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Standing herbage mass: An integrated indicator of management practices for examining how fertility and defoliation regime shape the functional structure of species-rich grasslands

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ABSTRACT

Characterising the functional composition of ecosystems is now recognised as an essential step for predicting the services they provide. However, predicting functional composition from environmental variables and management practices faces the difficulty of accurately describing the latter, especially for managed grasslands. We suggest using a plant nutrient index (PNi) and the maximum standing herbage mass at harvest (SHM) as indicators. The objective of this study was to evaluate whether these indicators reflected well effects on plant functional composition, which was defined as community-level weighted mean plant traits (CWMi) and indices of functional divergence (FDi).

We studied 18 grassland plant communities located in the Pyrenees mountains (southern France) differing in fertility, past use and defoliation regimes (cut twice per year, grazed in spring then cut, or only grazed). Four plant traits (specific leaf area (SLA), leaf dry matter content (LDMC), flowering time and vegetative plant height (VPH)) were chosen for their relevance to provisioning services (e.g. forage production and quality) and supporting services (e.g. providing nutrients).

For CWM plant traits, VPH increased and LDMC decreased (both significantly) in response to increasing PNi. All FD indices decreased in response to increasing PNi. These trends were greater for grazed grasslands than for cut grasslands because the former, never reaching the reproductive phase, had lower SHM. CWM plant traits were significantly correlated with SHM (LDMC and flowering times negatively, SLA and VPH positively) regardless of defoliation regime and PNi.

Cutting (compared to grazing) and high nutrient availability reduced plant FDi, probably due to increased plant competition. FDi significantly and negatively correlated with SHM. These results suggest that SHM is an integrated indicator of the effects of soil fertility, fertilisation and defoliation regime, thus helping to understand how management shapes the functional structure of species-rich grasslands. It thus can assess fertility and consider interactions between the defoliation regime and nutrient availability.

1. Introduction

Recent research has shown the relevance of the functional approach for analysing the effects of land-use change on ecosystem behaviour in grasslands, especially at large spatial scales (Garnier et al., 2007). This approach follows the idea that plant functional traits that respond to environmental variables and have effects on ecosystem services may help identify key properties governing the functioning of ecosystems and how they relate to ecological gradients (Lavorel and Garnier, 2002). On a small spatial scale (e.g. a valley), plant traits can be used to evaluate the services provided by species-rich grasslands (Ansquer et al., 2009a; Quetier et al., 2007). In this paper, we highlight how management practices shape the functional divergence (FD) of grassland communities. To this end, we used a framework relying on environmental gradients, performance filters and trait distribution (Webb et al., 2010) adapted to the specificities of the agroecosystem under study to specify stress, perturbation factors and plant traits (Fig. 1). For managed grasslands, this requires accurate assessment of the response of plant community functional structure to soil fertility, fertilisation rate and defoliation regime (Duru et al., 2005). This remains challenging because most situations combine grazing and cutting, as well as a wide range of cutting dates and grazing intensities either with or without organic and/or mineral fertilisation (Ansquer et al., 2004).

Difficulties arise when assessing environmental gradients because they are related to differences in fertilisation amounts and defoliation regimes whose effects are not independent. This is particularly the case when animals consume herbage and

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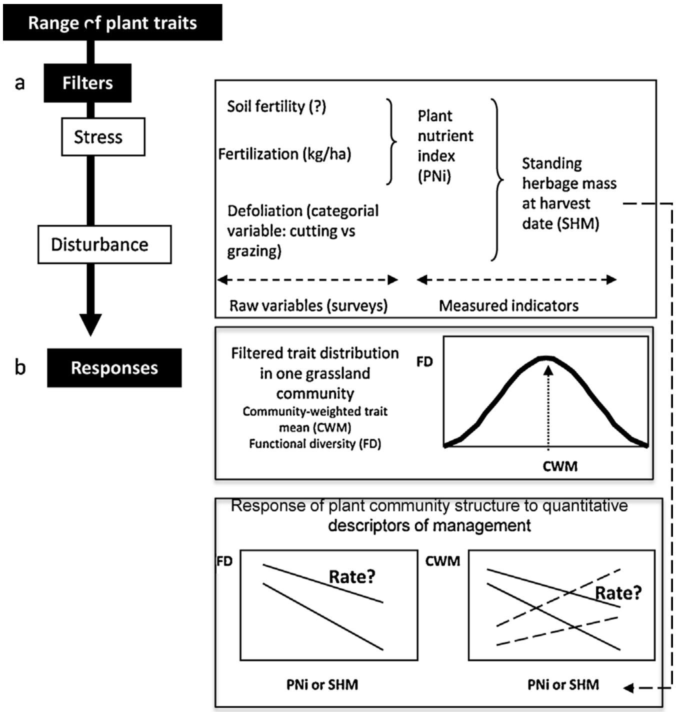

Fig. 1. A conceptual model for examining the effect of filters on grassland functional composition: (a) detailed characterisation of filters (? means that there is no simple indicator for soil N fertility); (b) hypothetical relationships between community weigthed plant trait (CWM) or functional diversity index (FD) and indicators of stress and disturbance (PNi: plant nutrient index; STH: standing herbage mass) for a set of grassland communities.

return nutrients to the grassland in their excreta. Only considering fertiliser applications (kg per ha and per year) and defoliation management (cutting vs. grazing) to assess their effects on plant functional divergence leads to poor estimates of the functional response to management practices, except when considering contrasting or extreme situations (e.g. grassland abandonment and grazed situations, with or without fertiliser applications) (Doležal et al., 2011). Thus, plant trait response is usually analysed by comparing a few defoliation treatments (e.g. Garnier et al., 2007) and recording applied fertiliser and/or stocking rate (e.g. Farruggia et al., 2006). However, this comparison is an over-simplification because current management practices vary in intensity, timing and frequency. To overcome these difficulties, we suggest the simple but efficient use of two plant indicators.

To assess resource availability (mainly N and P) that depends on natural soil fertility, animal excreta, and applied organic or mineral fertiliser, we used a generic integrated index of plant nutrient status (PNi) (Lemaire and Gastal, 1997) (stress factor in Fig. 1a). Characterising nutrient status directly through the amount of fertiliser, or indirectly through stocking density, does not consider natural soil fertility, particularly since soil analysis performs well for P but not for N. An integrated index, such as the Ellenberg indicator value (EIV), usually performs better for assessing nutrient availability (e.g. Schaffers and Sykora, 2000) but is questionable when related to plant traits, because EIV and plant traits at the plant-community level are calculated from species abundance. Defoliation, considered as a disturbance factor, varies in intensity, timing and frequency; so, its effect cannot be assessed easily through one of these components. According to previous results of the effect of standing herbage mass at harvest resulting from current management practices (SHM) on only one plant trait (leaf dry matter content (LDMC), Duru et al., 2010a), we examined whether similar results are observed for a larger number of plant traits relevant for evaluating forage provision. We hypothesised that SHM encapsulates both the effects of defoliation regime and nutrient availability (Fig. 1a). A long regrowth time, achievement of the reproductive phase and increased nutrient availability increases SHM.

Using measured quantitative indicators of changes in nutrient status and defoliation (PNi and SHM: Fig. 1a) induced by management, we examined two indices of plant community structure: the community-weighted mean plant trait (CWMi) and the functional divergence index (FDi) (Dıaz et al., 2007; Lavorel et al., 2008) for their responses to nutrient availability and defoliation regimes (Fig. 1b). These indices were calculated for traits related to forage provision: specific leaf area (SLA), LDMC, vegetative plant height (VPH) and flowering time (Ansquer et al., 2009a). SLA and LDMC locate a species on a resource capture/use-availability axis (Wilson et al., 1999). Species adapted to poor resource availability (usually slow-growing) have low SLA and high LDMC (Louault et al., 2005). VPH is considered the most relevant trait for indicating capacity for competitive dominance (Hodgson et al., 1999), because it expresses an ability to capture light (Vesk et al., 2004). Flowering time depends on environmental stress (Craine et al., 2011) and is related to plant growth rate and the capture and use of nutrients (Sosebee and Weibe, 1973). Plant-trait functional divergence usually decreases as land-use intensification increases (Flynn et al., 2009). We examined how CWMi and FDi responded to nutrient availability for different defoliation regimes by focusing on the reaction of plant community functional structure to different management practices applied over many years. The hypotheses tested were:

- CWMi increase (e.g. SLA and VPH) or decrease (e.g. LDMC and flowering time) in response to increasing PNi and FDi decreases in response to increasing PNi.
- A difference exists among defoliation regimes for plant-trait response to PNi, but expressing CWMi and FDi as a function of SHM includes fertility.

Based on these hypotheses, we examine whether PNi and SHM at harvest are relevant for describing how grassland management shapes the functional structure of species-rich grasslands. The latter index can be used to integrate the effect of soil fertility, fertiliser supply and defoliation regime. In the discussion section, a cross-sectional analysis examines the two hypotheses.

2. Materials and methods

2.1. Experimental design

The experiment was performed on 18 grassland communities located in the Pyrenees (42°51′N, 1°17′E). They were selected to represent a wide range of agricultural practices characterised by contrasting defoliation management (grazing and/or cutting for hay production) and nutrient availability (Ansquer et al., 2004). Located from 615 to 970 m a.s.l., plots showed no significant difference in mean temperature due to more solar exposure of higher fields. Soil parent material varied from alluvium in the valley to shale or granite on the slopes. Mean annual temperature was 10 °C, and annual rainfall was 1080 mm (over the last 10 years).

We studied 3 defoliation regimes: (i) grasslands cut twice per year then grazed in autumn (C), (ii) grazed in spring then cut (GC), and (iii) only grazed (G). Each defoliation regime had 2 levels of fertility (denoted + and −), giving a total of 6 management types (Table 1). There were 3 fields (i.e. replicates) per management type. To measure plant traits and nutrient status in each, we maintained