Effect of the method of assessing and weighting abundance on the interpretation of the relationship between plant clonal traits and meadow management

Jak je interpretace vztahu mezi klonálními vlastnostmi rostlin a obhospodařováním louky ovlivněna metodou zjišťování abundance a vážením abundancí?

Jitka K l i m e š o v á[1], Štěpán J a n e č e k[1], Jan H o r n í k[2,3] and Jiří D o l e ž a l[1]

D e d i c a t e d t o t h e m e m o r y o f L e o š K l i m e š

[1]*Institute of Botany, Academy of Sciences of the Czech Republic, Department of Functional Ecology, Dukelská 135, CZ-379 82 Třeboň, Czech Republic, e-mail: klimesova@butbn.cas.cz;* [2]*Centaurea, Society for Landscape Monitoring and Management, Stolany 53, CZ-538 03 Heřmanův Městec, Czech Republic;* [3]*University of South Bohemia in České Budějovice, Department of Botany, Na Zlaté stoce 1, CZ-370 05 České Budějovice, Czech Republic*

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The role of clonal traits in a plant's response to changes in management of semi-natural grasslands is poorly known and the few studies examining their importance have yielded contradictory results. For a better understanding of the role of plant functional traits in determining competitive ability and clonal growth in response to early changes in management, we mowed and applied fertilizer to 22 wet meadows in the Železné hory Mts, Czech Republic. We used two methods of assessing abundance (plant cover and species frequency) to determine whether changes in frequency induced by changes in management are better predicted by clonal traits while changes in cover are mainly determined by competitive traits such as plant height. We evaluated (i) the response of individual species to changes in management and (ii) the response of the whole community, with and without taking abundance of individual plants into account, in order to separate the effect of local extinction and immigration from changes in abundance. The plant functional traits tested were generally found to be important soon after the changes in the management of the semi-natural grasslands occurred: competitively superior resident species (possessing tall erosulate, monocyclic shoots) that are able to spread far and multiply clonally (having a high clonal index) were favoured by applying fertilizer and/or suppressed by mowing. Some other traits supposed to be important in the response to changes in management did not change (persistence of connection between ramets). Results for the two methods of assessing abundance differed; however, neither was better at detecting the response of particular types of traits (i.e. relevant to clonal growth and competitive ability). The initial response of the whole community, with and without taking abundance of individual plants into account, was consistent indicating that species that went extinct possessed the same traits as those that decreased in abundance. The clonal index proved to be a useful characteristic of meadow plants. Our results further imply that (i) the method used to assess abundance significantly affects the output of analyses of the response of functional traits, and (ii) a comparison of analyses based on weighting abundance and unweighted means resulted in a deeper insight into the changes in the spectra of functional traits that occurred after changes in meadow management.

K e y w o r d s: abandonment, clonal traits, clonal index, fertilization, mowing, plant height, semi-natural grasslands, SLA

Introduction

The most serious losses in plant species diversity in temperate Europe are connected with changes in land use, namely the application of fertilizer and abandonment of semi-natural grasslands, and their fragmentation and conversion into arable land (Stöcklin et al. 2000, Isselstein et al. 2005, Rudmann-Maurer et al. 2008). Besides changes in species diversity and species composition, changes in the spectra of functional traits are also recorded (Maurer et al. 2003, Kahmen & Poschlod 2004, 2008, Díaz et al. 2007, Garnier et al. 2007, Römermann et al. 2008, Pakeman et al. 2009, Pakeman & Marriott 2010); following both abandonment and the application of fertilizer, tall competitive plants with erosulate shoots and high specific leaf area (SLA) replace smaller plants with rosette shoots and low SLA. The clonal traits, which are important for local spread and plant persistence, have so far only rarely been assessed in semi-natural grasslands subjected to changes in management. A comparative analysis of the clonal growth organs of plant species on red lists vs those in entire floras indicate that plants with root tubers are especially prone to extinction (Klimeš & Klimešová 2000). On the other hand, there is much controversy about how other clonal traits change with abandonment. Some studies record that the meadow species that spread after the cessation of management are typically those with a high lateral spread and high rate of multiplication (Kahmen et al. 2002, Pakeman & Marriott 2010), while others report opposite trends (Kahmen & Poschlod 2008, Sammul 2011). Studies on clonal growth in relation to environmental gradients indicate that plants attaining dominance after the application of fertilizer or abandonment are characterized by the ability to spread laterally over great distances and split up connections among ramets (Klimešová et al. 2011). However, detection of a general pattern might be difficult as results of analyses are affected by the way the traits are scaled at the community level, i.e. whether plant abundance is taken into account and which measurement of plant abundance is used (Guo 2003, Sammul 2011).

Plant communities are usually dominated by a few species and the other species are less abundant. Therefore species-based and abundance-weighted analyses can produce different results (Pakeman et al. 2008), as is also demonstrated for clonal traits (Latzel et al. 2011, Sammul 2011). Many authors (e.g. Grime 1998, Cingolani et al. 2007, Mokany et al. 2008) argue that dominant species better reflect ecosystem processes than subordinate species. The rare species are, however, important for species richness and might be characterized by unique functional traits that substantially affect ecosystem functioning (Grime 1998) and the functional richness of a community (Thompson et al. 2010). Because rare plants are more prone to random extinction when habitats change, their inclusion in analyses may affect the results, and in the case that the rare species have unique traits will result in the loss of part of the functional diversity, but the reason for their extinction is not necessarily their unique traits but their rarity (Grime 1998). These random effects diminish with time and do not affect the results of studies that focus on the consequences of changes in management for plant traits in a community long after the first application of different treatments (e.g. Kahmen & Poschlod 2008, Pakeman & Marriott 2010). However, they might be important when assessing the initial response of plants in a community with the aim of detecting the key traits that play a role at the beginning of the process as a whole.

To understand the role of functional traits in the divergent developments that follow the establishment of different management treatments, we focused on the early course of events in the responses of meadow species and whole plant communities. We expected shifts in species abundance rather than substantial changes in species composition. In this case, weighting the data by species abundance or not have implications as a community mean calculated from presence/absence data reflects changes in species composition and is affected by local extinction of rare species, whereas a community mean weighted by species abundance includes effects of changes in abundance.

To study the response of plants with different clonal traits to management, we performed a manipulative experiment in 22 wet meadows spread across a landscape mosaic in the Železné Hory Mts, Czech Republic. Different management treatments combining mowing and application of fertilizer were applied for three years in a fully factorial design in each meadow. Besides the seldom studied focal clonal traits we tested whether the clonal index (defined by Johansson et al. 2011) as a proxy of the degree of clonal growth responds to changes in management. We also included in the analysis the more often studied traits relevant to competitive ability and carbon economy.

There are several methods for assessing species abundance, e.g. plant cover, plant frequency, shoot density and biomass (Kent & Coker 1992, Dierschke 1994, Bråkenheim & Liu 1995, Mucina et al. 2000, Röttgermann et al. 2000, Brathen & Hagberg 2004). While in some methods the abundance of a plant species having the same number of shoots is affected by shoot size (plant cover, biomass), in others it is affected by shoot number (plant density and frequency in small plots). The relationship between plant functional traits and meadow management might therefore be affected by the method used to assess plant abundance (e.g. Chiarucci et al. 1999, Pavlů et al. 2009, Sammul 2011). In our study two assessments of abundance, cover and frequency, were used. We may expect that estimates of cover are more sensitive to changes in management because it records the increasing/decreasing size of individual shoots together with changes in their number, whereas frequency assessment records only changes in shoot number. It is moreover expected that changes in plant cover are explained better by traits connected with plant dominance and carbon economy, whereas changes in plant frequency will be explained better by traits connected with clonal growth.

We presumed that (i) competitive resident species with tall erosulate and monocyclic shoots would be able to spread far, multiply clonally and have annual shoots, and that their large SLA and splitting rhizomes would be favoured by the application of fertilizer and/or suppressed by mowing; (ii) assessments of abundance using plant frequency would be more sensitive for detecting the response of plants that employ different clonal traits, while cover will be more sensitive for detecting the response of plants that employ different competitive traits; and (iii) the results at the community level would be affected by the method of weighting abundance and thus the same results from particular analyses would mean that the extinct species and species with decreasing abundance did not differ in traits.

Methods

Study area

The study area was located at an elevation of 340 to 550 m a.s.l. in the Železné hory Mts, eastern Bohemia, Czech Republic. The landscape consists of a mosaic of forests, arable land, intensively managed meadows and urban areas. Semi-natural, species-rich wet meadows occupy less than 5% of the area (Fig. 1), but host more than 70% of endangered plant species (Horník & Hrázský 2009). For the experiment we selected 22 wet meadows (Electronic Appendix 1) distributed over an area of 9 × 21.5 km, covering a range of soil moisture, fertility, soil reaction values and types of management.

Experiment

Blocks of experimental plots 4.5 × 4.5 m in size were established in spring 2007 at each of the 22 meadows. Each block consisted of 4 plots (2 × 2 m) representing four treatments in full factorial design: application of fertilizer and mowing, application of fertilizer and abandonment, no application of fertilizer and mowing, no application of fertilizer and abandonment. The buffering zone between the plots was 0.5 m wide. Plant cover was assessed in the plots, using the following scale: r = rare plant with 1–3 individuals, + = cover less than 1%; cover higher than 1% was visually estimated with an accuracy of 1% (up to 20%) and 5% (over 20%), respectively. The semi-quantitative values + and r were transformed for analyses as: r = 0.001% and + = 0.5%. In total the plant cover in 88 plots was assessed during the season. Plant frequency was assessed for plant shoots rooting in 10 × 10 cm quadrates in the central 1 × 1 m quadrate of a plot, altogether there were 88 assessments per season (2007, 2009). Baseline data on vegetation composition were recorded in the first half of July 2007. Mowing was done after vegetation assessment and then in the following years at the same time of year. Fertilizer was applied at a dosage of 20 g mineral NPK (10% N, 10% P_2O_5, 10% K_2O) per m^2 at the end of July 2007 and 50 g/m^2 in the second half of April 2008 and 2009. The dosage represents the upper amount recommended by the producer for extensive grasslands (30–50 g/m^2).

Data on the response to the short period of management were collected in the first half of July 2009. Abundance was assessed by two or three observers who worked together and consulted over identification and adjusted cover estimates in order to avoid identification or estimation biases (for species list, see Electronic Appendix 2).

Plant functional traits

We selected eight functional traits indicating (i) competitive ability (shoot height, shoot cyclicity, shoot architecture), (ii) clonal growth (multiplication rate, lateral spread, clonal index) and (3) carbon economy (SLA, persistence of ramet connection) (for details, see Table 1).

Statistical analysis

Both univariate and multivariate analyses were performed to reflect the BACI (Before-After/Control-Impact) design of the experiment. In this design, the main interest is not the effect of the treatment itself but its effect on changes that occur after treatment was applied.

Fig. 1. – Land cover map of the Železné hory Mts with their location in the Czech Republic. Corine land cover categories: 1 – Artificial surfaces (including Discontinuous urban buildings, Industrial or commercial units, Mineral extraction sites, Sport and leisure facilities); 2 – Forests (including Coniferous forest, Mixed forests, Transitional woodland-shrub); 3 – Land principally used for agriculture, with significant areas of natural vegetation; 4 – Non-irrigated arable land; 5 – Pastures; 6 – Water bodies. Blue dots (1–22) denote the localities studied; for their characteristics see Table 1. ▶

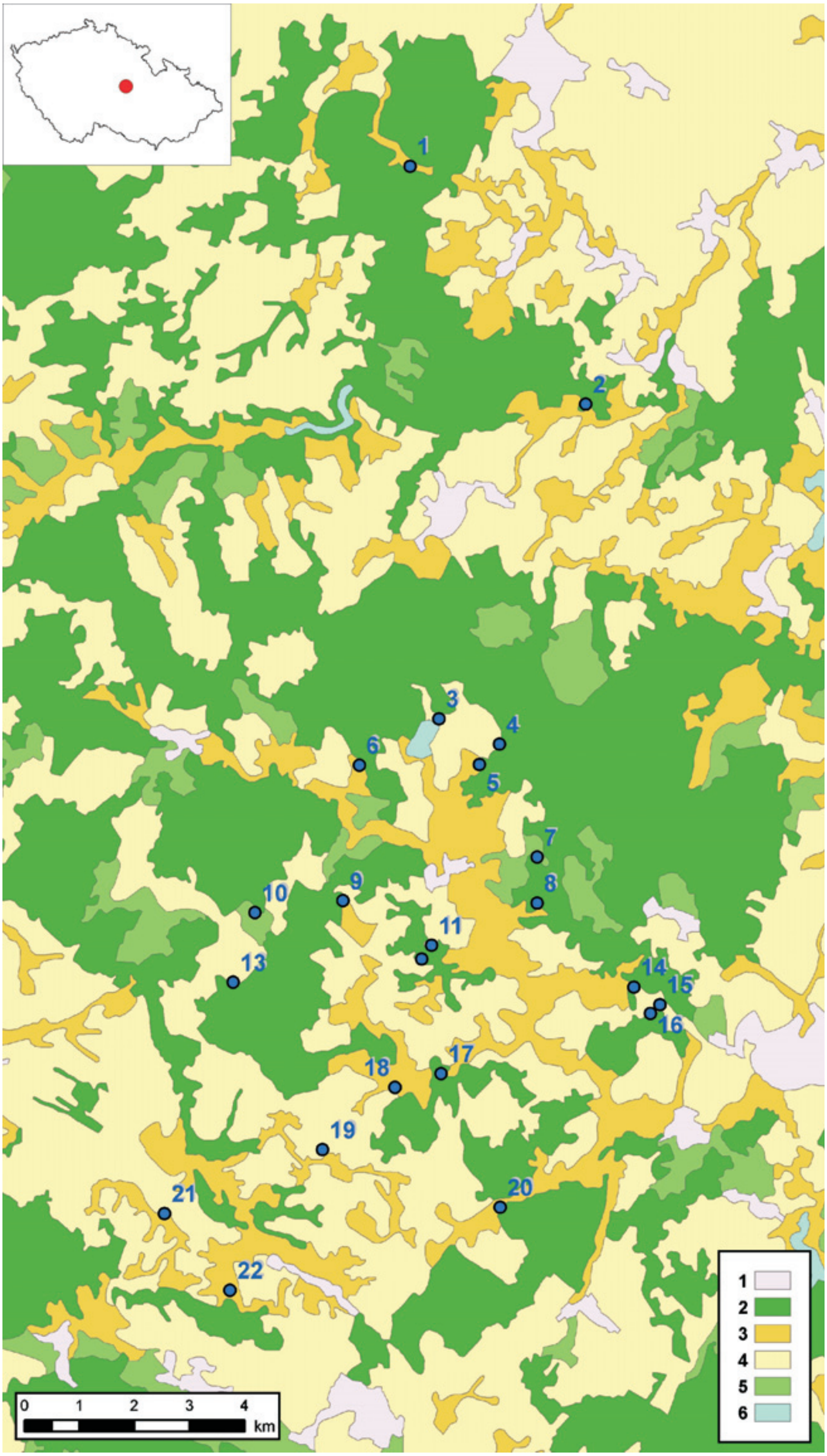
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Table 1. – Plant functional traits used in the analyses.

Function	Trait	Attributes	Source
Competitive ability	shoot height	cm	Kubát et al. 2002
	shoot cyclicity	1; 2; > 2 years	CLO-PLA database[1]
	shoot architecture	rosulate; semirosette; erosulate	CLO-PLA database[1]
Clonal growth	multiplication rate	< 1; 1; 2–10; >10 shoots per mother shoot per year	CLO-PLA database[1]
	lateral spread	< 0.01; 0.01–0.25; > 0.25 m per year	CLO-PLA database[1]
	clonal index	sum of ordinal values of multiplication rate and lateral spread	CLO-PLA database[1] according to Johansson et al. 2011
Carbon economy	specific leaf area	gram per m^2	LEDA traitbase[2]
	persistence of ramet connection	1/2/>2 years	CLO-PLA database[1]

[1]Klimešová & Klimeš 2006, [2]Kleyer et al. 2008.

Effect of the application of fertilizer/mowing on the composition of the vegetation

To test the effect of treatment on changes in the composition of the vegetation (in terms of plant frequency or plant cover) we used redundancy analysis (RDA) with the Monte Carlo permutation test in the Canoco 4.5 program (ter Braak & Šmilauer 2002). Our analyses were analogous to those described by Lepš & Šmilauer (2003, p. 215–235). RDA represents the constrained form of principal component analysis (PCA), in which the canonical axis is defined (constrained) by linear combinations of explanatory variables.

In our analyses, following the BACI design of our experiment, we were interested in the effect of Treatment (mowing or application of fertilizer) × Year interaction. As we used only one explanatory variable in each of the analyses (the interaction), the explanatory variable was fully associated with the first ordination axis (see Table 1). We used as covariates (i) the interaction between year and treatment that was not included in the explanatory interaction term to eliminate the vegetation changes caused by this factor and (ii) the plot identifiers (Plot ID) coded as 88 dummy variables, to eliminate between-plot variation. Because the Plot IDs were used as covariates the main effect (application of fertilizer and mowing) does not explain any variability and we finally did not include it as a covariate. In the sample-species matrix, data were centred by species and non-standardised by samples.

Data on percentage cover were log (y+1) transformed as recommended by Lepš & Šmilauer (2003, p. 13–15). Using the Monte Carlo permutation test a split-plot permutation design was employed: assessments of abundance made in different years in the same plot were considered as split-plots, whereas individual plots represented the whole plots. Permutations at both split-plot and whole-plot levels were performed 499 times. Species scores on the first (canonical) axis, the one determined by our single explanatory variable, represented the responses of the species to individual treatments and were used in the following analysis as the plant characteristics that were to be associated with particular plant traits. For more details on the RDA analysis in CANOCO see ter Braak & Šmilauer (2002) or Lepš & Šmilauer (2003), in R software Borcard et al. (2011).

Effect of the application of fertilizer/mowing on plant traits: response of individual species

In these analyses we aimed to explain plant responses to treatments (responses were determined by RDA scores from previous analyses) in terms of particular plant traits. These analyses were performed for 93 species of plants, which were present in more than eight plots. Rare species were excluded as recommended by Lepš & Šmilauer (2003) as they may not to be responding, because they are missing from most of the plots both before and after the treatment.

Individual plant traits (except for shoot architecture) were considered quantitative variables. The quantitative traits were calculated considering semi-quantitative categorization in the CLO-PLA database and the number of records for each category. If plant traits were classified into more than one semi-quantitative category in the CLO-PLA database (Klimešová & Klimeš 2006), we calculated the weighted mean of the trait. In this case, weighting by number of records in the category was used, e.g. when four records of lateral spread were in category 2 (0.01–0.25 m/year) and seven in category 3 (> 0.25 m/year), then the used value in the analyses was $((4×2)+(7×3))/(4+7) = 2.64$. To analyse the effect of plant traits on plant response to management we used backward stepwise selection in general regression models (STATISTICA for Windows; Statsoft 2010a, b). To avoid co-linearity among explanatory variables (plant traits) we (i) excluded the dichotomous variable "erosulate" where the erosulate plant species were coded, because this variable was fully collinear with two other dichotomous variables (rosette and semi-rosette), and (ii) calculated a correlation matrix and tolerance values for the remaining variables (Electronic Appendix 3). Tolerance for a variable is defined as 1 minus the r^2 of this variable with all other independent variables in the regression and it is recommended that variables with a tolerance value lower than 0.1 are excluded (Quinn & Keough 2007). As the lowest tolerance value detected was 0.29, we left all explanatory variables in the model. Plant height was log-transformed to decrease the effect of the tallest species *Phragmites australis*.

Effect of the application of fertilizer/mowing on plant traits: frequency versus cover data

To test if individual plant traits cause different responses to management from the frequency vs plant cover point of view we calculated general linear models with split-plot design. Species represented the whole plots and the type of its response to treatment (RDA scores calculated from frequency or cover data) was treated as a within-plot factor. The interactions between individual traits and within-plot factors were tested.

Effect of the application of fertilizer/mowing on plant traits: response of the community

We calculated community means and community-weighted means considering both frequency and cover data for individual plant traits for each plot before the 2007 and after the 2009 treatment. In these calculations all plant species (including the rare ones) were considered. The community mean was calculated as mean trait value of all species in the plot, whereas the community weighted mean was calculated by weighting the trait value by plant abundance (simply $\bar{x} = \frac{\sum_{i=1}^{n} w_i t_i}{\sum_{i=1}^{n} w_i}$, where w_i is the cover or frequency and t_i is the trait value of species *i*). The effects of treatments on changes in the community means and community weighted means were analysed by split-plot designed ANOVA, where time represented the within-plot factor. Locality identification was used as a random factor in the analyses.

Results

Effect of the application of fertilizer/mowing on the composition of the vegetation

The response of the plant species to mowing and the application of fertilizer differed significantly, but only accounted for a low percentage of total variability (Table 2). Most of the variability (more than 87% in all analyses) was determined by co-variables.

The responses of species to changes in management were similar when both ways of assessing abundance were used, as is revealed by the correlation between RDA scores for frequency and RDA scores for plant cover ($n = 97$; application of fertilizer, $r = 0.397$, $P < 0.01$; mowing $r = 0.663$, $P < 0.01$).

Plant traits: response of individual species

The correlations with traits relevant to competitive ability were more often significant than those with clonal traits. Shoot cyclicity correlated positively with the response of plant cover to mowing; plant height correlated negatively with plant cover and response in plant frequency to mowing but positively with cover and response in the frequency of plants to the application of fertilizer; SLA correlated positively with the response of plant cover to the application of fertilizer. Plants with a distinct shoot architecture responded differently to mowing in terms of frequency and to application of fertilizer in terms of cover (Table 3). The three clonal traits, lateral spread, multiplication rate and persistence of ramet connection correlated neither with species responses based on frequencies nor with those based on relative cover after changes in management (Table 3). Clonal index showed only one significant (positive) correlation, i.e. the response of plant frequency to the application of fertilizer (Table 3).

Effect of the application of fertilizer/mowing on plant traits: frequency vs cover

In evaluating the effects of plant traits on the different responses of plants to treatment based on either frequency or cover, three out of nine traits tested – persistence of ramet connection, SLA and shoot architecture (rosette plants) – had a significant effect (Table 4, Fig. 2). These traits were, however, significant only when responses to the application of fertilizer were tested (Table 4). Plants that produced ramets that remained connected to the mother plant for a short period exhibited a more positive response to the application of fertilizer in terms of cover than frequency, whereas plants with a low SLA showed a more positive response in terms of frequency than cover. Rosette plants showed a more positive response in terms of frequency than cover (Fig. 2).

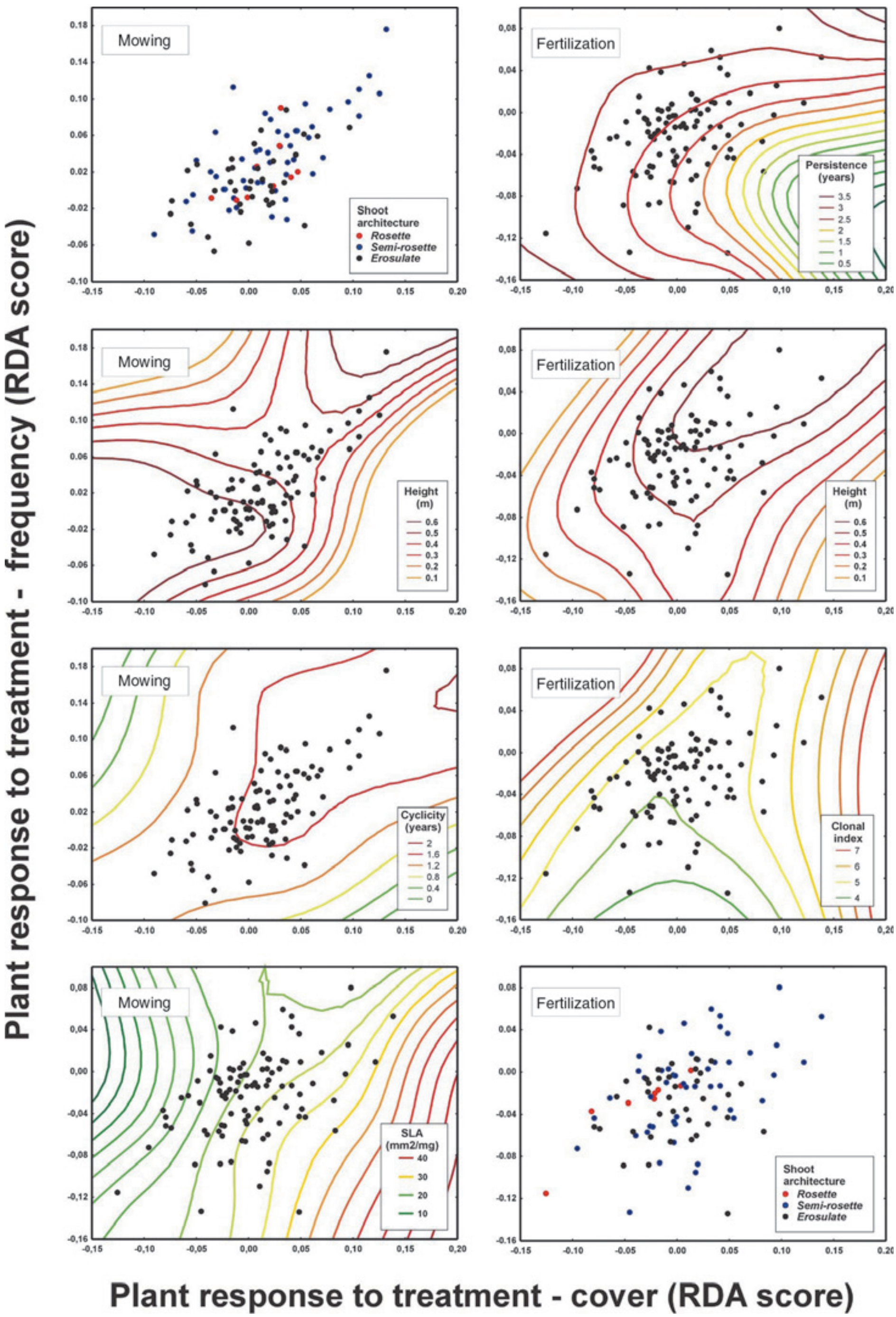

Fig. 2. – Regressions of the responses (RDA score) of individual species to management (mowing or application of fertilizer), based on plant abundance assessed in terms of cover (x-axis) and frequency (y-axis). Particular curve colours represent different continuous trait values, whereby plants of different categorical traits (shoot architecture) are colour-coded. Only traits that were significantly affected by the treatment (Table 4) and/or relationships that differed significantly when the two methods used to assess abundance were used (Table 5), are shown.

Table 2. – Effect of application of fertilizer and mowing on the composition of the vegetation of 22 wet meadows. Abundance expressed either as plant cover or plant frequency. F – fertilizer applied, M – mowing, Yr – Year number (2007: 0, 2009: 1), PlotID – identifier of each plot, % exp. var. – percentage of species variability explained by the first (constrained) axis, r – species-treatment correlation on the first axis, P – significance.

Method of abundance assessment	Explanatory variables	Covariables	% exp. var.	r (1st axis)	F-ratio	P-value
Plant cover	Application of fertilizer*Yr	Yr, PlotID, M*Yr	0.2	0.635	1.633	0.018
	Mowing*Yr	Yr, PlotID, F*Yr	0.2	0.630	1.737	0.004
Plant frequency	Application of fertilizer*Yr	Yr, PlotID, M*Yr	0.3	0.623	2.708	0.002
	Mowing*Yr	Yr, PlotID, F*Yr	0.4	0.624	4.024	0.002

Table 3. – Effect of plant traits on plant response to treatments analysed by using general linear models with backward stepwise selection. Only traits with a significant response (P < 0.05) are shown. β – correlation coefficient.

Mowing				Application of fertilizer			
Cover		Frequency		Cover		Frequency	
Traits	β	Traits	β	Traits	β	Traits	β
Cyclicity	0.2327	Semi-rosette	0.3497	Height (log)	0.2800	Height (log)	0.2564
Height (log)	–0.2948	Height (log)	–0.2442	SLA	0.3482	Clonal index	0.2307
				Semi-rosette	0.2455		

Table 4. – Effects of plant traits on differences in plant responses to treatments based on cover and frequency data. General linear models with split-plot design were used. Plant species represented the entire plots and plant response types, (i.e. responses calculated using frequency or cover data), were treated as within-plot factors. Interactions between plant traits and within factors were tested. F-values are shown, significant effects are in bold: * 0.05 > P > 0.01, ** P < 0.01, ns – non-significant; effect df = 1; error d.f. = 93 (except for SLA analyses, where error d.f. = 89 as we do not have SLA values for all plants).

Response to	Clonal index	Cyclicity	Persistence of connection	Multiplication rate	Lateral spread	Plant height	SLA	Rosette	Semirosette	Erosulate
Mowing	0.45^{ns}	0.05^{ns}	0.70^{ns}	0.14^{ns}	2.14^{ns}	0.81^{ns}	0.33^{ns}	0.28^{ns}	2.25^{ns}	1.47^{ns}
Fertilizer applied	0.84^{ns}	1.59^{ns}	**16.48****	0.05^{ns}	0.51^{ns}	0.08^{ns}	**12.84****	4.21*	0.72^{ns}	0.12^{ns}

Plant traits: response of community

Considering frequency, the application of fertilizer led to an increase in clonal index, multiplication rate and plant height both in terms of changes in abundance (weighted mean) and species composition (unweighted mean). Some of these trends were also obvious when cover was used (Table 5). Mowing, on the other hand, led to increased cyclicity, but lower lateral spread only when weighted means were used. A decreased representation of erosulate shoots was found irrespective of weighting. Multiplication rate and the representation of semi-rosette shoots positively responded to both types of management in both weighted and unweighted analyses (Table 5). Only one functional trait, persistence of ramet connection, did not show any response to change in management at the community level.

Table 5. – Effect of treatments on changes in individual community traits analysed by repeated-measures ANOVA with time as a within plot factor. F-values are shown, significant effects are in bold: * 0.05 > P > 0.01, ** P < 0.01, n.s. – non-significant; effect d.f. = 1; error d.f. = 21.

Explanatory variable (data used) Dependent variable	Clonal index	Cyclicity	Persistence of connection	Multiplication rate	Lateral spread	Plant height	SLA	Rosette	Semi-rosette	Erosulate
Mowing × Time (cover)										
Community mean	0.40^{ns}	2.74^{ns}	0.17^{ns}	2.76^{ns}	3.48^{ns}	1.19^{ns}	0.05^{ns}	**4.34***	7.17*	3.68^{ns}
Community-weighted mean	0.07^{ns}	20.12**	0.05^{ns}	20.12**	**5.87***	12.28**	1.25^{ns}	2.50^{ns}	**21.34****	14.07**
Mowing × Time (frequency)										
Community mean	1.97^{ns}	0.40^{ns}	1.13^{ns}	0.12^{ns}	2.78^{ns}	2.61^{ns}	3.34^{ns}	0.91^{ns}	**10.48***	6.60*
Community-weighted mean	0.41^{ns}	**6.07***	2.02^{ns}	0.01^{ns}	**8.97****	14.39**	5.87*	1.89^{ns}	**22.11****	11.44**
Application of fertilizer × Time (cover)										
Community mean	3.74^{ns}	1.02^{ns}	0.05^{ns}	1.02^{ns}	3.84^{ns}	**9.04****	1.24^{ns}	0.64^{ns}	0.21^{ns}	0.71^{ns}
Community-weighted mean	**4.42****	0.10^{ns}	0.10^{ns}	0.10^{ns}	0.24^{ns}	**4.54***	10.56**	9.88**	4.45*	0.28^{ns}
Application of fertilizer × Time (frequency)										
Community mean	**4.67***	0.07^{ns}	0.54^{ns}	**4.73***	2.98^{ns}	**4.35****	0.06^{ns}	0.18^{ns}	1.91^{ns}	1.68^{ns}
Community-weighted mean	**25.29****	0.63^{ns}	3.29^{ns}	**25.41****	0.53^{ns}	**21.35****	0.04^{ns}	**9.63****	5.14*	1.43^{ns}

Summary of results

All traits important at the species level were important in the analysis at the community level when data were weighted by plant abundance. Also the analyses at the community level, which treated all species equally and reflected changes in species composition in communities after changes in management with one exception, were confirmed by the analyses that took plant abundance into account (Table 6). However, all three methods produced the same result only for three traits: clonal index, plant height responding positively to the application of fertilizer and semirosette shoots responding positively to mowing. While the response in terms of plant height to the application of fertilizer was consistent using both methods of assessing abundance, the response of two other traits were consistent only when frequency was used (Table 6). The traits are moreover the same for rare and common species, whereas traits which responded to changes in species composition (community mean) – rosette and erosulate shoots, multiplication rate – were probably typical of rare species.

The analysis using community-weighted means produced the highest number of significant responses as it combined two effects: changes in abundance and changes in species composition (Table 6).

Discussion

Analysis of the results of a short-term experiment in which 22 wet meadows in central Europe were managed by mowing or applying fertilizer revealed that: (i) as expected, applying fertilizer favoured whereas mowing suppressed dominant, competitive species with tall erosulate and monocyclic shoots that can spread and multiply clonally over long

Table 6. – Summary of results showing the effects of plant traits on their responses to treatment (species) and effects of treatments on changes in community mean and community-weighted mean trait values. R – rosette; S – semi-rosette; E – erosulate. Note that the factor erosulate was not tested in the analyses of effects of traits on plant responses to treatment (see Statistical analyses for details).

Treatment Type of abundance measurement	**Method**	**Clonal index**	**Cyclicity**	**Persistence**	**Multiplication rate**	**Lateral spread**	**Plant height**	**SLA**	**R**	**S**	**E**
Mowing (cover)	species		↑				↓				
	community mean								↓	↑	
	community-weighted mean		↑		↑	↓	↓			↑	↓
Mowing (frequency)	species						↓			↑	
	community mean									↑	↓
	community-weighted mean		↑			↓	↓	↑		↑	↓
Application of fertilizer (cover)	species						↑	↑		↑	
	community mean						↑				
	community-weighted mean	↑					↑	↑	↓	↑	
Application of fertilizer (frequency)	species	↑					↑				
	community mean	↑			↑		↑				
	community-weighted mean	↑			↑		↑		↓	↑	

distances (have a high clonal index); (ii) although the results were affected by method of assessing abundance there was no clear relationship between abundance and two groups of traits; responses of plant cover to management were not better predicted by traits related to competitive ability, and that of plant frequency to management were not better predicted by clonal traits; (iii) trends at the species level in several cases occurred also at the community level as immigration and extinction had already occurred in the communities three years after the change in management, and plants that became extinct locally (and hence were rare) had (at least partly) the same traits as plants that decreased in abundance.

Plant traits

The trait that characterized the changes in species composition in the mowing treatment was shoot architecture; ratio of plants with semirosette shoots increased at the expense of plants with either rosette or erosulate shoots (Table 6). This result accords well with the finding that plants with semirosette shoots are at an advantage in grassland managed by mowing, because their shoot ontogeny is synchronised with the management (Klimešová et al. 2008). As shoot architecture correlates with shoot cyclicity (see Electronic Appendix 3) and responded to the mowing treatment we can conclude that our analyses confirm the idea that abandonment favours plants with erosulate shoots and a short lifespan (low cyclicity). Similar trends, although weaker, occurred in the response to the application of fertilizer, which did not affect plants with erosulate shoots and low cyclicity but favoured those with semirosette shoots, which increased in importance.

Other clonal traits rarely responded to mowing: multiplication rate increased and lateral spread decreased. These two opposite trends resulted probably from a lack of response in the clonal index, which is based on the two traits. On the other hand, the importance of the clonal index increased in the treatment in which fertilizer was applied, in which multiplication rate increased but lateral spread was unaffected. The clonal index proposed by Johannson et al. (2011) was the only clonal trait responding at all three levels analysed (plant species, community mean and community-weighted mean, see below) and proved to be a useful and better parameter of the degree of clonality than the simple division into clonal and non-clonal species in those communities where clonal plants prevail.

Traits associated with carbon economy, persistence of connections between shoots and SLA, responded very weakly. On the other hand, plant height, the most often used trait in studies determining the response of functional traits to management (e.g. Díaz et al. 2001, 2007, Vesk et al. 2004), responded consistently: low growing plants were favoured by mowing and tall plants were favoured by the application of fertilizer, which accords with the expectations (see also Klimešová et al. 2010).

Methods of assessing abundance

The method used to assess abundance affected the results of this experiment (see also Pavlů et al. 2009). Although our results differed from those obtained using individual methods of assessing abundance, they were not contradictory as was, for example, found for seed size (Chiarucci et al. 1999, Guo 2003). Contrary to our expectations, the two methods used to assess abundance (frequency and cover) did not affect the sensitivity of the analysis in terms of trait types (clonal, competitive and carbon economy). It is difficult, however, to combine different methods of assessing abundance in one analysis (see Garnier et al. 2007, Sammul 2011).

We compared results obtained using the two methods of assessing abundance considering only their principal differences as proposed by Chiraucci et al. (1999), i.e. effect of shoot size on cover data and number of shoots on frequency data, without taking into account the accuracy of the description of the vegetation obtained using these methods. Studies that evaluate the quality of data collected using the different method for assessing abundance (e.g. Lepš & Hadincová 1992, Klimeš 2003, Vittoz et al. 2010) indicate that the data are constrained by misidentifications, difficulties with estimating cover of species with similar and inconspicuous growth forms, overestimating large and conspicuous species, different skills of the observers participating in the monitoring, etc. We aimed to limit these methodological difficulties as much as possible; although our field study would not have been possible without the participation of numerous observers, minimally two or three trained observers worked together, compared their estimates and consulted over plant identifications. Although estimating cover is the most inaccurate technique for repeated sampling, the results were not in contradiction with those obtained by assessing frequency. However, it gives results that are the least consistent for all three analyses (see below).

Species vs community level, weighting by abundance

By combining the three analyses of the dataset: the species, the community mean and the community-weighted mean enabled us to separate the effects of changing plant cover (the species level), immigration and extinction (the community mean). Only three traits were found to consistently respond at all tree levels: semirosette shoots increased with mowing, clonal index and plant height increased after the application of fertilizer. The method combining both effects (community-weighted mean) logically was the most sensitive measure of trait changes that occurred in our study and with one exception confirmed trends revealed by the two other methods. Although it would be convenient if the community-weighted mean was the most powerful tool for such analyses, we advocate that the selection of the method should be determined by the research question being addressed (see Pakeman et al. 2008).

Preceding studies using abundance weighting together with community means for trait parameters combined with both the methods for separating the role of environmental filtering (whether the species can immigrate into the community) from performance of species in a community (whether the species can spread in the community by seeds or clonal growth) (Cingolani et al. 2007, de Bello et al. 2007, Pakeman et al. 2008, Latzel et al. 2011, Sammul 2011). Here we show that in short-term experiments the two methods can separate the effect of changes in species composition (immigration and extinction) from changes in the abundance of resident species. Although fluctuations in species composition shortly after the change in management might be partly caused by random processes (see Introduction), the traits found to respond only to changes in species composition (rosette and erosulate shoots, multiplication rate) can be considered important for meadow species. This implies that early responses in species composition to changes in management are (at least partly) caused by filtering of traits based on the type of management.

Conclusion

Clonal index as a proxy of the degree of clonal growth is a better measure of clonality than the more often used division into clonal and non-clonal species. Our results further imply that (i) the method of assessing abundance significantly affects the analysis of the response of functional traits to changes in management at the community level, and (ii) comparison of analyses based on abundance weighting and unweighted means results in a deeper insight into the changes in the spectra of functional traits that occur after a community is disturbed.

See http:///www.preslia.cz for Electronic Appendix 1–3.

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Souhrn

Role klonálních vlastností v reakci rostlin na změny v obhospodařování polopřirozených trávníků je málo známá a několik málo studií, které se jí zabývají, dochází k protichůdným závěrům. Pro lepší porozumění úlohy funkčních vlastností rostlin, týkajících se kompetiční schopnosti a klonálního růstu v časné reakci na změnu obhospodařování, jsme založili experiment s variantami koseno/nekoseno a hnojeno/nehnojeno na 22 mokrých loukách v Železných horách. Použili jsme dvě metody určování abundance (pokryvnost a frekvenci) abychom zjistili, zda

změny ve frekvenci druhů způsobené změnou obhospodařování jsou lépe vysvětlitelné jejich klonálními vlastnostmi, zatímco změny v pokryvnosti jsou určeny kompetitivními vlastnostmi, jako je výška rostliny. Zjišťovali jsme (1) odpověď na změnu obhospodařování u jednotlivých druhů a (2) odpověď celého společenstva s tím, že jsme použili jen přítomnost druhů, nebo jsme druhy vážili jejich abundancí ve společenstvu, abychom oddělili vliv druhových změn od vlivu změn v abundanci. Testované funkční vlastnosti byly obecně důležité pro časnou reakci rostlin na změnu obhospodařování polopřirozených trávníků: kompetičně zdatné druhy (s vysokými, bezrozetovými a monocyklickými prýty) schopné laterárního šíření a rozmnožující se klonálně (s vysokou hodnotou „klonálního indexu“) byly podpořeny hnojením, případně potlačeny kosením. U některých dalších vlastností (např. vytrvalost spojení mezi rametami) jsme nezjistili žádnou odezvu. Výsledky našich analýz se lišily v závislosti na dvou metodách zjišťování abundance, ale žádná z metod se neukázala vhodnější pro detekci odpovědi určitého typu rostlinných vlastností (tj. těch, které se týkaly klonálního růstu a kompetiční schopnosti). Časná odpověď celého společenstva jen částečně závisela na vážení druhů jejich pokryvností, což naznačuje, že lokálně vyhynulé druhy měly některé vlastnosti stejné jako druhy se snižující se abundancí (klonální index, polorozetové prýty a výška rostliny) a některé vlastnosti unikátní (rosetové a bezrozetové prýty a klonální multiplikace).

Z našich výsledků dále vyplývá, že (1) klonální index se osvědčil jako užitečná charakteristika lučních rostlin, (2) metoda zjišťování abundance významně ovlivňuje výsledky analýzy funkčních vlastností a (3) srovnání analýz založených na vážení abundancí a analýz, kde je počítáno s prostou přítomností druhů, umožňuje hlubší vhled do změn spektra funkčních vlastností následkem změn obhospodařování lučního společenstva.

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Fanta J. & Siepel H. (eds.)

Inland drift sand landscapes

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A large area of The Netherlands is covered with drift-sand. Therefore, in the geology of The Netherlands there is a great emphasis on the Quaternary. This interest is expressed also in this book, which is edited by Professors Josef Fanta and Henk Siepel. They have assembled a large team of 21 coauthors, three of which, including one of the editors, J. Fanta, are Czech. They present different views on inland drift-sand landscapes in terms of the ecological processes, historical aspects of spatiotemporal changes, conservation and/or restoration of this special ecotope. This overview is important because of the "belt character" of the patches of aeolian drift sand, which occur in several European countries, along a west-east axis. Moreover, at present these landscapes are currently conserved as important Natura 2000 priority habitats despite the fact that for centuries they were seen as a threat to society, mainly agriculture, housing and/or infrastructure.

Inland drift-sand was mainly deposited during the period of transition from the last ice age to the Holocene and more recently due to human activity in sandy areas. Drift-sand is not the same as the cover sand in periglacial areas or loess sediments at the opposite end of the material gradient. They consist mainly of wind-blown particles in areas that were at least periodically vegetated after periods of great disturbance, which is related not only to a change in climate but also to human exploitation of landscapes. Surprisingly, the items of literature associated with drift-sand habitats are rare, starting with the geology and finishing with landscape ecology.

This book is divided into five parts. The first mainly deals with the origin and geological development of drift-sand, but includes an account of the vegetation and the effect of man's activities in drift-sand areas. The second part deals with the habitat variables from microclimate of drift sand areas, their soils including humus development and nutrient cycling, fauna and mycoflora. Part three deals with other organisms such as lichens, bryophytes and their fauna, mainly in the context of succession. In summary these chapters are a multidisciplinary approach to what is a very special environment. The fourth part presents the results of forestation of inland drift-sand. Natural processes, such as spontaneous succession, are viewed as results of interaction of the ecosystem independent (environmental conditions) and dependent (behaviour of woody species) factors which together regulate the degree of the stand differentiation. The logical conclusion is that this interaction results in the establishment of different types of forest. A small, but important part of chapter five deals with the practical implications for the development of this type of landscape, and the protection and management of the ecosystem studied.

The book has simple hierarchical structure. Themes of the chapters are clearly stated and illustrated by numerous coloured photographs printed on high-quality paper. It would be advantageous if an index is included in future editions. There are some minor orthographical and nomenclatorical problems but they do not reduce the significance and general value of this book on what is a rare subject. The chapters that deal with restoration or problems of nature protection in this special context should be recommended reading for ecologically oriented schools or faculties. The interdisciplinary approach and the drawing of general conclusions makes this book a valuable contribution in the field of landscape ecology and provides an interesting perspective of ecological complexity.

Pavel Kovář