4 b	15.3 a
<i>Poa dusenii</i>	Small	18.2 b	1.9 b	22.0 a	25.7 a	32.2 a
	Big	28.9 a	18.1 a	14.0 b	17.7 b	21.3 b
<i>Carex andina</i>	Small	18.0 a	5.2 b	5.1 b	23.2 a	48.5 a
	Big	15.7 a	16.2 a	11.1 a	32.5 a	24.5 b
Ca						
<i>Festuca pallescens</i>	Small	6.8 b	2.3 b	5.8 a	68.3 a	16.8 b
	Big	12.5 a	28.7 a	6.3 a	22.3 b	30.2 a
<i>Stipa chrysophylla</i>	Small	15.3 b	6.3 b	18.2 a	39.7 a	20.5 a
	Big	27.2 a	37.1 a	12.6 a	9.7 b	13.4 a
<i>Poa dusenii</i>	Small	10.3 a	2.2 b	24.2 a	24.1 a	39.2 a
	Big	17.2 a	22.2 a	16.1 a	17.4 a	27.1 b
<i>Carex andina</i>	Small	10.4 a	4.6 b	7.0 b	22.3 a	55.7 a
	Big	9.3 a	14.8 a	15.8 a	31.7 a	28.4 b

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