

Functional diversity in low-input grassland farming systems: characterisation, effect and management

Michel M. Duru, J Tallowin, Pablo Cruz

▶ To cite this version:

Michel M. Duru, J Tallowin, Pablo Cruz. Functional diversity in low-input grassland farming systems: characterisation, effect and management. Agronomy Research, 2005, 3 (2), pp.125-138. hal-02676364

HAL Id: hal-02676364 https://hal.inrae.fr/hal-02676364

Submitted on 31 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Review

Review article

Functional diversity in low-input grassland farming systems: characterisation, effect and management

M. Duru¹, J. Tallowin² and P. Cruz¹

¹UMR ARCHE, Chemin de Borde Rouge, BP52627, 31326 Castanet Tolosan, France ²Institute of Grassland and Environmental Research, North Wyke, Okehampton, Devon EX20 2SB, UK

Abstract. High biodiversity in grasslands is widely perceived to have a major role in maintaining or enhancing the amenity and cultural value of landscapes in Europe. In this paper, we focus mainly at community level, evaluating factors that appear to influence biodiversity at farm and landscape levels. In order to establish generic principles we examine the maintenance of biodiversity in terms of maintaining or enhancing functional diversity (FD). We define plant functional types (PFTs), groups of species having the same function and/or the same effect in the grassland ecosystem, species identified on the basis of plant traits. These traits reflect ecological responses to nutrient input and/or defoliation frequency, and they can also have an effect on ecosystem properties. We reviewed the literature, examining the relationship between several leaf and plant traits and principal ecological factors and, in turn, how these traits could influence the feed value of the grassland vegetation for herbivores. FD was determining as the range of relevant PFTs at community, farm and landscape levels. We propose a practical method of assessing agronomic value of semi-natural grasslands based on the determination of dominant PFTs by measuring traits in situ, or through using a trait database coupled to species abundance records. We then assess the relevance of the method for semi-natural grasslands subjected to several management practices.

Key words: biodiversity, grassland, defoliation, fertilisation

INTRODUCTION

At the livestock farm scale, specific and functional diversity of the vegetation depends greatly on how farmers manage grasslands and meadows, and how they are spatially arranged in the landscape. Adoption by livestock farmers of management practices that enhance biodiversity depends on subsidies they receive and on their objectives for animal performance, production costs and labour. Biodiversity has a range of functional roles within agroecosystems at a range of scales (Altieri, 2002). However, most studies have been done at just one scale, the plant community (plot level) or landscape level (Freckleton, 2004).

High grassland biodiversity is generally associated with low-input livestock systems that support less than 1 LU per ha (Duru & Hubert, 2003). Today biodiverse grasslands only survive where economic drivers towards intensification can not operate

or where there is adequate compensation against intensification via agri environment subsidies (Hodgson et al., 2005). Biodiversity rich areas are often characterized by marked differences in management between fields that reflect topographic and environmental differences. Although grassland biodiversity may provide a diversity of potential utilitarian functions (Swift et al., 2004) at an ecosystem or landscape level such as sequestration of carbon, purification and filtration of surface water, provision of amenity facilities for society, to the livestock farmer the essential function is to feed herbivores (Guérin & Bellon, 1990).

In this paper, we use plant functional traits, to characterize the functional diversity of grasslands at different spatial scales. We hypothesize that this approach could be a bridge linking management practices to the vegetation structure and to their productivity and quality. We exclude sown grasslands and we consider only ecological factors on which farmers could act upon through management of nutrient inputs and defoliation regime (mowing and/or grazing). These are the most important environmental factors that drive the structure and the composition of plant communities (Grime, 1988; Kleyer, 1999).

We define functional diversity (FD) of a grassland community using a combination of plant functional traits which reflect the influence of ecological factors on functional diversity and on the ecosystem properties. We examined a range of plant and/or leaf traits in order to identify ones that were specific to particular ecological factors. Two approaches were used, one based on plant functional types (PFTs) and a database of species having the same strategy for resource acquisition and use, and the second based on plant trait measurement *in situ*. We review the advantages and limitations of a functional-trait based approach to the categorisation of grasslands examining issues relating to the plant plasticity, and the comparison of plant growth forms. We also evaluate the relevance of both approaches to assess grassland functional diversity at farm and landscape scales.

From plant functional traits to functional diversity at plant community level: some methodological aspects

A functional classification of species based on plant traits

It has been recognized that predicting the response of species and neighbour relationships to variations in resources and climatic change requires a functional classification of species (McIntyre, 1999). It could be based on traits directly linked to growth and development functions of plants, or strongly correlated to other variables describing these functions (Weiher et al., 1999). A short list of key plant functional traits has been identified (Diaz & Cabido, 1997), which has led to the development of the concept of plant functional type (PFT). PFTs are defined as non-phylogenetic groupings of species exhibiting common biological traits that enable them to fulfil specific functions in a similar way within an ecosystem (Gitay & Noble, 1997). PFTs are regarded as a concept enabling the identification of general principles for the functioning of organisms which can be used for making predictions, but also as a practical tool to reduce a wide diversity of species to a small number of entities. The basis of PFT rests on an analysis of the traits developed by plants growing in communities. One distinguishes traits of response, which are those whose values change in response to factors applied to the community, and traits of effect that act on

the processes of the ecosystem (productivity and nutrient cycling among others) (Lavorel & Garnier, 2002).

Plant traits as indicators of environmental factors (response traits)

Land management acts upon the composition and the dynamics of plant communities through changes in nutrient availability and defoliation regime. Nutrient availability depends on fertilizer supplied, amount and kind (quality) of litter and excrete through grazing. Defoliation regime could have an indirect effect modifying the light incoming at different heights of the canopy, and also direct effects making gaps, or removing vegetative or reproductive plant components (Bullock & Marriott, 2000).

Prediction of community or ecosystem response to changes in land management has driven a search for key traits that take account of: (i) the capacity to exploit resource-rich or -poor environments; (ii) the capacity for competitive dominance; (iii) the response to disturbance (Wilson et al., 1999). Modelling vegetation dynamics for predicting the rate at which the vegetation changes needs extensive studies on plant strategy for regeneration, avoidance, and tolerance, and most often the interaction with the climatic circumstances that are not considered here.

Certain leaf traits can be used to indicate the morphogenetic strategies of species to exploit resource-rich or -poor environments. For example, fast growing species have low tissue density and short organ lifespan (Ryser, 1996). Slow growing species have low area per leaf mass (SLA) and long leaf lifespan (LLS) indicative of slow turnover of plant parts, long nutrient residence times, and slow response to favourable growth conditions (Westoby et al., 2002). Wilson et al., (1999) showed that leaf dry matter content (LDMC) was much less variable than the other leaf traits, being largely independent of leaf thickness and a better predictor of location on the resource capture/use-availability axis (Garnier et al., 2001). High correlation was found between LDMC and the density of tissues, which is the key variable to distinguish the strategies of morphogenetic development of species.

Managing or knowing the response of plants within a community to nutrient availability needs to take into account the capacity of individual species to exploit the resources, but also their capacity for competitive dominance. Ryser and Urbas (2000) showed that a nutrient-conserving strategy with long LLS is of advantage in nutrient rich environments when no external disturbance removes the conserved nutrient.

Analysing the response of plant species within a community to a defoliation regime needs to take account of their individual capacities for competitive dominance. Specific shoot height (SSH) is considered to be the most relevant trait indicating capacity for competitive dominance (Hodgson et al., 1999), because it expresses an ability to capture light (Vesk et al., 2004). However, in cut or grazed grasslands this trait alone can not predict a species' capacity for competitive dominance. Others plant traits are related to meristem position (Bonser et al., 1996), resprouting and branching abilities (Lavorel et al., 1999). The timing of managements such as mowing, if imposed at the same time each year, will eventually lead to selection of phenological traits such as start of flowering and timing of seed set that are adapted to the particular management regime. After abandonment of any fixed agricultural management regime,

seed production is no longer time-limited, which appears to explain the increase in late flowering species (Kahmen & Poschlod, 2004).

Plant traits determining effects of plants on vegetation characteristics influencing feed value for domestic herbivores

Porter and Remkes (1990) showed that species with low relative growth rate (RGR), longer LLS, lower SLA and higher leaf tissue density (Reich et al., 1992), also contained proportionally more cell wall material (lignin, hemicelluloses, cellulose) than species with higher RGR. The latter contained proportionally more cytoplasmic elements such as protein and sterols (i.e. compounds in solution) (Ryser, 1996). Species with high RGR have high leaf water content, low leaf specific mass, low proportion of cell wall per unit of leaf area, high proportion of mesophyll protoplast per unit volume and high organic nitrogen concentration. Different proportions of leaf mesophyll (highly digestible tissue) among herbaceous species result in a large range of nutritive values (Van Arendonk & Poorter, 1994). Differences in tissue anatomy and chemical composition have a major influence on the digestibility of plant components (Wilson, 1993). Leaves having long LLS tend to have a high fibre/crude protein ratio, high lignin concentration and low nitrogen and phosphorous concentration (Nelson, Moser, 1994). Long LLS is very important for storing nutrients (Escudero et al., 1992). Low specific leaf area is also often associated with increasing concentrations of secondary compounds and starch (Aerts & Chapin, 2000).

During the reproductive period, herbage growth pattern depends greatly on the rate and duration of stem growth, whereas during vegetative regrowth, it depends mostly on the leaf lifespan (Duru et al. 2002). Over the vegetative period, the herbage bulk density is also highly correlated with leaf plant traits (Duru et al., 2004), species having higher LDMC also have higher bulk density.

From plant traits to functional diversity

The nutrient factor shows considerable overlap between response and effect traits. Leaf traits that are indicators for resources capture and utilization are also predictors for herbage growth rate, herbage nutritive value and leaf toughness. Timing of initiation and of flowering that determines the beginning and the end of stem elongation act upon the herbage growth pattern over the reproductive period. Specific shoot height which depends on defoliation management acts upon sward structure. On the other hand, demographic and regeneration traits, associated with response to disturbance, are known to have little connection with adult traits involved in plant ecophysiology (Lavorel & Garnier, 2002). They would be of little relevance to assess vegetation characteristics.

Functional diversity characterizes the extent of complementarity among species' trait value by estimating the dispersion of species in trait space (Mason et al., 2003). When the number of species is small, they generally present a high level of similarity in their plant features and could be related to the same functional group.

Some key questions for functional diversity assessment

Comparison of leaf traits in a set of species growing in pure stand showed that LDMC values separated the species into three life form classes (grasses, rosette forbs and upright forbs, $P \le 0.001$) while this is not the case for SLA and LLS. Rosettes and

upright forbs are respectively defined as dicotyledonous having, at the vegetative stage, entire wide leaves without stems and not entire leaves with stems or/and large petioles (Cruz et al., 2002). This result was confirmed when comparing SLA and LDMC for grass and rosette life forms growing in the same community (Viegas et al., 2005): the average values for LDMC were, respectively, 160 and 270 g kg⁻¹ for rosette forbs and grasses, whereas the SLA was the same $(26 \text{ m}^2 \text{ kg}^{-1})$ for both plant life form. Consequently, LDMC should not be measured without considering separately plant life forms, unless the study is only on grasses. The choice of grasses is also justified by their high abundance in natural grasslands and their similar morphology (one botanical family) which avoid changes or adaptations in the procedure of trait measurements. Furthermore, when measuring only grass populations, the loss of information is low with respect to the whole community (Ansquer et al., 2005).

Evidence that species ranking for plant traits is strongly influenced by environmental conditions was shown in pot studies on *Dactylis glomerata* and *Brachypodium pinnatum* grown in different environmental conditions: 3 nitrogen x 3 phosphorus nutrient levels (Ryser & Lambers 1995). LDMC varied from 160 to 220 g kg⁻¹ for *D. glomerata*, and from 260 to 320 for *B. pinnatum*. For SLA, it was 28 to 42, and from 23 to 28, respectively. Therefore, under these controlled experimental conditions although plant traits appear to be environment dependent, the species ranking was not affected (Cruz et al., 2005; Poozesh et al., 2005). Species ranking was also compared at the plant population and plant community levels (Table 1). It is apparent that for these species the plant traits showed great variability reflecting therefore considerable phenotypic plasticity. Nevertheless the species ranking remained consistent.

Table 1. Comparison of average values of LDMC (g kg ⁻¹) for some grasses growing in
pure stand (Toulouse : 150m asl, with or no N application) or in plant communities having great
differences in P and N herbage nutrient status (Ariège, Central Pyrenees (1°17'E, 42°51'N,
600-900m asl), data 2001, P. Cruz, unpublished data).

Species	LDMC of s	pecies in pure	LDMC of species in grassland			
	species stands: mean and		communities (1 to 4 spring seasons):			
	(SD) for 3 growing		mean and (SD); n=number of plots			
	seasons		· · ·			
	N+	N-	different N and P	min and max		
			plant status	measured values		
Holcus lanatus	208 (24)	219 (20)	235 (26) $n = 28$	173-280		
Lolium perenne	220 (42)	246 (31)	246 (25) $n = 18$	193-269		
Dactylis glomerata	237 (35)	250 (24)	270 (22) $n = 29$	249-329		
Agrostis capillaris	256 (30)	270 (28)	283 (26) $n = 11$	263-355		
Festuca rubra	273 (48)	302 (42)	304(38) $n = 9$	272-335		

Use of plant trait measurement for plant functional diversity assessment and management

A plant functional approach to grassland community classification could be developed from a database of plant functional types, or directly in the field through measurement of plant traits.

A database, containing a list of relevant response and effect plant traits for a large range of grassland species, needs to be developed to show groups of species that have close similarity in plant trait values. The database would then be used to position different grasslands on an ecological gradient and classify them in terms of their agronomic characteristics. It would, however, be necessary to assess variation in FD within and between plant communities by comparing the abundance of different functional types (Petchey & Gaston, 2002). The agronomic characteristics of the pasture can then be deduced from those of the dominant functional type. This is the case of communities growing in nutrient-rich environments where competition for light lead to elimination of slow growing species. By contrast, under lower competition levels, several functional types can coexist (Lavorel & McIntyre, 1999). An example of database is given in Appendix 1.

Plant traits that are easy to measure in the field could be used to assess the position of a plant community on an ecological gradient, and to measure FD. An index proposed by Mason et al. (2003) allows for the inclusion of small functional differences between species, which might be ignored by the database approach. It should be possible to quantify functional diversity and functional richness with this approach. FD index reflects the range of character values present in a given area, so it does not have the same significance for all plant traits. To assess the potential (maximum) FD index in a given area, we used the minimum and the maximum recorded values.

Advantages and limitations to characterizing grassland communities using either the plant functional type method, in which a database on individual species is required, or the plant functional trait approach are summarized in Table 2.

	Plant functional type	Plant functional trait
Advantages	Opportunity to study correlations	Takes account of trait plasticity
	between a set of plant traits (leaf, phenological; some of them being hard to measure)	Low botanical knowledge needed
	Species typology based on several plant traits	
	Linking with ecological factor and vegetation properties inside the database	
Limitations	Trait plasticity	Only a limited number of plant
	Some botanical knowledge needed	traits easily measurable at field
	Number of species in the database	level
	-	Requires knowledge on the
		relevance of plant traits for a given
		ecological factor and for the
		vegetation properties

Table 2. Comparison of two met	thods that could be used to characterized the functional
diversity within and between grassland	plant communities.

Assessment and management of grassland functional diversity: some examples from natural grasslands used for cutting and grazing

Within plant community

To assess FD within plant community, we used a long-term trial (17 years), conducted on a natural grassland in Rio Grande do Sul (Brazil), where the grazing pressure by cattle was maintained at four levels of intensity (Table 3). The vegetation structure of the most intensively grazed treatment (4% dry matter allowance) was homogeneous. The productivity of the grassland in this treatment was very low, in some extent due to low light interception. Grassland production and animal performance were higher in the 12 and 16% intensity treatments. These lenient grazing treatments allowed the cattle to select preferred forage species, which created structural heterogeneity with tall grass patches dominated by ungrazed or only lightly grazed species and tightly grazed short sward areas containing preferred species. Increasing grazing pressure reduced the FD. FD was higher when analysed using SLA values compared with LDMC values in all the treatments. There was, however, a tendency for LDMC to increase and SLA to decrease at lower grazing pressures.

The animal performances per animal or per ha were the lowest for the highest stocking rate treatment that coincide to the lower FD. In contrast, the lenient grazing treatments that allowed a better spread of forage over the year coincide with a higher FD.

Defoliation regime introduces changes of species either directly (via mortality following removal of apices) or indirectly (via change in competitive relations between species), which will result in differences in the dynamics of accumulation of herbage mass during regrowth. In the case of pastures that are exclusively grazed, these dynamics can result in substantial heterogeneity of the vegetation. Low grazing pressure conditions will favour several types of vegetation structures, each with species belonging to a different functional group.

Considering the minimum and the maximum LDMC and SLA observed at field level in the studied area, we computed the FD for a community having 50% of species of each leaf traits; it give respectively 0.50 and 0.75. It means that results shown in Table 3 express only a small fraction of the maximum diversity, respectively 20 and 28%.

under differe	under different grazing intensities, Cruz and Theau (unpublished data).								
Grazing	Number	SL	А	LDMC		Live weight gain**			
intensity *	of species					kg per animal	kg ha⁻¹		
		Mean	FD	mean	FD	day ⁻¹¹			
4%	10	16.3	0.12	307	0.03	0.2	80		
8%	13	15.7	0.21	313	0.06	0.4	125		
12%	10	13.2	0.21	350	0.10	0.5	145		
16%	11	13.3	0.18	337	0.09	0.5	110		

Table 3. Average SLA (m² kg⁻¹) and LDMC (g kg⁻¹) values for 4 plant communities (data for grasses only which constituted more than 45% of the total herbage mass) that had developed under different grazing intensities, Cruz and Theau (unpublished data).

* in kg of DM per 100 kg of live weight per day (grazing pressure adjusted monthly during seventeen years)

** from Nabinger et al., 1999

Between plant communities

For these illustrations, we focused on natural grasslands that were cut for hay and grazed most often heavily in spring or in autumn, in such a way that there was only little effect of dietary choices of animals. Consequently, diversity is expected to be greater between plant communities than within.

To illustrate the relationship between management, measured functional diversity and agronomic characteristics, we used grassland communities located high in the central Pyrenees. There were large differences in herbage N and P status and defoliation regimes (Table 4).

Table 4. Leaf plant traits (average value and FD) for some upland grassland communities differing in their defoliation regime and nutrient status (grasses only). Proportion of the different functional types: A, B, C (see appendix 1).

Defoliation regime	Sward nutrient		$SLA (m^2 kg^{-1})$		LDMC (g kg ⁻¹)				
C: cut;	sta	atus							
G grazing	Ν	Р	average	FD	average	FD	fur	octior	nal
(l: lax; s: severe)	index	index					t	ypes	
(defoliation score)							(A,	В,	C)
C - C - G(1)	82	63	24.4	0.10	245	0.03	41	42	7
	61	100	24.9	0.10	261	0.03	39	45	6
Gs – C– G (2)	81	86	24.7	0.09	250	0.03	56	43	3
	66	70	21.6	0.04	264	0.01	35	65	5
Gl - C - G(3)	70	76	24.2	0.18	260	0.03	28	41	31
	68	49	14.6	0.15	287	0.03	4	3	93
G - G - G(4)	76	69	23.7	0.14	267	0.02	25	13	62
	66	44	18.9	0.16	270	0.03	15	20	75

Measured and computed (see appendix 1) plant traits were highly correlated, respectively 0.67 (P < 0.01) with SSH (Specific Shoot Height), 0.65 (P < 0.01) for LDMC, and 0.82 (P < 0.001) for SLA. There was also significant correlation between plant traits: SSH vs LDMC: 0.76***, SSH vs SLA: 0.61*, SLA vs LDMC: 0.75***, indicating that a single one could not be a specific response trait.

FD is low for LDMC and higher for SLA, and there is a trend to have higher FD for SLA when there was no cut or a lax spring grazing. Considering the minimum and the maximum LDMC and SLA observed at field level in the studied area (respectively 175 and 350 g kg⁻¹, and 12 and 36 m² kg⁻¹), we computed the FD for a community having 50% of species of each leaf trait value; it gave respectively 0.34 and 0.63. It means that results shown in Table 5 express only a small fraction of the maximum diversity, respectively 8 and 29%.

We found that the plant trait LDMC was highly correlated with spring forwardness (date at which herbage mass reach 200g m⁻²), the daily herbage growth rate over the linear phase, and the date at which herbage ceiling yield for reproductive spring growth was reached (correlation coefficients were, respectively: 0.93 (P < 0.001), -0.82 (P < 0.01) and -0.82 (P < 0.01). SLA and flowering date were the plant traits best correlated with the maximum standing herbage (0.84, P < 0.01) and the date at which it occurred (r = 0.65, P < 0.10).

The relevance of plant functional approach to assess an ecological factor was assessed first using plant trait measurements. Given data from Table 4, we show that LDMC and SLA were both well correlated to the herbage nutrient index ($r^2 = 0.75$; P < 0.001), and that SSH was the trait which was best correlated with the defoliation regime ($r^2 = 0.71$; P < 0.001). When using computed plant traits instead of measured ones, coefficients of correlation were significant but at lower levels. There was not a plant trait specific to nutrient availability and defoliation regime. Finally, LDMC assessed both factors according to the following equation LDMC= 332 –1.3 NPi+3.79 defoliation, $r^2 = 0.81$ (NPi: sward nutrient index; defoliation: defoliation score).

However, in a sample of 80 meadows and grasslands, we observed that plant functional types based on the LDMC database responded to defoliation regime and nutrient availability (Table 5), which meant that LDMC was not specific to an ecological factor. Furthermore, the proportion of plant functional types established on the LDMC basis depended on both nutrient availability and defoliation regime. There was a trend for a more even distribution of plant functional types in plant communities that had a lower nutrient herbage status, and those that were only grazed. The number of species was greatest when the proportion of the different functional types was more evenly distributed; i.e. when the competition for light was lowest (low nutrient, and/or early defoliation in spring).

Ansquer et al, 2004).						
	Defoliation regime:	Hei	Herbage nutrient status			
Criteria	C = cut; G = grazed	low	low medium hig			
	CCG		52-40-8			
Functional	GCG	28-31-41	48-34-18	65-28-7		
diversity	GGG		25-28-47			
	CCG		21			
Number of species	GCG	32	28	21		
	GGG		30			

Table 5. Functional diversity assessed at grassland community level through the proportion of different functional groups of grasses (A, B, C: see appendix), and species diversity of 80 grasslands differing in defoliation regime and nutrient herbage status (from Ansquer et al, 2004).

At farm and landscape levels

Surveys conducted on four commercial farms showed that each of them had grasslands dominated by one of the three PFT. This diversity between grasslands allows farmers to fulfil a set of functions (Guérin, Bellon, 1990). However, the proportion of each vegetation type varied greatly according to farm (Table 6). For example, type C occupied from 6 to 28% of the grassland area.

Farms 1 and 3 with the higher stocking rates had the highest proportion of grasslands in which the type A functional group was dominant. (Table 6). However, the proportion of *Chaerophyllum aureum*, an undesirable invasive species growing in nutrient-rich habitat and particularly when there is no spring grazing (Magda et al., 2003), was also more abundant on vegetation type A. This species was most abundant in grasslands in the valley bottom, due probably to more favourable soil conditions compared with the slopes.

Level		tage of gra		Production system characteristics				
			onal groups					
	A, B, C	C are domi	nant					
	А	В	С	stocking rate (cow ha ⁻¹)*	proportion of undesirable species			
Farms								
1	60 ^a	34	6	1.20 ^a	0.75^{a}			
2	37 ^b	39	23	1.05 ^b	0.35 ^b			
3	47 ^a	33	19	1.22 ^a	0.40 ^b			
4	43 ^a	28	28	0.95 ^b	0.27 ^b			
Landscape								
Valley bottom	57 ^a	39	4		0.70 ^a			
Slope	30 ^b	27	40		0.14 ^b			

Table 6. Functional diversity assessed at farm and landscape levels in terms of the proportion of different functional groups of grasses (A, B, C); the computed averages over three vears are shown. Values with different superscript letters are significantly different (P < 0.05).

At landscape level there was clustering of the landscape units, for example the valley bottoms being mainly occupied by type A, which corresponds to grasslands having the higher nutrient level, and/or being not heavily grazed in spring.

In areas where most of the grasslands were cut for hay at least once per year the plant functional diversity was higher at farm and landscape levels than at community level. Differences in the timing of hay harvest between fields due to topographic and edaphic reasons, for example, probably had a major influence on grassland FD at the farm/landscape level. Greater functional diversity in grasslands at the farm/landscape levels probably also reflected the needs of individual farmers, such as the ability to maximise the duration of the grazing season and thus vary the management regime at the field level between years depending on between year variations in weather.

CONCLUSIONS

Management practices implemented to fulfil different functions in livestock feeding systems generate functional diversity in plant communities between fields within a given farm. Furthermore, topographic field characteristics determine the spatial distribution of the management practices within the farmland. Unfavourable field characteristics, such as steep slope, poor drainage or distance from the farm, determine the management practices of paddocks and consequently the vegetation types. As spatial and temporal scales increase (from field to farmland; from a season to a year or years) particularly where there is considerable variability in soil type, slope, elevation, aspect and climatic conditions, these factors drive an increase in vegetation diversity (White et al., 2004). In other words, grassland community diversity has a functional role in farmland management, and this role of diversity can only be assessed over the entire managed area at farm level. White et al. (2004) argue that a functionally diverse plant community over the entire managed area should be promoted in terms of potential for livestock farming sustainability, as well as for the biodiversity benefits of localized species diversity within grasslands. The farmland area could be a field used in continuous grazing (with high functional diversity) or a set of fields used in rotation grazing or for grazing and hay, leading to high diversity at farm level, but each of them having low functional diversity. The maintenance of a range of grazing intensities at the landscape level can allow the conservation of a wide diversity of herbaceous plants (McIntyre et al., 2003).

Plant traits derived from measurements or databases are useful to assess grassland community characteristics, but they are not specific to a single management practice. There is a challenge to use them for growth modelling (Viegas et al., 2005). On the other hand, further researches should be done on linking planned and associated diversity (Altieri, 1999). Indeed, in less favoured areas, one role of grazing animal is maintenance or enhancement of sward structural heterogenity, and thus botanical and faunal diversity, by selective defoliation due to dietary choices, treading, nutrient cycling and propagule dispersal (Rook & Tallowin, 2003).

REFERENCES

- Aerts, R. & Chapin, F.S. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* **30**, 2–67.
- Agreil, C. et al. 2002. Prospects for ecological habitat conservation: a new modelling approach to evaluate grazing of broom shrubland. EGF, La Rochelle (FRA), 27-30/05/02. Multifunction grasslands - Quality forages, animal products and landscapes. Durand J. L., Emile, J. C., Huyghe, C., and Lemaire, G. pp. 752–753.
- Altieri, M.A. 2002. Agroecology: the science of natural resource management for poor farmers in marginal environments. *Agriculture, Ecosystems & Environment* **93**, 1–24.
- Ansquer, P. et al. 2004. Caractérisation de la diversité fonctionnelle des prairies naturelles. Une étape vers la construction d'outils pour gérer les milieux à flore complexe. *Fourrages* **179**, 353–368.
- Ansquer, P. et al. 2005. How to simplify tools for natural grassland characterisation based on biological measures without losing too much information? IGC, Glagow, June 2005 (in press).
- Bonser, S.P. & Aarssen L.W. 1996. Meristem allocation: a new classification theory for adaptive strategies in herbaceous plants. *Oikos* 77, 347–352.
- Bullock, J.M. & Marriott C.A. 2000. Plant responses to grazing and opportunities for manipulation. Eds Rook A.J. and penning P.D. BGS Occasional Symposium 34, pp.17– 26.
- Cruz, P. et al. 2002. Une nouvelle approche pour caractériser la valeur d'usage des prairies naturelles et semi-naturelles. *Fourrages* **172**, 335–354.
- Cruz, P. et al. 2005. Leaf dry matter content of native grassland species under contrasting N and P supply. IGC, Dublin, June 2005 (in press).
- Diaz, S. & Cabido, M. 1997. Plant functional types and ecosystem functions in relation to global change. *Journal of Vegetation Science* **8**, 463–474.
- Diaz, S. et al. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology* **38**, 97–508.
- Duru, M. et al. 1998. Fonctionnement et dynamique des prairies permanentes. Exemple des Pyrénées centrales. *Fourrages* 153, 97–113.
- Duru, M. et al. 2002. Modelling net herbage accumulation of an orchardgrass sward. *Agronomy Journal* 94, 1244–1256.
- Duru, M. & Hubert, B. 2003. Management of grazing systems: from decision and biophysical models to principles for action. *Agronomie* **23**, 689–703.
- Duru, M. et al. 2004. Using plant traits to compare sward structure and composition of grass species across environmental gradient. *Applied Vegetation Science* 7, 11–18.

- Escudero, A. et al. 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia* **90**, 80–87.
- Freckleton, R.P. 2004. The problems of prediction and scale in applied ecology: the example of fire as a management tool. *Journal of Applied Ecology* **41**, 599–603.
- Garnier, E. et al. 2001. Consistency of species ranking based on functional leaf traits. *New Phytologist* **152**, 69–83.
- Gitay, H. & Noble, I.R. 1997. What are plant functional types and how should we seek them ? In: Smith, T.M., Shugart, H.H. and Woodward, F.I. (eds) *Plant functional types: their relevance to ecosystem properties and global change*. Cambridge University Press, Cambridge, pp. 3–19.
- Grime, J.P 1988. Comparative Plant Ecology: A Functional Approach to Common British Species. Unwyn-Hyman, London.
- Guérin, G. & Bellon S. 1990. Analyse des fonctions des surfaces pastorales dans des systèmes de pâturage méditerranéens. *Etudes et Recherches Syst. Agraires Dév.* 17, 147–158.
- Hodgson, et al. 1999. Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* **85**, 282–294.
- Hodgson, J.G.G. et al. 2005. How much will it cost to save grassland diversity? *Biological Conservation* **122**, 263–273.
- Kahmen, S. & Poschlod P. 2004. Plant functional trait responses to grassland succession over 25 years. *Journal of Vegetation Science* **15**, 21–32.
- Kleyer, M. 1999. Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. *Journal of Vegetation Science* **10**, 697– 708.
- Lavorel, S. & McIntyre, S. 1999. Plant functional types: is the real world too complex? In People and Rangelands: Building the Future. Proceedings of the VI International Rangeland Congress. Townsville, Australia, July 19–23, pp. 905–911.
- Lavorel, S. et al. 1999. Functional groups for response to disturbance in Mediterranean old fields. *Oikos* 84, 480-498.
- Lavorel, S. & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**, 545–556.
- Magda, D. et al. 2003. Hay-meadows production and weed dynamics as influenced by management. *Journal of Range Management* **56**, 127–132.
- Mason, W.H. et al. 2003. An index of functional diversity. *Journal of Vegetation Science* 14, 571–578.
- McIntyre, S. 1999. Plant functional types recent history and current developments. In *Proceedings of the VI International Rangeland Congress*, Townsville, Australia, 2, pp. 891–892.
- McIntyre, S. et al. 2003. The relative importance of cattle grazing in subtropical grasslands: does it reduce or enhance plant biodiversity? *Journal of Applied Ecology* **40**, 445-457.
- Nasbinger, C. et al. 1999. Campos in Southern Brazil in Grassland ecophysiology and grazing ecology. Eds: Lemaire, G., Hodgson, J., A de Moares, PC de F Carvalho et C Nabinger, pp. 355–376.
- Nelson, C.J. & Moser L.E. 1994. Plant factors affecting forage quality. In Fahey, G.C. (ed.): *Forage quality, evaluation and utilization*, pp. 115–154.
- Petchey, O.L. & Gaston K.J. 2002. Functional diversity species richness and community composition. *Ecology Letters* 5, 402–411.
- Poorter, H. & Remkes, C. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* **83**, 553–559.
- Poozesh, V. et al. 2005. Are leaf traits stable enough to rank native grasses in contrasting growth conditions? IGC, Dublin, Juin2005 (in press).

- Reich, P.B. & Walters, M.B. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**, 365–392.
- Rook, A.J. & Tallowin, J. 2003. Grazing and pasture management for biodiversity.
- Ryser, P. 1996. The importance of tissue density for growth and life span of leaves and roots: a comparaison of five ecollogically contrasting grasses. *Functional Ecology* **10**, 717–723.
- Ryser, P. & Urbas P. 2000. Ecological significance of leaf life span among Central European grass species. *Oikos* **91**, 41–50.
- Ryser, P. & Lambers, H. 1995. Root and leaf attributes accounting for the performance of fastand slow-growing grasses at different nutrient supply. *Plant and Soil* **170**, 251–265.
- Ryser, P. & Aeschlimann, U. 1999. Proportional dry-mass content as an underlying trait for the variation in relative growth rate among 22 Eurasian populations of *Dactylis glomerata* s.l. *Functional Ecology* **13**, 473–482.
- Shipley, L.A. et al. 1999. Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. *Oikos* **84**, 55–68.
- Swift, M.J. et al. 2004. Biodiversity and ecosystem services in agricultural landscapes are we asking the right questions? *Agriculture, Ecosystems & Environment* **104**, 113–134.
- Van Arendonk, J.C.M. & Poorter, H. 1994. The chemical composition and anatomical structure of leaves of grass species differing in relative growth rate. *Plant Cell & Environment* **17**, 963–970.
- Vandermeer, J. et al. 1998. Global change and multi-species agroecosystems: concepts and issues. *Agriculture, Ecosystems & Environment* **67**, 1–22.
- Vesk, P.A. 2004. Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *Journal of Applied Ecology* **41**, 22–31.
- Viégas, J. et al. 2005. Variation of LDMC and SLA relationship between growth forms in natural grasslands. IGC, Dublin, June 2005 (in press).
- Weiher, E. et al. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* **10**, 609–620.
- Westoby, M. et al. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33** 125–159.
- White, T.A. et al. 2004. Vegetation diversity, growth, quality and decomposition in managed grasslands. *Agriculture, Ecosystems & Environment* **10**, 73–84.
- Wilson, J. R. 1993. Organization of forage plant tissues. In Jung, H. J., Buxton, D. R., Hartfield, R. D. & Ralph, J. (eds.): *Forage cell wall structure and digestibility*, pp. 1–32.
- Wilson, P.J. et al. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* **143**, 155–162.

Appendix 1: Database used for designation of plant functional types (PFT).

Seed of 17 grass species collected from meadows in the Pyrenees were sown in pure stands at Toulouse and grown with two N application rates. Measurements were taken once for time of flowering and SSH) or three (LDMC, SLA) growing seasons.

We show that LDMC was a reliable plant trait measure because it was well correlated to flowering time, plant digestibility, and herbage growth rate. Four significant groups were determined (from Ansquer et al., 2004).

	Date of flowering		LDMC		SLA
Species	(Julian days)	(cm g-0,33)	$(g kg^{-1})$	LDMC classes*	$(m^2 kg^{-1})$
Lolium perenne	141	44	196	А	28.2
Holcus lanatus	131	41	198	А	32.6
Arrhenatherum elatius	138	43	218	В	32.5
Festuca arundinacea	150	51	222	В	18.7
Anthoxanthum odoratum	96	20	222	В	28
Dactylis glomerata	134	41	225	В	25.2
Poa trivialis	143		238	В	34.2
Trisetum flavescens	158	37	240	C	26.5
Agrostis capillaris	176	31	242	C	31.4
Phleum pratense	175	26	247	C	30.8
Festuca rubra	134	29	249	C	21.8
Avena pubesens	162	41	250	C	20.5
Festuca ovina	150	34	257	D	16.9
Cynosurus cristatus	121		262	D	19
Deschampsia cæspitosa	176	32	266	D	14.2
Briza media	146	37	274	D	18.9
Molinia cærulea	172		302	D	19.9
Brachypodium pinnatum	162	41	313	D	22.3