A functional classification of 63 common Poaceae in the "Campos" grasslands of South America

Pablo Cruz[1,✉]; Lucrecia Lezana[2]; Martín Durante[3]; Martin Jaurena[4]; Mercedes Figari[5]; Leandro Bittencourt de Oliveira[6]; Jean-Pierre Theau[1]; Ernesto Massa[2]; Julio Viegas[6] & Fernando L. Ferreira de Quadros[6]

[1] AGIR, Université de Toulouse, INRA, INPT, INP-EI PURPAN, Castanet-Tolosan, France. [2] EEA INTA Paraná, Entre Rios, Argentina. [3] EEA INTA Concepción Del Uruguay, Argentina. [4] Instituto Nacional de Investigación Agropecuaria, INIA, Uruguay. [5] DGDR-MGAP, Tacuarembó, Uruguay. [6] Universidade Federal de Santa Maria, Santa Maria, Brazil.

Abstract. The natural grasslands that form part of the "Campos" of South America contain a large number of species at the paddock level (high α diversity), but little differentiation among paddocks (low β diversity). Thus, forage resources at the farm level have slightly different seasonal growth peaks, in part due to the low frequency of fertilization, the lack of differential grazing management and mowing of these plant communities. To stimulate diversification of these forage resources, it is possible to take advantage of differential responses of each type of plant community to changes in their use. Characterizing species by functional traits allows to orient the use of forage resources according their functional composition, thus increasing the diversity of vegetation types, which favors differentiation of growth peaks among paddocks. After an initial division between C_3 and C_4 species, 63 Poaceae species were classified into eight groups or plant functional types (PFT) according to their preferred degree of soil fertility and use intensity. Based on the leaf dry matter content (LDMC) measured in experiments in Brazil, Uruguay and Argentina, we distinguished four PFT, two for C_3 species and two for C_4 species, with LDMC less than or equal to 300 mg/g. The species of these four PFT are adapted to fertile environments and intensive defoliation. Fertilizing and using more intensively vegetation dominated by species with these low LDMC can diversify the use value of paddocks, thus facilitating use of forage resources at the farm level.

[Keywords: diversity, LDMC, C_3 and C_4 species, management]

Resumen. Una clasificación funcional de 63 Poáceas comunes de los pastizales naturales de Sudamérica. Los pastizales naturales que forman parte de los "Campos" de América del Sur se caracterizan por tener un gran número de especies a nivel de potrero (alta diversidad α) y una diferenciación entre potreros relativamente baja (baja diversidad β). Esto significa que, a nivel de predio, se dispone de un conjunto de recursos forrajeros con picos de crecimiento estacionales poco diferenciados. En parte, esto es consecuencia del uso escaso de prácticas diferenciales de fertilización, de manejo del pastoreo y de corte sobre dichas comunidades vegetales. Para incentivar la diversificación de los recursos forrajeros (aumentar la diversidad β) se puede aprovechar la respuesta diferencial de los pastizales frente a cambios en su uso. Caracterizar las especies a través de sus rasgos funcionales permite orientar el uso del recurso al aplicar el tratamiento adecuado a su composición, aumentar la diversidad de tipos de vegetación y favorecer, de esta manera, el escalonamiento de la producción entre distintos potreros. Luego de una primera división entre especies C_3 y C_4, se clasificaron 63 Poáceas en 8 grupos o tipos funcionales de plantas (PFT) según su preferencia por sitios más o menos fértiles e intensidades de uso más o menos altas. Sobre la base de los valores de contenido en materia seca foliar (LDMC) obtenidos en varios experimentos en Brasil, Uruguay y Argentina se separaron cuatro PFT, dos de especies en C_3 y otros dos de especies en C_4, que presentan valores inferiores o muy cercanos a 300 mg/g. Las especies de estos cuatro PFT están adaptadas a ambientes fértiles y defoliadas con gran intensidad, a diferencia de los cuatro PFT restantes. Fertilizar y usar de forma más intensa la vegetación donde dominan las especies con esas bajas LDMC permitirá diversificar el valor de uso de los potreros, lo que facilita el aprovechamiento de los recursos forrajeros a nivel de predio.

[Palabras clave: diversidad, LDMC, especies C_3 y C_4, manejo]

Introduction

The "Campos" grasslands of southeast South America, that extends from approximately 30-35° S, is mainly covered by multispecies grasslands dominated by Poaceae species. This area is part of a much larger region called "Pastizales del Río de la Plata" (28°-38° S; 47°-67° W), a grassland region that covers southeastern Brazil, central-eastern Argentina and Uruguay (Soriano 1991). The climate of the region ranges from subtropical humid in the north to temperate humid in the south. In this region, grasslands have a high α diversity with about 30 species/m² (Overbeck et al. 2005), characterized by the coexistence of grass species with both metabolic pathways C_3 and C_4 grass species. Their proportions in a given area depend on nutrient availability (Pallares et al. 2005), the seasonal water availability, the season of the year and, especially, mean annual temperature (Epstein et al. 1997; Sage et al. 1999).

Livestock production based on the natural grassland, that covers most of the area, is an important economic activity. Grazing such diverse vegetation is complex, since it is affected by the vegetation's phenological heterogeneity (Nabinger et al. 2011; Guido et al. 2014) and climate variability (Cruz et al. 2014). Nonetheless, the coexistence of vegetation containing C_3 and C_4 species can be considered an advantage because the latter have offset growth periods, which provides the ability to increase resource diversity (Fidelis 2009). Grassland vegetation of the Campos is managed extensively, practically without inputs (Pallares et al. 2005; Modernel et al. 2016). As β diversity (differentiation among communities) is linked mainly to historical disturbance levels (Hanke et al. 2014), the homogeneous management across the region could explain the low inter-paddock diversity. At the farm scale, observing subtle differences in species composition between paddocks may facilitate to adopt practices that increase these differences to create different types of vegetation for different purposes (i.e., mown or deferred paddock grazing when its growth is high to use it in events of fodder crisis, as low temperature or low water availability [Nabinger et al. 2011]).

Traditionally, management of natural vegetation relies on a relatively detailed description of its botanical composition (Balent 1991), an approach that addresses difficulties of performing potentially complex vegetation surveys. Most agricultural advisors, however, do not have the time to describe botanical composition nor the botanical skills to recognize all the species present. Given these limitations, researchers have proposed simplifying description of grassland vegetation by replacing botanical composition with functional composition (Ansquer et al. 2004b; Cruz et al. 2010a). Grassland vegetation can be described simply by the relative abundance of plant functional types (PFT). Although some expertise is always necessary to identify species in grasslands to determine the proportions of PFT, this approach (Theau et al. 2010) requires much less botanical knowledge because it is limited to dominant species of the Poaceae family (Ansquer et al. 2005).

To establish PFT for use by agronomic advisors, Ansquer et al. (2004a) used LDMC, which classifies Poaceae species according to growth rate. They obtained five PFT that allowed to describe the use value of native grasslands at the farm level. Later, this classification was modified by including other functional traits, such as specific leaf area (SLA), leaf life span (LLS) and tensile strength (Cruz et al. 2010b), which did not necessarily improve the definition of PFT compared to those of Ansquer et al. (2004a). The LDMC, a proxy of tissue density (Hodgson et al. 2011), provides information about the morphogenic potential of a species, which determines its growth strategy (Ryser and Lambers 1995). Low tissue density allows, for a given mass, larger volumes of organs to capture more resources (resource-capture strategy). In contrast, species with higher tissue density capture fewer resources and conserve them longer (resource-conservation strategy) according to a recognized trade-off, widely described in the literature (Reich et al. 1992; Ryser 1996; Wright et al. 2004). Species with low tissue density are more abundant in high-fertility conditions and respond strongly to an increase in nutrient availability (e.g., mineral or organic fertilization). This response will increase efficiency of fertilizer use if grasslands are dominated by species that have a growth strategy orientated towards resource capture. Otherwise, when grasslands have similar compositions, their vegetation can be oriented towards a dominance of resource-capture or resource-conservation PFT if they are fertilized or not, respectively (Brambilla et al. 2012).

In the present study, our objective was to broaden this functional approach to the high

α diversity grasslands of the Campos biome. Functional description of the species of these grasslands can reveal small differences in the use value, which could improve the use of herbaceous resources at the farm level with an adequate management (Ansquer et al. 2005; Cruz et al. 2010a; Sosinski and Pillar 2004). We examined different environmental conditions in the Campos, assuming that interspecific differences are greater than intraspecific trait variation (Kazakou et al. 2014) and that trait-based ranking of functional groups is consistent across environments. Changes in environmental conditions, however, may alter leaf morphological traits (Chapin et al. 1987; Hodgson et al. 2011) and change trait-based ranking of species (Rose et al. 2013; Siebenkäs et al. 2015). If these trait-based rankings vary, then the ability of functional group classification to predict community responses to agricultural practices may be limited (Lepš et al. 2011). In the present study, leaf traits were measured on the youngest adult leaves and on plants growing under solar radiation (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Thus, we measured standardized leaves to capture the potential of each species and not the effects of biotic or abiotic factors on this potential. Under these conditions, we hypothesized that intraspecific trait variation did not change the ranking of species when they are characterized by their LDMC, making it possible to develop homogeneous PFT based on this trait.

MATERIALS AND METHODS

Two leaf traits, LDMC and SLA, known for their ability to predict resource-use strategy (Wilson et al. 1999), were measured on 63 species of Poaceae (20 C_3 and 43 C_4) in a set of experiments at multiple sites located in Brazil, Uruguay and Argentina. In all sites, green leaf lamina samples were weighted as green material, scanned and oven dried to constant dry weight for calculating LDMC and SLA according to the Cornelissen et al. (2003) protocol. Considering all the sites, more than 80 species were identified and measured, but commercialized genotypes (e.g., *Dactylis glomerata*, *Brachiaria decumbens*) and species for which the minimum number of individuals (set at 10) could not be reached were excluded from analysis, resulting in a final list of 63 species (Table 1). More than 7000 measurements were taken from these species.

Brazil

In Porto Alegre, 34 species of Poaceae were cultivated in the botanical garden of the park of the Faculty of Agronomy, Universidade Federal do Rio Grande do Sul (UFRGS), and two experiments in natural grasslands, one with three levels of nitrogen (0, 100 and 200 kg N.ha^{-1}.year^{-1}) and the other with four levels of daily forage supply (4, 8, 12 and 16 kg of dry matter per 100 kg of live weight.ha^{-1}.day^{-1}). All grass species, representing at least 90% of the biomass of Poaceae species in the Campos, were collected (N=22 and 49 species for the first and second experiment, respectively). In Santa Maria, Poaceae species came from a) a field experiment (Restinga area) in which availability of nutrients and water was tested in 32 species, and b) a greenhouse experiment (Universidade Federal de Santa Maria, UFSM) that studied effects of phosphate fertilizer on leaf traits of 4 species.

Uruguay

In Tacuarembó, Poaceae species came from a grazing experiment in which cattle were excluded, and the 23 most abundant grass species after 70 days of vegetative regrowth were harvested and measured. Two other experiments were performed, one with three levels of nitrogen (0, 100 and 200 kg N.ha^{-1}.year^{-1}) and the other to follow the evolution of leaf trait values during the growth cycle (30, 60 and 120 days of regrowth)

Argentina

In Concepción (C) del Uruguay, 48 Poaceae species were a) cultivated in pots and 17 species b) came from an experiment in which grazing frequency (approximately every 2 or 4 months) and fertilization (no input or an input of 150 kg N+100 kg P.ha^{-1}.year^{-1}) were varied.

Analysis procedure

Leaf traits (LDMC and SLA) were measured on the entire last expanded leaves (blade without sheath) that were healthy, undamaged, well exposed to solar radiation and rehydrated for 8 hours in the dark at 4 °C, according to the protocol of Cornelissen et al. (2003) and Pérez Harguindeguy et al. (2013). After rehydration and drying in an oven at 60 °C until constant mass was reached, leaf mass was measured with an electronic balance with a precision of at least 0.1 mg. The minimum

area of measured leaves was set at 2 cm². If a single leaf did not reach this area, many leaves were measured until they reached this threshold. These areas were measured according to each site's equipment, either an optical area meter or computer software.

To determine PFT, species were first divided into groups based on their metabolic pathway (C_3 or C_4). This choice was justified by phenological differences between the pathways, a variable of primary importance when deciding how to manage these grasslands due to differences in the seasonality of forage production. In each metabolic group, homogeneous PFT groups were obtained from LDMC values alone using ascending hierarchical classification according to Ward's method (Euclidean distance) calculated with Statgraphics Centurion software (Statpoint Technologies, Inc., The Plains, VA, USA).

Using LDMC alone avoids classifying species using traits that are correlated with each other, such as LDMC and SLA or LDMC and leaf strength. Moreover, LDMC predicts primary production of plant communities more accurately than SLA (Smart et al. 2017). We used the relations measured between LDMC and SLA to locate species and PFT in the "worldwide leaf economics spectrum" (Wright et al. 2004), compare our results to those from a broad database (Garnier et al. 2001b; Flores et al. 2014) and verify that our results corresponded well to a general model of vegetation functioning. Nitrogen content, which was also analyzed, was not used because of its high variability. Indeed, nitrogen content depends much more than other leaf traits on environmental factors such as nitrogen availability and, as explained by Garnier et al. (2001a), is the trait that ranks species among seasons, years and sites with the lowest repeatability.

We tested whether LDMC modified trait-based species ranking due to the response to different treatments: a) nutrient availability (Tacuarembó and Santa Maria), b) days of regrowth (Tacuarembó), c) frequency of grazing and fertilization (C. del Uruguay), and d) forage supply and fertilization (Porto Alegre). Stability of the ranking based on LDMC was analyzed for the species shared by all treatments of an experiment; thus, species from experimental collections that had no treatments (Porto Alegre, C. del Uruguay) and in experiments with fewer than three species in common (e.g., Restinga, UFSM) were excluded from the analysis. For all treatments that could be analyzed, the Spearman rank test was used to test the effect of the treatments on changes in the ranking of species based on LDMC.

Results

The C_3 and C_4 metabolic groups had similar ranges of LDMC and SLA. SLA values varied from 5.82 (*Jarava plumosa*) to 38.28 m²/kg (*Phalaris aquatica*) for C_3 species and from 9.23 (*Aristida venustula*) to 33.39 m²/kg (*Chloris canterae*) for C_4 species (Table 1). LDMC values varied from 156.2 (*Phalaris aquatica*) to 432.7 mg/g (*Piptochaetium montevidensis*) for C_3 species and from 198.0 (*Stenostaphrum secundatum*) to 492.1 mg/g (*Aristida laevis*) for C_4 species (Table 1). *J. plumosa* had the lowest coefficient of variation (CV) of LDMC (3.7%)
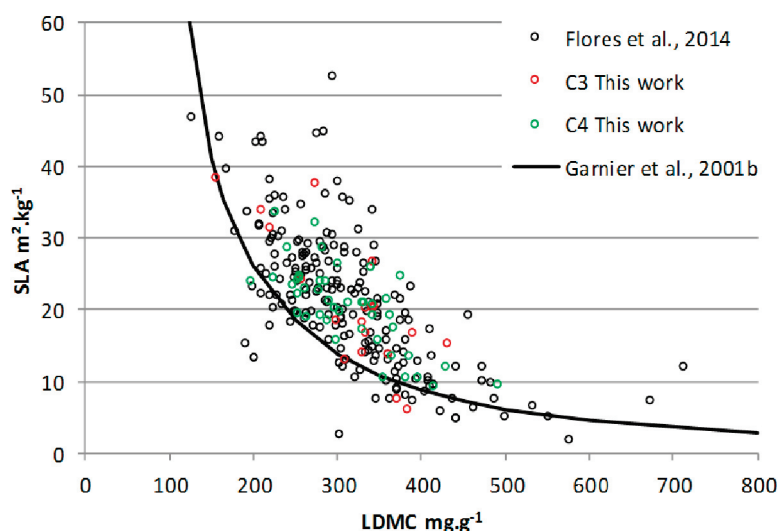

Figure 1. Relation between specific leaf area (SLA) and leaf dry matter content (LDMC) for the C_3 and C_4 Poaceae species measured in the present study; comparison with results of Flores et al. (2014) for Poaceae and with the model from Garnier et al. (2001b) for herbaceous species.

Figura 1. Relación entre el área foliar específica (SLA) y el contenido de materia seca foliar (LDMC) en las especies C_3 y C_4 medidas en este trabajo; comparación con los resultados de Flores et al. (2014) para especies Poáceas y con el modelo establecido por Garnier et al. (2001b) para especies herbáceas.

Table 1. Species name, code, mean and standard deviation (SD) of leaf dry matter content (LDMC, mg/g) and specific leaf area (SLA, m²/g), and number of individuals (n) measured.

Tabla 1. Nombre de las especies, código, media y desvío standard (SD) del contenido de materia seca foliar (LDMC, mg/g) y del área foliar específica (SLA, m²/g) y número de individuos (n) medidos.

C3 species	Code sp.	LDMC	SD LDMC	SLA	SD SLA	n
Agrostis montevidensis Nees	AGRMON	310	33	12	4	22
Briza minor L.	BRIMIN	275	51	37	6	61
Bromus auleticus Trin. ex Nees	BROAUL	299	35	18	4	101
Chascolytrum subaristatum (Lam.) Desv.	CHASUB	334	52	16	4	130
Danthonia rhizomata Swallen.	DANRIZ	210	22	33	3	20
Deyeuxia viridiflavescens (Poir.) Kunth var.	DEYVIR	334	24	20	3	20
Glyceria multiflora Steud.	GLYMUL	221	17	31	2	20
Hordeum stenostachys Godr.	HORSTE	330	20	18	1	20
Jarava plumosa (Spreng.) S. W. L. Jacobs & J. Everet	JARPLU	384	14	5	0	20
Leersia hexandra Sw.	LEEHEX	342	39	26	4	20
Melica macra Nees	MELMAC	331	16	13	1	20
Nassella charruana (Arechav.) M.E.Barkworth	NASCHA	342	85	20	7	29
Nassella hyalina (Nees) Barkworth	NASHYA	345	85	20	7	25
Nassella neesiana (Trin. & Rupr.) Barkworth	NASNEE	389	56	16	3	147
Nassella nutans (Hack.) Barkworth	NASNUT	372	51	7	1	20
Panicum sabulorum Lam	PANSAB	255	59	24	7	194
Phalaris aquatica L.	PHAAQU	156	31	38	4	12
Piptochaetium bicolor (Vahl) É.Desv.	PIPBIC	362	14	13	1	20
Piptochaetium montevidense (Spreng.) Parodi	PIPMON	432	86	15	4	276
Poa lanigera Ness	POALAN	259	47	24	5	33
C4 species	**Code sp.**	**LDMC**	**SD LDMC**	**SLA**	**SD SLA**	**n**
Andropogon lateralis Nees	ANDLAT	343	54	19	6	162
Andropogon ternatus (Spreng.) Nees	ANDTER	359	33	21	2	12
Aristida jubata (Arechav.) Herter	ARIJUB	356	34	10	1	23
Aristida laevis (Nees) Kunth	ARILAE	492	61	9	2	66
Aristida murina Cav.	ARIMUR	385	40	13	3	25
Aristida uruguayensis Henrard	ARIURU	430	25	11	2	29
Aristida venustula Arechav.	ARIVEN	416	87	9	4	13
Axonopus argentinus Parodi	AXOARG	278	48	22	5	62
Axonopus compressus (Sw.) P.Beauv.	AXOCOM	242	43	28	9	23
Axonopus fissifolius (Raddi) Kuhlm.	AXOFIS	255	50	24	4	358
Bothriochloa laguroides (DC.) Herter	BOTLAG	302	32	26	4	84
Bothriochloa saccharoides (Sw.) Rydb.	BOTSAC	286	27	23	1	20
Bouteloua megapotamica (Spreng.) Kuntze	BOUMEG	332	56	20	5	33
Chloris canterae Arechav.	CHLCAN	226	20	33	2	20
Chloris grandiflora Roseng. & Izag	CHLGRA	330	39	17	4	29
Cynodon dactylon (L.) Pers.	CYNDAC	284	38	28	6	38
Eleusine tristachya (Lam.) Lam.	ELETRI	303	26	19	1	20
Eragrostis bahiensis Roem. & Schult.	ERABAH	264	16	18	2	20
Eragrostis lugens Nees	ERALUG	363	47	19	2	63
Eragrostis neesii Trin.	ERANEE	282	34	18	2	41
Eragrostris plana Ness	ERAPLA	365	69	13	1	13
Eustachys paspaloides (Vahl) Lanza & Mattei	EUSPAS	275	32	32	11	27
Eustachys retusa (Lag.) Kunth	EUSRET	280	56	23	2	29
Eustachys uliginosa (Hack.) Herter	EUSULI	248	15	23	2	20
Mnesithea selloana (Hack.) de Koning & Sosef	MNESEL	331	49	20	3	303
Paspalum dilatatum Poir.	PASDIL	262	23	22	3	138
Paspalum nicorae Parodi	PASNIC	292	57	20	4	61
Paspalum notatum Flügeé	PASNOT	298	42	19	4	521
Paspalum paucifolium Swallen	PASPAU	288	25	18	3	43
Paspalum plicatulum Michx.	PASPLI	300	54	15	5	196
Paspalum pumilum Ness	PASPUM	224	31	24	3	51
Paspalum unispicatum (Scribn. & Merr.)	PASUNI	254	19	22	2	20
Paspalum urvillei Steud.	PASURV	253	48	19	3	64
Sacharum angustifolium (Nees) Trin.	SACANG	382	46	10	3	20
Schizachyrium microstachyum (Desv. ex Ham.) Roseng.	SCHMIC	343	73	20	8	146
Schizachyrium spicatum (Spreng.) Herter	SCHSPI	375	55	24	5	30
Setaria parviflora (Poir.) M.Kerguelen	SETPAR	254	51	24	3	158
Setaria vaginata Spreng.	SETVAG	314	86	20	3	40
Sorghastrum pellitum (Hack.) Parodi	SORPEL	350	39	15	2	21
Sporobulus indicus (L.) R.Br.	SPOIND	397	72	10	5	173
Steinchisma hians (Elliott) Nash	STEHIA	340	35	25	3	56
Stenotaphrum secundatum (Walter) Kuntze	STESEC	198	21	23	3	20
Trachypogon montufari (Kunth) Nees	TRAMON	367	30	17	2	29

and *Setaria parviflora* the highest (27.4%); the mean CV of all 63 species was 13.6%. Relations between LDMC and SLA values corresponded well to those that Flores et al. (2014) obtained for Poaceae species and seemed to show no differences between C$_3$ and C$_4$ species (Figure

1). The relations measured in the present study also overlapped the relation predicted by the model of Garnier et al. (2001b) for herbaceous non-Poaceae (Figure 1).

Hierarchical classification of LDMC values resulted in eight PFT groups, four (A to D)

for each metabolic pathway (C_3 or C_4 [Table 2]). For each metabolic pathway, differences in mean LDMC values (Table 2) between the four groups were highly significant ($P<0.001$). Relations between mean values of LDMC and SLA for the eight PFT groups revealed slightly higher mean LDMC and SLA than predicted

Table 2. Grouping of 63 species in eight plant functional types (PFT) obtained by the Ward's method of hierarchical classification according to mean (standard deviation) of leaf dry matter content (LDMC) and specific leaf area (SLA). Letters A-D correspond to different PFT of species with C3 and C4 photosynthetic pathways. Different lowercase letters indicate significant differences ($P<0.001$). See Table 1 for species codes.

Tabla 2. Agrupamientos de las 63 especies en ocho tipos funcionales de plantas (PFT) obtenidos mediante una clasificación jerárquica según el método de Ward con los valores medios (desvíos estándar) del contenido de materia seca foliar (LDMC) y el área foliar específica (SLA). Las letras A-D corresponden a diferentes TFP de especies con vía fotosintética C_3 o C_4. Letras minúsculas diferentes indican diferencias significativas ($P<0.001$). Los códigos de las especies son los de la Tabla 1.

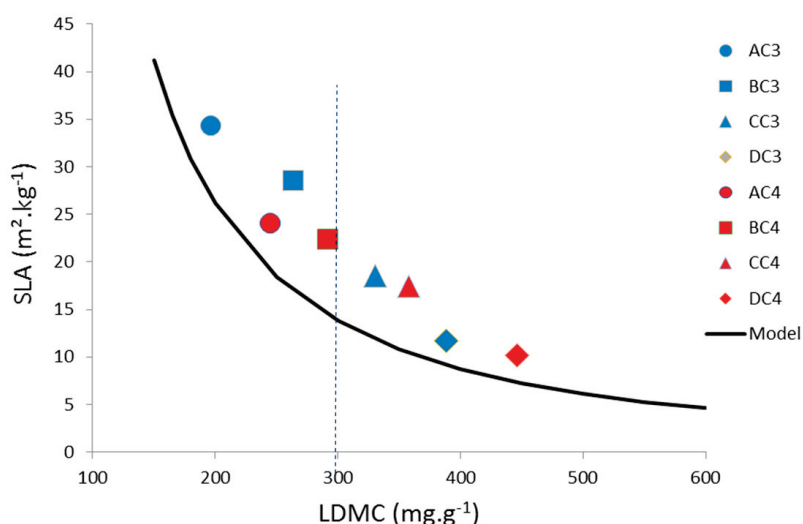| Group	C_3 Species (code)	Mean LDMC (mg/g)	Mean SLA (m²/kg)	C_4 Species (code)	Mean LDMC (mg/g)	Mean SLA (m²/kg)
A	Danrhi, Glymul, Phaaqu	195.9[a] (34.8)	34.4 (3.6)	Axocom, Axofis, Chlcan, Erabah, Eusuli, Pasdil, Paspum, Pasuni, Pasurv, Setpar, Stesec	244.1[a] (20.0)	24.1 (4.0)
B	Brimin, Pansab, Poalan	263.3[b] (10.6)	28.6 (7.8)	Axoarg, Botsac, Botlag, Cyndac, Eletri, Eranee, Eusret, Euspas, Pasnic, Pasnot, Paspau, Paspli, Setvag	291.2[b] (11.7)	22.4 (4.5)
C	Agrmon, Broaul, Chasub, Deyvir, Horste, Leehex, Melmac, Nascha, Nashya	330.2[c] (15.4)	18.5 (4.1)	Andlat, Andter, Arimur, Arijub, Boumeg, Chlgra, Eralug, Erapla, Mnesel, Sacang, Schmic, Schspi, Spoind, Sorpel, Stehia, Tramon	357.9[c] (20.5)	17.5 (4.9)
D	Jarplu, Nasnee, Nasnut, Pipbic, Pipmont	388.4[d] (27.0)	11.7 (4.8)	Arilae, Ariuru, Ariven	446.3[d] (40.3)	10.2 (1.4)

Figure 2. Relations between mean specific leaf area (SLA) and mean leaf dry matter content (LDMC) for the eight functional groups of C_3 and C_4 Poaceae species determined in the present study, compared to predictions of a model from Garnier et al. (2001b) for herbaceous non-Poaceae species. The vertical line represents a LDMC threshold above which all species would be classified as having a resource-conservation (or low-growth) strategy.

Figura 2. Relación entre valores medios del área foliar específica (SLA) y del contenido de materia seca foliar (LDMC) para los ocho grupos funcionales de gramíneas C_3 y C_4 comparados con las predicciones del modelo de Garnier et al. (2001b) para especies herbáceas no Poáceas. La línea vertical representa el umbral de LDMC por encima del cual las especies serian de tipo conservación de recursos (estrategia de crecimiento lento).

Table 3. Stability of species ranking among treatments based on leaf dry matter content LDMC in experiments including grazing as a factor of variation. Coefficient of correlation of Spearman and *P*-value (probability of maintaining ranking): *P-0.1; **P≤0.05; ***P-0.001. ns: the ranking of species changed. 3A, Porto Alegre: 4, 8, 12 and 16 kg of dry matter per 100 kg of live weight.ha⁻¹.day⁻¹. 3B, Concepción del Uruguay: F+F+: fertilized and high frequency of grazing; F+F-: fertilized and low frequency of grazing; F-F+: not fertilized and high frequency of grazing and F-F-: not fertilized and low frequency of grazing. Fertilized=150 kg N and 100 kg P.ha⁻¹.year⁻¹. High and low frequency of grazing: every 2 or 4 months, respectively. See Table 1 for species codes.

Tabla 3. Estabilidad del ranking de especies entre tratamientos según el contenido de materia seca foliar (LDMC) en experimentos que incluyeron el pastoreo como un factor de variación. Coeficiente de correlación de Spearman y nivel de probabilidad de conservación de rangos: *P-0.1; **P≤0.05; ***P-0.001; ns: el rango de especies fue modificado. 3A, Porto Alegre: 4, 8, 12 y 16 kg de materia seca por 100 kg de peso vivo.ha⁻¹.día⁻¹. 3B, Concepción del Uruguay: F+F+: fertilizado y alta frecuencia de pastoreo; F+F-: Fertilizado y baja frecuencia de pastoreo; F-F+ No fertilizado y alta frecuencia de pastoreo; F-F-: No fertilizado y baja frecuencia de pastoreo. Fertilizado: 150 kg N y 100 kg P.ha⁻¹.año⁻¹. Alta y baja frecuencia de pastoreo: cada 2 ó 4 meses, respectivamente. Los códigos de las especies son los de la Tabla 1.

3A	4 kg	8 kg	12 kg
8 kg	0.90*		
12 kg	0.90*	1.00***	
16 kg	1.00***	0.90*	0.90*

Species (5): Andlat, Axocom, Pasnot, Pipmon, Setpar

3B	F+F+	F+F-	F-F+
F+F-	0.71ns		
F-F+	0.77ns	0.94**	
F-F-	0.83*	0.89*	0.77 ns

Species (5): Broaul, Mnesel, Nasnee, Pasdil, Pasnot, Schmic

Table 4. Stability of the species ranking among treatments based on LDMC in experiments in which grazing was not a factor of variation. Coefficient of correlation of Spearman and *P*-value (probability of maintaining rankings): *P≤0.1; **P≤0.05; ***P-0.001. 4A. Tacuarembó: 0, 100 and 200 kg N.ha⁻¹.year⁻¹. 4B. Tacuarembó: 30, 60 and 120 days of regrowth. 4C. Santa Maria: 0 NP, NP (100 g N and 50 mg P/kg of soil) y P (50 mg P/kg of soil). See Table 1 for species codes.

Tabla 4. Estabilidad del ranking de especies entre tratamientos según el contenido de materia seca foliar (LDMC) en experimentos en los que no se incluyó el pastoreo como factor de variación. Coeficiente de correlación de Spearman y nivel de probabilidad de la conservación de rangos: *P≤0.1; **P≤0.05; ***P≤0.001. 4A, Tacuarembó: 0, 100 y 200 Kg N.ha⁻¹.año⁻¹. 4B, Tacuarembó 30, 60 y 120 días de rebrote. 4C. Santa María: 0 NP, NP (100 g N and 50 mg P/kg de suelo) y P (50 mg P/kg de suelo). Los códigos de las especies son los de la Tabla 1.

4A	0 N	100 N
100N	1.00***	
200N	0.96**	0.96**

Species (7): Axofis, Botlag, Mnesel, Stehia, Pasdil, Pasnot, Paspli

4B	30 d	60 d
60 d	0.95**	
120 d	0.89**	0.96**

Species (5): Botlag, Mnesel, Pasdil, Pasnot, Paspli

4C	0 NP	NP
NP	1.00***	1.00***
P	1.00***	

Species (4): Andlat, Arilae, Axofis, Pasnot

by the model of Garnier et al. (2001b [Figure 2]). Half of the groups (A and B) lay below a threshold of 300 mg/g of LDMC, below which species are classified as having a resource-capture strategy (Figure 2).

When the Spearman rank test was applied to experiments in which grazing was a treatment, the ranking of species did not change significantly regardless of the treatments compared (Porto Alegre [Table 3A]) or changed slightly for 3 out of 6 treatments compared (C. del Uruguay [Table 3B]). For experiments in which nitrogen availability (Tacuarembó [Table 4A]), time of regrowth (Tacuarembó [Table 4B]) or nitrogen and phosphorus availability (Santa Maria [Table 4C]) were treatments, no change in the ranking of species was observed.

DISCUSSION

Our results supported the hypothesis which establishes that intraspecific trait variation did not change the ranking of species when they were characterized by their LDMC. We analyzed information form several experiments and species rankings appeared stable along the gradients of factors studied. Out of 21 comparisons of rankings between treatments, only 3 rankings changed slightly. Thus, LDMC can be considered a reliable functional marker, making it possible to develop homogeneous PFT based on this trait.

In contrast with previous studies, we focused on Poaceae species and included both metabolic groups (C_3 and C_4). We found higher LDMC and SLA values than those predicted by the Garnier et al. (2001b) model, which was developed with dicotyledonous species. This difference from predicted values can be explained by the fact that Poaceae species integrate veins into their leaf lamina

to provide structure, while dicotyledonous species obtain structure from their petioles, which lie outside the leaf lamina. Cruz et al. (2010b) worked with C_3 Poaceae species and classified them by resource-use strategy and phenology based on four functional traits (LDMC, SLA, LLS and tensile strength). Our classification was based only on LDMC, a trait that distinguishes species by resource-use strategy. Resource capture species prefer higher soil fertility and defoliation intensity than resource conservation species (Ansquer et al. 2004b; Cruz et al. 2010a). We found similarity in the ranges of trait values between the two metabolic groups. However, as C_3 species grow in autumn, winter and spring, while C_4 species grow mainly in spring and summer, separating metabolic pathways before constructing PFT based allows separating species by phenology.

Of the four groups that make up each metabolic pathway, groups A and B follow a resource-capture strategy because their mean LDMC values are the lowest. In contrast, groups C and D, with the highest mean LDMC values, tend to follow a resource-conservation strategy (Ryser 1996). That these groups of growth strategies are located on either side of the threshold value of 300 mg/g of LDMC agrees with a previous study performed in a temperate climate with only C_3 species (Cruz et al. 2010b). Ranges of trait values are sufficiently large to distinguish groups of species that should respond differently to an increase in resource availability. Thus, for both metabolic pathways, species in groups A and B should respond more strongly than those in C and D to any factor increasing growth, such as fertilization, irrigation, or an increase in access to sunlight, which may occur due to defoliation.

It is interesting to note that nearly all species of the same genus follow the same strategy.

This is true for C_3 (*Nasella* sp. and *Piptochaetium* sp.) and C_4 (*Andropogon* sp., *Aristida* sp. and *Schizachyrium* sp.) species with a resource-conservation strategy and for C_4 species with a resource-capture strategy (*Axonopus* sp., *Paspalum* sp., *Botriochloa* sp., *Eustachys* sp. and *Setaria* sp.). Only the genus *Eragrostis* divides its species between resource conservation (*E. lugens* and *E. plana*) and resource capture (*E. bahiensis* and *E. neesii*). This pattern reveals strong phylogenetic consistency among species of the same genus, which may allow identification of the resource-use strategy of other species belonging to the genera we studied.

Assuming that managing grasslands communities is complex and that it could be facilitated by high inter-paddock functional diversity, these functional types allow the identification of paddocks in which forage production or its use can be intensified. This is true for grasslands in which species with resource-capture strategies (groups A and B) dominate. In contrast, in paddocks dominated by species of groups C and D, intensification must be lower. For example, grassland whose species abundance is dominated by *Axonopus* sp., *Paspalum* sp. or *Botriocholoa* sp. will be more suited to receive fertilizer applications or to be more frequently or intensely defoliated (by grazing or mowing) than those dominated by *Andropogon* sp., *Aristida* sp. or *Bouteloa* sp. In the absence of high inter-paddock functional diversity, it will be necessary to create and maintain it. In practice, PFT composition of herbaceous vegetation can be determined by the De Vries and De Boer (1959) method or the Theau et al. (2010) simplification of it. In summary, the classification of PFT reported in the present work provide a basis for the development of differential management of forage resources in time and space, applicable to livestock farms.

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