



Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: <http://www.elsevier.com/locate/rama>

Controls of Carrying Capacity: Degradation, Primary Production, and Forage Quality Effects in a Patagonian Steppe[☆]

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ARTICLE INFO

Article history:

Received 4 August 2014

Accepted 2 March 2015

Keywords:

grazing
harvest index
range management
sustainability

ABSTRACT

Rangeland carrying capacity depends on aboveground net primary production (ANPP) and on the sustainable harvest index (Hlsust), the portion of ANPP that livestock can consume without undermining the production capacity of the system. At a regional scale, the observed harvest index (Hlreal) increases with ANPP, but at a landscape scale the pattern is less clear, and controls of Hlreal and Hlsust are unknown. We analyzed the landscape patterns of variation of Hlreal and Hlsust across gradients of ANPP, pastoral value of vegetation (PV), and degradation. In 15 plots of a 2 753-ha paddock in a western Patagonian grass–shrub steppe, we estimated ANPP, consumption, forage pastoral value, and degradation. To estimate degradation we used PV weighed by forage cover because it was negatively correlated with a combination of ecosystem traits formerly linked to grazing-induced degradation. We calculated Hlreal (consumption/ANPP) and Hlsust (consumption removing 40% of aerial biomass of the key species/ANPP). We choose *Festuca pallelescens* as the key species because of its high abundance and moderate preference. As the paddock was grazed with low stocking rate to maximize among-plots selection, Hlreal was lower than Hlsust. As in regional models, Hlsust and Hlreal increased with ANPP within the paddock ($R^2 = 0.33$ and 0.30 , respectively). Multiple regressions showed that Hlreal increased with ANPP and degradation, while Hlsust increased with ANPP but decreased with degradation ($R^2 = 0.64$ and 0.77 , respectively). This suggests that at stocking rates lower than carrying capacity, sheep choose highly productive stands and, at a given level of ANPP, they prefer degraded stands. In contrast, carrying capacity increases with productivity and decreases with degradation. Management systems based on Hlsust may result in severe biomass removal of species more preferred than the key species (*Poa ligularis*), and it is necessary to include strategies to preserve their individuals and populations.

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Introduction

Estimating carrying capacity is a prerequisite for designing sustainable management systems of natural grasslands. Livestock carrying capacity is the animal density that an area can sustain without degrading forage resources and maintaining a level of secondary production coherent with landowner objectives and available management options (Holechek et al., 1989; Scarnecchia, 1990; Golluscio, 2009; Golluscio et al., 2009). Livestock carrying capacity can be estimated as the ratio between the amount of forage that can be sustainably consumed and

the amount of forage that each individual animal must consume during a given period to attain the prefixed objectives of secondary production (Johnston et al., 1996). On the basis of the model of energy flux across the ecosystem (Odum, 1972), the forage that can be sustainably consumed is a fraction of aboveground net primary production (ANPP) beyond which plant productivity, energy supply to decomposers, integrity of nutrient cycles, and floristic composition are degraded (Golluscio, 2009).

Livestock carrying capacity is highly variable among years because of the high interannual variability of precipitation. As this variability is higher in arid than in humid zones (Paruelo and Lauenroth, 1998), it even questions the concept of carrying capacity in certain African ecosystems (Ellis and Swift, 1988). In addition, livestock carrying capacity depends on grazing management, which in turn can increase (e.g., McNaughton, 1985) or decrease ANPP (Milton et al., 1994). Finally, both forage resources and animal behavior are highly variable at different spatial scales, from region, to landscape, to community, to

[☆] Research was funded by INTA, UBA (G045, G497) and Agencia Nacional de Promoción de la Ciencia y la Tecnología (PICT 463, PICT 1276).

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paddock (Senft et al., 1987). Within this conceptual framework, only long-term average carrying capacity may be roughly estimated on the basis of ANPP, individual animal consumption, and the proportion of ANPP that can be sustainably consumed. Here, this is called the sustainable harvest index (Hlsust; Eq. (1)), also known as “safe” level of forage utilization (Johnston et al., 1996).

$$CC = ANPP \times Hlsust \times IAC^{-1} \quad (1)$$

Where:

CC = Carrying capacity for livestock production (animals · ha⁻¹)
ANPP = Aboveground net primary production (kgDM · ha⁻¹ · year⁻¹)

Hlsust = Harvest index sustainable for both ecosystem functioning preservation, and animal production under man-defined production objectives (kgDM · kgDM⁻¹)

IAC = Individual annual consumption required as a function of the man-defined production objectives (kgDM · animal⁻¹ · year⁻¹)

ANPP depends mainly on environmental factors, and IAC depends mainly on animal traits. Instead, the estimation of Hlsust is a key component of carrying capacity assessment because it defines the real harvest index (Hlreal) to be used, the variable most sensitive to human manipulation of rangelands (Golluscio et al., 1998a, 2009; Golluscio, 2009). As a consequence, it is essential to know the controls of Hlsust at regional, landscape, and community scales. The regional scale allows quantifying the energy flux for broad ecosystem types and may be critical for government decisions (Oesterheld et al., 1992), while landscape and community scales are crucial in terms of ranch management (Senft et al., 1987; Golluscio et al., 1998a).

For South American rangelands most available information refers to Hlreal (Hlreal = observed consumption/ANPP), which does not necessarily coincide with Hlsust. In addition, the patterns differ between spatial scales. At a regional scale, the main control of Hlreal is ANPP, as shown by the direct relationship between HI and ANPP^{0.5} derived by Golluscio et al. (1998a) from the double-logarithmic relationship between herbivore biomass and ANPP, obtained by Oesterheld et al. (1992). Thus, at a regional scale, livestock stocking rate increased in correspondence with a simultaneous increase of both ANPP and Hlreal. However, when analyzing the same relationship for the subset of data corresponding to Patagonian steppes (ANPP < 1 500 kgDM · ha⁻¹ · y⁻¹), Hlreal decreased rather than increased with ANPP (Golluscio, 2009). This suggests that, at these community and landscape scales, controls other than ANPP would affect Hlreal, even linked to environment (cold, snow, drinking water availability, predators, etc.) or to human management (real stocking rate, temporal use of forage resources, etc.).

The concept of Use Factor could aid to estimate Hlsust. The Use Factor (Holechek et al., 1989) is the proportion of forage biomass of the “key species” that can be consumed by livestock without affecting plant production or floristic composition across time. The “key species,” in turn, is that which can be used to estimate grassland trend and condition, mainly because of its moderate preference and/or abundance (Stoddart et al., 1955). For North American grasslands similar to those of Patagonia, Holechek et al. (1989) proposed an empirical Use Factor of 50% to 30%, decreasing according to the ecological fragility of sites. In this paper we calculated Hlsust by adding to measured animal consumption the biomass of the key species that would have been consumed under a Use Factor of 40%.

Hlsust may be affected by ecosystem degradation induced by grazing because it often reduces ANPP and forage quality. The relatively common reduction of ANPP (Moën and Oksanen, 1998; Oksanen and Oksanen, 2000) and forage value of plant communities (Hofmann, 1989; Clauss and Lechner-Doll, 2001; Clauss et al., 2002)

induces a reduction of carrying capacity, which commonly is not accompanied by a reduction of stocking rate, leading to a positive feedback that exacerbates the negative effect of grazing on the ecosystem (Le Houerou, 1977; Fisher and Turner, 1978; Dregne, 1983; Dodd, 1994; Prince et al., 1998). However, in certain cases, ANPP or forage quality may not be reduced under poor grazing management because preferred species may be replaced by other highly productive species, such as prostrate herbaceous species (Altesor et al., 2005) or shrub species (Archer, 1995; Aguiar et al., 1996). Additionally, grazing may favor certain highly palatable species that were subordinate to other less palatable but more aggressive species (Cingolani et al., 2005).

The Patagonian grass–shrub steppe dominated by *Festuca pallelescens* is a good case study to analyze the controls of harvest index. First, it is one of the most productive communities of the Patagonian Phytogeographic Province (Paruelo et al., 2004). Second, it is one of the most studied communities in terms of carrying capacity, and both ANPP and forage quality have been included in local models to estimate carrying capacity of these steppes (Nakamatsu et al., 1998; Golluscio et al., 1998a; Elissalde et al., 2002; Golluscio et al., 2009; Golluscio, 2009). Third, several indicators of grazing-induced degradation have been identified for this community. From a physiognomic point of view, degradation was associated with a reduction of total cover and grass cover, as well as an increase of cover of litter, erosion pavements, and shrubs (Soriano and Brun, 1973; León and Aguiar, 1985; Perelman et al., 1997; Bertiller and Bisigato, 1998; Cesa and Paruelo, 2011). From a floristic point of view, degradation was associated to a reduction of the cover of several preferred grass species, such as *Bromus pictus*, *Poa ligularis*, *Festuca pallelescens*, and *Pappostipa speciosa* (León and Aguiar, 1985; Cesa and Paruelo, 2011), and an increase in the cover of unpreferred grasses, such as *Pappostipa major*, and unpreferred shrubs and subshrubs, such as *Senecio filaginoides* (Soriano, 1956; León and Aguiar, 1985), *Mulinum spinosum* (León and Aguiar, 1985), and *Acaena splendens* (Cesa and Paruelo, 2011).

Our objective was to analyze the within-paddock patterns of Hlreal and Hlsust and relate them to ANPP, degradation, and forage quality. Under the hypothesis that forage availability will increase as ANPP and forage quality increase and degradation decreases, we predicted that in stands located within the same paddock and landscape unit, and dominated by the same set of species, both Hlreal and Hlsust would be positively related to ANPP and forage quality and negatively related to degradation. We tested this prediction by simple and multiple regressions on information obtained from a mensurative experiment done in 15 plots located within a paddock under controlled grazing. On each plot we measured consumption, ANPP, forage value of vegetation, and several degradation indicators. In order to estimate Hlsust we first calibrated a nondestructive method to calculate the proportion of biomass removed from a visual scale of defoliation for the three most conspicuous species in the diet and then determined the key species on the basis of their abundance in the community and their preference by sheep.

Materials and Methods

Study Site

The work was done in the NW Chubut Province (Center West of Patagonia), a region with dissected relief and arid soils (Del Valle, 1998). Climate is cold-temperate, with mean temperatures from 4°C in July to 16°C in January and intense Western winds. Annual precipitation varies from 150 to 300 mm from West to East and is concentrated in winter. Precipitation is much lower than annual potential evapotranspiration (~600 mm, concentrated in summer), leading to a water balance with marked summer deficit and winter excess (Paruelo et al., 1998). The most conspicuous plant communities are the grass–shrub steppes of *Festuca pallelescens*, *Pappostipa speciosa*, *Poa ligularis*,

and *Mulinum spinosum* and the shrub-grass steppes of *Mulinum spinosum*, *Senecio* spp., *Pappostipa speciosa*, and *Poa lanuginosa* (León et al., 1998; Paruelo et al., 2004). Prairies are located following the drainage network, dominated by *Juncus balticus*, *Poa pratensis*, and *Festuca pallescens* (“sweet” mallines) or by *Distichlis* spp., *Juncus balticus*, and *Festuca pallescens* (“salt” mallines), the last ones more frequent toward the eastern region (Paruelo et al., 2004).

Experimental Layout

The experiment was done in fifteen 30 × 30 m plots located in grass-shrub steppe stands within the “Nevado” paddock (2 753 ha; estimated annual precipitation of 500 mm) of Estancia Montoso (Chubut Province, Patagonia, Argentina) (Table S1, available online at <http://dx.doi.org/10.1016/j.rama.2015.03.002>). This paddock was chosen because it was ungrazed during the previous 10 months, had only 0.2% of area covered by the previously mentioned prairies (mallines), and had a large plane zone where herbivore behavior was not affected by topographical factors. During seven years before the experiment, it was grazed only three months every year with 15 000 ewes, equivalent to an instantaneous stocking rate of 5.4 ovine units · ha⁻¹ and an annual stocking rate of 1.36 ovine units · ha⁻¹ (one ovine unit, OU, equals one 40 kgLW wether; Elissalde et al., 2002). The plots were located on the plane zone, at less than 2 500 m from the water point to guarantee the visit of sheep (Holechek et al., 1989), but at more than 500 m from refuges and water points, which are frequently visited by sheep even in the absence of forage.

The 15 plots were edaphically and floristically similar. Twelve of them had a clay loam texture with more than 50% of silt, one had a silty texture with more than 80% of silt, and the other two had a loam texture with more than 30% of lime. Vegetation physiognomy was a grass-shrub steppe dominated by *Festuca pallescens*, *Pappostipa speciosa*, *Senecio filaginoides*, and *Adesmia volckmannii* (see details in Tables S1 and S2, available online at <http://dx.doi.org/10.1016/j.rama.2015.03.002>).

During the experiment, the paddock was grazed by wethers with an instantaneous stocking rate of 4.5 OU · ha⁻¹ from April 15 to May 7 of 2002, and 1.7 OU · ha⁻¹ from May 23 to June 16, when using the paddock became excessively risky because of the high probability of snowstorms. This low intensity of use (equivalent to an annual stocking rate of 0.39 OU · ha⁻¹) was set to allow the animals to freely choose among plots within the paddock.

Measurements and Calculations

ANPP

As a consequence of a markedly Mediterranean pluviometric regimen and cold temperatures, ANPP shows a clear seasonal peak at December–January and becomes nearly zero in winter (Paruelo et al., 2004). As a consequence, we estimated ANPP as the total biomass accumulated at the end of the growing season (i.e., harvested before the beginning of grazing, April 15, see earlier). We assumed that the eventual carryover of biomass from the previous year was compensated for by the eventual biomass death and fall during the current year. Both fluxes are much smaller than current-year biomass production (Sala and Austin, 2000; Jobbagy et al., 2002).

Animal Consumption

We estimated animal consumption as the reduction of aerial biomass between the beginning and ending of grazing. Measurements were done by harvesting a 0.2 m × 5 m (1 m²) rectangle randomly located within each plot (Fernández et al., 1991). Biomass was separated into *Festuca pallescens*, *Poa ligularis*, *Pappostipa speciosa*, *Hordeum comosum*, *Bromus* spp., other grass species, woody species, and herb species and dried in an oven at 85°C until constant weight was achieved. It was possible to

estimate consumption as the difference in plant biomass before and after grazing, not only because the carryover of biomass from the previous year is negligible but also because the period of study coincided with the season of water deficit (Paruelo et al., 2004), making unnecessary any correction for simultaneous ANPP (Oesterheld and McNaughton, 2000). Our climatic records show that the only precipitation event (80 mm) occurred in June, 12 days before the ending of the experiment and with very low air temperature. As a consequence, it seems plausible to assume it had no effect on ANPP during the experiment (Table S3, available online at <http://dx.doi.org/10.1016/j.rama.2015.03.002>).

Forage Value of Vegetation

We estimated the forage value of vegetation as the Pastoral Value (PV) (Daget and Poissonet, 1971), which represents the mean specific quality index (SQI) of all the species composing the plant community, weighted by their cover (Eq. (2)).

$$PV = [0.2 \times \sum(\text{Cov}_i \times \text{SQI}_i)] \times (\sum \text{Cov}_i)^{-1} \quad (2)$$

Where:

PV = Pastoral Value (adimensional: 0–1)

Cov_i = Plant cover for each species i (adimensional: 0–1)

SQI_i = Specific quality index for each species i (adimensional: 0–5)

0.2 = Scalar parameter (fix a top value of 1 to PV)

To calculate PV, within the first 15 days of April, we estimated the cover of each species by the point-intercept method (Greig Smith, 1983), in a linear transect of 100 points separated 2 m, whose first 30 m were included into the 30 × 30 m plot (Nakamatsu et al., 1998; Elissalde et al., 2002). We only recorded the sheep-edible fractions of each species: green and yellow foliar tissues of grasses, young shoots of shrub, and aerial tissues of herbs (Elissalde et al., 2002). The SQI of each species (SQI_i) varied between 0 and 5 and was established according to animal preference, nutritive quality, and seasonal availability (Elissalde et al., 2002). Taking into account our personal observations, we also included the floral tissues of *Poa ligularis* and *Bromus* spp. and corrected the SQI of *Festuca pallescens* from two (Elissalde et al., 2002) to three because it is clearly more preferred than *Pappostipa speciosa* (SQI = 2; Elissalde et al., 2002) (Soriano, 1956; Golluscio et al., 1998a).

Grazing-Induced Degradation

We used the stand-level Pastoral Value (PVstand) as an inverse indicator of grazing-induced degradation. PVstand, which varies between 0 and 100%, results from the product between the previously described PV and the cover of forage species (i.e., those with SQI ≥ 1), which varies between 0 and 100% (Nakamatsu et al., 1998). If two stands have the same floristic composition based on relative cover, they will have the same PV. However, their PVstand will differ if they have different absolute forage cover. As degradation is strongly related to forage cover, we expect that degradation will be inversely related to PVstand.

To test the relationship between PVstand and grazing-induced degradation we made a preliminary study consisting of a multivariate analysis of 20 floristic censuses taking into account the cover of all the degradation indicators mentioned in the introduction and listed in Table 1. We excluded forage cover because it is part of PVstand and cover of the functional types “preferred” or “unpreferred” grasses and shrubs because we included their dominant species, which explain most of the cover of both plant functional types (see details in Table 1). All censuses were performed between 2001 and 2004 with the methodology described earlier, in stands of the sheep-grazed grass-shrub steppes of *Festuca pallescens* located between 42°37′42.7″ and 44°11′10.0″ S lat and between 69°59′40.9″ and 71°05′06.9″ W long. The censuses were ordered by reciprocal averaging (RA; Hill, 1973), using the

Table 1

Attributes indicating land degradation used in multivariate analyses, with their respective eigenvalues for the first two ordination axes (reciprocal averaging). For each axis, asterisks indicate the significance of the correlation between the cover of each attribute on each census and the position of the census in the axis (* 0.05 > P > 0.01; ** P < 0.01). We show the eigenvalues and the percent of variance explained by the two first axis (0.0426 and 12.4%, respectively, for RA 3).

PCA axes traits	Ordination axis		RA 1	RA 2
	Explained variance	(%)	33.6	23.6
	Eigenvalue		0.1151	0.0809
Ecosystem traits (cover %): Mean (max-min)	Herbs	12 (28-3)	44	168**
	Plant cover	55 (77-22)	27	38
	Bare soil	9 (28-0)	-215 **	-72
	Erosion pavement	14 (58-1)	59	-231**
	Litter	9 (19-4)	-75 *	92
	<i>Mulinum spinosum</i>	5 (25-0)	-321 **	26
	<i>Pappostipa speciosa</i>	3 (11-0)	122	99
	<i>Festuca pallescens</i>	15 (38-3)	72	-21
	<i>Poa ligularis</i>	4 (9-0)	123 *	-117*
	<i>Senecio filaginoides</i>	2 (8-0)	-68	-203*
	<i>Pappostipa major</i>	0.05 (1-0)	346	576
	<i>Acaena</i> spp.	0 (3-0)	111	495**
	<i>Bromus</i> spp.	1 (4-0)	71	262**

Chi-squared distance as a measure of compositional dissimilarity (PCORD software).

The first three RA axes explained 70% of the variability among censuses. In the first RA axis the proportion of bare soil, the cover of litter, and that of the shrub *Mulinum spinosum* had significant negative loadings, and the cover of *Poa ligularis* had significant positive loadings. The dominant grass species, *Festuca pallescens* and *Pappostipa speciosa*, tended to have positive loadings, but they were not significant ($P < 0.15$). The increase of bare soil and *M. spinosum* cover at the expense of the cover of *F. pallescens* and other preferred grasses coincided with a previous independent description of the grazing-induced degradation in this plant community (León and Aguiar, 1985). This suggests that the location of censuses along the first RA axis is proportional to its degradation level. Because PVstand significantly increased along the first RA axis and did not change along the second RA axis ($r = 0.52, P < 0.05$, and $r = 0.20, P > 0.10$, respectively), we accepted PVstand as an indicator oppositely related to grazing-induced degradation (Table 1).

Real Harvest Index

We calculated HIreal as the ratio between animal consumption and ANPP.

Sustainable Harvest Index

To calculate HIsust we algebraically summed to animal consumption the differential of consumption that would have been attained under a use factor of 40% for the key species (average between 30% and 50% proposed by Holechek et al., 1989). Livestock can actually consume a proportion of key species' biomass higher or lower than the recommended use factor. As a consequence, we calculated HIsust by adding to animal consumption (of key and other species) the key species' biomass that would have been consumed under a use factor of 40% (when the key species was consumed < 40%) or by subtracting the consumed biomass of the key species exceeding a use factor of 40%. This procedure to estimate HIsust is not perfect because in both extremes it ignores the changes in the consumption of species other than the key species, associated with the change on the consumption of the key species algebraically summed to HIreal.

The calculation of HIsust required a characterization of the proportion of different plant species in sheep diet, the dynamics of defoliation of the three most important plant species in the diet, and the dynamics of the proportion of removed biomass (RB%) for each of them. The proportion of different species in the diet, combined with its proportion in plant cover (Table S2 available online at <http://dx.doi.org/10.1016/j.rama.2015.03.002>), allowed us to define the key species (Stoddart et al., 1955). The dynamics of RB%, estimated from that of defoliation,

allowed us to determine how far from an RB% of 40% was the animal consumption of each species during the experiment.

Proportion of Different Species in Animal Diet

We obtained fresh fecal samples at 26 and 57 days of the beginning of grazing and subjected them to microhistological analysis (Holechek and Gross, 1982) in the Laboratory of Microhistological Analyses of EEA INTA Bariloche (Somlo et al., 1997). In most cases it was possible to identify species, except in the cases of *Pappostipa* spp., *Eleocharis* spp., *Bromus* spp., *Armeria* spp., and *Junellia* spp., where only genera were identified. Grasses and graminoids constituted 82% of diet, and 71.8 % corresponded to only three species: *Festuca pallescens*, *Poa ligularis*, and *Pappostipa* spp. (Table 2).

Defoliation Dynamics of the Three Most Important Forage Species

On each plot we measured every 10 days the defoliation degree of five individuals of the three plant species most important in the diet. We used a visual scale of five (*P. ligularis*) or six (*F. pallescens* and *P. speciosa*) defoliation degrees, based on the three-degrees scale developed for *P. speciosa* by Golluscio et al. (1998b), which takes into account the proportion of tillers consumed in each plant and the height of the remaining stubble (Table 3).

Table 2

Proportion in the diet (%) of all species identified in sheep feces along the experiment (days 26 and 57 from grazing start). Species are ordered according to their mean proportion in the diet.

Species	Life form	Day 26	Day 57	Cumulative average
<i>Festuca pallescens</i>	Grass	42.6	45.4	43.8
<i>Poa ligularis</i>	Grass	18.4	16.5	61.3
<i>Pappostipa</i> spp.	Grass	7.5	13.4	71.8
<i>Juncus balticus</i>	Graminoid	6.5	8.0	79.1
<i>Hordeum comosum</i>	Grass	2.6	3.5	82.1
<i>Cerastium arvense</i>	Herb	3.3	2.5	85
<i>Rhodophiala elwesii</i>	Herb	5.2	0	87.6
<i>Eleocharis</i> spp.	Graminoid	1.7	3.2	90
<i>Mulinum spinosum</i>	Shrub	4.0	0.6	92.3
<i>Acaena pinatifida</i>	Herb	1.3	2.5	94.2
<i>Carex antarctica</i>	Graminoid	1.7	0.6	95.4
<i>Rhizidosperra</i> spp.	Grass	1.6	0	96.4
<i>Bromus</i> spp.	Grass	0.7	1.2	97.3
<i>Berberis heterophylla</i>	Shrub	0.8	0.2	97.8
<i>Armeria</i> spp.	Herb	0.6	0	98.1
<i>Junellia</i> spp.	Shrub	0.3	0	98.3
Others		1.6	2.5	100

Table 3
Scale of defoliation degrees for *Poa ligularis*, *Festuca pallescens*, and *Pappostipa speciosa*.

Defoliation degree	<i>Poa ligularis</i>	<i>Festuca pallescens</i>	<i>Pappostipa speciosa</i>
0	No defoliation	No defoliation	No defoliation
1	Only one tiller at 3 cm	Only one tiller at 5 cm	Only one tiller at 5 cm
2	25% of tillers at 3 cm	25% of tillers at 5 cm	25% of tillers at 5 cm
3	50% of tillers at 3 cm	50% of tillers at 5 cm	50% of tillers at 5 cm
4	75% of tillers at 3 cm	75% of tillers at 5 cm	75% of tillers at 5 cm
5	100% of tillers at 3 cm	100% of tillers at 5 cm	100% of tillers at 5 cm
6		100% of tillers at 3 cm	100% of tillers at 3 cm

Dynamics of the Proportion of Removed Biomass for Each Species

To estimate the dynamics of the proportion of removed biomass for the three most conspicuous species in the diet, we calibrated specific regression models between defoliation degree and percentage of removed biomass. These models provided a nondestructive method to estimate the proportion of removed biomass from the degree of defoliation. To develop those models we measured the height and diameter of 160 individuals of *Poa ligularis*, 138 of *Festuca pallescens*, and 126 of *Pappostipa speciosa*. Then we randomly subdivided the sets of plants into five (*P. ligularis*) or six (*F. pallescens* and *P. speciosa*) subgroups. Each subgroup was defoliated with scissors at one of the defoliation degrees defined in Table 3. The removed and remnant biomass fractions were oven dried at 85°C until constant weight was achieved and weighed. The proportion of removed biomass was calculated as the ratio between “removed” and “removed plus remnant” biomass. Several simple and multiple regression models were fitted, including those with allometric variables, with the minimal squares algorithm. The three species showed highly significant quadratic models between the defoliation degree (D) and the proportion of removed biomass (RB%): (a) *Poa ligularis* (RB% = 1.23 D² + 6.39 D - 1.60, R² = 0.87, P < 0.0001), (b) *Festuca pallescens* (RB% = 0.99 D² + 6.11 D - 0.80, R² = 0.90, P < 0.0001), and (c) *Pappostipa speciosa* (RB% = 1.01 D² + 1.10 D + 1.21, R² = 0.78, P < 0.0001). The inclusion of allometric traits as independent variables did not improve the models. The RB% of 40% corresponded to a defoliation degree of 4 for *F. pallescens* and *P. ligularis* and 5–6 for *P. speciosa*. On the basis of these calibrated relationships, we calculated the dynamics of biomass removal from defoliation degree measured in the field.

Statistical Analyses

We evaluated the simple linear regressions of ANPP, PV, and PVstand (independent variables) with Hlreal and Hlsust (dependent variables). However, Milchunas et al. (1988) suggested that along a gradient of increasing precipitation, ANPP, forage quality, and forage cover may vary, probably leading to correlations among the three independent variables of this study. Given such a lack of independence among the three independent variables, we applied Path Analysis (Sokal and Rohlf, 1981) to evaluate to what extent the correlation between two variables was mediated by the relationship of the independent variable with another independent variable. In addition, we analyzed all the multiple regression models including two or three independent variables. All statistical analyses were performed with α = 0.05, using Infostat software (Di Rienzo et al., 2008).

Results

By the end of the experiment, sheep had consumed on average 65% the aerial biomass of *Poa ligularis*, but only 15% of *Festuca pallescens* and practically none of *Pappostipa speciosa*. This indicates that the two most abundant species (*F. pallescens* and *P. speciosa*) were subutilized, while the least abundant and most preferred (*P. ligularis*) was overutilized (Fig. 1). The degree of defoliation of any

species did not depend on the degree of defoliation of the other species (data not shown). *Festuca pallescens* was the key species because it was moderately consumed and had simultaneously the highest proportion in sheep diet (Table 3) and high abundance (Table S2 available online at <http://dx.doi.org/10.1016/j.rama.2015.03.002>).

The final proportion of removed biomass (RB%) did not increase with ANPP or PV nor decrease with degradation (inverse of PVstand) for any species (Fig. 2). Surprisingly, the proportion of biomass of *Festuca pallescens* removed by sheep decreased with ANPP and increased with degradation (Fig. 2D and F, respectively). However, these relationships must be taken with caution because they become not significant when the stand with the lowest biomass remotion is left out of the analysis (P < 0.15 in both cases). The RB% of *Poa ligularis*

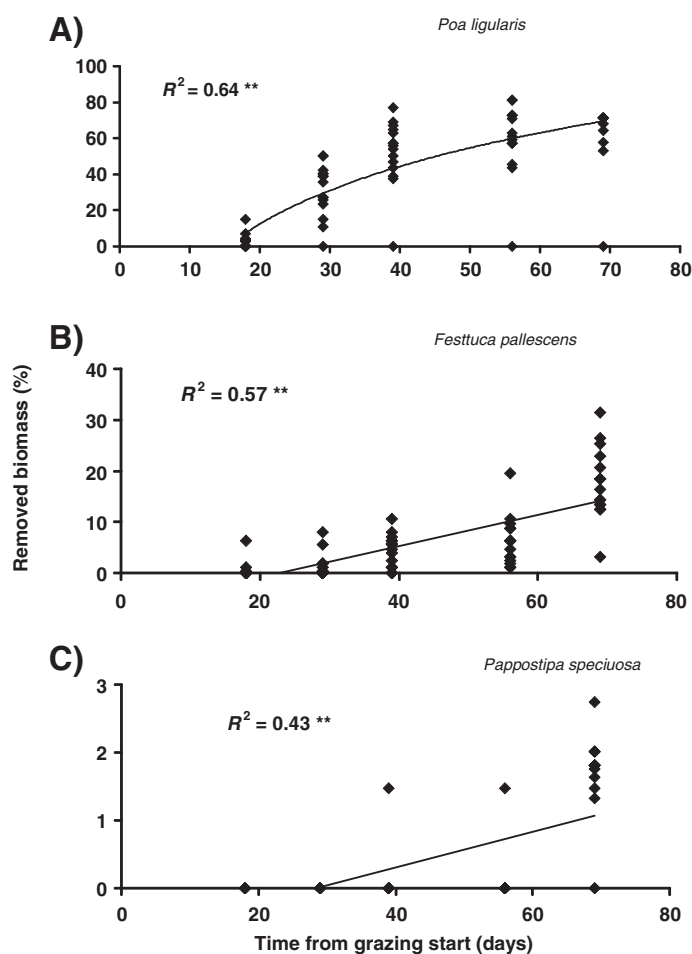


Fig. 1. Variation of the proportion of removed biomass (percent) along the paddock occupation period for *Poa ligularis* (A), *Festuca pallescens* (B), and *Pappostipa speciosa* (C). (N = 15). Note that all y-axes have different scales. The linear regressions of y-variable as a function of time are consigned (y = a + b.Ln(x) for *P. ligularis*, and y = a + b.x for *F. pallescens* and *P. speciosa*; ** P < 0.01).

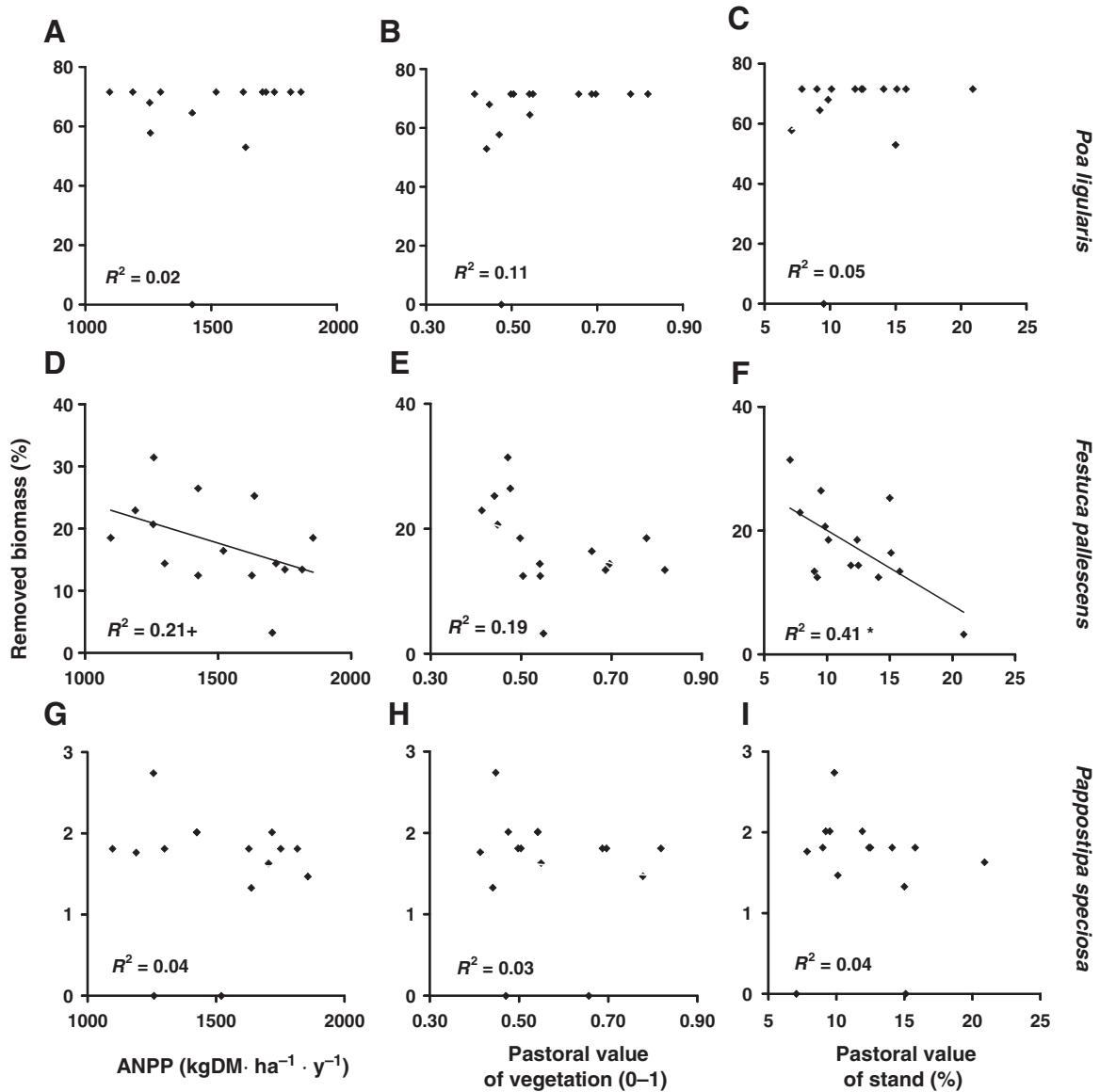


Fig. 2. Relationship between the proportion of biomass removed at the end of the experiment and ANPP (A, D, G), PV (B, E, H), and PVstand (C, F, I) for *Poa ligularis* (A, B, C), *Festuca pallescens* (D, E, F), and *Pappostipa speciosa* (G, H, I). * 0.05 > P > 0.01; + 0.10 > P > 0.05.

and *Pappostipa speciosa* (extremely high and low, respectively) were not correlated with any of the three variables (Fig. 2).

The Hlreal was positively correlated with ANPP and PV (Fig. 3A and B). In turn, ANPP was positively correlated with PV ($r = 0.57$, $P = 0.03$) and was not significantly correlated with PVstand ($r = 0.43$, $P = 0.11$), while PV was not correlated with PVstand ($r = 0.10$, $P = 0.73$). As a consequence of the described correlation matrix among the independent variables, the relationship between Hlreal and ANPP was determined by ANPP itself, not by its correlation with the other two independent variables (see table inserted in Fig. 3A). Instead, the correlation between PV and Hlreal was determined indirectly by the correlation between PV and ANPP (Fig. 3B). Finally, the lack of correlation between Hlreal and PVstand resulted from the balance between a negative direct effect of PVstand on Hlreal and an indirect positive effect of ANPP on PVstand (Fig. 3C). All the patterns described in this paragraph remained unchanged when one or both lowest Hlreal values were discarded.

The multiple regression including the three independent variables highly improved model fitting (R^2 increased from 0.35, for

the best univariate model, to 0.68 for the three-variate model; Table 4). In the three-variate model, Hlreal was again positively related to ANPP but was not related at all with PV. Instead, PVstand appeared significant with a negative coefficient, as had been suggested by the negative direct effect of PVstand on Hlreal shown in Fig. 3C.

The bivariate regression model including ANPP and PVstand, inverse of degradation, explained a higher proportion of Hlreal than the other two potential bivariate models (Table 4). It showed a positive effect of ANPP but a negative effect of PVstand, both with similar importance ($Hlreal = -1.7 + 0.004 ANPP - 0.21 PVstand$, $R^2 = 0.64$, $\beta_{ANPP} = 0.82$, and $\beta_{PVstand} = -0.65$, both slopes different from 0 $P < 0.001$; Fig. 4A).

The Hlsust was positively correlated with ANPP and PVstand but not with PV (Fig. 3D–F). PVstand was more important than ANPP in determining Hlsust because PVstand had a direct effect while ANPP had an indirect effect mediated by its relationship with PVstand (Fig. 3D and F).

The multiple regression relating Hlsust with the three independent variables showed a marginally better fitting than the univariate correlation with PVstand (R^2 increased from 0.72 to 0.78), with only the slope of PVstand being significantly different from 0 (Table 4). In

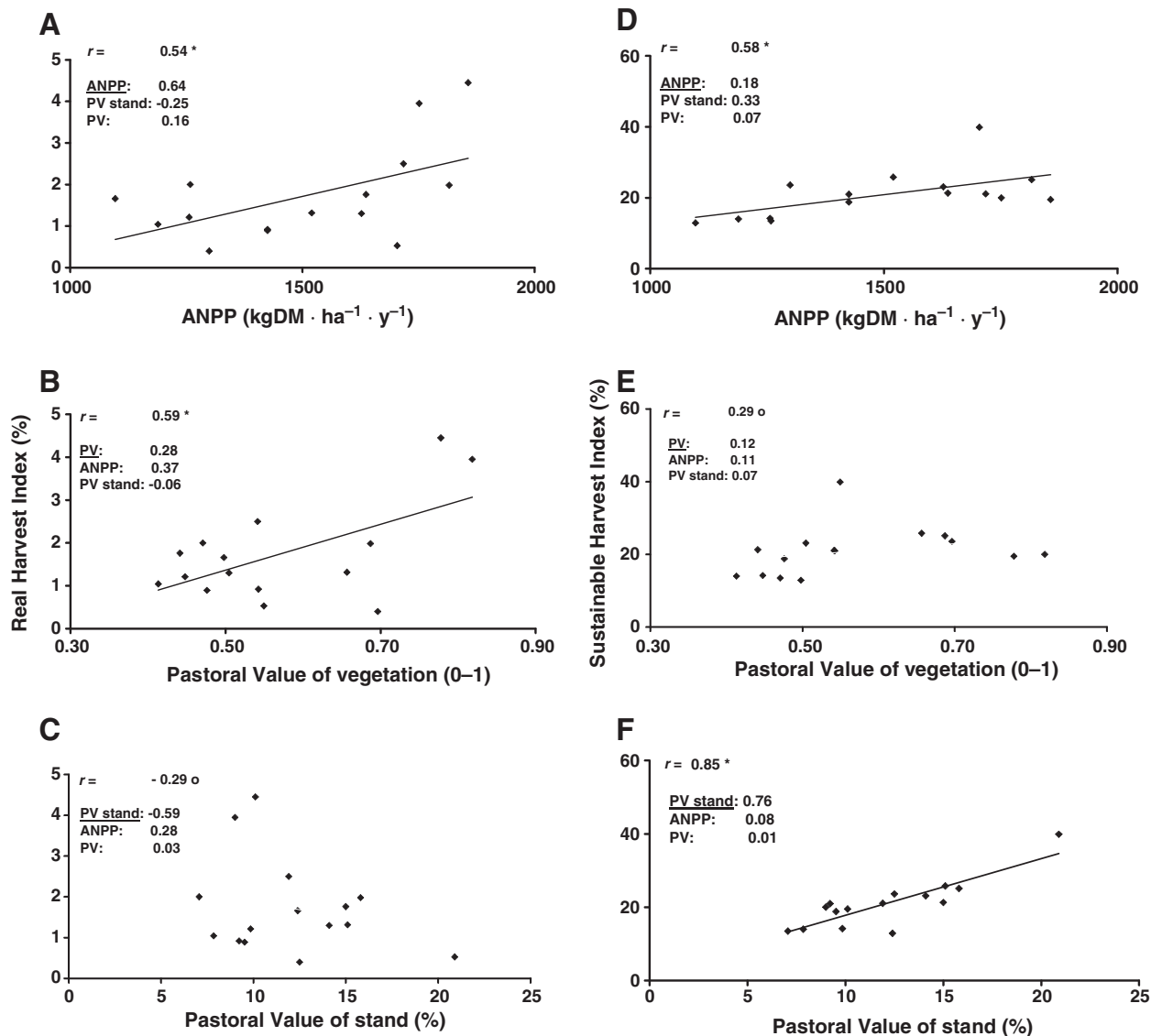


Fig. 3. Linear regressions between real harvest index (A, B, C) or sustainable harvest index (calculated for a use factor of 40% for the key species, *Festuca pallescens*) (D, E, F), and ANPP (A, D), PV (B, E), and PVstand (C, F). In the simple linear regressions, the Pearson correlation coefficient and the Path Analysis results show the relative importance of the direct effect of each independent variable (highlighted) and the indirect effect mediated by the correlation with other independent variables.

Table 4

Regression analyses performed between Hlreal or Hlsust and the three independent variables included in this study: aboveground net primary production (ANPP), pastoral value of vegetation (PV), and pastoral value of stand (PVstand). The y-intercept (a), the partial slopes, the overall R², and the P-value are included for each model. Asterisks indicate y-intercepts or partial slopes significantly different from zero. P-values indicate that the model explains a significant portion of the overall variance (P < 0.05).

Harvest index	Model	a	ANPP	PV	PVstand	R ²	P-value
Hlreal	a+bx	-2.14	0.0026*			0.3	0.036
		-1.31		5.34*		0.35	0.022
		2.83*			-0.09	0.09	0.296
Hlsust	a+bx1+cx2	-2.62	0.0015	3.73		0.41	0.0429
		-1.73	0.0039*		-0.21*	0.64	0.0025
		-0.15		5.66*	-0.11	0.46	0.0236
Hlsust	a+bx1+cx2+dx3	-2.05	0.0031*	2.51	-0.19*	0.68	0.0045
		-2.93	0.016*			0.33	0.0241
		12.1		15.6		0.09	0.286
Hlsust	a+bx1+cx2	2.29			1.55*	0.72	<0.0001
		-2.57	0.0168	-3.12		0.34	0.086
		-6	0.0072		1.34*	0.77	<0.0001
Hlsust	a+bx1+cx2+dx3	-3.65		11.24	1.51*	0.77	<0.0001
		-6.78	0.0049	6.26	1.39*	0.78	0.0006

the best bivariate model, Hlsust showed a significant relationship with ANPP and PVstand, with an R² practically identical—but more significant—than the three-varied multiple regression (Hlsust = -6.0 + 0.00715 ANPP + 1.344 PVstand, R² = 0.77, β_{ANPP} = 0.26, and β_{PVstand} = 0.74; Fig. 4B). However, the PVstand slope was significantly higher than 0 (P < 0.01), while that of ANPP was only marginally different from 0 (P = 0.11). Finally, the Hlsust calculated from the bivariate model (Hlsust = f(ANPP, PVstand)) was similar to that estimated from Oosterheld et al. (1992) model (r = 0.58, P < 0.05) (see solid line in Fig. 4B).

Discussion

As our initial hypothesis proposed, at low stocking rate Hlreal increased with ANPP. However, in opposition to our hypothesis, Hlreal increased with degradation, which was estimated as the inverse of the forage value of vegetation weighed by total forage cover (Fig. 3A–C). These findings must be carefully extrapolated because they could change at higher stocking rates. Taking into account this

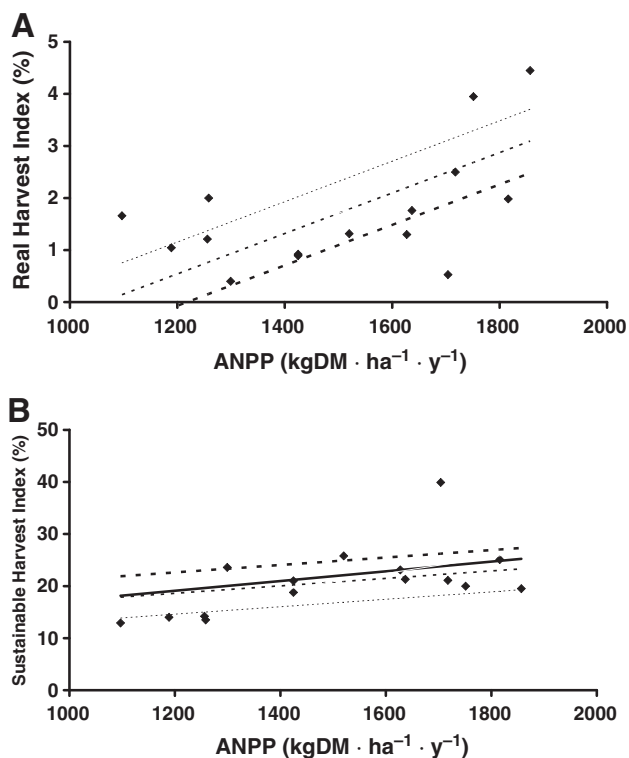


Fig. 4. Multiple regressions between real harvest index (A) or sustainable harvest index (calculated for a use factor of 40% for the key species, *Festuca pallescens*) (B), and both ANPP and PVstand. The three dotted lines represent the values estimated as a function of ANPP and three fixed values of PVstand (mean: central line; 25% higher than mean: coarse line; 25% lower than mean: thin line; $N = 15$). In panel B, the coarse entire line represents the HI estimated from ANPP using the regional model of Oesterheld et al. (1992). * $0.05 > P > 0.01$; ** $P < 0.01$.

precaution, our results suggest that when animal demand is relatively low, as in our study, sheep consume more intensely the most productive sites, but at a given ANPP level they prefer the most degraded sites. This response is consistent with the trend to a higher proportion of biomass of *Festuca pallescens* removed by sheep as degradation increased (Fig. 2F). We speculate that with increasing degradation, the within-year accumulation of dead plant material decreases and then forage biomass is more accessible. As a consequence of higher grazing pressure, degraded areas may have also younger, shorter, and more digestible grasses than undegraded areas because they have lower cellulose and lignin concentrations (Wilmshurst et al., 2000) and greater nutrient concentrations (Jarrell and Beverly, 1981). In addition, sheep may be more protected against predators, like puma (*Felis concolor*) or zorro colorado (Patagonian red fox, *Lycalopex culpaeus*), in the most degraded sites because of higher visibility (Bertiller and Ares, 2008). A similar pattern was also described for wild African herbivores (Riginos and Grace, 2008).

In agreement with the hypothesis, HIsust increased with ANPP (Fig. 3D) and decreased with degradation (Fig. 3F). This implies that ANPP is one of the main controls of carrying capacity but that degradation has an even more important direct negative effect. Our values of HIsust were closely similar to the “safe levels of forage utilisation” of 15–20% obtained by Johnston et al. (1996) for Queensland, Australia (average precipitation of 16 meteorological stations = 562 mm [www.bom.gov.au, website of the Bureau of Meteorology of Australia Government], highly similar to the annual precipitation of the study site),

Our results provide new insights on the contradiction between regional and subregional scale models that related HIsust and ANPP (Oesterheld et al., 1992; Golluscio, 2009). Across a wide, 300–7 000 kgDM · ha⁻¹ · y⁻¹ gradient of ANPP, HIsust increased

from 6% to 22% (Oesterheld et al., 1992). In contrast, for the low, Patagonian end of that gradient (300–1 500 kgDM · ha⁻¹ · y⁻¹), a subregional model predicted that HIsust decreased from 22% to 5% (Golluscio, 2009). The pattern of HIsust revealed in the present work was similar to the pattern of HIsust estimated from the regional model (Oesterheld et al., 1992). This suggests that HIsust is close to HIsust at the broadest regional scale, but controls different from ANPP prevent HIsust to reach HIsust at a smaller scale (Fig. 4B). These regional HIsust values are similar to those attained in this study site under normal circumstances (3.5 times the annual stocking rate used in this experiment). Severe overgrazing would exist at the least productive end of the short gradient, probably linked to the high proportion of familiar and pastoralist production systems under more restrictive environmental conditions, whose low economic profitability induces the use of high stocking rates (Golluscio et al., 2009). At the most productive end of the short gradient, the positive correlation between ANPP and PV led us to discard the hypothesis that it is forage quality which constrains harvest index. Instead, we propose that it may not be possible to reach HIsust because of the low accessibility due to the accumulation of dry biomass, at the scale of individual plant (Cingolani et al., 2005), and the winter inaccessibility of *Festuca pallescens* grasslands, currently subjected to severe snowfall (Soriano, 1956), at the paddock scale. Another factor limiting the attainment of HIsust at this most productive end of the short gradient is the structural and logistical restrictions at the scale of ranch, namely poor subdivision, difficulties to move animals, and impossibility to maintain high animal stocks during winter (Golluscio et al., 1998a).

The visual scale of defoliation degree developed in this work correlated with the proportion of removed biomass of different plant species. As a consequence, biomass consumption was estimated in real time by a nondestructive method. This allowed making a large number of replications within a reasonable time frame, covering the spatial heterogeneity in the distribution of both plant populations and animal consumption. It also allows making repeated measurements of defoliation over time on the same individuals, therefore discarding the effect of the among-plants consumption heterogeneity. In the specific case of our experiment, the defoliation degree of the key species, *Festuca pallescens*, allowed us to acceptably estimate HIsust. On the other hand, although HIsust was not predicted by the defoliation degree of any individual species, it was correlated with the mean proportion of biomass removed for all the species, weighed by their respective plant cover ($r = 0.55$), and with both the cover and defoliation degree of the key species (R^2 of bivariate model = 0.62). These findings suggest that, as the measurement of both defoliation degree and plant cover is simple and nondestructive, their simultaneous monitoring may be a useful tool to prevent ecosystem degradation and loss of animal condition.

The extrapolation of our results must be careful because they were obtained in a single year and a single paddock. Additional research is required to explore the effect of temporal and spatial heterogeneity on the patterns of plant production and consumption. Taking into account this precaution, our work seems to confirm that a use factor of 40% for the key species may not guarantee a HIsust for the entire plant community. For more than 50 y it has been stated that the use intensity for a plant community may not necessarily depend on a linear relationship between the defoliation degree of a key species and that of the entire community (Holechek et al., 1989; Stoddart et al., 1955; Vallentine, 2001). Our experiment shows that monitoring grazing intensity on the three most important forage species of the community is better than monitoring the key species only. Even with the low HIsust achieved in our study, the proportion of biomass removed from the most preferred species, *Poa ligularis*, was above 60%, much higher than the 40% recommended for the key species (Fig. 2A). On

the other hand, *Pappostipa speciosa* was hardly consumed. To develop sustainable grazing systems for this plant community, it is necessary to determine the effect of even higher biomass removal (Fig. 1A) on the growth and survival rates of individuals and populations of *P. ligularis*. If some of these effects were deleterious for this species, the grazing systems aiming to reach the HIsust at the community level would cause a severe floristic impoverishment because of the reduction of density and/or vigor of the most preferred species.

Implications

Management alternatives that can allow reaching a harvest index closer to the sustainable one, without endangering the survival of the species more preferred than the key species, must be explored. Some of these strategies are deferred grazing or successive grazing with high stocking rates of animal categories of decreasing nutritional requirements during short time periods (Golluscio et al., 1998a; Briske et al., 2008; Golluscio et al., 2009). These strategies are relatively compatible with the rangeland management systems commonly applied in the Patagonian region, ranging from strict continuous grazing, to seasonal use of paddocks, to adaptive management experiences here described and others more closely linked to the holistic management school. However, rest rotation strategy represents a radically different management paradigm, providing paddocks with a full-year recovery period every alternate year. This strategy allows sheep to heavily utilize paddocks in one year and then rest those paddocks the next year, allowing vigor recuperation of most preferred species (Kirkman and Moore, 1995). Within this framework, a use factor higher than 40% for the key species is an obvious requisite to maintain the stocking rate at the overall ranch scale. However, under normal climatic conditions, probably grasses that are heavily grazed in one year may recover vigor and biomass during the next full-year resting period. Clearly, this range management strategy deserves more attention in fragile ecosystems as the Patagonian steppes.

The increase of Hlreal with site degradation suggests that under low stocking rate there would be a positive feedback between grazing and degradation: Because animals prefer the most degraded sites, these sites will deteriorate quicker than the less degraded ones. Two of the most widespread methods to estimate carrying capacity in the Patagonian steppes take into account either ANPP or PVstand, an inverse indicator of degradation (Golluscio et al., 2009). Perhaps one of the most important contributions of this work is the conceptual model (Fig. 4B), which estimates HIsust taking into account both ANPP and PVstand, thus integrating primary production, forage quality, and degradation. However, this strategy must be accompanied by monitoring the grazing intensity on a group of indicator species with different abundance and animal preference in order to promptly detect degradation processes.

Acknowledgements

José Paruelo, Marina Omacini, Juan Carlos Guevara, Viviana Nakamatsu, Gonzalo Irisarri, Fernando Cavagnaro, Magalí Valenta, and Guillermo García Martínez enriched early versions of the manuscript with their valuable comments. We also greatly acknowledge the comments of the journal editors and two anonymous reviewers.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.rama.2015.03.002>.

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