

MEADOW PRODUCTIVITY RELATED TO SOIL MOISTURE AND THERMAL TIME IN SOUTHERN PATAGONIA, ARGENTINA

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ABSTRACT

In Southern Argentine Patagonia, meadows are wetland ecosystems that require integrated grazing management, in which water dynamics, climatic components, and soil and vegetation characteristics are crucial factors for maintaining ecosystem functionality. The objectives of this study were to characterize and relate the productive parameters of the wet and dry meadow sectors to soil moisture and thermal time. Plant height, accumulated aerial biomass (AAB), live biomass (LB), dead biomass (DB), live AAB, daily vegetation growth rate (DGR), daily vegetation regrowth rate (DRR), soil moisture (SM), water table depth (WTD), and thermal time (TT) were determined monthly from October to April during three consecutive growing seasons in two extra-Andean meadows. AAB was analyzed using a factorial arrangement in a completely randomized design with three replications. Plant height and biomass were related to TT and SM by polynomial regressions, while DGR, DRR, and LB were related to SM and TT using multiple regression models. AAB in the wet sector was higher than in the dry sector from December to April, whereas biomass in both sectors was associated with TT and SM. In the wet sector, DGR, DRR and LB varied with SM, which was negatively associated with WTD. Overall, across both wet and dry meadow sectors, soil moisture emerged as the most relevant variable for guiding optimal management recommendations.

Keywords: South American wetlands, hydric edaphic, climate and vegetation variables.

INTRODUCTION

In Patagonia, meadows, locally known as ‘mallines’ represent a type of wetland located mainly in low-lying areas of the landscape, where surface and subsurface runoff from adjacent higher areas accumulate (Horne, 2015). Meadows provide water, forage for livestock and wildlife, and are reservoirs of biodiversity, among other environmental services (Gaitan et al., 2010). Extra-Andean meadows cover 5% of the total wetlands in Argentina (Navarro et al., 2022) and occupy 3.5% of the surface area in the southern continental region (Mazzoni, 2021). They are located mostly in alluvial plains, glaci-fluvial and glaciolacustrine plains, and slopes of basaltic plateaus (Epele et al., 2022).

Patagonian meadows contribute approximately 40% of the net forage production of rangelands; however, in recent decades, they have experienced a significant reduction in forage supply associated with degradation processes affecting about 30% of these ecosystems, primarily due to overgrazing and decreased vegetation cover, as well as increased bare soil (Bonvissuto et al., 2008). Additional contributing factors include the proliferation of invasive and unpalatable species (Collantes et al., 2013), higher soil bulk density, enhanced water evaporation, salinization, and hydric erosion processes (Utrilla et al., 2020). Curcio et al. (2023) reported that 55% of meadows analyzed in Patagonia (250,000 ha) showed severe degradation associated with a decline in aboveground net primary production, resulting in a reduction of regional stocking by 73,000 sheep (equivalent to an 8% decrease in carrying capacity) between 2002 and 2018.

Meadows are characterized by an intrinsic spatial heterogeneity defined by a gradient of soil moisture influenced by water table level, vegetation diversity (Gaitán et al., 2010), and soil type (Cisternas et al., 2025). Temporal heterogeneity is defined by seasonal and interannual changes in hydrological dynamics (Ciari, 2009; Horne and Polla, 2021), primary production (Buono et al., 2010), and forage nutritional quality (Utrilla et al., 2006).

In this context, topography and soil physicochemical properties define the internal water gradient of the meadow, which is represented by three sectors: humid, sub-humid, and dry, located in the central (flooded and near the riverbed), intermediate, and peripheral (in contact with the steppe) zones, respectively (Enriquez et al., 2015; Mazzoni, 2021).

In addition, seasonal water dynamics in these environments is characterized by a recharge phase during autumn-winter and early spring

driven mainly by phreatic ascent from rainfall and snow, and groundwater recharge and/or snowmelt. The discharge phase occurs from mid-spring to summer, driven by a deeper water table as a result of decreased rainfall and reduced stream flow (Horne and Polla, 2021). Likewise, the combination of soil physical and hydric factors defines the type of vegetation present in the different sectors of the meadow (Horne, 2015). In the wet sector (WS), graminoids (*Juncus balticus*, *Carex gallana* and *Eleocharis albibracteata*) predominate, accompanied by grasses (*Poa pratensis* L., *Hordeum pubiflorum* Hook. f., *H. halophyllum*, *Agrostis stolonifera*, *Agrostis* spp., *Alopecurus* sp., and *Deschampsia caespitosa*), herbaceous and legumes (*Taraxacum officinale* and *Trifolium repens*) (Bonvissuto et al., 2008; Gaitan et al., 2010). In contrast, in the dry sector (DS), *Festuca pallescens* is abundant, accompanied by other grasses (*Hordeum* spp., *Poa pratensis*, *P. spiciformis*, *Poa* spp., and *Carex* spp.) (Collantes et al., 2009; Gaitan et al., 2010; Chimner et al., 2011; Filipová et al., 2012). Several studies reported higher values of primary productivity (Buono et al., 2010; Vargas, 2017) and vegetation nutritional quality in the WS compared with the DS (Utrilla et al., 2006).

Efficient and sustainable meadow management under grazing involves adjusting stocking rates according to paddock receptivity, separating meadows from the steppe, and selecting the most appropriate grazing season and rest periods (Utrilla, 2019). Accordingly, the integrated management of these environments requires an understanding of seasonal biomass growth across meadow sectors, which is closely related to soil moisture and temperature (Vargas, 2017) and can help identify potential sustainable stocking rates. However, information on this ecosystem that integrates data on water, soil, vegetation, and climate components over several years remains limited; only preliminary studies have partially addressed this issue (Utrilla et al., 2006).

The present study tests the hypothesis that the interaction of hydric, edaphic, and climatic factors determines vegetation productivity across meadow sectors. Therefore, the objectives of this work were to characterize and relate the productive parameters of the wet and dry sectors to soil moisture and thermal time in meadows of Southern Patagonia, Argentina.

MATERIALS AND METHODS

Location and description of experimental sites

Based on the favorable conditions of the plains and valleys in the southern continental region

for meadow formation, the study was conducted in two meadows (locally known as 'vegas' in Santa Cruz Province), under continuous mixed grazing (cattle and sheep). The sites were located on fluvio-glacial valley floors (Mazzoni, 2021). The first site was the Glencross (GL) meadow (51°49'21.3" S, 71°37'18.6" W) (110 m.a.s.l. and 96.9 ha), located in the lower basin of the Turbio River within the Wet Magellanic Steppe. The second site was the La Leona (LL) meadow (51°27'29.8" S, 69°56'14.1" W) (64 m.a.s.l. and 178.1 ha), located in the middle basin of the Coyle River within the Dry Magellanic Steppe. Both sites are situated in the southwest and south of Santa Cruz Province, respectively.

The GL and LL meadows are located in the subhumid and semiarid, very cold climatic zones, respectively, as classified by Almonacid et al. (2023) for the period 1995-2014 in Santa Cruz Province. In each meadow, two sectors with moderate degradation were selected based on indicators such as bare soil, the presence of degradation-indicator species, and mulch cover (Suárez et al., 2010):

i) wet Sector (WS): near the main riverbed of the meadow, with a predominant vegetation of grasses (*Poa pratensis*, *Hordeum pubiflorum* and *Agrostis* sp.) accompanied by graminoids (*Eleocharis* sp. and *Carex gallana*), legumes (*Trifolium repens*) and herbaceous (*Taraxacum officinale*); ii) dry Sector (DS): on the periphery of the meadow, covered mainly by *Festuca pallescens* accompanied by *Poa spiciformis*, *P. pratensis*, *H. comosum*, *Juncus balticus* and *T. officinale* (Utrilla et al., 2008. Cited by Utrilla et al., 2014).

In the WS, the soil profile of the LL meadow consists of an organic surface layer (0-10 cm) over a deeper layer (10-25 cm), whereas the GL meadow is characterized by organic and sandy loam soils in the surface and deep profiles. In the DS, the soil profile of the GL meadow is characterized by organic and loam soils, while in the LL meadow it is sandy loam in both horizons. In general, pH values across sectors and profiles of both meadows are moderately acidic (5.6 and 5.7), with moderate organic matter contents (16.2 and 6.5%) and total nitrogen values (0.76 and 0.37%) (La Manna et al., 2011), with no salinity constraints.

From the start of the study (10 December 2003), vegetation parameters, water table depth (WTD), soil moisture (SM), and air temperature were evaluated in each meadow and sector. Measurements were taken monthly from 10 December to 12 April during 2003-2004 and, prior to installation of the study, during the 2004-2005 and 2005-2006 (08 October-12 April) periods.

Climatic measurements and thermal time determination

Daily air temperature was recorded with a datalogger (® HOBO TEMPERATURE, RH ©1996 ONSET), with an hour interval. Rainfall was recorded using a collector with a digital counter (Pluviometer II, No. 7852M. Standard and Industrial, ® Davis Instruments, 1996). Mean daily temperatures (MDT) in the GL and LL meadows ranged from 5.3 °C and 6.9 °C (September-October) to 6.8 °C and 8.6 °C (March-April), respectively. Maximum temperature values ranged from 12.2 °C to 14.7 °C in January-February, with LL being consistently higher than GL by 2.5 °C (Fig. 1a, b).

Then, using MDT values by year, accumulated thermal time (TT), defined as the sum of heat units expressed as degrees days (°C d), or phyllochron, a relatively constant parameter for a given species (Lemaire and Agnusdei, 2000), was calculated for each sampling date and for the intervals between monthly measurement using the following formula: MDT - base temperature for growth initiation (4° C) * Number of days in the interval (Ruolo and Nanning, 2024).

The rainfall recorded in the intervals 10 Dec-12 Apr and 06 Sep-12 Apr of the years 2003-2004 (Cycle 1), 2004-2005 (Cycle 2), and 2005-2006 (Cycle 3) was, respectively, 83.0, 264.0, and 293.5 mm (GL), and 80.8, 166.9, and 198.3 mm (LL). Likewise, the spring-summer rainfall distribution was homogeneous and higher in summer respect to spring in Cycles 2 and 3, respectively (Fig. 1a, b).

Vegetation measurements

Soil cover and botanical composition

Three permanent enclosures (1.5 m × 1.2 m × 0.6 m) were installed nearby in each sector (i.e., six per meadow) to measure total vegetation cover, mulch, and bare soil. Vegetation was characterized by measuring the relative aerial cover (%) of plant species classes (Daubenmire, 1959) or functional groups.

Accumulated aerial biomass and plant height

Manual forage cuts were performed monthly (30±3 days) at a height of 3-4 cm using a 0.1 m² frame in each permanent enclosure, according to MDT, from 10 Dec (Cycle 1) and 08 Oct (Cycles 2 and 3), following previous rangeland mowing, to 12 Apr (all three cycles), covering the growing season. Previously, within each frame, the modal height of three plants belonging to the most frequent rangeland species was measured using a graduated ruler. In the laboratory, the forage samples were dried in an oven at 60 °C until constant weight to determine the accumulated

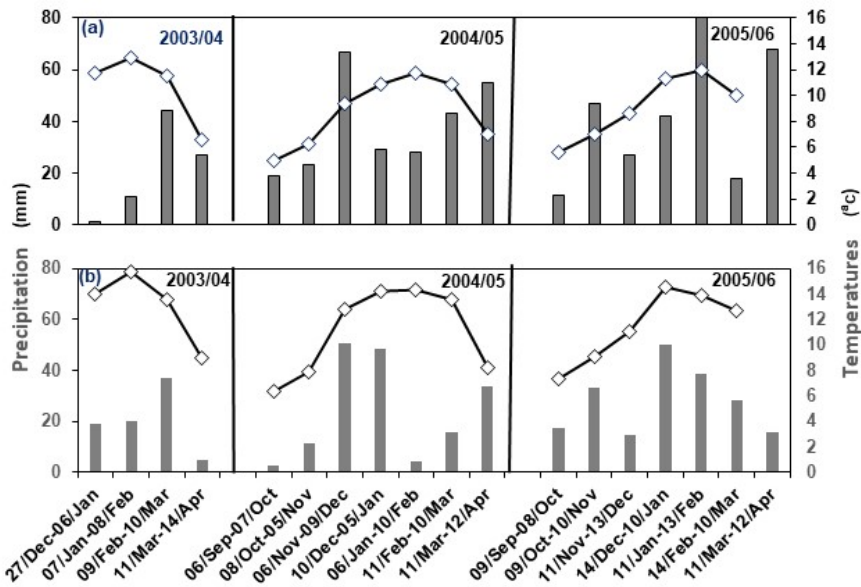


Fig. 1. Distribution of precipitation (bars) and mean daily temperatures (lines) by period in the Glencross (a) and La Leona (b) meadows during the study years.

aerial biomass (AAB, kg DM ha⁻¹), calculated using the formula: AAB (g) x 100.

Growth and regrowth rates, live and dead material, and live aerial biomass

Daily growth rate (DGR) of vegetation was estimated between cutting dates in kg DM ha⁻¹ day⁻¹ as the difference in AAB between two consecutive measurements divided by the length of the interval. Furthermore, daily regrowth rate (DRR) was calculated in kg DM ha⁻¹ day⁻¹ as the aerial biomass accumulated during regrowth divided by the number of days between two consecutive sampling dates. Samples of accumulated rangeland forage were subsequently separated into live biomass (LB; green leaves and stems) and dead biomass (DB; senescent leaves and stems and spikes) to determine their relative proportions based on total dry material. Live accumulated aerial biomass (LAAB) in kg DM ha⁻¹ was calculated using the formula AAB x proportion LB.

Water table depth and soil moisture measurements

One phreatometer was installed near each enclosure at depths of 1.5 m (WS) and 2.0 m (DS) to measure WTD. Perforated polyvinyl chloride (PVC) tubes and wire mesh were installed at the base to avoid possible obstructions when using a measuring tape to determine WTD. Likewise, in each enclosure and on each rangeland cutting date, a soil sample was collected at a depth of 30 cm using a manual rotary auger (Meridiens ®)

and kept in plastic bags to determine SM content on dry mass basis using the gravimetric method. For this purpose, in the laboratory, the wet samples were weighed using a digital electronic scale (Precisa ® 6000 D, Swiss Quality; precision: 0.1 g) and then, after manual separation of roots from the WS, dried in a forced-air oven at 60 °C until constant weight, ensuring complete removal of soil water content to determine dry mass. SM percentage was calculated using the formula: wet weight - dry weight/dry weight x 100 (Tanriverdi et al., 2016).

Experimental design and statistical analysis

The AAB of the rangeland was analyzed using a 2 x 2 x 7 factorial arrangement, i.e., Site (fixed factor; Glencross meadow and La Leona meadow), Sector (fixed factor; Wet and Dry), and Date (fixed factor: October, November, December, January, February, March, and April). The factorial arrangement was analyzed under a completely randomized design with three replications (corresponding to three growing seasons). The experimental units, defined by each site and sector of the meadow, were characterized by the average of measurements taken from the three enclosures (pseudoreplicates) installed to obtain a more reliable estimate of the response variable. The results were subjected to analysis of variance (ANOVA) using the mixed-model procedure for repeated measures (ProcMixed, SAS 2002-2008) according to the following model:

$$y = \mu + \text{Site} + \text{Sector} + \text{Date} + \text{Site} \times \text{Sector} + \text{Site} \times \text{Date} + \text{Sector} \times \text{Date} + \text{Site} \times \text{Sector} \times \text{Date} + \text{Error}$$

Where:

y = AAB; μ = overall mean; Site = Glencross meadow and La Leona meadow; Sector = wet and dry; Date: cutting date = October, November, December, January, February, March, and April.

Subsequently, AAB means by site and meadow sector, as well as differences among interaction means described in the analysis model, were compared with the Tukey's test and adjusted with the Tukey-Kramer procedure with a 5% significance level in both cases. Likewise, plant height, AAB, LAAB, and DGR values by meadow sector were related to TT and SM using polynomial regression models (PROC REG, SAS 2002-2008, and InfoStat, 2008). The relationships between plant height and LAAB, and between WTD and SM, were analyzed using Pearson's correlation index (PROC CORR, SAS 2002-2008). In turn, DGR, DRR, and LB by meadow sector were related to SM and TT using linear and quadratic regression models (PROC REG, SAS 2002-2008) with the stepwise selection procedure. In this context, predictor variables associated with the parameters of interest were included in

the multiple analysis model with a significance level of 20% ($p = 0.20$), and model selection was based on the coefficient of determination (R^2).

RESULTS

Soil cover and botanical composition

In the GL meadow, values (mean \pm standard deviation) for vegetation cover (VC) of 86.5 ± 7.8 and $80.6 \pm 8.7\%$, litter (L) 12.5 ± 7.3 and $17.3 \pm 8.5\%$ and bare soil (BS) 1.1 ± 2.2 and $1.9 \pm 2.5\%$ were recorded in the WS and DS, respectively. Likewise, in both sectors of the LL meadow, VC, L, and BS were 87.1 ± 9.0 and $83.1 \pm 6.5\%$, 12.2 ± 8.6 and $9.8 \pm 6.0\%$ and 0.9 ± 1.8 and $7.1 \pm 5.7\%$, respectively. The main VC in both meadows and sectors was represented by grasses (Fig. 2). In both sectors of the LL meadow, graminoid cover was approximately 4.5-5.0-fold higher than the mean values reported in GL. In addition, the cover of herbaceous species, subshrubs, and lichens found in the DS of both meadows was relatively higher than that of the same functional groups in the WS (Fig. 2).

Accumulated aerial biomass and plant height

The analysis of AAB (mean \pm standard error) of the rangeland revealed significant effects ($p < 0.05$) of Site, Sector, Date, and the Sector \times Date

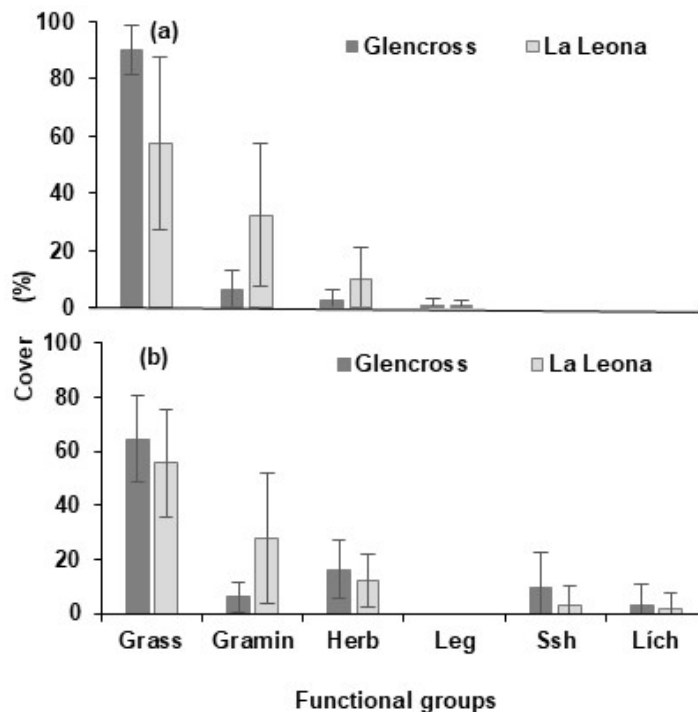


Fig. 2. Cover means (% \pm standard deviation) ($n = 62$) from grasses (Grass), graminoids (Gramin), herbaceous species (Herb), legumes (Leg), subshrubs (Ssh) and lichens (Lich) by site and wet (a) and dry (b) sectors.

interaction. In this context, the GL meadow parameter exhibited higher AAB (1.4-fold) than that of the LL meadow ($3371 \pm 288a$ vs. $2380 \pm 288b$ kg DM ha⁻¹), while AAB in the WS was substantially higher (8.5-fold) than in the DS ($5147 \pm 288a$ vs. $603 \pm 288b$ kg DM ha⁻¹). Likewise, forage accumulation in January, February, March and April ($3771 \pm 327a$, $4374 \pm 327a$, $4715 \pm 327a$ and $4563 \pm 327a$ kg DM ha⁻¹) was greater (ranging from 1.9- to 33-fold) than in October, November, and December ($142 \pm 396c$, $557 \pm 382c$, and $2004 \pm 327b$ kg DM ha⁻¹). Regarding the Sector \times Date interaction, from December onwards AAB in the WS exceeded the forage accumulated in the DS until the final sampling date, with differences ranging from 6-fold (December) to 12-fold (April) (Table 1). In addition, values observed in the WS in February, March, and April were higher than those recorded on previous dates, while January values were significantly higher compared with those in December and, in both cases, higher with respect to those in October and November (Table 1). In contrast, AAB in the DS did not differ significantly ($p > 0.05$) among dates.

Furthermore, in line with the increase in TT observed in both meadows, plant height (mean \pm standard deviation) measured in the WS and DS varied in the October-April period, from 6 ± 2 to 37 ± 6 cm and from 4 ± 1 and 8 ± 4 cm, respectively. Variation in this parameter was related to TT and SM, as described by the following quadratic polynomial regression models:

WS: $y = 0.01 + 0.09x - 0.0001x^2$; $R^2 = 0.68$; $p < 0.0001$ (TT); $y = 1.17x - 0.0097x^2$; $R^2 = 0.40$; $p < 0.0001$ (SM).
DS: $y = 1.59 + 0.02x - 0.00001x^2$; $R^2 = 0.56$; $p < 0.0001$ (TT); $y = 0.65x - 0.0113x^2$; $R^2 = 0.65$; $p < 0.0001$ (SM).

Daily growth and regrowth rates, live and dead material, and live aerial biomass

In the WS, DGR and DRR decreased from 3.0-4.4 to 1.6-1.7-fold in the October-January period, coinciding with reductions in TT (from 1.8 to 1.1-fold) and higher SM values (>75%) (Table 2). Following peak DGR and DRR values, both parameters decreased in association with the reduction of SM, which was negatively correlated with WTD ($r = -0.81$; $p < 0.0001$) (Table 2). In contrast, in the DS, DGR and DRR showed minor fluctuations, with higher values observed between November and December and between October and November. These patterns were accompanied by slight reductions in SM, associated with WTD ($r = 0.53$; $p = 0.001$) (Table 2).

Live material collected in the WS was highest in the October-January period, corresponding to higher edaphic water content, and subsequently declined by half as the season progressed, in

parallel with a similar decrease in SM (Table 2). In the DS, this parameter also reached its highest values in the October and November period, followed by a marked decline in accordance with successive reductions in SM (Table 2). Conversely, dead material harvested in both sectors showed a substantial increase (2.0 to 4.0-fold) during the February-April period with respect to the preceding interval (Table 2).

Table 1. Means (\pm standard error) of the accumulated aerial biomass (kg DM ha⁻¹) by meadow sector and cut-off date (n = 4 and 6).

Meadow sector	Cutt-off Day						
	08/Oct	08/Nov	10/Dec	08/Jan	11/Feb	11/Mar	12/Apr
Wet	85*(560) aD	787*(541) aD	3438(463) aC	6716(463) aB	7988(463) aA	8594(463) aA	8424(463) aA
Dry	198*(560) aA	328*(541) aA	571(463) bA	826(463) bA	759(463) bA	836(463) bA	702(463) bA
p Value	0.8874	0.5516	<.0001	<.0001	<.0001	<.0001	<.0001

*, value adjusted for missing data.

Different lowercase and uppercase letters indicate significant differences ($p < 0.05$) between meadow sectors within dates and between dates within meadow sectors, respectively.

Table 2. Means (\pm standard error) of live and dead biomass (LB-DB, %) by meadow sector and cut-of-day, daily growth rate (DGR, kg DM ha⁻¹ day⁻¹), daily regrowth rate (DRR, kg DM ha⁻¹ day⁻¹) by meadow sector (n= 4 and 6) and interval (days) between cuts, thermal time (TT, °C day), soil moisture (SM, %) and water table depth (WTD, cm).

Meadow sector	Cut-of-Day and days between cuts	Variable									
		LB	DB	DGR	DRR	TT	SM	WTD			
Wet	08-Oct (30)	81.6(6.5)	18.4(6.5)	9.0(2.1)	9.0(2.1)	61.5(15.8)	88.8(14.1)	25.1(5.1)			
	08-Nov (31)	87.3(6.9)	12.8(6.9)	27.8(11.4)	39.8(12.8)	112.7(26.5)	85.7(15.8)	38.5(6.7)			
	10-Dec (32)	81.4(4.0)	18.6(4.0)	78.2(22.4)	68.0(5.7)	191.8(18.3)	85.9(13.9)	44.1(4.9)			
	08-Jan (27)	87.8(1.8)	12.3(1.8)	126.0(10.2)	38.5(7.1)	225.1(28.8)	76.3(14.1)	51.2(4.8)			
	11-Feb (32)	70.0(5.1)	30.0(5.1)	47.7(15.8)	21.3(5.3)	303.9(20.1)	59.2(11.5)	72.1(4.4)			
	11-Mar (29)	67.9(6.2)	32.1(6.2)	23.5(9.2)	13.6(4.3)	234.3(25.0)	45.6(7.9)	83.2(4.8)			
	12-Apr (31)	42.7(4.2)	57.3(4.2)	23.3(22.7)	13.0(3.5)	114.5(18.5)	34.9(1.8)	75.5(7.0)			
	Dry	08-Oct (30)	70.2(13.2)	29.9(13.2)	4.5(0.3)	4.0(0.7)	61.5(15.8)	35.0(10.2)	143.0(14.8)		
08-Nov (31)		80.3(3.8)	19.7(3.8)	3.5(2.1)	14.5(14.8)	112.7(26.5)	24.6(8.3)	143.3(16.3)			
10-Dec (32)		77.0(5.9)	23.0(5.9)	11.5(2.8)	11.3(3.1)	191.8(18.3)	23.2(4.9)	138.5(17.0)			
08-Jan (27)		71.3(3.0)	28.7(3.0)	8.8(3.2)	12.8(3.2)	225.1(28.8)	19.7(3.3)	141.8(17.7)			
11-Feb (32)		51.1(2.4)	48.9(2.4)	0.5(0.4)	5.3(1.4)	303.9(20.1)	15.2(3.0)	147.8(19.3)			
11-Mar (29)		45.4(6.1)	54.6(6.1)	3.7(2.6)	6.0(3.1)	234.3(25.0)	15.9(4.2)	156.3(20.3)			
12-Apr (31)		35.5(5.9)	64.5(5.9)	1.0(0.7)	2.5(0.7)	114.5(18.5)	19.4(7.8)	164.7(31.0)			

Oct: October, Nov: November, Dec: December, Jan: January, Feb: February, Mar: March, Apr: April

AAB and LAAB displayed contrasting patterns between meadow sectors as TT increased. Mean (\pm standard error) values of AAB are presented by sampling date in Table 1. LAAB values ranged from 235 \pm 385 to 3469 \pm 315 kg DM ha⁻¹ in the WS and from 126 \pm 385 to 271 \pm 315 kg DM ha⁻¹ in the DS in the October-April period. Furthermore, both parameters showed contrasting responses between meadow sectors to changes in SM. Accordingly, variation in these variables was related to TT (Fig. 3a,b) and SM (Fig. 3c,d), as

described by the following quadratic polynomial regression models:

WS: AAB: $y = -408.18 + 17.64x - 0.0086x^2$; $R^2 = 0.77$; $p < 0.0001$; LAAB: $y = -172.89 + 13.93x - 0.0081x^2$; $R^2 = 0.70$; $p < 0.0001$ (TT); DS: AAB: $y = 60.03 + 2.23x - 0.0014x^2$; $R^2 = 0.45$; $p < 0.0001$; LAAB: $y = 81.23 + 1.14x - 0.0008x^2$; $R^2 = 0.38$; $p < 0.0001$ (TT).

WS: AAB: $y = 1.595,9 + 192.86x - 1.7114x^2$; $R^2 = 0.39$; $p < 0.0001$; LAAB: $y = 882.29 + 131.61x - 1.1169x^2$; $R^2 = 0.36$; $p < 0.0001$ (SM); DS: AAB: $y = -38.11 +$

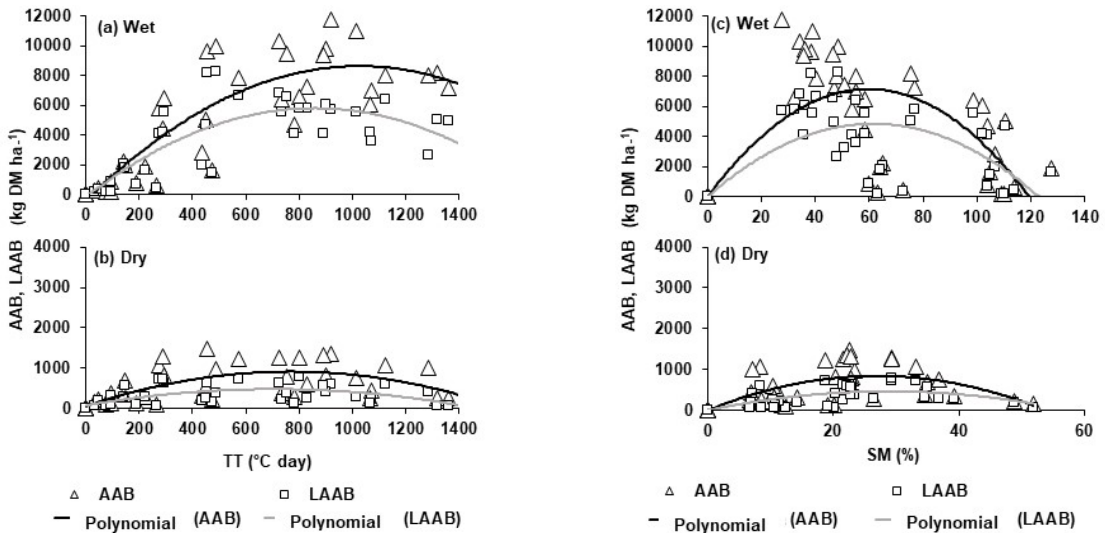


Fig. 3. Relationship between accumulated aerial biomass (AAB) and live accumulated aerial biomass (LAAB) in wet and dry meadow sectors as a function of thermal time (TT) (a, b) and soil moisture (SM) (c, d).

$$65.89x - 1.2194x^2; R^2 = 0.44; p < .0001; \text{LAAB: } -40.75 + 35.69x - 0.6187x^2; R^2 = 0.49; p < .0001 \text{ (SM)}.$$

In this context, LAAB in the WS and the DS was positively correlated with plant height ($r = 0.92$ and 0.86 , respectively; $p < .0001$ in both cases). Likewise, DGR exhibited contrasting responses between meadow sectors to changes in TT and SM. Accordingly, variation in this parameter by sector was related to TT (Fig. 4a,b) and SM (Fig. 4c,d) as described by the following quadratic polynomial regression models:

$$\text{WS: } y = 12.94 + 0.21x - 0.0002x^2; R^2 = 0.34; p < 0.0001 \text{ (TT); DS: } y = 4.97 + 0.0046x - 6E-06x^2; R^2 = 0.097; p = 0.2176 \text{ (TT)}.$$

$$\text{WS: } y = 2.87 + 1.50x - 0.01x^2; R^2 = 0.14; p = 0.07 \text{ (SM); DS: } y = -0.06 + 0.38x - 0.0045x^2; R^2 = 0.20; p = 0.0057 \text{ (lineal) (SM)}.$$

Relationship between daily growth and regrowth rates and live biomass with soil moisture and thermal time by multiple analysis

In the WS, the multivariate model for DGR primarily selected TT as the main explanatory variable. In contrast, SM was the main variable selected in the models for DRR and LB (Table 3). In the DS, the same main explanatory variable was selected across the DGR, DRR and LB analysis models, respectively (Table 3).

DISCUSSION

Vegetation cover and composition

Vegetation cover was consistently high in the WS, comparable to that reported for extra-Andean wet meadows of southern Patagonia (Utrilla and Jaurena, 2017; Vargas, 2017). However, floristic composition varied in response to hydrological dynamics. In this context, the WS was dominated by *Poa pratensis* and *Agrostis stolonifera*, in accordance with patterns observed in wet meadows of southern region (Utrilla et al., 2020). In contrast, the DS showed higher representation of *P. pratensis* and *Festuca pallescens* adapted to drier conditions (Gaitan et al., 2010), and a floristic composition similar to that of dry meadows in southern Patagonia (Utrilla et al., 2020). These differences highlight the role of hydrological conditions in structuring vegetation composition across wet and dry meadow sectors, consistent with patterns reported in riparian meadows in North-America (Castelli et al., 2000; Dwire et al., 2006) and wet meadows of northern Patagonia (Gaitan et al., 2010).

Plant height and aerial biomass

The predominance of taller species in the WS with respect to the DS may explain the greater variation in plant height observed during the study period. In turn, the AAB observed in the WS was higher than that in the DS from December onwards, likely due to more favorable edaphic

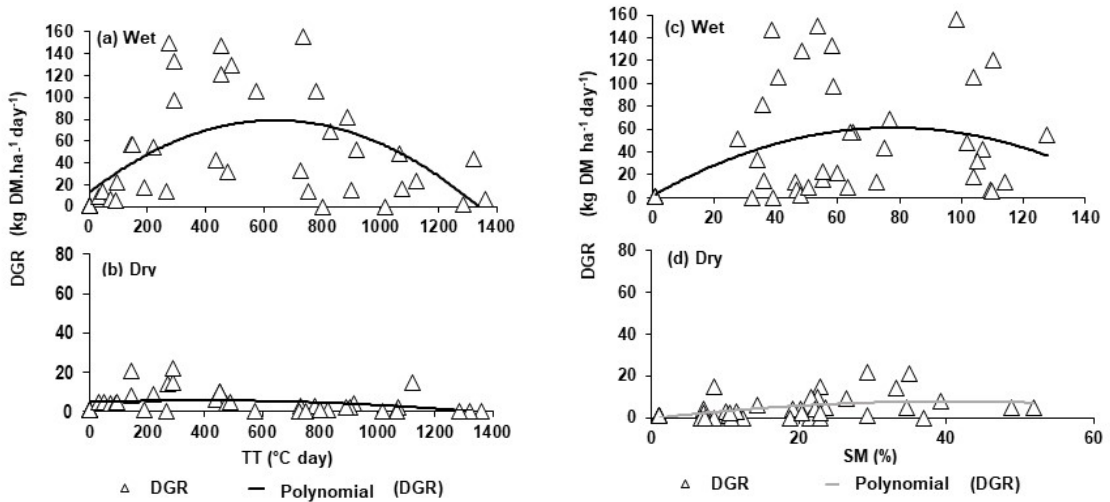


Fig. 4. Relationship between the daily growth rate (DGR) in wet and dry meadow sectors as a function of thermal time (TT) (a, b) and soil moisture (SM) (c, d).

Table 3. Relationship of daily growth rate (DGR), daily regrowth rate (DRR), and live biomass (LB) in wet and dry meadow sectors with soil moisture (SM) and thermal time (TT), based on multiple regression analysis (stepwise procedure).

Parameter	Meadow		Partial R ²	Model R ²	Significance (p = 0.20)
	sector	Multiple regression model			
DGR	Wet	$y = -15.28 + 0.68TT - 0.001TT^2$	TT=0.06	0.06	0.1639
	Dry	$y = -2.54 + 0.58SM - 0.01SM^2$	TT ² =0.05 SM=0.12 SM ² =0.05	0.11 0.12 0.17	0.1636 0.0404 0.1757
DRR	Wet	$y = 12.47 + 0.27SM$	SM=0.12	0.12	0.0433
	Dry	$y = 3.84 + 0.20SM$	SM=0.11	0.11	0.0607
LB	Wet	$y = 32.78 + 1.10SM - 0.06SM^2$	SM=0.15 SM ² =0.05	0.15 0.20	0.0179 0.1683
	Dry	$y = 48.24 + 0.63SM$	SM=0.15	0.15	0.0198

water conditions, consistent with patterns reported for riparian meadows (Dwire et al., 2004; 2006). Peak biomass values were comparable to those reported in the northern (Enriquez et al., 2015), central (Buono et al., 2010), and southern (Vargas, 2017; Cipriotti et al., 2018; Utrilla et al., 2020) meadows of extra-Andean Patagonia. In contrast, AAB in the DS was limited, consistent with drier peripheral zone of these environments (Buono et al., 2010; Vargas, 2017; Utrilla et al., 2020). These results indicate that edaphic hydric heterogeneity within meadows generates marked productivity gradients between meadow sectors.

Daily growth and regrowth rates, live and dead material, and live aerial biomass

The higher values of DGR and DRR in the

WS of meadows would be determined by the combination of effects of high SM associated with a shallow water table, characteristic of riparian meadows (Castelli et al., 2000), and the seasonal hydric dynamics typical of Patagonian meadows (Horne and Polla, 2021). In addition, more favorable thermal conditions in spring further enhance net forage accumulation (Parson, 1988). In contrast, reduced SM in summer, resulting from a deeper water table due to decreased stream flow (Horne and Polla, 2021), is associated with lower daily productivity values observed in this meadow sector. Similarly, the peripheral DS areas, characterized by lower SM and greater phreatic depth (Castelli et al., 2000), would determine that the magnitude of change was slight, consistent with the predominant

vegetation type in this meadow sector (Utrilla et al., 2020) and the reduced summer growth typical of water-limited steppe ecosystems (Ferrante et al., 2014). In this context, these findings should be taken into account to ensure proper grazing management. Furthermore, the higher proportion live fraction collected in spring may be explained by an active rangeland growth at the expense of the accumulated dead material, particularly in central meadow, promoted by more favorable hydric edaphic conditions (Utrilla et al., 2006). Thus, it is evident that the predominance of dead material harvested at the end of summer in both sectors reflects the hydric edaphic restrictions characteristic of the period in Patagonian meadows (Horne and Polla, 2021).

Regarding the dissimilar evolution of the accumulated and live aerial biomass and DGR in relation to TT and SM between the WS and DS of the meadows, could be explained by differences in leaf life cycle dynamics (Lemaire and Chapman, 1996) and the progression of plant maturity, which is influenced by low SM conditions typical of summer, as reported by Utrilla et al. (2023) for introduced grasses in the Dry Magellanic Steppe. Overall, these findings showed that the interaction between SM availability and phenological cycles regulates both the magnitude and timing of forage productivity.

Relationship between daily growth and regrowth rates and live material with soil moisture and thermal time by multiple analysis

Multiple regression analysis revealed that SM positively influenced both DGR and the proportion of live material in both sectors, although excessive or limiting parameter values produced negative, non-linear effects. This response is consistent with the seasonal hydric dynamics of humid Patagonian meadows (Horne and Polla, 2021) and with greater phreatic depths observed in the DS. It also aligns with the conditions described for the peripheral zones of riparian meadows (Castelli et al., 2000) under severe water deficit (Horne, 2015). In contrast, in the WS, TT was poorly associated with the DGR of the rangeland due to the limiting SM in the summer caused by a deeper water table as reported by Horne and Polla (2021) for the Patagonian meadows.

These results underscore the dominant role of SM in regulating vegetation productive parameters in both meadow sectors, with TT exerting a secondary influence on rangeland productivity, which contrasts with the growth dynamics typically reported for temperate ecosystems species (Parson, 1988).

CONCLUSIONS AND IMPLICATIONS

Integrated management of meadows requires an understanding of the long-term interactions among water, soil, vegetation, and climatic components. In this context, the present study demonstrates that edaphic hydric heterogeneity within meadows can generate different vegetation compositions and marked productivity gradients between sectors. Collectively, these results support the central hypothesis of this study: that the productivity of Patagonian meadows is determined by the combined influence of hydric-edaphic and climatic factors, with soil moisture emerging as the primary driver of seasonal biomass production across meadow sectors. Accordingly, these findings support the selection of the most appropriate grazing season and the identification of potential sustainable stocking rates.

The results suggest that sustainable grazing management of meadows must consider hydrological regimes, as alterations in groundwater depth or seasonal water availability could significantly reduce productivity. Under scenarios of climate change and altered precipitation, these insights provide a framework for anticipating sector-specific responses and for designing strategies to safeguard the plant composition and productive dynamics of Patagonian meadows.

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Author contributions

Víctor Utrilla, Miguel Andrade, Daniela Ferrante: Collection, analysis, and writing of the manuscript; Pablo Peri: Review and writing of the article; Gervasio Humano, Juan Carlos Kofalt: Collection of the dates. All authors approved the final version of the manuscript.

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