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Community aggregated traits disclose functional responses to seasonal resource fluctuations and spatial heterogeneity

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Nomenclature
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Abstract

Aim: To investigate changes in community-level functional responses to rainfall seasonality in Neotropical grasslands through the analysis of community aggregated traits.

Location: Semi-natural grasslands in the Río Grande de Matagalpa watershed, Nicaragua.

Methods: We measured 14 functional response traits that are indicators of plant resource-use strategies, across 32 herbaceous and four woody species in eight permanent plots: leaf size, specific leaf area, leaf dry matter content, leaf lifespan, foliar concentrations of P, N, Ca, K and Mg, plant height, lateral spread by clonal growth, root depth, start of flowering period and length of the period from flowering to seed shed. We calculated the community-weighted means (CWM) with trait values weighted by species cover for five different paddocks 11 times (between 2 Jul 2007 and 26 May 2008), and grouped them into four periods according to rainfall seasonality: early rainy season, late rainy season, early dry season and late dry season.

Results: Community aggregated values of specific leaf area, leaf dry matter content, leaf lifespan, foliar concentrations of P, N, Ca, K and Mg, length of the period from flowering to seed shed, and to a lesser extent lateral spread by clonal growth responded to temporal variations in rainfall, and corresponded to a considerable extent to expectations based on plant resource-use strategies along resource supply gradients. Community aggregated values of specific leaf area and foliar nutrient concentration were higher in the rainy season than in the dry season, while we observed an opposite trend with leaf dry matter content and leaf lifespan.

Conclusions: Semi-natural grasslands of central Nicaragua experience shifts in plant trait dominance that correspond with changes in resource supply given by rainfall seasonality, indicating that the stabilizing function of net primary productivity found in earlier studies can in part be a consequence of temporal differentiation in functional responses.

Introduction

Despite increasing consensus that biological diversity underpins the capacity of plant communities to support resilience and cope with environmental change by sustaining and stabilizing function (Ospina et al. 2012; Jucker et al. 2014; Zang et al. 2014), our knowledge of how this capacity is associated with functional responses of organisms to the environment is limited. Evidence increasingly indicates that the diversity of functional adaptations of co-existing plants is central to this response capacity (Westoby et al. 2002). A number of recent studies document high trait differentiation and functional diversity within communities (Bermúdez & Retuerto 2014; Carmona et al. 2015). Craine et al. (2013) in their global study showed that drought

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tolerance traits in grasses were well distributed across climates and phylogenies, suggesting that most native grasslands were likely to contain a high diversity of trait expressions, a property which could help maintain ecosystem functioning in response to environmental change (Loreau et al. 2001). One possible mechanism that is involved in stabilizing function, other than niche differentiation in space, could be temporal shifts in the dominance of different response traits, triggered by temporal changes in resource supply (Carmona et al. 2015).

Most studies on trait responses to the environment address spatial variability (Kraft & Ackerly 2010; de Bello et al. 2013), and those addressing temporal shifts have generally studied inter-annual fluctuations (Carmona et al. 2015), but fine-grain temporal responses, revealing functional differences among species that can both help understand co-existence mechanisms and the implications of functional diversity on stabilizing ecosystem function are few (Bermúdez & Retuerto 2014). Seasonally dry environments, as is the case in our study, provide an opportunity to investigate fine-scale community-level shifts in trait dominance in response to intra-annual changes in resource supply.

Individual plant responses to resource availability are governed by physiological and morphological trade-offs; determining a fundamental axis of specialization and adaptation (Grime et al. 1997), i.e. the *leaf economics spectrum* (Wright et al. 2004) and its broader extension to plant, community and ecosystem scales (*plant economics spectrum*; Reich 2014) entails contrasting strategies of resource use associated with different resource supply conditions. These strategies consist of high rates of resource acquisition and circulation, and low resource use efficiency when resources are in high supply; and a strategy of conservative resource use and low demand, associated with resource-poor conditions (Díaz et al. 2004; Wright et al. 2004).

A number of morpho-ecophysiological traits are related to these resource-use strategies. Foliar traits such as specific leaf area (SLA), leaf dry matter content (LDMC), leaf lifespan (LLS) and leaf nitrogen and phosphorus concentrations (N and P, respectively) are robust indicators of resource use (Garnier et al. 2004; Ordoñez et al. 2009). High values of SLA, N and P correspond to high resource acquisition and circulation, and high values of LDMC and LLS indicate a resource conservative strategy. In addition, leaf K correlates positively with leaf N and P and, in turn, leaf N, P, K, Ca and Mg correspond with rapid growth under favourable growth conditions (Grime et al. 1997).

The capacity of vegetative spread correlates with nutrient supply, which in turn, is coupled to water resources, and linked to resource-use strategies in an integrated plant economics spectrum (Reich 2014): fertilization increases vegetative mobility and branching (Sammul et al. 2003), and low rates of lateral spread have been found where there is low soil fertility in alpine snow-bed plants (Rusch et al. 2011). In the case of root traits, differentiation in water use strategies is evidenced by differences in root depth (RD). For instance, grasses consistently use water in the shallow soils layers, while forbs can use soil water from greater depths when the upper horizons become dry (Nipper & Knapp 2007).

Flowering phenology, i.e. the start of the flowering period (SFP) and length of the period from flowering to seed shed (LFS) is associated with plant development and a temporal differentiation of resource use over seasonal periods (Roscher et al. 2004), but a linkage of phenological traits and resource-use strategies is unclear. However, in a parallel study (Ospina et al. 2009, S. Ospina, unpubl. data), species with shorter LLS had shorter LFS, and *vice versa*.

Plant size, anatomy and architecture are usually linked to resource gradients (Westoby 1998; Westoby et al. 2002), but these relationships vary strongly with life form (Cornelissen et al. 2003). Small leaf size (LS) generally corresponds with stressful environments (dry, disturbed; Wright et al. 2004; Niinemets et al. 2007), and plant height (PH) is positively related to gradients of soil resources (Fonseca et al. 2000; Cornelissen et al. 2003; Rusch et al. 2009).

The particular functional traits of individuals and populations can be scaled up to communities and ecosystems (Díaz et al. 2004; Violle et al. 2007) through community-weighted mean values of a trait (henceforth, CWM) or the community aggregated trait, representing the dominant trait values in a community (Violle et al. 2007), and which is a good indicator of trait–environment relationships (Schellberg & Pontes 2012). Our case study area is dominated by Neotropical savannas and grasslands that experience pronounced rainfall seasonality; the temporal pattern of rainfall is the most important cause of resource supply variation in these systems, which is reflected in the pattern of herbaceous above-ground primary productivity in the area (Ospina et al. 2012; Rusch et al. 2014). There is also evidence of different species attaining dominance at different times of the growing period in similar savanna systems (Sarmiento 1984, 1992). In this study, we used CWM of traits associated with resource use as metrics to explore seasonal trends in community-level functional responses to resource availability and, specifically, the extent to which shifts in resource supply are reflected in the predominant resource-use strategies. We specifically hypothesized that: (i) CWMs of SLA, N and P would be higher in the rainy season, while CWM of LDMC and LLS would be lower in the rainy season, increasing in the dry season. Also CWM of leaf Ca, K and Mg concentrations would be higher in the rainy season than in the dry season; (ii) CWM of RD would be shallower in the rainy season when superficial water supply is high; (iii) CWM of lateral spread by clonal growth (LSCG) would be longer in the rainy season than in the dry season; (iv) CWM of LFS would present a seasonal trend similar to CWM of LLS, increasing in the dry season; and (v) CWM of LS and PH would be larger in the rainy season.

Methods

Study site

The study was conducted in the Río Grande de Matagalpa watershed in Central Nicaragua (12°31′–13°20′ N; 84°45′–86°15′ W). The area is located in the municipality of Muy Muy, at sites within an altitudinal range of 280–380 m a.s.l. There is a clear contrast between rainy and dry periods, and the predominant land use is livestock farming with relatively homogeneous livestock management. The natural vegetation of the region corresponds to a transitional tropical sub-humid forest (Holdridge 2000) with semi-deciduous vegetation, and is referred to as seasonally dry tropical forest by Bullock et al. (1995). The typical vegetation is an assemblage of native and naturalized species including grasses, herbs and woody plants. The grassland vegetation develops after forest clearing, or on fallow land, and is maintained by grazing and weed control.

Rainfall recorded between Nov/Dec 2007 and Apr/May 2008 was <10% of the mean annual rainfall (1971–2000) for Muy Muy (1547.1 ± 147 mm) and the annual mean air temperature was 24.3 °C (http://www.ineter.gob.ni/direcciones/meteorologia/clima%20nic/caracteristicasdelclima).

The topography is undulating, with slopes between 5% and 40%. The bedrock consists of Tertiary volcanic tuff, a type of pyroclastic rock. Tuff in the area seems to be impermeable, which explains the limited infiltration often observed in flat areas during the rainy season. In most flat areas, it is common to find soils with Vertic properties (A. Nieuwenhuyse, J.A. Arauz-Ubeda & S. Ospina, unpubl. data).

Species selection and trait measurements

Thirty-two herbaceous and four common woody species were selected based on earlier studies that assessed the composition of the grasslands (Ospina 2005; Ospina et al. 2012). Our target species comprised various life forms of annual and perennial plants including two pteridophytes, representing various vascular plant families with a wide range of functional traits (Appendix S1).

The traits were studied in plants occurring in eight paddocks with sizes ranging between 2.5 and 5.0 ha. The paddocks were at least 12 yr old, and were managed with cattle grazing, hand weeding at least once a year, and no fertilizer application. At the beginning of the rainy season 2007 (early June), the paddocks were mown to ground level to homogenize the height of the sward at the start of the trait study. Woody species taller than 20 cm were cut at ground level and the harvested biomass was removed from the paddocks. Soon after mowing, one permanent sampling plot (PSP) of 100 m × 100 m was randomly delimited in each paddock. Fourteen traits were measured: nine foliar traits: leaf size (LS), specific leaf area (SLA), leaf dry matter content (LDMC), leaf lifespan (LLS) and foliar concentrations of P, N, Ca, K and Mg; three whole plant traits: plant height (PH), lateral spread by clonal growth (LSCG) and root depth (RD); and two phenological traits, start of flowering period (SFP) and the length of the period from flowering to seed shed (LFS). The procedures for trait measurement, including the number of replicates, are listed in Table 1 and explained in detail in Appendix S2.

Species cover, soil and climate data

Species cover was studied in five paddocks with similar topsoil: organic matter (4.9–7.8%), pH_{water} (6.1–6.6), with relatively high levels of Ca (12–30 $mg \cdot kg^{-1}$) and no deficit of Mg (4.0–10.0 $mg \cdot kg^{-1}$) or K (0.30–1.10 $mg \cdot kg^{-1}$). Further details of species cover, soil and climate data are provided as supplementary material (Fig. S3, Table S3-a in Appendices S3, S4, S5).

We estimated plant cover in four 1 m × 1 m quadrats located in each plot between 2 Jul 2007 and 26 May 2008. Surveys started after 21 days of grazing exclusion following 1/2 days of grazing and were subsequently followed by monthly observations. In total, we obtained 440 vegetation cover records: five plots, four quadrats per plot, two times (at the start and the end of each grazing exclusion period), and 11 periods. Species cover was estimated visually (Greig-Smith 1983) using a 1 m × 1 m metallic frame subdivided into 5 cm × 5 cm squares (in total 400 per quadrat). The cover of each species was estimated as a proportion of the projected area of the plant, added over the 400 squares, independently from the cover of other species. With this methodology, total cover can exceed 100% per subplot due to the species aerial overlap.

Daily rainfall data were collected from three rain gauges located in three villages within the study area (three plots). Additional data came from a weather station of the Nicaraguan Institute of Land Studies (INETER) located <5.7 km from the survey plots (two plots). We considered that the rainy season began when the daily average rainfall reached and remained above 11.5 mm for seven consecutive days in at least two of the rain gauges. The rainy season ended when the daily average rainfall decreased

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Table 1. List of measured species traits with measurement unit, type of statistical variable, number of replicates, brief procedure for measurement, and references.

Trait Type	Trait	Measurement Unit	Statistical Type	Number of Replicates	Mode of Measurement	Reference
Leaf	Leaf size (LS)	mm^2	Interval	9–30	On scanned leaves, average size of simple and compound leaves, including petioles	Cornelissen et al. (2003)
	Specific leaf area (SLA)	$mm^2 \cdot mg^{-1}$	Ratio	9–30	Fresh lamina area/oven dry lamina mass, including petioles	Cornelissen et al. (2003)
	Leaf dry matter content (LDMC)	$mg \cdot g^{-1}$	Ratio	9–30	Oven-dry mass/ Fresh mass, including petioles	Cornelissen et al. (2003)
	Leaf lifespan (LLS)	Weeks	Interval	10	Weekly counts of leaves of each species on about 900-1000 leaves tagged from leaf emergency to leaf fall into eight different isolated modules set up for this study	Ryser and Urbas, (2000); Cornelissen et al. (2003)
	Leaf nitrogen concentration (N)	$mg \cdot g^{-1}$	Ratio	1 Compound sample ≥100 individuals	With an auto-analyzer (ThermoFinnigan, Flash EA 1112) by the total combustion method. Total amount of N / Leaf dry mass	Cornelissen et al. (2003)
	Leaf phosphorus concentration (P)	$mg \cdot g^{-1}$	Ratio	1 Compound sample ≥100 individuals	Colorimetry using molybdate and stannous chloride and read by spectrophotometer UV/V (absorbance at 660 nm). Total amount of P / Leaf dry mass	Cornelissen et al. (2003)
	Leaf calcium concentration (Ca)	$mg \cdot g^{-1}$	Ratio	1 Compound sample ≥100 individuals	With spectrophotometer of atomic absorption (Equipment Analysis 100, Perkin Elmer), Total amount of Ca / Leaf dry mass	
	Leaf potassium concentration (K)	$mg \cdot g^{-1}$	Ratio	1 Compound sample ≥100 individuals	With flame emission spectrometry (absorbance at 768 nm). Total amount of K / Leaf dry mass	
	Leaf magnesium concentration (Mg)	$mg \cdot g^{-1}$	Ratio	1 Compound sample ≥100 individuals	With spectrophotometer of atomic absorption (Equipment Analysis 100, Perkin Elmer),Total amount of Mg / Leaf dry mass	
Whole plant	Plant height at onset of flowering (PH)	(cm)	Interval	30	The shortest distance between the highest photosynthetic tissue and ground level at the beginning of flowering	Cornelissen et al. (2003)
	Lateral spread by clonal growth (LSCG)	(cm)	Interval	8	The horizontal yearly growth of ramets followed over time	Knevel et al. (2005) with modification
	Root depth	(cm)	Interval	10	Digging of trenches and taking samples from three walls of each trench to determine the depth of the root systems for each species	Schuster, (1964) with modification
Phenological	Start of flowering period (SFP)	Week of the year (WOY)	Interval	8 per week	Continuous weekly surveys by observing the phenological status of individuals present along a 50 m long transect	–
	Length of the period from flowering to seed shed (LFS)	Weeks	Interval	8 per week		–

and remained below 2.0 mm. Accordingly, the rainy season 2007 started on 21 Jun and ended on 30 Nov, and the dry season 2008 started on 1 Dec 2007 and ended on 26 May 2008. Daily rainfall records were accumulated between 2 Jul 2007 and 26 May 2008, and both the rainy season 2007 and the dry season 2008 were divided in two periods (early/late) of approximately similar duration to characterize within-season variation on community-aggregated traits: Early rainy season 2007 (2 Jul–14 Sep 2007), late rainy season 2007 (15 Sep–30 Nov 2007), early dry season 2008 (1 Dec–27 Feb 2008) and late dry season 2008 (1 Mar–26 May 2008).

Data analysis

We calculated the CWM for each trait and each cover plot combining the species cover data of the eight subplots for each of the 11 seasonal periods, weighting the trait values by species cover data using f-Diversity software (Casanoves et al. 2011).

The distribution of mean species' values of all foliar traits (SLA, LDMC, LLS, leaf N and leaf P concentrations) had skewness ≤ 0.77; therefore, their trait values were suited for analysis without transformation. Mean values of traits with skewness ≥ 1 were transformed in order to reduce the effect of asymmetry before conducting the CWM analysis. We used log functions in the case of leaf traits (LS, leaf Ca, K and Mg concentrations), whole plant (PH and RD) and the phenological trait, SFP, and rank transformation in the case of LFS.

Since trait CWMs can vary in time and also in space, we tested the relative contribution of these sources of variation. Since CWMs were repeated in time and variances did not fulfil homoscedasticity assumptions, we used general linear mixed models that allowed modelling the variances and correlating data (Di Rienzo et al. 2011). Trait CWMs were modelled as a response to seasonal period (four levels) and "cover plot" as the random factor, and the two-way interaction term. The best-fitted models were selected with the AIC and the Bayesian information criterion (BIC), and the normality assumption was tested with the Shapiro-Wilk test. To compare means, we used the Fisher's least significant difference (LSD) test (significance level = 0.05). The data were analysed using the rlme function (R Foundation for Statistical Computing, Vienna, AT) implemented in the InfoStat statistical software, v 2009 (Di Rienzo et al. 2009). The soil chemical analyses and the PCA on soil properties are described in Fig. S3, Table S3-a in Appendix S3).

Results

All sites experienced similar seasonal rainfall fluctuations. The accumulated rainfall was correlated in all cover plots for all periods (between 2 Jul 2007 and 26 May 2008; $r^2 = 0.9880$, $P < 0.0001$) and also in: early rainy season 2007 ($r^2 = 0.9950$, $P < 0.0001$), late rainy season 2007 ($r^2 = 0.9643$, $P < 0.0001$), early dry season 2008 ($r^2 = 0.9602$, $P < 0.0001$) and late dry season 2008 ($r^2 = 0.9082$, $P < 0.0001$). The daily rainfall values for the individual sites are provided in Appendix S5.

Seasonal variation of the aggregated functional traits

Total plant cover varied little within the period studied (Table S4, Appendix S4). However, significant temporal differences were observed for the CWMs of most traits. CWM of foliar traits such as LS, SLA, LDMC and LLS, foliar nutrients (P, N, Ca, K and Mg) and LSCG and LFS changed significantly among seasons (Table 2, Fig. 1). There was a general trend of the CWM of foliar nutrients to increase slightly through the rainy season and to decline from the

Table 2. *F*-Statistics of community weighted means of foliar, whole plant and phenological traits in response to plot and four seasonal time periods in semi-natural grasslands of Central Nicaragua. Sources of variation with *F* values. One, two and three asterisks indicate significance levels at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Trait Type	CWM Traits	Source of Variation		
		Seasonal Period (*t*)	Plot (*p*)	*t* × *p*
Foliar Traits	LS	5.57**	27.01***	1.72
	SLA	8.45***	29.50***	2.45*
	LDMC	10.43***	22.53***	2.72*
	P	5.11**	43.65***	1.86
	N	16.76***	46.61***	0.44
	Ca	9.32***	52.29***	0.98
	K	33.74***	73.80***	2.87**
	Mg	13.27***	26.71***	2.73*
	LLS	25.52***	10.85***	1.86
Whole Plant Traits	PH	2.35	1.51	1.16
	LSCG	3.81*	138.86***	5.63***
	RD	0.44	71.53***	1.61
Phenological Traits	SFP	1.91	90.48***	0.58
	LFS	32.24***	27.12***	2.19*

Leaf size (LS), specific leaf area (SLA), leaf dry matter content (LDMC), leaf phosphorus concentration (P), leaf nitrogen concentration (N), leaf calcium concentration (Ca), leaf potassium concentration (K), leaf magnesium concentration (Mg), leaf lifespan (LLS), plant height (PH), lateral spread by clonally growth (LSCG), root depth (RD), starting flowering period (SFP) and length of the period from flowering to seed shed (LFS).

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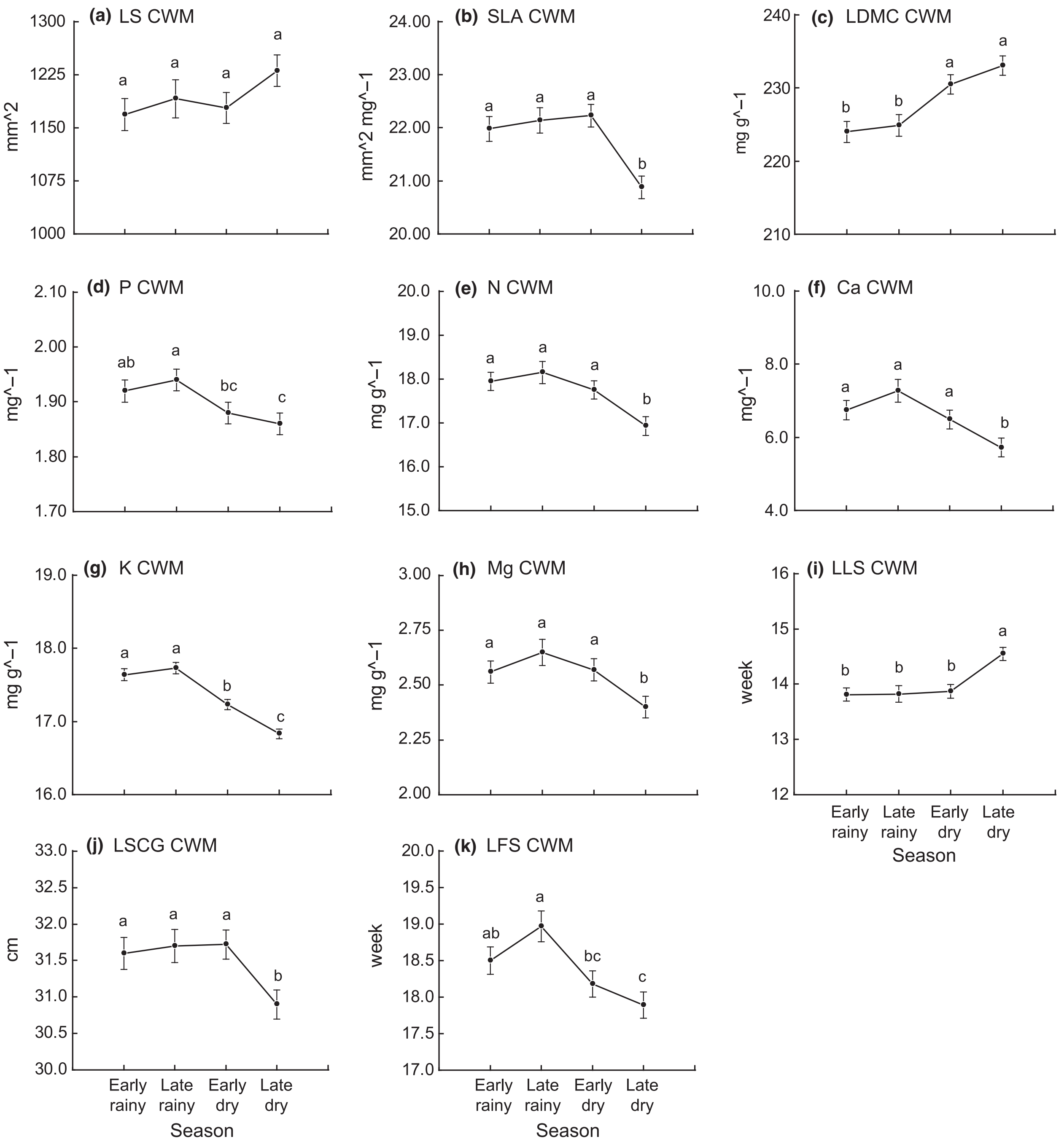

Fig. 1. Mean ± SE of functional traits weighted by species cover during a continuous period (2 Jul 2007 to 26 May 2008) in five plots with semi-natural grasslands of Central Nicaragua. CWM: community-weighted mean. (**a**) LS, leaf size, (**b**) SLA, specific leaf area, (**c**) LDMC, lead dry matter content, (**d**) P, leaf phosphorus concentration, (**e**) N, leaf nitrogen concentration, (**f**) Ca, leaf calcium concentration, (**g**) K, leaf potassium concentration, (**h**) Mg, leaf magnesium concentration, (**i**) LLS, leaf lifespan, (**j**) LSCG, lateral spread by clonal growth and (**k**) LFS, length of the period from flowering to seed shed. The letters on each point indicate statistical differences among the seasonal periods according to the Fisher LSD test at $P < 0.05$.

start of the dry season. Specifically, and as expected, there were higher CWM of foliar P, N, Ca, K and Mg, and higher SLA and longer LSCG in the late rainy season compared to the late dry season, and in the early dry season compared to the late dry season (Fig. 1b,d,e,f,g,h,j). The seasonal variation of the CWM of SLA was similar to that of LSCG (Fig. 1b,j). In contrast, CWM of LDMC and LLS (Fig. 1c,i) showed an opposite pattern, with low values in the late rainy season and high values early in the dry season.

The CWM of LFS (Fig. 1k) changed strongly with season, with longer reproductive periods in the rainy season compared to the dry season; and, contrary to our expectations, with an opposite trend to that of LLS (Fig. 1i), i.e. shorter leaf longevity in the rainy season. Leaf lifespan increasing with decreasing resource availability. CWM of LFS was, on the other hand, positively associated with CWM of leaf nutrient concentration (Fig. 1d,e,f,g,h). Finally, CWM of LS changed significantly with season (ANOVA $F_{5.57}$ $P = 0.0031$), but these differences were not reflected in the Fisher's LSD test (Fig. 1a).

Site heterogeneity and its effects in the variation of the aggregated functional traits

The two-first axes of a PCA explained 77% of the variation in soil properties. Axis I (48% of the variation) was determined by the relative proportion of sand and clay particles, and Mg and Ca concentrations; Axis II (29% of the variation) was determined by the levels of available P and pH. Soils in plots 15, 13 and 8 had higher proportions of sand and lower concentrations of Mg and Ca than plots 14 and 7. Plots 7, 8 and 13 had higher available P and lower soil pH, while plots 14 and 15 showed the opposite trend (Fig. S3, Table S3-a in Appendix S3).

The CWMs of all foliar traits, the two phenological traits and of LSCG and RD showed significant differences among plots (Table 2, Fig. 2). In the case of LLS and LFS, the seasonal variation was stronger than plot differences, but for the others (except for pH with no differences); plot differences were the main source of variation (Table 2). Differences among plots were the only significant source of variation for CWM of RD and SFP (Fig. 2k,l), and an important source for SLA and leaf K concentration (Fig. 2b,g). However, the variation in CMW of SLA, leaf K and RD did not correspond well with the axes of soil differentiation among the plots (Fig. 2b,g,k). Plot 15 differs significantly in the CWM of various traits, the majority indicating an over-representation of trait values associated with resource acquisition strategies, i.e. higher values of LS, foliar P, N, Ca and Mg, and low LDMC and LLS (Fig. 2a,e,f,h,i). CWM of clonal growth (LSCG) and RD also differed significantly (Fig. 2j,k) as well as that of LFS (Fig. 2m). There was also a significant interaction term of time and plot ($P < 0.05$) for six aggregated traits, SLA, LDMC, K, Mg, LSCG and LFS.

Discussion

We investigated whether there were shifts in the dominance of resource-use strategies along a resource availability variation determined by rainfall seasonality in semi-natural grasslands in Nicaragua. We hypothesized that along with a seasonal sequence, there would be a turnover in relative abundance of species, and that those changes in dominance between species would signal different strategies of resource use across the seasons. In agreement with this hypothesis, we found that community averages of SLA, LDMC, LLS and leaf P, N, Ca, K and Mg concentrations, LFS, and to a lesser extent, LSCG responded to temporal variation in rainfall. The community means of SLA and foliar nutrient concentration increased in the rainy season, while those of LDMC and LLS decreased. These findings suggest that the species-level trade-off between resource acquisition and conservation has functional significance and allows co-existing species to partition their use of resources when these fluctuate through time. An unaccounted source of variation that could strengthen the signal of seasonal responses is that resulting from within-species differences in trait expression: when CWMs are calculated for traits that could differ in values according to treatment level, i.e. in this case according to season, then differences in CWM can be caused not only by changes in species composition but also by within-species trait variability (de Bello et al. 2011; Carmona et al. 2015).

Our results highlight the relevance of rainfall seasonality in controlling functional changes of grassland communities. However, it is also relevant to note that all aggregated traits analysed except plant height were significantly affected by among-site heterogeneity, and differences in local conditions can also be important in determining the temporal patterns of community trait composition, since several time x plot interactions were significant. However, we found no clear correspondence between soil texture and chemistry and community-weighted traits as would be expected from the plant resource–economics postulates. Although we used common indicators of soil fertility (mineral concentrations and soil texture), other soil factors may be better predictors of growth conditions. In particular, the soils in the area of the study have generally high clay content, low hydraulic conductivity and a tendency to seasonal water-logging, conditions which may override the importance of nutrient content as a limiting factor (Ospina et al. 2012; Rusch et al. 2014). Differences in the relative composition of major plant life forms among sites could also have been important in determining the differences in trait averages observed among plots. For example, in relation to the others, CWMs in plot 15 showed consistently larger leaves, more superficial roots, higher concentrations of foliar nutrients such as N, Ca and Mg, longer duration of phenological stages, shorter lateral spread by clonal growth, shorter leaf longevity and lower dry matter content. It is unlikely that the obvious different values for plot 15 resulted only from soil differences. Rather, these characteristics seem to reflect that plot 15 could have a higher

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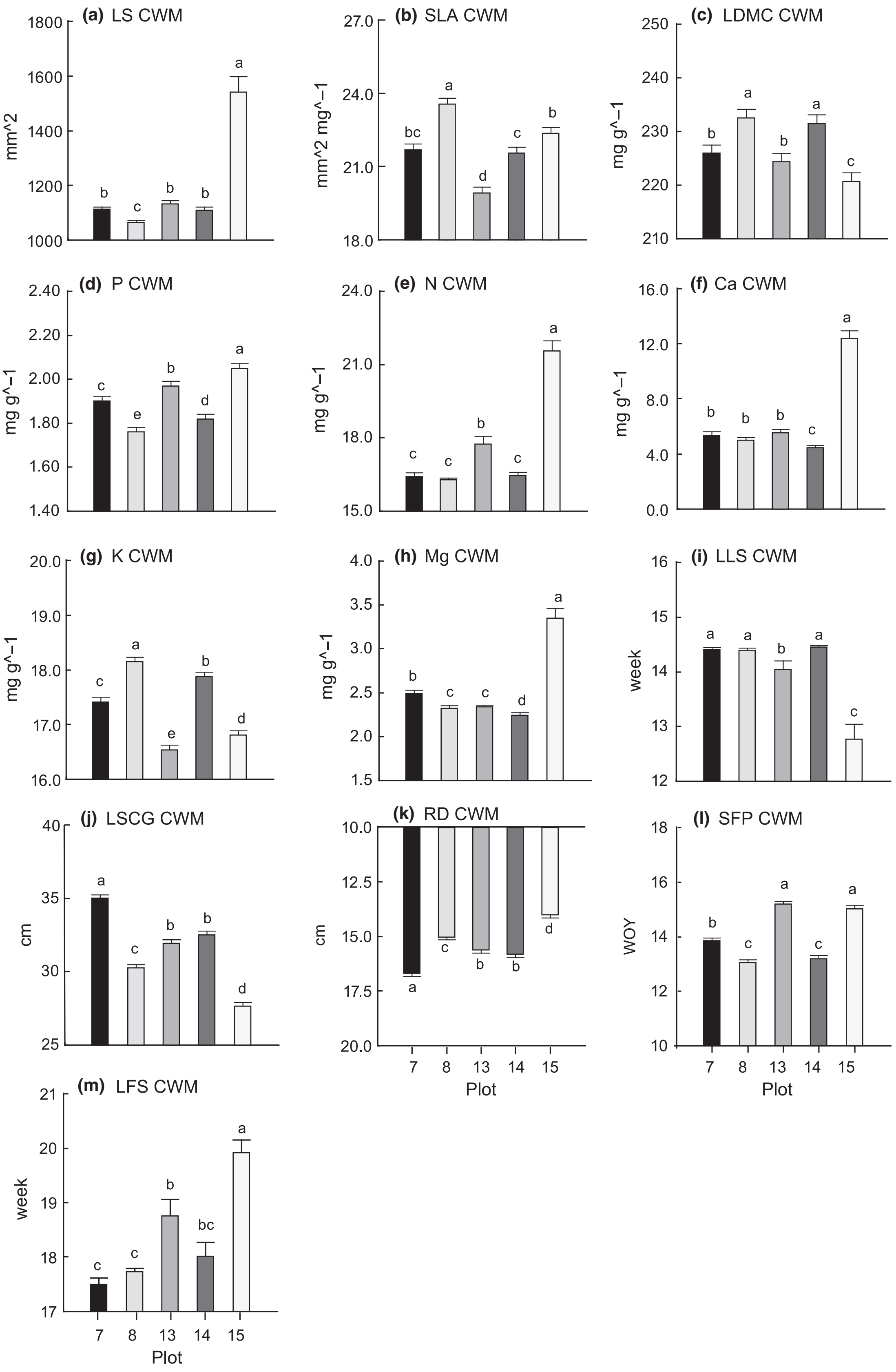
(a) LS CWM
mm^2
1800
1600
1400
1200
1000
b c b b a
(b) SLA CWM
mm^2 mg^–1
27.0
24.0
21.0
18.0
bc a d c b
(c) LDMC CWM
mg g^–1
250
240
230
220
210
b a b a c
(d) P CWM
mg g^–1
2.40
2.20
2.00
1.80
1.60
1.40
c e b d a
(e) N CWM
mg g^–1
24.0
21.0
18.0
15.0
c c b c a
(f) Ca CWM
mg g^–1
16.0
12.0
8.0
4.0
0.0
b b b c a
(g) K CWM
mg g^–1
20.0
19.0
18.0
17.0
16.0
c a e b d
(h) Mg CWM
mg g^–1
4.0
3.5
3.0
2.5
2.0
1.5
b c c d a
(i) LLS CWM
week
16
15
14
13
12
a a b a c
(j) LSCG CWM
cm
40
35
30
25
a c b b d
(k) RD CWM
cm
10.0
12.5
15.0
17.5
20.0
a c b b d
7 8 13 14 15
Plot
(l) SFP CWM
WOY
18
16
14
12
10
b c a c a
7 8 13 14 15
Plot
(m) LFS CWM
week
21
20
19
18
17
c c b bc a
7 8 13 14 15
Plot

Fig. 2. Mean ± SE of functional traits weighted by species cover in five plots with semi-natural grasslands in Central Nicaragua. (**a**) LS, leaf size, (**b**) SLA, specific leaf area, (**c**) LDMC, lead dry matter content, (**d**) P, leaf phosphorus concentration, (**e**) N, leaf nitrogen concentration, (**f**) Ca, leaf calcium concentration, (**g**) K, leaf potassium concentration, (**h**) Mg, leaf magnesium concentration, (**i**) LLS, leaf lifespan, (**j**) LSCG, lateral spread by clonal growth, (**k**) RD, root depth, (**l**) SFP, starting of flowering period and (**m**) LFS, length of the period from flowering to seed shed. The letters on each bar indicate statistical differences between cover plots according to the Fisher LSD test, at $P < 0.05$.

proportion of short-lived herbs than the other plots. Also, it is expected that CWM of LLS and leaf K concentration could be affected by the relative cover of perennial and annual species (S. Ospina, unpubl. data). These differences in species composition appear to be more related to land-use history rather than to soil conditions (Ospina et al. 2009) and indicate the potential of anthropogenic influences on primary ecological functioning.

Studies on grassland assemblages show that spatial gradients of soil resources interact with temporal resource availability and with species composition in shaping the productivity of grasslands and species assemblages (Maestre et al. 2006; Maestre & Reynolds 2007). Our results complement and support these studies, since site heterogeneity (spatial variation) interacted with seasonal changes in resource supply, and modified functional responses along the rainfall variation. The findings in this study are consistent with those in Ospina et al. (2012), where seasonal biomass stability in diverse grasslands was higher than in pasture monocultures that ceased growth earlier in the dry season. The presence of species with a wider set of strategies and a capacity of some species to make use of more unreliable and scarce resources enabled the continued growth beyond the peak of the rainy season (Ospina et al. 2012). The effect of seasonal fluctuations in rainfall on the morpho-phenological traits of the community of 32 species in our study matched predictions from published literature. We found that in the rainy season, the dominant grassland species had higher aggregated values of traits with well documented correspondence with high levels of resource supply, such as SLA, leaf concentrations of N and P, while in the dry season, species with resource conservative traits such as high LLS and LDMC gained dominance (Cornelissen et al. 2003; Garnier et al. 2004).

Likewise, the responses of foliar and whole plant traits with less well-documented correspondence with the resource economy axis confirmed our expectations. The association of a high capacity for clonal growth with resource acquisitive strategies matched the findings of previous studies at species and community level, showing the correspondence of high capacity for LSCG with high levels of resource supply (Sammul et al. 2003; Rusch et al. 2011).

Contrary to our expectations, the length of the reproductive period was longer in the rainy season than in the dry season. This finding contradicts suggestions that long LFS is associated with a strategy of resource conservation at the species level, where LLS and LFS were positively correlated (S. Ospina, unpubl. data). The lack of correspondence between CWMs of LFS and LLS could be due to the fact that, in these communities, the period in which there is active growth in the dry season is comparatively shorter than in the rainy season, so species that attain dominance in the dry season have a narrow time window for reproduction. Similarly, species with different life forms and life cycles flowered at different times, and all annuals and some sedges and forbs had the onset of flowering early in the rainy season. Towards the mid- and late rainy season a large number of perennial species reached flowering, and it is likely that for them, a longer LFS could be also related to other factors not considered here, such as, a competition for pollinators during the peak growing season, or particular climatic factors (e.g. irradiance and air humidity) that could affect reproductive phenology (Michalski & Durka 2007; Sola & Ehrlén 2007).

The results for CWMs of RD did not fit the expectations: no significant differences in RD could be detected between the seasons. One reason might be the nature of the trait variation and the methodological approach. RD responds plastically to soil properties (Hodge 2004; Roumet et al. 2006), and Nipper & Knapp (2007) identified different water use strategies when upper soil horizons became dry. In this study, RD measurements were made in the rainy season, when the soils in the area are friable and it is feasible to carry out manual excavations of roots. Therefore, if the species' RD changed with growing conditions over the seasons, our method would not capture this variation, which would explain why CWM of RD appears not to be responsive to the shifts in the dominance during the seasons.

Conclusions

Grasslands provide an important benefit to humans by maintaining a storehouse of genetic material, referred to as the "genetic library" *sensu* Myers (1997) in Sala & Paruelo (1997), a service that is comparable to resource harvest (Barbier 2007). This resource is particularly important in a climate adaptation context. One of the three key recommendations in the latest IPCC report (Field et al. 2014) for climate change adaptation is to protect genetic diversity to ensure the capacity of society to adapt to new climatic, ecological and socio-economic contexts. Grassland plants include a range of adaptations to stressful conditions (i.e.

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periods of water shortage, nutrient limitation) and disturbance (herbivory, trampling, mowing). Compared to monocultures, diverse Neotropical grasslands can stabilize primary production in seasonal climates (Ospina et al. 2012). In this study, we observed coordinated shifts in plant trait dominance that resulted from changes in species cover due to temporal changes in resource supply produced by rainfall seasonality, indicating that the stabilizing function can be in part the consequence of a differentiation in functional traits through the season. Heterogeneous and variable response patterns have given support to the idea of deliberately using spontaneous selection and adaption effects as a management strategy under climate change conditions (Kahmen et al. 2005), especially when a strong directional selection for more tolerant individuals or species takes place (Zang et al. 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species used for trait analysis by family, life cycle and life form.

Appendix S2. Detailed procedures for trait measurements.

Appendix S3. Methodology and results on the soil properties of vegetation cover plots.

Appendix S4. Mean values of species cover of the target group, the open ground cover and the total cover of five plots in four seasonal periods that represent shifts in the resource availability gradients in semi-natural grasslands in Central Nicaragua.

Appendix S5. Daily rainfall plotted against four seasonal periods: early rainy season 2007, late rainy season 2007, early dry season 2008, and late dry season 2008.

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