Translational Animal Science, 2023, **7**, 1–14
https://doi.org/10.1093/tas/txad028
Advance access publication 10 March 2023
Forage Based Livestock Systems

Supplement feed efficiency of growing beef cattle grazing native *Campos* grasslands during winter: a collated analysis

Fiorella Cazzuli[†,1], Javier Sánchez[‡], Andrés Hirigoyen[||], Pablo Rovira[$], Virginia Beretta[¶], Alvaro Simeone[¶], Martín Jaurena[†], Martín Durante[†,**], Jean Victor Savian[††], Dennis Poppi[‡‡], Fabio Montossi[||||], Ximena Lagomarsino[$$], Santiago Luzardo[||||], Gustavo Brito[||||], J. Ignacio Velazco[$], Carolina Bremm[¶¶], and Fernando A Lattanzi[****].

[†]Instituto Nacional de Investigación Agropecuaria (INIA), Programa Pasturas y Forrajes, Estación Experimental INIA Tacuarembó, Tacuarembó, Uruguay
[‡]Department of Health Management, Atlantic Veterinary College, University of Prince Edward Island, Charlottetown, PEI, Canada
[||]Instituto Nacional de Investigación Agropecuaria (INIA), Programa Forestal, Estación Experimental INIA Tacuarembó, Tacuarembó, Uruguay
[$]Instituto Nacional de Investigación Agropecuaria (INIA), Programa Carne y Lana, Estación Experimental INIA Treinta y Tres, Treinta y Tres, Uruguay
[¶]Animal Science Department, Universidad de la República, Paysandú, Uruguay
[**]Estación Experimental Agropecuaria Concepción del Uruguay, Concepción del Uruguay, Argentina
[††]Instituto Nacional de Investigación Agropecuaria (INIA), Programa Pasturas y Forrajes, Estación Experimental INIA Treinta y Tres, Treinta y Tres, Uruguay
[‡‡]School of Agriculture and Food Sciences, The University of Queensland, Gatton, Australia
[||||]Instituto Nacional de Investigación Agropecuaria (INIA), Programa Carne y Lana, Estación Experimental INIA Tacuarembó, Tacuarembó, Uruguay
[$$]FCA-UDE, Facultad de Ciencias Agrarias, Universidad de la Empresa, Montevideo, Uruguay
[¶¶]Grazing Ecology Research Group, Federal University of Rio Grande do Sul, Porto Alegre, Brazil
[****]Instituto Nacional de Investigación Agropecuaria (INIA), Programa Pasturas y Forrajes, Estación Experimental INIA La Estanzuela, Colonia, Uruguay
[1]Corresponding author: fcazzuli@inia.org.uy

ABSTRACT

Supplementing growing cattle grazing native subtropical *Campos* grasslands during winter improves the low, even negative, average daily weight gain (ADG) typical of extensive animal production systems in Uruguay. Nonetheless, to render the practice profitable, it is crucial to control supplement feed efficiency (SFE), that is, the difference in ADG between supplemented and control animals (ADGchng) per unit of supplement dry matter (DM) intake. Little has been studied specifically on how SFE varies in these systems. The objective of this study was to quantify the magnitude and variation in SFE of growing beef cattle grazing stockpiled native *Campos* grasslands during winter and assess putative associations with herbage, animals, supplements, and climatic variables. We compiled data from supplementation trials carried out in Uruguay between 1993 and 2018, each evaluating between one and six supplementation treatments. The average ADG of unsupplemented and supplemented animals were 0.13 ± 0.174 and 0.49 ± 0.220 kg/animal/day, respectively. In both cases, ADG decreased linearly as the proportion of green herbage in the grazed grassland was lower, but the ADG of unsupplemented animals was further reduced when winter frosts were numerous. Estimated SFE were moderately high, with an average of 0.21 ± 0.076 ADGchng/kg DM, resulting from average ADGchng of 0.38 ± 0.180 kg/animal/day in response to an average supplementation rate of 1.84 ± 0.68 kg supplement DM intake/animal/day (0.86% ± 0.27% body weight). No association was found between SFE and supplementation rate or type (protein vs. energy-based; $P > 0.05$), but forage allowance negatively affected it, and herbage mass positively affected it, yet in a smaller magnitude, suggesting that a balance is needed between the two to maximize SFE. Weather conditions during trials affected SFE ($P < 0.05$), with greater SFE in winters with lower temperatures and more frosts. Daytime grazing time was consistently lower in supplemented animals compared to their unsupplemented counterparts, whereas ruminating time during the day was similar, increasing as the proportion of green herbage decreased. Herbage intake estimated from energy balance suggested the existence of some substitution effect. This agrees with the moderately high SFE and with the total digestible nutrients-to-protein ratio of these subtropical humid grasslands being higher than in semi-arid rangelands and dry-season tropical pastures but lower than in sown pastures.

LAY SUMMARY

Beef cattle are reared on native grasslands worldwide. In the native *Campos*—the subtropical humid grasslands part of the Pampa biome in southern South America—animals often lose weight during winter due to insufficient quantity or quality of available forage. Therefore, supplementation with concentrates is advocated. Notwithstanding its productive impact, this practice is unprofitable when supplement feed efficiency (SFE) is low. We collated data from 25 trials carried out from 1993 to 2018 in Uruguay to better understand how and why SFE varies in growing

Received October 3, 2022 Accepted March 9, 2023.

cattle grazing stockpiled *Campos*. On average, animals gained 0.21 kg of body weight per kg of consumed supplement, but variation was large. Winters with more frosts resulted in greater responses, rendering the practice more efficient. The amount of forage per animal negatively affected efficiency, while overall forage availability positively affected it (yet in a smaller magnitude), suggesting that in order to be more efficient, a balance between them is needed. Protein concentration of supplements was associated with SFE. Nonetheless, the proportion of green biomass in offered herbage did correlate with weight gain and grazing behavior of the cattle. The total digestible nutrients-to-protein ratio of *Campos* winter herbage—halfway between that of rangelands and sown pastures—would explain the observed relatively high SFE.

Key words: concentrate supplementation, growing cattle, native grasslands, nutritive value, protein, supplement feed efficiency

INTRODUCTION

Native grasslands are the foundation of extensive animal production agro-ecosystems worldwide (Jaurena et al., 2021). However, the nutrients they provide are not always sufficient to meet the desired animal performance goals. This is often the case for growing ruminants during winter or the dry season, when available herbage is either insufficient or of limited nutritive value (Hall et al., 1998; Williams et al., 2018; Orcasberro et al., 2021).

Complementing the diet of grazing animals with energy, protein, and mineral supplementation, can help overcome such constraints and enhance production, but it also increases economic and financial risks whenever profits are sensitive to changes in costs, as is often the case for extensive systems (DelCurto et al., 2000; De Figueiredo et al., 2007; Bowen and Chudleigh, 2020). Therefore, it is crucial to anticipate the economic efficiency of supplementation, which is in part determined by the supplement feed efficiency (SFE). Usually, SFE is expressed as the difference in average daily liveweight gain (ADG) between supplemented and control (unsupplemented) animals (ADGchng) per unit of supplement intake, the latter typically expressed on a dry matter (DM) basis.

For animals grazing sown pastures, variation in SFE is often attributed to variation of substitution effects, that is, the decrease in intake of grazed herbage observed in supplemented animals (Grainger and Mathews, 1989; Moore et al., 1999; Clariget et al., 2021a). Therefore, SFE often correlates with herbage offer, allowance, and/or nutritive value because these modulate substitution effects. Conversely, for animals grazing native grasslands, analyses of what drives SFE are scarcer. In a comprehensive review, Moore et al. (1999) observed that supplementation consistently increased herbage intake of animals grazing native *prairies* of North America ($N = 55$), presumably improving SFE, whereas it decreased herbage intake in animals grazing sown pastures ($N = 132$). This differential response between these two forage bases was associated with the ratio of total digestible nutrients-to-protein (TDN:CP) of 7 in the grazed herbage Moore et al. (1999), and therefore to protein deficiency (DelCurto et al., 2000). The conclusion that the primary limiting nutrient is crude protein (CP) and substitution effects are small was also reached for cattle grazing Australian rangelands or tropical pastures during the dry season (Poppi et al., 2018).

The *Campos* are subtropical humid highly diverse native grasslands that foster extensive sheep and cattle production across the Pampa biome in Uruguay, southern Brazil, and center-eastern Argentina. These systems are currently facing the challenge of both increasing profitability and at the same time maintaining native grasslands as their main feed source in order to keep low system-wide costs (Jaurena et al., 2021), be resilient against extreme climatic events (Briske, 2017), and preserve the various valuable ecosystem services they provide (Modernel et al., 2016; Tittonell, 2021).

Campos grasslands benefit from relatively mild temperatures and no dry season, but during winter, dominant C4 grasses show rapid decreases in growth rate and loss of nutritive value, frequently resulting in reduction or loss of animal performance (Berretta et al., 2000) and well-being. Therefore, winter supplementation is advocated to ensure both adequate reproductive function of females and defined growth paths and slaughter ages of males (Simeone et al., 2010; Luzardo et al., 2014a, 2014b; Cazzuli et al., 2018). Yet, little is known about the magnitude and causes of variation in SFE in these systems. This increases uncertainty in assessing productive and economic impact of supplementation, impairing farmers' decision-making.

One source of variation in SFE might be the type of supplement. A wide range of subproducts are locally available for animal feed, such as rice (*Oryza sativa*) and wheat (*Triticum aestivum*) bran, maize (*Zea mays*) and sorghum (*Sorghum bicolor*) grain, dry distillers grains with solubles (DDGS), as well as high-protein concentrates (Montossi et al., 2014). Additionally, SFE might depend on the quantity and quality of herbage on offer, which depends on management of autumn stockpiling and winter stocking rate (Fedrigo et al., 2022; DoCarmo et al., 2018). Furthermore, in contrast to rangelands in other climates, *Campos* grasslands retain variable amounts of green biomass over winter, depending on the proportion of C3 species present in the sward and the number and intensity of frosts, which may affect the protein concentration of available herbage (Nuñez et al., 2022).

The aims of this study were 1) to quantify SFE and its variability in growing cattle grazing native *Campos* grasslands during winter, and 2) to assess whether SFE is associated with pasture, animal, supplement, or climatic variables to infer putative causes of its variation. To this end, we collated and analyzed a largely unpublished dataset of 25 trials of late autumn–winter concentrate supplementation of growing beef cattle grazing *Campos* grasslands carried out in Uruguay over the last 30 yr.

MATERIALS AND METHODS

Database Compilation

Data were gathered from 25 supplementation trials carried out between 1993 and 2018 in which growing beef cattle grazing native *Campos* grasslands in Uruguay were supplemented during late autumn and winter. These trials represent the totality of experiments carried out in Uruguay with those characteristics and within the mentioned period (1993–2018), and only cases using lick blocks as supplements were excluded, as well as validation experiences (no experimental control). All trials included an unsupplemented control treatment. Experimental units consisted of a group of animals grazing an independent paddock. On average, trials had 7 animals per paddock, but the variation was large, with a minimum of 4 and a maximum of 30. Most trials had several supplemented treatments, depending on their specific objective (comparison of supplement type, supplementation frequency, method, rate, etc.) and were carried out with 7–9 mo calves (male or female), but six trials used 18 mo steers. Cattle breeds were Hereford, Aberdeen Angus, their cross, or Braford.

Sixteen trials had two replicates spatially arranged in a completely randomized design, whereas nine trials had only one paddock per treatment (Table 1). The collated database comprised a total of 108 comparisons between an unsupplemented (control) and a supplemented treatment. Only two of these datasets were published as refereed articles. For the remaining cases, the responsible researchers were contacted to access the experimental protocol and original dataset. Annex 1 briefly summarizes each trial.

In all trials, paddocks were continuously stocked at a fixed stocking rate for the duration of the trial (stocking period). The trials' stocking period extended from June/July to September, i.e., the local winter, lasting 42–141 d (except for one that started late in May, and two that ended in mid-October). Herbage intake was always voluntary, by direct grazing of herbage stockpiled prior to the stocking period. Stockpiled herbage accumulated over variable periods of time, following either a mechanical cut or short-term heavy grazing in late summer/early autumn. Therefore, the amount and proportion of green mass present at the start of the stocking period varied greatly between trials. Concentrate supplements were fed either manually in their troughs (daily or every 2–4 d) or using selffeeders, at a rate of between 0.5% and 1.7% of body weight (BW).

Diverse concentrate supplements were used in each trial, including rice bran, DDGS, soy (*Glycine max*) and sunflower (*Helianthus annuus*) expellers, maize and high-moisture sorghum grain silage with or without added nitrogen. Supplements had similar metabolic energy concentration but varied widely in CP concentration. Consequently, the energy-to-protein ratio of supplements varied greatly between trials. Supplements were categorized according to their CP concentration: above 20% (Harris, 1980) supplements were considered protein based. In all trials, supplemented animals were gradually acclimated to supplements over a 7- to 10-d period prior to the stocking period.

Animal behavior was registered in 14 trials, with observers using binoculars throughout daylight hours (0700–1830 hours, approximately), registering the activity of all animals of each plot every 15 min and classifying them into grazing and ruminating, among other activities.

Response and Auxiliary Variables

Animals were weighed individually at the beginning and at the end of the stocking period. In most cases, shrunk weight was determined, using 12–16 h of fasting (Meyer et al., 1960; Watson et al., 2013), but in some cases only unshrunk weight was available and a 6% adjustment was applied to make all data more comparable following (Clariget et al., 2021b). Then ADG was calculated as final minus initial average BW of all animals in each paddock (experimental unit), divided by the stocking period (days). The response to supplementation was estimated as the difference in ADG between supplemented and unsupplemented animals (ADGchng).

Supplement intake of the group of animals in each experimental unit was measured on a DM basis as the total amount of supplement DM offered minus supplement DM refusal in the trough, which was collected and weighed. All trials had negligible amounts of supplement refusal.

Average sward height and herbage mass were measured at the beginning of each trial. In some cases, these assessments were repeated during or at the end of the trial. For nine trials, individual sward height records were available, and the frequency of heights were estimated for five strata (0–4, 4–8, 8–12, 12–16, >16 cm). Forage allowance was estimated as kg of DM per kg of BW on total (FA) and green mass basis (gFA; Table 2).

Chemical composition was determined in herbage samples taken at different moments throughout the stocking period, and in a sample of the concentrate supplement at the beginning of the stocking period. In the few cases where supplement chemical composition data were unavailable, average values from local tables were assumed (Mieres et al., 2004). All samples were oven-dried at 60 °C for 72 h. Neutral detergent fiber (NDF) and acid detergent fiber (ADF) concentrations were determined according to Van Soest et al. (1991), ash included, whereas DM content and CP concentrations were determined according to AOAC (1990). Dry matter digestibility (DMD, %) was estimated following Osítis et al. (2003) as $88.9 - 0.779 \times \text{ADF\%}$, and the concentration of metabolizable energy (ME, MJ/kg DM) was estimated as $(4.4 \times 0.82 \times \text{DMD\%}/\ 100) \times 4.184$ (Agricultural Research Council, 1980). In addition, the ME/CP ratio of supplements was calculated (units: 100 MJ/kgCP).

Meteorological data—daily rainfall, minimum, maximum, and average daily temperature, and the number of ground frosts—were obtained from the meteorological station nearest to each trial.

Statistical Analyses

The SFE data were collated across the 25 trials, rendering 65 independent comparisons. Simple average, and the 20%, 50% (median), and 80% percentile were estimated. Then, a logistic function was fitted to the distribution of SFE frequency (TBLCurve v2.0, Sigma).

To determine the relationship between variables, Spearman correlations between SFE and auxiliary variables were explored, and then simple and multiple regressions models fitted to estimate quantitative responses to putative determinants of SFE and the ADG of control and supplemented animals.

A mixed model was developed with SFE as the response variable, using trial as a random effect and all variables with Spearman coefficients between them and SFE which presented values above + 0.10 or below −0.10, as fixed effects (see below Spearman correlations). The best model was selected using the AIC criterion.

Statistical analyses were performed with the base package of R software (R Core Team, version 4.0.3, 2017) in combination with Infostat (Di Rienzo et al., 2015). The threshold for statistical significance was $P < 0.05$.

RESULTS

Sward, Animal and Supplement Type and Intake

There was little or no difference between control and supplemented treatments in initial animal BW, nor in the amount and nutritive value of herbage offered, within each trial (Figure 1), yet there was ample variation between trials. Thus, sward height ranged from 2.5 to 19.0 cm and herbage mass, from 460 to 6,160 kg DM/ha, whereas herbage CP

Table 1. Summary of collated trials on supplementation of cattle grazing native rangelands carried out in Uruguay between 1993 and 2018

Trial ID	Location, year	Supplementation treatments[a]	Breed and category	Duration (d)	Replicates	Animals/trial	*n* SFE[b]	Source
1[a]	La Magnolia, 2013	TMR with fiber	Braford male calves	97	2	40	6	Cazzuli et al. (2018)
2[a]	Glencoe, 2013	TMR with fiber	Hereford male calves	120	2	40	6	Cazzuli et al. (2018)
3[a]	La Magnolia, 2014	RB (ground and pelleted)	Braford male calves	68	2	40	8	Montossi et al. (2017)
4[a]	Glencoe, 2014	RB (ground and pelleted)	Hereford male calves	108	2	50	8	Montossi et al. (2017)
5[a]	Glencoe, 2015	Various (maize, expellers and RB)	Hereford male calves	141	2	50	8	Montossi et al. (2017)
6[a]	Glencoe, 2009	RB	Hereford male and female calves	113	2	48	6	Luzardo et al. (2014a)
7[a]	Glencoe, 2010	RB	Hereford male calves	111	2	48	6	Luzardo et al. (2014a)
8[a]	Glencoe, 2011	RB	Hereford male calves	119	2	48	6	Luzardo et al. (2014a)
9	Palo a Pique, 2009	HMSGS	British crossbred male calves	99	1	56	3	Rovira and Velazco (2014)
11	Palo a Pique, 2009	HMSGS	British crossbred male calves	84	1	54	4	Rovira et al. (2014)
12[a]	Palo a Pique, 2013	HMSGS	British crossbred steers	84	2	32	6	Rovira (2014a)
13	Salsipuedes, 2009	TMR	British crossbred female calves	84	1	90	2	Blasina et al. (2010)
14[a]	Ptas del Chuy, 2011	TMR	British crossbred male calves	81	2	48	4	Esteves et al. (2013)
15[a]	Palo a Pique, 2014	HMSGS	British crossbred steers	55	2	32	6	Rovira (2014a)
16[a]	Glencoe, 2007	RB	British crossbred male calves	98	2	24	2	Luzardo et al. (2014b)
17	Palo a Pique, 2012	TMR with fiber	British crossbred male calves	77	1	12	1	Rovira (2014b)
20	Palo a Pique, 2000	RB and TMR	British crossbred female calves	87	1	30	2	Campos and Terra (2002)
21	Glencoe, 2005	Various (maize, expeller and RB)	British crossbred male calves	96	1	40	4	Pittaluga et al. (2007)
22	Glencoe, 2011	RB	Hereford steers	97	1	18	2	Brito et al. (2011)
24[a]	Glencoe, 2004	Various (RB and expeller)	British crossbred steers	42	2	70	4	Arrieta et al. (2008)
25[a]	Glencoe, 2004	Various (RB and expeller)	British crossbred steers	78	2	70	8	Arrieta et al. (2008)
26	Palo a Pique, 1992	RB	Hereford female calves	89	1	80	3	Quintans et al. (1993)
27	Palo a Pique, 2008	TMR	British crossbred male calves	77	1	56	3	Rovira and Velazco (2012)
28[a]	Cañada del Pueblo, 2008	DDGS	Hereford female calves	89	2	40	2	Berretta et al. (2019)
29[a]	Tomás Gomensoro, 2008	DDGS	British crossbred male calves	84	2	40	2	Berretta et al. (2019)
Total						1156	108	

All trials included one unsupplemented control treatment.
TMR, total mixed ration; RB, rice bran; HMSGS, high-moisture sorghum grain silage (combined with protein supplements);
[a]Trial with 2 replicates;
[b]Number of calculated SFE values.

Table 2. Secondary calculations and estimations divided into categories according to what they describe (Type) using parameters from original datasets, protocols and publications from experiments on supplementation on native rangelands in Uruguay (1993–2018).

Type	Variable	Units	Observations
Conditions	Stocking period	Days	–
Pasture	0–4 cm	Frequency	Frequency calculation
Pasture	4–8 cm	Frequency	Frequency calculation
Pasture	8–12 cm	Frequency	Frequency calculation
Pasture	12–16 cm	Frequency	Frequency calculation
Pasture	16 + cm	Frequency	Frequency calculation
Pasture	ME	Mcal/kg	4.4 × 0.82 × DMD/100 (ARC, 1980)
Pasture	DMD	%	88.9 – (0.779 × ADF%) (Osítis et al., 2003)
Animal	ADG	kg BW/animal/d	(BW f—BW i)/(date f—date i)
Animal	ProdHa	kg BW/ha	(BW f—BW i)/area
Animal	ProdHa/d	kg BW/ha/d	(BW f—BW i)/area/day
Animal	Stocking rate BW	kg/ha	BW/area
Animal	Stocking rateLU	LU/ha	BW/380/area
Animal/supplement	SFE		kg DM/ADGchng
Animal/supplement	SuppRate		kg sDMI/kg BW
Animal/pasture	FA	kg/kg	kg DM/kg BW
Animal/pasture	gFA	kg/kg	kg green DM/kg BW
Animal/pasture		FAg/FA	–

Conditions, experimental conditions; Animal, animal related variables; Pasture, pasture related variables; Supplement, supplement related variables; I, initial; f, final; ProdHa, BW production/hectare; LU, livestock unit (380 kg BW); SuppRate, supplementation rate (%BW); sF, supplemented´s HDMI; cF, control´s HDMI..

concentration varied between 4.3% and 16.6%, and DMD, between 43% and 70% (Table 3). The proportion of green herbage in the standing biomass also varied widely, between 15% and 87% (Figure 1), and was negatively associated with total herbage mass and sward height ($r = -0.46$; $P < 0.01$) and positively with CP concentration ($r = 0.64$; $P < 0.01$; data not shown in tables).

Supplementation rate (0.86 ± 0.26%; min 0.3, max 2.0 % of BW) and supplement DM intake (1.84 ± 0.68 kg/animal/d; min 0.4, max 3.8 kg/animal/d) presented substantial variation among trials (Table 3). Supplements varied little in ME concentration (min. 10.1, max. 13.4 MJ/kg DM) but widely in CP concentration (min. 7.1, max. 43.9%), and therefore their ME/CP ratio was variable (Figure 1, Table 3). Considering a 20% threshold CP concentration (Harris, 1980), supplements categorized as "nonprotein based" (i.e., energy based) had mean ME and CP concentrations of 11.7 ± 0.807 MJ/kg DM and 14.1% ± 2.043%, respectively (data not shown), whereas protein supplements had on average almost the same ME concentration (11.5 ± 0.682 MJ/kg DM) but twice as great CP concentration (28.7 ± 8.170%).

ADG of Supplemented and Control Animals

The average ADG of unsupplemented animals (cADG) was positive yet low at 0.13 ± 0.174 kg/animal/d, ranging from −0.19 to 0.58 kg/animal/d. The average ADG of supplemented animals (sADG) was considerably greater at 0.49 ± 0.220 kg/animal/d, ranging from 0.05 to a maximum value of 1.24 kg/animal/d (Table 3, Figure 2). This resulted in ample variation in ADGchng, between −0.10 and 1.02 kg/animal/d, with an average of 0.38 ± 0.167 kg/animal/d.

SFE and its Relationship with ADGchng and Supplement Intake

The average SFE was 0.21 ± 0.076 ADGchng/kg DM, ranging between 0.07 and 0.40 ADGchng/kg DM. Expressed on a CP basis, SFE varied between 0.36 and 2.68 ADGchng/kg CP, and expressed as ME it ranged between 0.01 and 0.03 ADGchng/MJ (Table 3).

The distribution of SFE frequencies was asymmetrical, with few values below 0.10 ADGchng/kg DM, an average of 0.21 and a median of 0.19 ADGchng/kg DM. Three out of five values ranged between 0.15 and 0.29 ADGchng/kg DM (i.e., the 20% and 80% percentiles, respectively, Figure 2). When analyzing the association between SFE and its two components, variation in SFE appeared to be more closely associated with changes in ADGchng (and sADG and cADG) than in supplement intake or supplementation rate (Tables 4 and 5). Discriminating SFE between protein and "nonprotein based" (energy based) supplements yielded no distinct pattern in these relationships (Figure 3).

Relationship Between SFE and Auxiliary Variables

The mixed model's fixed effects explained 78% of its variability and it resulted in the following equation: SFE = 0.0435 + 0.00017 × HerbageMass—0.0684 × ForageAllowance ($P < 0.05$).

Neither of the variables describing the nutritive value of herbage were associated with SFE (Table 6). Opposite to what was expected, sADG was negatively associated with sward height, herbage mass and allowance, and cADG was negatively associated with initial herbage mass. Interestingly, the proportion of the paddock with sward heights below 4 cm was positively associated with both sADG and cADG. An association emerged between the proportion of green herbage

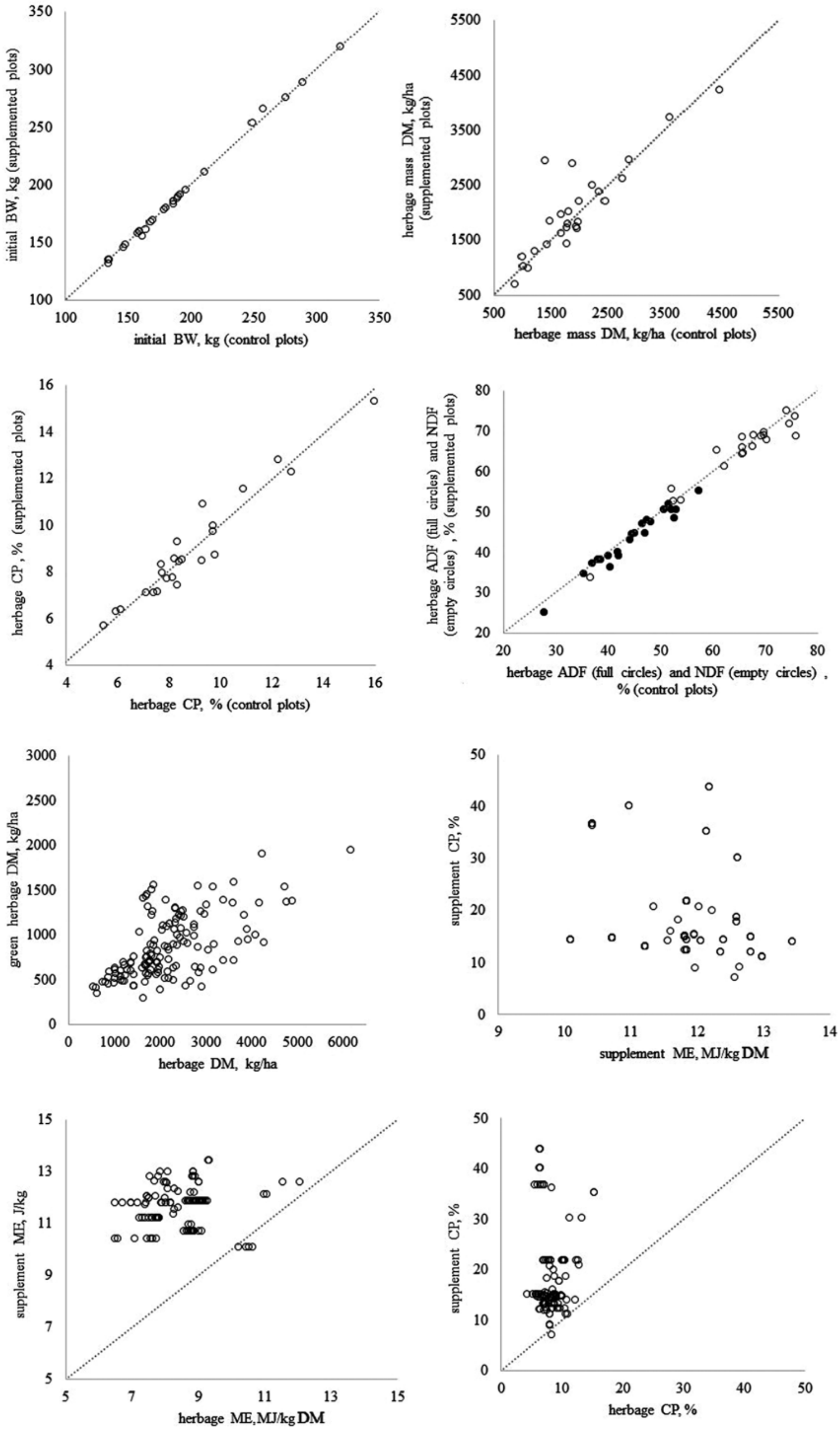

Figure 1. Main descriptive characteristics from sward, animal, and supplements of a database of supplementation experiments for young beef cattle on native grasslands in Uruguay (1993–2018). BW, body weight; DM, dry matter; CP, crude protein; ADF, acid detergent fiber; NDF, neutral detergent fiber; ME, metabolizable energy.

and sADG, cADg, and ADGchng, which in turn was dependent on climate (Figure 4).

Weather variables were associated with some of the relevant parameters explaining SFE (Table 6). Control ADG was negatively associated with the number of frosts that occurred 30 d before the beginning of the trials. On the other hand, the number of frosts that occurred 60 and 90 d prior to the trials were all positively associated with sADG. Additionally,

Table 3. Descriptive statistics (mean), standard deviation (SD), coefficient of variation (CV), minimum (min), and maximum (max) related to animals and pastures of a dataset of supplementation experiments for young beef cattle on native grasslands in Uruguay (1993–2018)

Variable	Mean	SD	CV	Min	Max
cADG, kg/animal/day	0.13	0.17	130	−0.19	0.58
sADG, kg/animal/day	0.49	0.22	45	0.05	1.24
ADGchng, kg/animal/day	0.38	0.18	48	−0.10	1.02
Shrunk average BW, kg	201	51	25	123	371
Stocking rate, kgBW/ha	429	119	28	217	755
Forage allowance (FA), kgDM/kgBW	5.2	3.0	57	1.1	19.1
Green forage allowance, kg green DM/kgBW	2.1	1.2	57	0.7	6.5
Green FA/FA	0.4	0.2	37	0.2	0.9
Sward height, cm	7.4	3.9	52	2.5	19.0
Herbage mass, kgDM/ha	2079	969	47	461	6163
Herbage DM content, %	0.5	0.1	21	0.2	0.7
Green Herbage mass, %	0.4	0.2	37	0.2	0.9
Herbage CP, %	8.4	2.1	25	4.3	16.6
Herbage ADF, %	43.7	7.3	17	23.7	59.1
Herbage NDF, %	65.3	8.3	13	30.7	81.1
Herbage energy, MJ ME/kg DM	8.5	1.1	12.9	6.5	12.1
Herbage DM digestibility, %	55.0	5.8	10	42.9	70.5
Forage ME/CP, 100MJ/kgCP	1.0	0.2	19	0.6	1.6
Supplementation rate, %BW	0.9	0.3	31	0.3	2.0
Supplement DM intake, kg/an/day	1.8	0.7	37	0.4	3.9
SFE, ADGchng/kg DM	0.21	0.08	41	0.07	0.40
SFE, ADGchng/kg CP	1.23	0.58	47	0.36	2.68
SFE, ADGchng/MJ	0.02	0.01	39	0.01	0.03
Supplement ME content, MJ/kg	11.7	0.7	6	10.1	13.4
Supplement CP content, %	18.4	8.3	45	7.1	43.9
Supplement ME/CP, 100MJ/kgCP	0.7	0.3	35	0.3	1.8
Stocking period, days	92.5	24.7	27	42.0	141.0

Green, green DM proportion.

Table 4. Multiple regressions with SFE as the response variable and supplement intake and ADGchng of a database of supplementation experiments for young beef cattle on native grasslands in Uruguay (1993–2018)

Regressor1	Estimate	*P*-value	Regressor2	Estimate	*P*-value	Regressor3	Estimate	*P*-value	R2	AIC
Supp Intake	−0.07	<0.0001	ADGchng	0.47	<0.0001	–	–	–	0.73	−383
Supp Intake	−0.16	<0.0001	(Supp Intake)^2	0.01	<0.0001	ADGchng	0.55	<0.0001	0.85	−451
Supp Intake	−0.06	<0.0001	ADGchng	0.61	<0.0001	(ADGchng)^2	−0.17	0.0132	0.74	−388
Supp Intake	−0.01	<0.0001	–	–	–	–	–	–	0.06	−252
ADGchng	0.13	0.0002	–	–	–	–	–	–	0.12	−255
Supp Intake	–	0.2144	(Supp Intake)^2	–	0.5741	–	–	–	0.06	−250
ADGchng	−0.72	<0.0001	(ADGchng)^2	−0.59	<0.0001	–	–	–	0.37	−290

Supp Intake = kg DM per animal per d; ADGchg = kg DM/kg BW change per animal per day.

ADGchng was positively associated with frosts occurring both 60 and 30 d before the trials began.

During the stocking period, in winter, both cADG and sADG were positively associated with minimum average temperatures and negatively associated with rainfall, yet only cADG was negatively affected by the number of winter frosts. Consequently, the number of frosts during the stocking period positively affected ADGchng.

Animal Behavior

In all trials, grazing time during the hours of daylight was consistently lower for supplemented animals than their control counterparts. Unsupplemented animals grazed for 8–9 h, while supplemented animals grazed 8 h or less and as little as 2–4 h in some cases (Figure 5). The magnitude of the difference was variable and not related to the nutritive value of offered herbage nor the climatic conditions (although

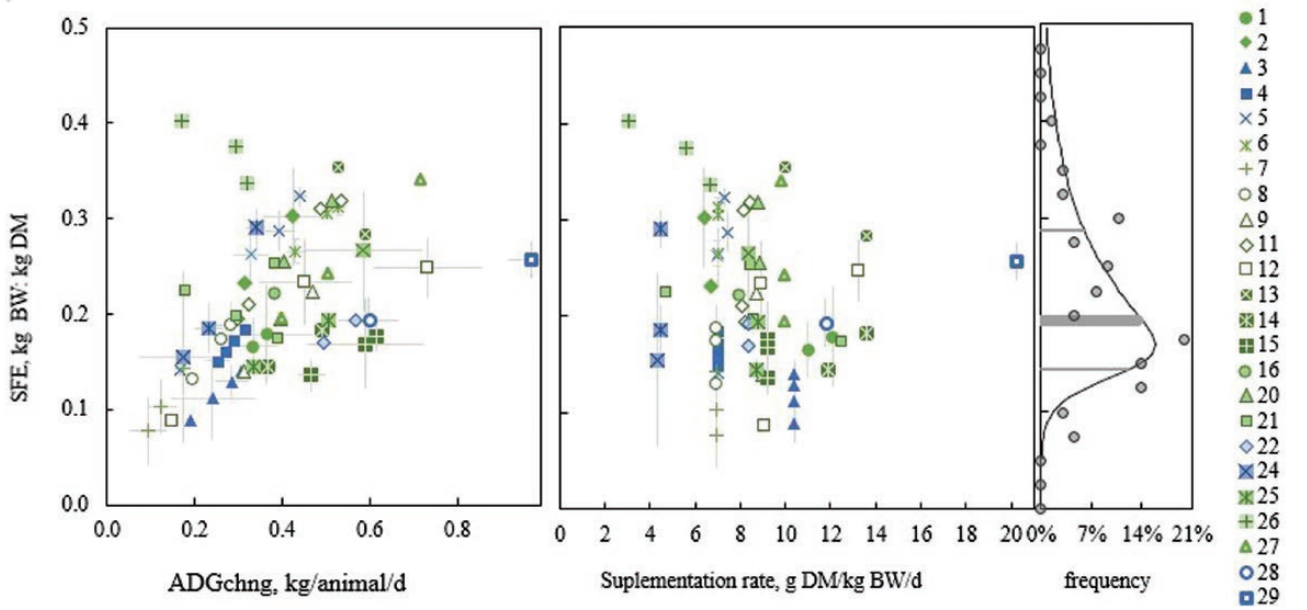

Figure 2. Supplement feed efficiency (SFE) by average daily gain change (ADGchng) and supplementation rate, and SFE values frequencies of a database of supplementation experiments for young beef cattle on native grasslands in Uruguay (1993–2018). BW, body weight; DM, dry matter. References on the right hand of the figure correspond to each trial's ID, as in Table 1.

Table 5. Spearman´s correlation coefficients between supplement feed efficiency and crude protein and metabolizable energy contents in forage and supplements and their intake both separately and of the whole diet of a database of supplementation experiments for young beef cattle on native grasslands in Uruguay (1993–2018)

SFE	*r*	*P*-value	SFE (ME)	*r*	*P*-value	SFE (CP)	*r*	*P*-value
SFE MJ	0,91	0,000						
SFE kgCP	0,57	0,000						
ME f	−0,12	0,214	ME f	−0.19	0.054	ME f	−0.24	0,012
ME s	−0,11	0,300	ME s	−0.19	0.058	ME s	0.07	0,517
ME s intake	−0,18	0,065	ME s intake	−0.22	0.020	ME s intake	0.07	0,472
CP f	−0,18	0,067	CP f	−0.28	0.004	CP f	−0.05	0,646
CP s	0,26	0,006	CP s	0.26	0.006	CP s	−0.53	0,000
CP s intake	0,04	0,650	CP s intake	0.06	0.571	CP s intake	−0.49	0,000
s DM intake	−0,17	0,072	s DM intake	−0.21	0.034	s DM intake	0.06	0,558
cADG	−0,34	0,006	cADG	−0.31	0.011	cADG	−0.39	0,001
sADG	0,21	0,027	sADG	0.17	0.078	sADG	0.17	0,079
ADGchng	0,58	0,000	ADGchng	0.51	0.000	ADGchng	0.45	0,000
Supp rate (%)	−0,17	0,077	Supp rate (%)	−0.21	0.028	Supp rate (%)	−0.08	0,403

f, forage; s, supplement; SuppRat,: supplementation rate (%BW).

maximal grazing time in control animals appeared to occur at intermediate values of the proportion of green biomass). Conversely, no difference in rumination time during the hours of daylight was observed between supplemented and unsupplemented animals, and both groups increased their rumination time from less than 0.5 h when the proportion of green herbage in the standing biomass was high, to more than 1.5 h when it decreased to less than 0.3 (Figure 5).

DISCUSSION

Overall positive responses to supplementation were observed. The average SFE of the database was 0.21 ± 0.076 ADGchng/kg DM, but SFE was quite variable, ranging from 0.05 to 0.40 ADGchng/kg DM. Variation between- and within-trials was more closely associated with variation in ADGchng than in supplement intake or supplementation rate (despite these being naturally associated with SFE because they are part of its calculation). Forage allowance negatively affected SFE, while herbage mass affected it in a positive yet smaller manner. On the other hand, when analyzing the Spearman correlations, it can be observed that neither sward height nor chemical composition of the herbage mass were directly associated with variation in SFE. Unlike reports from semi-arid rangelands and tropical pastures with a dry season (Moore et al., 1999; DelCurto et al., 2000; Poppi et al., 2018), little evidence was found for protein concentration playing a major role in determining SFE for growing cattle grazing native

Campos grasslands during winter. Weather variables, on the other hand, influenced SFE, with greater values observed in colder winters and milder autumns.

The response in animal performance relative to the cost of the additional nutrients provided is a key economic consideration when assessing the efficacy of supplementation in extensive animal production systems (McLennan et al., 2017). Since costs are, in part, associated with the amount of offered supplement, improving SFE is desirable (Wilkinson, 2011). For animals grazing sown pastures, negative association effects (substitution) are often observed, at least for supplementation rates above a certain threshold (Moore et al., 1999). For instance, Bowman and Sanson (1996) suggest that energy supplementation above 0.5% BW increases substitution and hence worsens SFE. In the present study, SFE and supplement DM intake were not associated or were less relevant than ADGchng. This was not due to the variation of supplement energy concentration which was relatively small. Within a wide range of supplementation rates (0.30–2.03%BW), the largest SFE values were observed at intermediate levels and without a distinct pattern, which means that the substitution effect mentioned in the literature (Bowman and Sanson, 1996) would not be operating through any particular supplementation rate threshold in our data. Thus, the substitution mechanism would not seem to be related to the supplementation rate, although considering that unsupplemented animals spent more time grazing than their supplemented counterparts, some amount of substitution may be assumed, nonetheless.

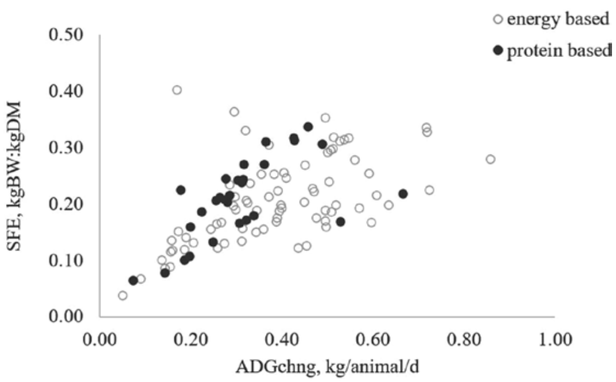

Figure 3. Supplement feed efficiency (SFE) by average daily gain change (ADGchng) by type of supplement of a database of supplementation experiments for young beef cattle on native grasslands in Uruguay (1993–2018). BW, body weight; DM, dry matter; energy-based supplement: <20% crude protein (CP, %) content; protein-based supplement: >20% CP content.

The ADG of unsupplemented animals was negatively affected by weather conditions, specifically by harsher conditions both before (autumn) and during the stocking period (winter). Kuinchtner et al. (2018) point out that limitations to young cattle performance during the cool season in native grasslands may be due to low forage quality that is a consequence of lower temperatures and frosts that inhibit growth of C4 grasses. Furthermore, our results suggest that frosts actually kill the accumulated biomass of C4 species. Indeed, the proportion of green herbage in the standing biomass was never above 50% in harsh winters. Even though not all pasture related variables were associated with cADG, the fact that the green proportion of the forage allowance (greenFA/FA) was positively associated with this may point in the same direction. In fact, with stockpiled native grasslands, Fedrigo et al. (2022) observed that as sward height increased from 5 to 10 cm, NDF and ADF increased while CP concentration decreased, meaning that unsupplemented animals would benefit from shorter, greener swards, compared to a taller pasture but with low green DM content. Additionally, other than the negative effect that low environmental temperature may have on digestibility (Christopherson and Kennedy, 1983), Sarker and Holmes (1974) concluded that frost formation on vegetation was the cause of a decreased daily grazing time, and this could also explain what was observed with our control animals, whose only nutrient source came from the pasture and always dedicated more time to grazing activities

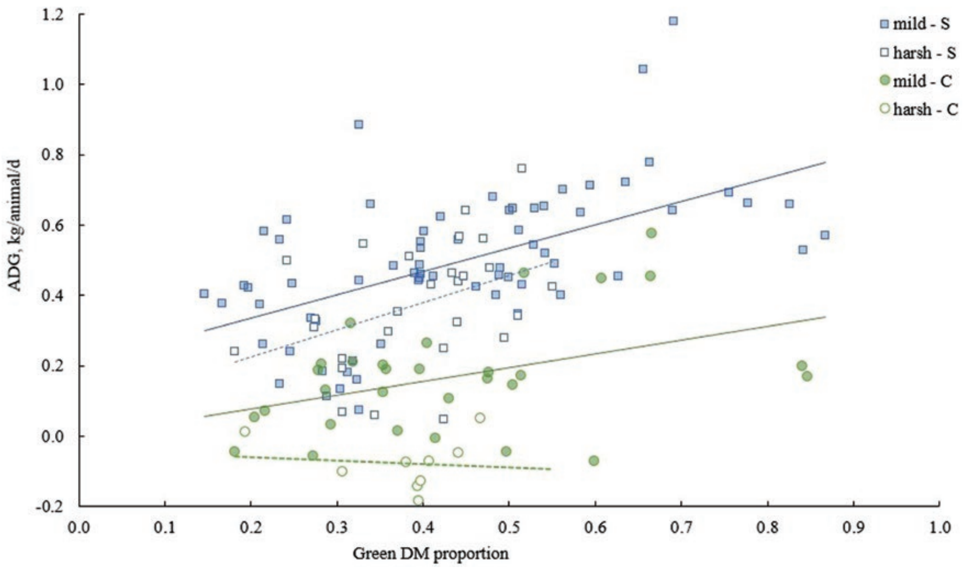

Figure 4. Average daily gain change (ADGchng) by green herbage dry matter (DM) proportion and type of weather of a database of supplementation experiments for young beef cattle on native grasslands in Uruguay (1993–2018). S, supplemented plots; C, control plots; mild weather: less than 20 frosts during trial; harsh weather: more than 20 frosts during trial.

Table 6. Spearman´s correlation coefficients between supplement feed efficiency and other variables of a database of supplementation experiments for young beef cattle on native grasslands in Uruguay (1993–2018)

Variable(1)	Variable(2)	Spearman	*P*-value
SFE	Sward height	0.17	0.082
SFE	Herbage mass	0.11	0.270
SFE	FA	0.14	0.153
SFE	forageCP	−0.18	0.070
SFE	tmin 90p	0.32	0.004
SFE	tmin 60p	0.29	0.011
SFE	F 90 p	−0.28	0.019
cADG	F Trial	−0.65	0.000
cADG	tmin Trial	0.60	0.000
cADG	F 30p	−0.50	0.001
cADG	PP 30p	0.41	0.002
cADG	F 90 p	0.45	0.002
cADG	%Grazing	−0.47	0.008
cADG	4–8 cm	−0.49	0.013
cADG	PP Trial	−0.33	0.014
cADG	PP 90p	0.31	0.023
cADG	greenFA/FA	0.28	0.028
cADG	0–4 cm	0.41	0.040
cADG	iHerbage mass	−0.28	0.046
sADG	Green herbage mass	0.58	0.000
sADG	greenFA/FA	0.57	0.000
sADG	Avg herbage mass	−0.38	0.000
sADG	Supplementation rate	0.36	0.000
sADG	Sward height	−0.36	0.000
sADG	PP Trial	−0.36	0.001
sADG	F 90 p	0.35	0.003
sADG	fHerbage mass	−0.34	0.003
sADG	iHerbage mass	−0.31	0.005
sADG	PP 90p	0.30	0.005
sADG	FA	−0.26	0.007
sADG	PP Trial	0.28	0.010
sADG	NDF	−0.28	0.010
sADG	tmin Trial	0.29	0.011
sADG	P Supl	0.27	0.012
sADG	F 60p	0.29	0.013
sADG	0 to 4 cm	0.36	0.018
ADGchng	F 30p	0.44	0.000
ADGchng	F Trial	0.36	0.002
ADGchng	PP 60p	−0.32	0.003
ADGchng	Bite rate	0.37	0.008
ADGchng	Green Herbage mass	0.25	0.015
ADGchng	F 60p	0.26	0.027
ADGchng	greenFA/FA	0.22	0.029

T min, minimum temperature, °C; PP, precipitations, mm; F, number of frosts; 30–60–90p, 30, 60, 90 d prior to beginning of trial; Green, green DM proportion; SH, sward height; I, initial.

than their supplemented counterparts (Figure 5). Even though ADGchng also correlated with harsh winter conditions, these associations were weaker than what was observed with control animals, but also the number of frosts that occurred 2 mo before the trial positively affected both ADGchng and sADG (Table 6). Wheeler et al. (2002) found that during 1 mo after the first killing frost, beef cows did not respond to supplementation, but later in the winter, supplementation improved the utilization of stockpiled bermudagrass forage. This could mean that even if frosts affected supplemented animals, the impact could have been of a relatively short term, or that it may vary throughout the supplementation period.

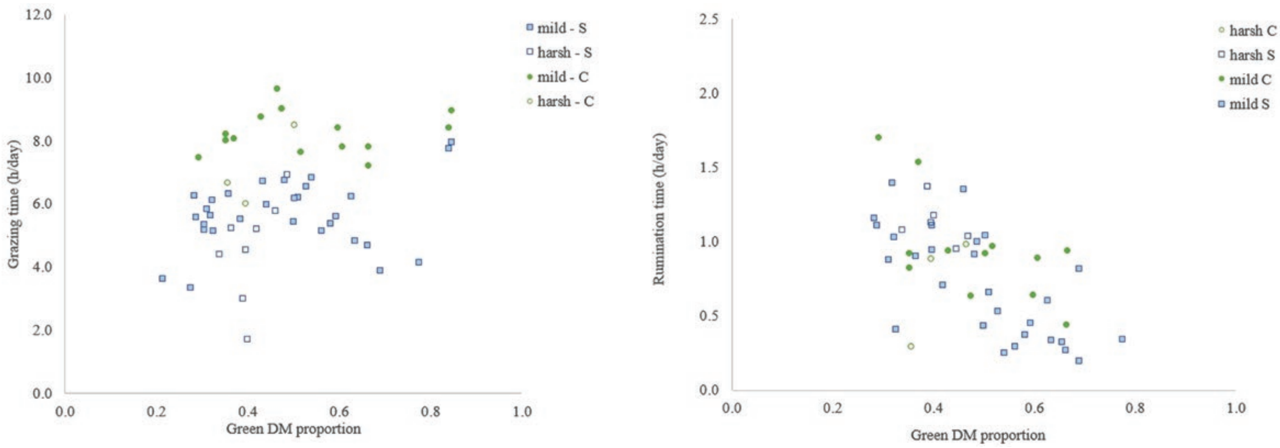

Figure 5. Grazing time (a) and rumination time (b) by dry green herbage dry matter (DM) proportion of a database of supplementation experiments for young beef cattle on native grasslands in Uruguay (1993–2018). S, supplemented plots; C, control plots; mild weather: less than 20 frosts during trial; harsh weather: more than 20 frosts during trial.

Our understanding of the relationship between supplementation and animal performance for rangelands is limited (Bohnert and Stephenson, 2016). In our research, very few associations could be established between SFE and most pasture-related variables, despite their great variability. Forage allowance was one notable exception, negatively affecting SFE, suggesting that more available forage, than what animals need, would go unutilized at some point, thus rendering inefficiencies. However, as herbage mass was the other exception, positively affecting SFA—even though its importance is less than that of FA—it could be thought that some balance is needed between allowance and mass, at least up to a certain point of herbage mass. Given that substitution is related to the herbage DM intake (HDMI) of unsupplemented animals (Stockdale, 2000), this would suggest some substitution existed in our database, which would explain inefficiencies. As McCollum and Horn (1990) stated in a protein supplementation review, an SFE of 0.33 may be considered a benchmark standard in growing cattle, which is higher than what was observed in our database, meaning that inefficiencies occurred, probably spurred by substitution effects. Furthermore, if the greater the HDMI, the greater the substitution rate, the lower the supplement response or ADGchng (Hills et al., 2015) SFE would be expected to decline.

To assess, at least to some extent this possibility, HDMI was estimated *via* energy balance (CSIRO Cattle Explorer, 2012), assuming a DMD of 65% of consumed herbage. We focused on the magnitude of the difference in HDMI between supplemented and unsupplemented animals and its relationship to the herbage total digestible nutrients-to-protein ratio (TDN:CP, Figure 6). There is an apparent concordance in the lack of large substitution or additive effects observed in our database with the fact that the ratio of TDN:CP of the *Campos* grasslands lies in-between that of sown pastures (large substitution effects) and native *prairies* (large additive effects).

Supplement response variability can be explained by substitution effects, due to the similarities or differences between the nutritive value of forage and supplement (Tonello et al., 2011), specifically by both pasture and supplement CP concentration and it may decrease when herbage CP increases (Detmann et al., 2014). In the review of Moore et al. (1999), the lowest response to concentrate supplementation was observed when molasses alone or with very low nitrogen addition were given to animals grazing native grasslands, whereas the greatest responses were observed on improved forages using balanced concentrates. Our data shows that ADGchng was relevant in determining SFE more than supplement DMI; therefore, the interaction between the nutrients offered from pasture and supplement could explain part of the variability. Additionally, the database presented enough variability on native grasslands' nutrient content, as well as on supplement CP, yet not so much on ME concentration. If we consider the CP concentration of sown pastures and their relation to SFE on the one hand (CP = 13% to 15%, SFE 0.11–0.10, (Clariget et al., 2021a) and on the other hand, we consider other native grasslands of the world, such as midlate winter of dormant native tallgrass prairie (CP = less than 6% in, Bodine and Purvis, 2003), or Australian tropical rangelands (CP = around 6%, White et al., 2010), we could place our *Campos* grasslands somewhat in the middle. Should this be the case, it could be assumed that native grasslands are in the CP deficit threshold, with some cases above and others below it.

Poppi et al. (2018) suggest that supplementation response is based on achieving the best combinations to increase metabolizable protein and ME supply when animals are grazing low CP concentration forage. The protein concentration of herbage in native *Campos* grasslands during winter varies, but 8.4% is commonly observed (Cazzuli et al., 2019; Fedrigo et al., 2021; Orcasberro et al., 2021), above what McLennan et al. (2017) consider "low CP forages" (<7% CP). This CP concentration is about one-third that of sown temperate pastures in winter (20% ± 6%, Mieres et al., 2004), but not as low as values reported for tropical grasslands during the dry season (e.g., less than 3% in Australian rangelands, Bowen et al., 2017). Again, this database appears to be somewhat in the middle of all other forage bases in terms of CP concentration. In addition, the actual consumed CP by the animals would be even greater since animal selection improves diet quality on this type of rangelands (Piaggio et al., 1995). When SFE and ADGchng were classified into protein and "non-protein based" (energy-based) supplementation treatments, no distinct pattern could be observed; if forage CP had been the

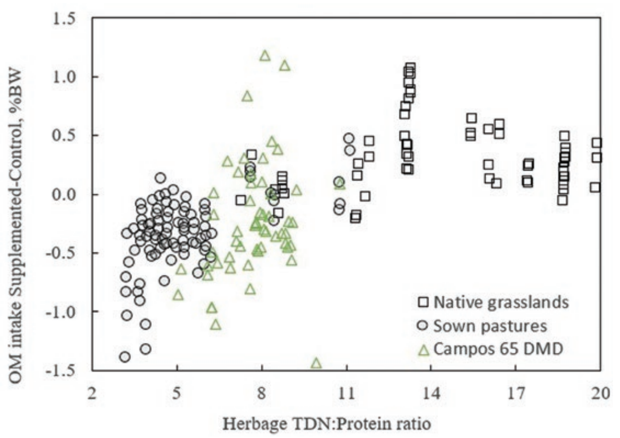

Figure 6. Difference between supplemented and control animals in organic matter (OM) intake by herbage TDN:CP by source of estimation. TDN, total digestible nutrients; CP, crude protein; "Native grasslands and sown pastures" from Moore et al. (1999); "Campos 65 DMD", estimation from database of supplementation experiments for young beef cattle on native grasslands in Uruguay (1993–2018).

most important limiting factor, some kind of distinction in either SFE or ADGchng should have been observed. When protein is limiting growth, protein deposition is linearly increased by protein supply (Schroeder and Titgemeyer, 2008). In our dataset—comprising growing cattle- no differential response could be found using high protein concentration supplements, nor a significant correlation between SFE and herbage CP. According to Poppi and McLennan (1995), protein intake is expected to be the main limiting nutrient for cattle in a growing phase, at least in tropical environments, something we did not find in our analysis. Additionally, McCollum and Horn (1990) affirmed that SFE lower than 0.33 suggest no N deficiency, in which case, our data would match this criterion, at least on average. In the case of Bowman et al. (2004), HDMI and NDF and CP intakes decreased linearly with increasing nonstructural carbohydrate supplementation of beef heifers on low quality forage-based diets (5.5 % CP, 49.0 ADF%, 71.3 NDF%), in which both forage and supplement digestible organic matter (DOM):CP seemed to be superior predictors of response to supplementation compared with forage CP levels alone. Actually, Lima et al. (1999) observed that DOM:CP was as important as CP concentration for beef heifers grazing a C4 grass in explaining ADG variations. All this suggests that protein may not be the most important limiting factor of these native grasslands production systems, not even for young growing cattle.

CONCLUSIONS

Positive responses to supplementation occurred in the 25 collated trials. In general, SFE were relatively high, with 80% of SFE above 0.15 ADGchng/kg DM. The average SFE was 0.21 ± 0.08 ADGchng/kg DM. Considering the variables directly related with SFE, a greater variation was observed with ADGchng than with supplementation rate. Forage allowance affected SFE in a negative way, while herbage mass positively affected yet it in a smaller magnitude, suggesting a balance between these two variable is needed to maximize SFE.

Weather conditions during the stocking period was the only variable that showed a significant effect on SFE, through its detrimental impact on the performance of unsupplemented animals in harsh winters that led to a greater supplement response (ADGchng) and thus greater SFE.

Little evidence was found on the existence of a major overriding role for protein deficiency on native *Campos* grasslands of the Pampa biome as the main factor limiting animal growth during winter. This is probably because the nutritive value of herbage of *Campos* grasslands seems to be higher than in other grasslands, such as tropical rangelands or North American prairies, because *Campos* retain a variable, and potentially high, proportion of green leaves over winter.

ACKNOWLEDGMENTS

We are grateful to Dr. Graciela Quintans for her preliminary comments on the paper general layout, to Dr. Zully Ramos for her continuous support and advice, and to Dr. Georgett Banchero for her final comments and suggestions to improve the paper. We acknowledge students and technicians that helped carry out the experiments. INIA Uruguay and the Agronomy School of the University of the Republic (FAgro/UdelaR) financed this research. FC is grateful to INIA for financial support via an Academic Excellence Scholarship for PhD studies.

CONTRIBUTIONS

FC and FL conceived the research work as a whole. FC gathered the datasets, with the help of PR, VB, AS, XL, SL, and GB. The analysis design was discussed between FC, FL, JSánchez, AH, PR, VB, AS, MJ, MD, JSavian, JIV, and XL. JSánchez ran the initial meta-analyses and meta-regressions, together with FC. The rest of the analyses were run by FC, FL, AH, and XL. The discussion of the results was carried out by FC, FL, AH, JSánchez, PR, VB, AS, MJ, MD, JSavian, DP, FM, XL, SL, GB, JIV, and CB. Finally, FC and FL led the manuscript writing, and all authors contributed critically to the drafts and gave their final approval for publication.

CONFLICTS OF INTEREST STATEMENT

None declared.

LITERATURE CITED

AOAC. 1990. *Official method of analysis*. 15th ed. Washington, DC: Assoc. Off. Anal. Chem.

ARC. 1980. *The nutrient requirements of ruminant livestock*. London, UK: Agric. Res. Coun., Commonwealth Agric. Bur. The Gresham Press.

Arrieta, G., X. Lagomarsino, J. Olivera, and G. Trindade. 2008. *Incidencia de diferentes dietas sobre el crecimiento animal, el rendimiento carnicero y la calidad de carne* [graduate thesis]. Montevideo: FAgro/UdelaR; p. 218.

Berretta, E. J., D. Risso, F. Montossi, and G. Pigurina. 2000. Campos in Uruguay. In: G. Lemaire, J. Hodgson, and A. Moraes, editors, *Grassland ecophysiology and grazing ecology*. Wallingford, UK: CABI; p. 377–394.

Berretta, V., A. Simeone, G. Castro, M. Ferrés, G. Legorburu, and M. Victorica. 2019. DDGS, campo natural y comederos de autoconsumo: una alianza estratégica para mejorar la recría en ganado de carne. In: Simeone, A., and Berretta, V., editors. *Jornada anual de la unidad de producción intensiva de carne: Pradera, campo natural, suplementación y corral: un medio campo para* *ganar el partido de la rentabilidad*. Paysandú: UPIC/FAgro/UdelaR, 21; p. 32–43.

Blasina, M., A. Piñeyrúa, and M. Renau. 2010. *Evaluación del sistema de autoconsumo para la suplementación invernal de terneras sobre pasturas naturales* [*graduate thesis*]. Montevideo: FAgro/UdelaR; p. 104.

Bodine, T. N., and H. T. Purvis. 2003. Effects of supplemental energy and/ or degradable intake protein on performance, grazing behavior, intake, digestibility, and fecal and blood indices by beef steers grazed on dormant native tallgrass prairie. *J. Anim. Sci*. 81:304–317. doi:10.2527/2003.811304x

Bohnert, D. W., and M. B. Stephenson. 2016. Supplementation and sustainable grazing systems. *J. Anim. Sci*. 94:15–25. doi:10.2527/jas.2016-0520

Bowen, M. K., and F. Chudleigh. 2020. An economic framework to evaluate alternative management strategies for beef enterprises in northern Australia. *Anim. Prod. Sci*. 61:271–281. doi:10.1071/an20125

Bowen, M. K., D. P. Poppi, and S. R. McLennan. 2017. Efficiency of rumen microbial protein synthesis in cattle grazing tropical pastures as estimated by a novel technique. *Anim. Prod. Sci*. 57:1702–1712. doi:10.1071/an15535

Bowman, J. G. P., and D. W. Sanson. 1996. Starch- or fiber-based energy supplements for grazing ruminants. In: Proc. 3rd Grazing Livestock Nutrition Conf. (July 17–19, 2016). Journal of Animal Science and the American Society of Animal Science, Park City, UT. p. 118–135.

Bowman, J. G. P., B. F. Sowell, L. M. M. Surber, and T. K. Daniels. 2004. Nonstructural carbohydrate supplementation of yearling heifers and range beef cows. *J. Anim. Sci*. 82:2724–2733. doi:10.2527/2004.8292724x

Briske, D. D. 2017. Rangeland systems: foundation for a conceptual framework. In: Briske, D. D., editor. *Rangeland systems: processes, management and challenges*. Cham, Switzerland: Springer International Publishing; p. 1–21.

Brito, G., S. Luzardo, X. Lagomarsino, F. Montossi, A. La Manna, J. Frugoni, J. Levratto, S. Hernandez, D. Bottero, W. Zamit, et al. 2011. Frecuencia de suplementación invernal en campo natural: su aplicación en la recría de novillos de sobreaño. In: *Propuestas tecnológicas para el incremento de productividad, la valorización y el ingreso económico para siste,as ganaderos del basalto*. Tacuarembó: INIA, Serie de Actividades de Dufisión 657; p. 39–40.

Campos, F., and G. Terra. 2002. *Comparación entre afrechillo de arroz y una formulación comercial como suplementos para terneros de destete pastoreando campo natural durante el invierno*. [*graduate thesis*]. Montevideo: FAgro/UdelaR; p. 124.

CattleExplorer. 2012 CattleExplorer spreadsheet. CSIRO GrazPlan. Available from http://www.grazplan.csiro.au/

Cazzuli, F., I. De Barbieri, M. Jaurena, C. Silveira, and F. Montossi. 2019. Restricted oats grazing and its frequency of allocation affects calves´ performance on native grasslands. *Arch. Zootec*. 68:220–227. doi:10.21071/az.v68i262.4140

Cazzuli, F., X. Lagomarsino, P. Boggiano, A. Saadoun, and F. Montossi. 2018. Self-feeding improved animal performance of calves grazing native grasslands during winter on extensive livestock production systems. *Agro. Sur*. 46:29–39. doi:10.4206/agrosur.2018.v46n1-04

Christopherson, R. J., and P. M. Kennedy. 1983. Effect of the thermal environment on digestion in ruminants. *Can. J. Anim. Sci*. 63:477–496. doi:10.4141/cjas83-058

Clariget, J. M., G. Banchero, S. Luzardo, E. Fernández, E. Pérez, A. La Manna, A. Saravia, M. del Campo, A. Ferrés, and M. E. Andrighetto Canozzi. 2021b. Effect of pre-slaughter fasting duration on physiology, carcass and meat quality in beef cattle finished on pastures or feedlot. *Res. Vet. Sci*. 136:158–165. doi:10.1016/j.rvsc.2021.02.018

Clariget, J. M., M. Lema, A. La Manna, E. Pérez, G. Banchero, and E. Fernández. 2021a. Estimated beef cattle performance under intensive grazing systems in Uruguay. *Agrocienc. Urug*. 25:1–14. doi:10.31285/AGRO.25.107

De Figueiredo, D. M., A. S. De Oliveira, M. F. L. Sales, M. F. Paulino, and S. M. L. R. Do Vale. 2007. Economic analysis of four supplementation strategies for growth and finish beef cattle in a pasture-supplement system. *Revista Bras. Zoot*. 36:1443–1453. doi:10.1590/S1516-35982007000600030

DelCurto, T., B. W. Hess, J. E. Huston, and K. C. Olson. 2000. Optimum supplementation strategies for beef cattle consuming low-quality roughages in the western United States. *J. Anim. Sci*. 77:1–16. doi:10.2527/jas2000.77e-suppl1v

Detmann, E., E. E. L. Valente, E. D. Batista, and P. Huhtanen. 2014. An evaluation of the performance and efficiency of nitrogen utilization in cattle fed tropical grass pastures with supplementation. *Livest. Sci*. 162:141–153. doi:10.1016/j.livsci.2014.01.029

Di Rienzo, J. A., F. Casanoves, M. G. Balzarini, L. Gonzalez, M. Tablada, and C. W. Robledo. 2015 InfoStat versión 2015 [computer program] Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Cordoba, Argentina.

Do Carmo, M., G. Cardozo, M. Jaurena, and P. Soca. 2018. Demonstrating control of forage allowance for beef cattle grazing Campos grassland in Uruguay to improve system productivity. *Trop. Grassl*. 17:35–47. doi:10.15232/pas.2016-01600

Esteves, M., S. Laxalde, and M. Nario. 2013. *Utilización de nitrógeno no proteico en programas de suplementación invernal basados en autoconsumo para terneros pastoreando campo nativo* [*graduate thesis*]. Montevideo: FAgro/UdelaR; p. 119.

Fedrigo, J. K., P. F. Ataide, J. C. R. Azambuja Filho, P. Bertoncelli, and C. Nabinger. 2022. Deferment associated to contrasting grazing intensities affects root/shoot biomass allocation in natural grasslands. *Appl. Veg. Sci*. 25:e12671. doi:10.1111/avsc.12671

Fedrigo, J. K., M. Jaurena, M. Fett Pinto, T. Devincenzi, M. Cadenazzi, I. Carassai, and C. Nabinger. 2021. Spring deferment and N-P fertilization in natural grasslands vulnerable to summer water deficit. *Agrocienc. Urug*. 25:1–14. doi:10.31285/AGRO.25.354

Grainger, C., and G. L. Mathews. 1989. Positive relation between substitution rate and pasture allowance for cows receiving concentrates. *Aus. J. Exp. Agric*. 29:355–360. doi:10.1071/EA9890355

Hall, W. B., G. M. McKeon, J. O. Carter, K. A. Day', S. M. Howden, J. C. Scanlan, P. W. Johnston, and W. H. Burrows. 1998. Climate change in Queensland's grazing lands: II. An assessment of the impact on animal production from native pastures. *Rangeland J*. 20:177–205. doi:10.1071/RJ9980177

Harris, L. E. 1980. Feedstuffs. In: FAO. Fish Feed Technology: lectures presented at the FAO/UNDP Training Course in Fish Feed Technology, 9 Oct 1978, Seattle, Washington. (USA). Rome: FAO. (Chapter 8). Available from www.fao.org/3/x5738e/x5738e09.htm

Hills, J. L., W. J. Wales, F. R. Dunshea, S. C. Garcia, and J. R. Roche. 2015. Invited review: an evaluation of the likely effects of individualized feeding of concentrate supplements to pasture-based dairy cows. *J. Dairy Sci*. 98:1363–1401. doi:10.3168/jds.2014-8475

Jaurena, M., M. Durante, T. Devincenzi, J. V. Savian, D. Bendersky, F. G. Moojen, M. Pereira, P. Soca, F. L. F. Quadros, R. Pizzio, et al. 2021. Native grasslands at the core: a new paradigm of intensification for the Campos of Southern South America to increase economic and environmental sustainability. *Front. Sustain. Food Sys*. 5:1–15. doi:10.3389/fsufs.2021.547834

Kuinchtner, B. C., F. L. F.Quadros, F. Jochims, P. T. Casanova, G. M. Dutra, F. Ongaratto, and R. M. R. de Carvalho. 2018. Performance and feed intake of beef heifers on rotational grazing of natural grassland receiving protein and energy supplement in cool season. *Ciênc. Rural*. 48:e20170563. doi:10.1590/0103-8478cr20170563

Lima, G. F., L. E. Sollenberger, W. E. Kunkle, J. E. Moore, and A. C. Hammond. 1999. Nitrogen fertilization and supplementation effects on performance of beef heifers grazing limpograss. *Crop Sci*. 39:1853–1858. doi:10.2135/cropsci1999.3961853x

Luzardo, S., R. Cuadro, X. Lagomarsino, F. Montossi, G. Brito, and A. La Manna. 2014a. Tecnologías para la intensificación de la recría en el basalto - uso estratégico de suplementación sobre campo natural y pasturas mejoradas. In: Berretta, E. J., F. Montossi, G. Brito, editors. *Alternativas tecnológicas para los sistemas ganaderos de Basalto*. INIA, Serie Técnica 217, Tacuarembó; p. 71–91. doi:10.35676/INIA/ST.217

Luzardo, S., R. Cuadro, X. Lagomarsino, F. Montossi, G. Brito, and A. La Manna. 2014b. Tecnologías para la intensificación de la recría bovina en el Basalto - suplementación infrecuente sobre campo natural y pasturas mejoradas en Basalto. In: Berretta, E., F. Montossi, and G. Brito, editors. *Alternativas tecnológicas para los sistemas ganaderos del Basalto*. INIA, Serie Técnica 217, Montevideo; p. 93–125. doi:10.35676/INIA/ST.217

McCollum, F. T., and G. W. Horn. 1990. Protein supplementation of grazing livestock: a review. *Prof. Anim. Sci*. 6:1–16. doi:10.15232/S1080-7446(15)32251-8

McLennan, S. R., J. M. Campbell, C. H. Pham, K. A. Chandra, S. P. Quigley, and D. P. Poppi. 2017. Responses to various protein and energy supplements by steers fed low-quality tropical hay. 2. Effect of stage of maturity of steers. *Anim. Prod. Sci*. 57:489473–489488. doi:10.1071/an15660

Meyer, J. H., G. P. Lofgreen, and W. N. Gareett. 1960. A proposed method for removing sources of error in beef cattle feeding experiments. *J. Anim. Sci*. 19:1123–1131. doi:10.2527/jas1960.1941123x

Mieres, J. M., L. Assandri, and M. Cúneo. 2004. Tablas de valor nutritivo de alimentos. In: Mieres, J. M., editor. *Guía para la alimentación de rumiantes*. INIA, Serie Técnica 142, Montevideo; p. 13–68.

Modernel, P., W. A. H. Rossing, M. Corbeels, S. Dogliotti, V. Picasso, and P. Tittonell. 2016. Land use change and ecosystem service provision in Pampas and Campos grasslands of southern South America. *Environ. Res. Lett*. 11:1130021–1130022. doi:10.1088/1748-9326/11/11/113002

Montossi, F. 2017. Sistemas de suplementación mediante autosuministro para la mejora de la recría invernal de terneros sobre campo natural en el norte del Uruguay. In: Montossi, F., editor. *Auto-suministro y suplementación sobre campo natural*. INIA; Serie Técnica 234, Tacuarembó; p. 70.

Montossi, F., J. M. Soares de Lima, G. Brito, E. J. Berretta. 2014. Impacto en lo productivo y económico de las diferentes orientaciones productivas y tecnologías propuestas para la región del basalto. In: Berretta, E. J., F. Montossi, G. Brito, editors. *Alternativas tecnológicas para los sistemas ganaderos del basalto*. Montevideo: INIA, Serie Técnica 217; p. 557–568.

Moore, J. E., M. H. Brant, W. E. Kunkle, and D. I. Hopkins. 1999. Effects of supplementation on voluntary forage intake, diet digestibility, and animal performance. *J. Anim. Sci*. 77:122–135. doi:10.2527/1999.77suppl_2122x

Núñez, N., A. Hirigoyen, M. Durante, J. M. Arroyo, F. Cazzuli, C. Bremm, and M. Jaurena. 2022. What factors control the crude protein content variation of a basaltic "Campos" native grassland of South America? *Agronomy*. 12: 1756. doi:10.3390/agronomy12081756

Orcasberro, M. S., C. Loza, J. Gere, P. Soca, V. Picasso, and L. Astigarraga. 2021. Seasonal effect on feed intake and methane emissions of cow–calf systems on native grassland with variable herbage allowance. *Animals*. 11:8821–8812. doi:10.3390/ani11030882

Osítis, U., S. Strikauska, and A. Grundmane. 2003. *Lopbarības Analīžu Rezultātu Apkopojums*. LLU, SIA Jelgavas tipogrāfija. 62, 1.

Piaggio, L., E. Prates, C. Rinaldi, and P. Soca. 1995. Diet quality and diet selection of steers grazing in a rotational system at four levels of forage allowance on a rangeland. *Ann. Zootech*. 44:119. (Abstr). doi:10.1051/animres:19950589

Poppi, D., and S. McLennan. 1995. Protein and energy utilization by ruminants at pasture. *J. Anim. Sci*. 73:278–290. doi:10.2527/1995.731278x

Poppi, D. P., S. P. Quigley, T. da Silva, and S. R. McLennan. 2018. Challenges of beef cattle production from tropical pastures. *Rev. Bras. Zootec*. 47:1–9. doi:10.1590/rbz4720160419

Pittaluga, O., G. Brito, P. Cuadro, S. Díaz, R. San Julián, and C. Silveira. 2007. *Incidencia de diferentes períodos de suplementación invernal de terneros y novillos sobre el crecimiento animal, el rendimiento carnicero y la calidad de carne*. INIA, Serie de Actividades de Difusión 511, Tacuarembó. p. 11–15.

Quintans, G., D. Vaz Martins, and E. Carriquiry. 1993. Efecto de la suplementación invernal sobre el comportamiento de terneras. In: *Jornada de Campo Natural*. Treinta y Tres: INIA, Serie de Actividade de Difusión, 49; p. 35–53.

R Core Team. 2017. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.r-project.org/.

Rovira, P. 2014a. Efecto de la adición de urea al grano húmedo de sorgo en el desempeño productivo de novillos suplementados sobre campo natural. In: Rovira, P., editor. *Suplementación de bovinos con grano húmedo de sorgo y fuentes proteicas sobre campo natural*. Montevideo: INIA; p. 59–67.

Rovira, P. 2014b. Suplementación de terneros en autoconsumo con raciones con fibra (sin limitador de consumo). In: *Estrategias de intensificación ganadera*. Treinta y Tres: INIA, Treinta y Tres; p. 6–15.

Rovira, P., and Velazco, J. I. 2012. Evaluación de un sistema de autoconsumo restringido con distinto contenido de sal en la ración en terneros suplementados sobre campo natural. In: Rovira, P., and J. I. Velazco, editors. *Suplementación de bovinos en pastoreo: autoconsumo*. Montevideo: INIA, Serie Técnica 199; p. 23–31.

Rovira, P., and J. I. Velazco. 2014. Efecto del agregado de fuentes proteicas al grano húmedo de sorgo en el crecimiento de terneros suplementados sobre campo natural. In: Rovira P., editor. *Suplementación de bovinos con grano húmedo de sorgo y fuentes proteicas sobre campo natural*. Montevideo: INIA; p. 17–27.

Rovira, P., J. I. Velazco, and F. Montossi. 2014. Desempeño productivo de terneros sobre campo natural suplementados con grano húmedo de sorgo y distintos niveles de nitrógeno de liberación lenta (rumenfeed). In: Rovira P., editor. *Suplementación de bovinos con grano húmedo de sorgo y fuentes proteicas sobre campo natural*. Montevideo: INIA; p. 47–58.

Sarker, A. B., and W. Holmes. 1974. The influence of supplementary feeding on the herbage intake and grazing behaviour of dry cows. *Grass Forage Sci*. 29:141–143. doi:10.1111/j.1365-2494.1974.tb01242.x

Schroeder, G. F., and E. C. Titgemeyer. 2008. Interaction between protein and energy supply on protein utilization in growing cattle: a review. *Livest. Sci*. 114:1–10. doi:10.1016/j.livsci.2007.12.008

Simeone, A., V. Beretta, M. Blasina, A. Piñeirúa, and M. Renau. 2010. Winter response of weaned beef calves to self-fed supplementation on native pastures. In: Proc. Aust. Soc. Anim. Prod. p. 5. (Abstr).

Stockdale, C. R. 2000. Levels of pasture substitution when concentrates are fed to grazing dairy cows in northern Victoria. *Aust. J. Exp. Agric*. 40:913–921. doi:10.1071/ea00034

Tittonell, P. 2021. Beyond CO_2: multiple ecosystem services from ecologically intensive grazing landscapes of South America. *Front. Sustain. Food Syst*. 5:1–11. doi:10.3389/fsufs.2021.664103

Tonello, C. L., A. F. Branco, C. Y. Tsutsumi, L. B. Ribeiro, S. M. Coneglian, and R. Castañeda, 2011. Suplementação e desempenho de bovinos de corte em pastagens: Tipo de forragem. *Acta Sci. - Anim. Sci*. 33:199–205. doi:10.4025/actascianimsci.v33i2.8130

Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods for dietary fiber, neutral de- tergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *J. Dairy Sci*. 74:3583–3597. doi:10.3168/jds.S0022-0302(91)78551-2

Watson, A. K., B. L. Nuttelman, T. L. Klopfenstein, L. W. Lomas, and G. E. Erickson. 2013. Impacts of a limit-feeding procedure on variation and accuracy of cattle weights. *J. Anim. Sci*. 91:5507–5517. doi:10.2527/jas.2013-6349

Wheeler, J. S., D. L. Lalman, G. W. Horn, L. A. Redmon, and C. A. Lents. 2002. Effects of supplementation on intake, digestion, and performance of beef cattle consuming fertilized, stockpiled bermudagrass forage. *J. Anim. Sci*. 80:780–789. doi:10.2527/2002.803780x

White, I. A., L. P. Hunt, D. P. Poppi, and S. R. Petty. 2010. Sampling requirements for predicting cattle diet quality using faecal near-infrared reflectance spectroscopy (f.NIRS) in heterogeneous tropical rangeland pastures. *Rangeland J*. 32:435–441. doi:10.1071/rj09021

Wilkinson, J. M. 2011. Re-defining efficiency of feed use by livestock. *Animal*. 5:1014–1022. doi:10.1017/S175173111100005X

Williams, G. D., M. R. Beck, L. R. Thompson, G. W. Horn, and R. R. Reuter. 2018. Variability in supplement intake affects performance of beef steers grazing dormant tallgrass prairie. *Prof. Anim. Sci*. 34:364–371. doi:10.15232/PAS.2017-01720