Plant Soil
DOI 10.1007/s11104-011-0782-2

REGULAR ARTICLE

Effect of slight vegetation degradation on soil properties in *Brachypodium pinnatum* grasslands

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Received: 16 December 2010 / Accepted: 24 March 2011

Abstract The interrelationship of soil and vegetation degradation is an emerging issue, where most studies have addressed severe degradation so far. We aimed at revealing changes in soil accompanying slight vegetation degradation in a case study involving xeromesophilous grasslands from Hungary. Slight degradation is of special interest here because the target community (*Euphorbio pannonicae—Brachypodietum pinnati* association) has great nature conservation value. Vegetation status was related to chemical and structural soil properties by principal component analysis and redundancy analysis. Vegetation conditions were assessed by species abundances and by fine-scale spatial structure, which is proposed here for soil-vegetation studies. Slight vegetation degradation clearly manifested itself in soil properties. Differences in vegetation status when assessed by species abundances were mirrored in chemical soil properties. When structural vegetation descriptors were used, a soil structure property (bulk density) was responsible for the segregation according to naturalness. Vegetation-soil relationships were more consistent over biogeographic regions, when vegetation structural descriptors were used. Differences in chemical soil properties reflected species abundance pattern, as was found in most non-grazing related degradation studies. However, changes to soil structure also accompanied slight degradation, and their importance was revealed when vegetation structure was taken into account.

Keywords Base-rock influence · Geographic variation · Naturalness · Soil structure · Vegetation structure

Introduction

While considerable knowledge has accumulated about plant-soil relationships, these mostly encompass single-species studies (Morales-Sillero et al. 2009; Schafer and Mack 2010). Less is known about vegetation-soil interactions and about how vegetation status, including degradation is reflected in soils. In natural communities, coexisting species may change soil characteristics directly, but also modify the reaction of each other to soil (Harrison and Bargett 2010), therefore soil requirements of individual species are not necessarily reflected in the occurrence

Responsible Editor: Jeffrey Walck.

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pattern within the community. Ample expert knowledge has accumulated about vegetation-soil relationships (Goodall 1989–2005), but quantitative studies are relatively rare (Elberling et al. 2008). It appears, however, that soil conditions do not only vary with species composition or plant associations. Elberling et al. (2008) have found the variation within a plant community may be as large as among communities. Such variation is possibly due to the different status of the communities within the vegetation dynamics process.

Currently, studying the effects of human use and disturbance on soil and vegetation simultaneously is receiving increased attention, since many of the Earth's ecosystems are threatened by intensification of use. Most authors reported significant differences in soil properties under vegetation disturbed to various degrees in several aspects including chemistry and physical attributes as well (Critchley et al. 2002; Müller et al. 2004; Myklestad 2004; Li et al. 2009). On the contrary, Lindell et al. (2010) found no differences in the characteristics of soils under native vegetation versus agricultural use. However, in most of these studies degradation was studied in its severe form. An exception is Cheng et al. (2007), who studied a full degradation gradient and also found differences in soil conditions typical to slight and severe degradation.

The conclusion of soil-vegetation studies regarding degradation may differ for a number of reasons. A major reason is surely the source of disturbance. A less obvious reason is the type of vegetation assessment. Early detection of slight degradation requires sensitive vegetation assessment, which might be the reason why severe degradation has been typically considered so far in soil-vegetation studies. Vegetation is typically characterised by species richness in soil-vegetation studies for generality and simplicity (Amorim and Batalha 2008; Pohl et al. 2009; Laurance et al. 2010). However, increasing number of studies have provided evidence that community responses to disturbances or degradation manifest less in changes of local species richness and more in changes in the structure, the fine-scale spatial complexity of the community (Campetella et al. 2004; Standovár et al. 2006; Virágh et al. 2008). Another reason, why conclusions can differ is, that vegetation-soil relationships often vary with geographical regions (Gough et al. 2000; Hájková et al. 2007; van Dobben and de Vries 2010). Even if the relationship would be comparable over regions, change in the species composition due to biogeographic reasons can mask this. Therefore, using species abundances as a mean to capture vegetation complexity in relation to soil, which is widespread nowadays (e.g. Somodi and Botta-Dukát 2004; Costa et al. 2005; Li et al. 2008), may lead to ambiguous results if the study is conducted over biogeographic regions or broad management regimes (e.g. Myklestad 2004). Changes in descriptors of vegetation structure are potentially more predictable than species composition, and therefore, it is a promising way to overcome such difficulties (Romme et al. 2009; Walker et al. 2010). A useful family of diversity-related, multiscale functions for quantifying vegetation structure and keeping most of its complexity has been introduced by Juhász-Nagy (Juhász-Nagy 1976, 1984, 1993; Bartha et al. 1998). These functions and related measures are capable of characterising the co-occurrence pattern of species at multiple scales, which allows assessing the studied vegetation in its full complexity.

There is a special interest in the naturalness of *Brachypodium pinnatum* dominated grasslands in Hungary. Although, the increasing dominance of *B. pinnatum* poses a threat to biodiversity in the Atlantic region of Europe (Bobbink and Willems 1987, 1992), in semiarid areas of the continent such as in Hungary, *Brachypodium* grasslands are remnants of the native wooded steppe vegetation. As the native wooded steppe has been largely removed by agriculture, such remnants are considered to be vulnerable. They are characterized by high species richness (45–50 species in 4 m^2 quadrats, Horváth 2010) and contain numerous elements of the former oak woodland (e.g. *Campanula persicifolia, Tanacetum corymbosum, Peucedanum cervaria*); thus they have great nature conservation value (Fekete et al. 1998). *Brachypodium* grasslands in Hungary belong to the grassland component of wooded steppe (*Euphorbio pannonicae—Brachypodietum pinnati* association, Horváth 2010), and typically occur on the north and north-east facing hillsides, at about 35^o steep slopes, at 150–300 m above sea level. For further detailes of floristic composition and habitat conditions of this grassland community see Horváth (2010). Nomenclature follows Tutin et al. (2001).

The first aim of this study was to explore whether and how slight vegetation degradation appears in soil characteristics of these grasslands. To assist this aim we formulated the following questions:

1. Can the compositional differentiation of samples from different vegetation conditions (degraded, undistrubed) be coupled with specific soil patterns?
2. Is there a difference in the generality of soil-vegetation relationships whether vegetation is characterised by abundance relationships or fine-scale structure?
3. Does the level of site influence of these relationships differ with the type of vegetation assessment?

Material and methods

Sampling

12 natural and 12 degraded stands of *Brachypodium* grasslands were sampled. To provide more general results these samples originated from two geographic regions within Hungary (Mezőföld N47°6′15″, E18°32′ 0″; Gödöllő-hills, N47°32′29″, E19°21′41″). While the community remains the same, distinct biogeographic differences make the actual species composition of the stands in the different regions slightly different. Sampled stands were selected a priori so as to represent the natural and slightly degraded status, however they were similar in every other aspects as much as possible including the association they belong to. Natural stands sampled were located within nature preserves, were surrounded by natural vegetation and therefore were subject to natural disturbances only. In the past, more than 30 years ago, all the sampled grasslands (both now degraded and natural) from the region of Mezőföld were moderately grazed. No major past disturbances to natural stands are known from the other region. Degraded stands in both locations have been subjected and are still exposed to occasional human disturbance (including fire, trampling, moto-cross, planting of electricity pillars). Nevertheless, the occurrence of these disturbances is sporadic; therefore they do not change the main character of the vegetation. Degraded stands, as a contrast to natural ones, are surrounded by arable fields or by strongly degraded vegetation, which again influence the target vegetation. The difference between degraded and natural stands regarding vegetation is yet subtle, both kinds of stands can still be considered exemplars of the *Euphorbio pannonicae—Brachypodietum pinnati* association. Differences do not appear either in species richness or diversity. Stands of different status here mainly differ in their physiognomy, e.g. some tall, ruderal dicots are present in degraded stands (*Solidago gigantea, Ononis spinosa, Stenactis annua, Erigeron annuus* and *Artemisia vulgaris*) and in their within-stand spatial heterogeneity, i.e. spatial organisation and structure (Virágh et al. 2008). Dynamic processes are slow in these communities; thus they can be considered dynamically stable at the decade-scale (Virágh et al. 2008).

Vegetation data

Vegetation sampling was carried out at the beginning of July according to the standard sampling protocol optimised for collecting data for information statistical analysis (see also Virágh et al. 2008). Natural stands were sampled in 2004, degraded ones in 2005. Soil analysis was carried out in 2008. In general, sampling in different years can influence vegetation comparisons, but the status of the grasslands studied here has been shown to be stable at the decade scale (Virágh et al. 2008). Namely, they were found to fluctuate in terms of species composition and structure in distinct regions according to degradation status; therefore we can assume that sampling dates do not influence our analyses.

Presence of rooted species were recorded in 25 cm^2 contiguous microquadrats along a 52 m long circular transect in each sample stand. Abundance of each species was quantified by the frequency of their individuals recorded in 1040 units of microquadrats along this transect. In the present analyses of abundance data, however, only those species were included which were more frequent than 0.01 when taking all stands into account. Spatial structures of the vegetation stands were described by two of Juhász-Nagy's information statistical functions: compositional diversity (FD) and associatum (As). Compositional diversity is the Shannon diversity of the frequency distribution of species combinations. Associatum (As) is an information theory measure that describes the overall multi-species spatial dependence within the community. Both functions are calculated at a series of scales by merging microquadrats hierarchically; thus they synthesise the complexity of within-stand coexistence relationships (structural complexity of the community). For detailed explanation of the functions and the theoretical background of this multiscale methodology, which is based on Juhász-Nagy's information theory models consult Juhász-Nagy (1976, 1984, 1993), Juhász-Nagy and Podani (1983), and Bartha et al. (1998, 2004).

Soil sampling and laboratory analysis

For soil sampling, three replicate points were marked within each stand, where vegetation sampling was carried out. At each point five replicate soil samples were collected from the depths of 0–10 and 10–20 cm of the soil and analyses were performed separately for each depth. Exceptions are soil bulk density and penetration depth. The former was determined only from the top 0–5 cm, by collecting core samples with standard steal cylinders (0.0001 m^3). The latter was measured with a drop hammer penetrometer in the field. During each measurement a 1,000 g hammer was dropped from 50 cm height five times and subsequently, the penetration depth of the 60° cone on the 15 mm thick rod was measured (Campbell and Hunter 1986; Godwin et al. 1991; Herrick and Jones 2002).

Chemical attributes of the soil were determined by standard methods according to Sparks (1996) in the laboratory after samples had been air-dried. All these analyses were conducted in the laboratories of the Research Institute for Soil Science and Agricultural Chemistry of the Hungarian Academy of Sciences, Budapest. pH was measured at 1:2.5 soil : water ratio after 1 day equilibration time, $CaCO_3$ content was determined with Scheibler-calcimeter, and plant available potassium and phosphorus were determined with ammonium lactate-acetic (AL) extraction (Diest 1963). NH_4-N and NO_3-N were measured by steam distillation after the methods of Houba et al. (1990) and Bremmer (1965). In order to eliminate the effect of root-mass, soil organic matter was only determined in the 10–20 cm layer with Tyurin method, which is a proxi of the Walkley-Black method (cf. Moore and Chapman 1986).

Means and standard deviation of soil properties for the individual sampling stands are presented in Table 1.

Data analysis

Before the actual analyses, abundance data and soil data were analysed using detrended correspondence analysis (DCA) to determine whether linear or

Table 1 Soil properties of the sampled stands. Means and standard deviations are presented. Soil organic matter was only determined in the deeper layer to eliminate the effect of root-mass. Bulk density refers to the upper 5 cm of the soil. Penetration depth was determined from the surface of the soil

	natural stands in Mezőföld		degraded stands in Mezőföld		natural stands in the Gödöllő-hills		degraded stands in the Gödöllő-hills	
depth	upper 10 cm	10–20 cm	upper 10 cm	10–20 cm	upper 10 cm	10–20 cm	upper 10 cm	10–20 cm
pH	7.42±0.10	7.62±0.09	7.33±0.16	7.52±0.10	6.96±0.77	7.10±0.73	7.23±0.28	7.32±0.30
soil organic matter {%}		6.92±1.57		8.22±0.49		5.43±0.74		5.98±0.86
calcium carbonate {%}	7.36±4.65	9.12±4.86	3.03±1.82	3.77±1.07	3.19±1.77	4.26±2.49	2.58±2.68	2.82±2.45
available potassium {K_2O_AL, mg/kg}	360.02±72.89	193.95±26.71	259.51±65.61	180.74±35.86	299.92±89.50	241.29±77.80	255.76±35.04	141.73±19.72
phosphorus {P_2O_AL, mg/kg}	105.42±28.46	62.73±15.50	125.63±28.53	88.33±24.76	68.93±15.61	55.74±16.03	97.79±14.66	60.11±7.83
ammonium nitrogen {NO_3-N, mg/kg}	16.67±15.36	9.40±4.98	10.84±2.60	7.22±1.28	7.85±1.78	5.50±0.49	9.07±1.98	6.61±0.89
nitrate nitrogen {NH_4-N, mg/kg}	19.69±12.60	9.48±5.31	23.07±9.75	16.82±10.16	7.33±4.72	6.41±3.03	19.90±11.34	8.04±3.10
soil bulk density {g/cm^3}	0.89±0.09		0.80±0.04		0.81±0.05		0.79±0.05	
penetration depth {cm}	4.91±0.47		6.44±1.90		5.62±1.10		7.01±1.47	

unimodal methods would be appropriate in the analyses (Lepš and Šmilauer 2003). As the gradient length was short (1.75 and 1.62 for the first 2 axes and much less for other axes), linear ordinations, such as principal component analysis (PCA) and redundancy analysis (RDA) were applied. All analyses were carried out in the R statistical environment (R Development Core Team 2008).

First, unconstraint ordinations (principal component analyses) were undertaken to explore the similarity of stands of different naturalness in terms of geographic variation, species composition and vegetation structure. Soil variables were then projected post hoc onto the ordination, thus preserving an unbiased representation of the positions of groups of samples according to vegetation characteristics. The FactoMineR package (Husson et al. 2010) was used for this purpose.

Second, redundancy analysis (ter Braak and Šmilauer 1998; Lepš and Šmilauer P 2003) was performed with the vegan package of the R statistical environment (Oksanen et al. 2011). In these models species abundances or structural complexity measures of vegetation stands represented the response, soil variables were the explanatory variables, while location of samples regarding the two geographic regions was included as a conditioning variable with two levels referring to the two regions. The effect of conditional variables is partialled out from ordinations. This ensures that the vegetation-soil relationship was cleaned from site effects in our RDAs.

Soil variables were highly correlated, which would not have allowed any significance testing in RDA. To overcome this, first, pairwise Pearson correlation was calculated between each variable separately for abundance and vegetation structure data. Variables showing higher correlation then 0.7 were inspected. Correlated variables typically quantified the same soil parameter in different depths. For these variables (pH, calcium carbonate, phosphorus and ammonium nitrogen), values coming from different soil depths were merged (averaging vs. summing up according to meaningfulness). There was only one variable after these treatments which still showed high correlation with several others, soil organic matter content, which was removed. The procedure resulted in 10 uncorrelated variables. RDA was then performed using these variables. We also applied stepwise variable selection based on the AIC criterion to these models. Model significance, the significance of axes and that of the contribution of variables were tested using a permutation test (anova.cca function in the vegan package, also recommended for RDA), which calculates a pseudo-F value and so corresponds to the F-test statistics used for model comparison in linear modelling.

Although site effects have been removed from RDA models, proportions of variance explained by site vs. soil effects cannot be unambiguously interpreted because variable interactions would influence the values. So as to be able to interpret regional and soil effects quantitatively and separately, we carried out variance partitioning on the reduced models (varpart function in vegan package; Borcard et al. 1992).

Results

Comparisons of vegetation stands based on species abundance

PCA resulted in distinct groups separated by region and by the level of disturbance (natural vs. slightly degraded) (Fig. 1). The first axis explained 20.25% of the total variance in species composition. This axis

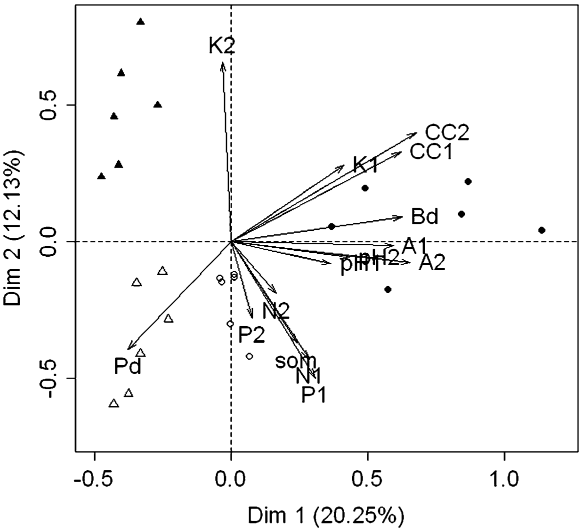

Fig. 1 Results of the PCA ordination of the sampling stands based on species abundance data. Circles refer to Mezőföld region, triangles to the Gödöllő region. Filled symbols indicate natural stands, open symbols degraded ones. Soil variables are added as supplementary variables. Abbreviations: CC—calcium carbonate, K—available potassium, som—soil organic matter, N—nitrate nitrogen, A—ammonium nitrogen, P—phosphorus, Bd - soil bulk density, Pd—penetration depth. Numbers refer to the depth samples were taken of: 1—upper 10 cm, 2–10–20 cm

can be interpreted as the main gradient differentiating our stands according to their geographic locations. Degraded stands from different regions were closer in the multivariate space than natural stands, i.e. they exhibited less compositional variability. At the same time their segregation according to geographic locations was still apparent. The second axis explained 12.13% of the variance, and this axis differentiated our stands according to the level of (past) disturbance (natural vs. disturbed/degraded states).

According to the post hoc projection of all measured soil attributes onto the PCA ordination, sample groups differentiated by species abundances also possess distinct soil characteristics (Fig. 1). One of the groups containing natural samples from undisturbed/protected sites (Mezőföld region) were characterised with higher pH, higher amount of available potassium in the top 10 cm of the soil (K1) and ammonium nitrogen (A1, A2), calcium carbonate (CC1, CC2) in both depths, as well as with higher bulk density (Bd) and lower penetration depth (Pd). The other group containing natural stands (from the Gödöllő-hill region) could be characterised with higher amount of potassium in the deeper layer of the soil. At the same time lower Pd, available phosphorus (P1, P2) and nitrate nitrogen (N1, N2) contents were indicated. Degraded stands, in contrast were characterized with increased nutrient levels both regarding phosphorus and nitrate nitrogen, as well as with more soil organic matter and greater penetration depth. These samples were located on the lower end of the potassium gradients regardless of the depth where the sample was taken, as well as at the lower end of the pH, calcium carbonate and ammonium nitrogen content and bulk density gradient. The latter was especially pronounced in the case of the degraded site in the Gödöllő-hills region.

Redundancy analysis (RDA) followed by stepwise variable selection underlined the importance of base-rock related soil characteristics: potassium levels in different depths and calcium-carbonate content (Fig. 2). The relationship between vegetation and soil was significant according to the model as well as the first three axes (Table 2). All the variables had significant contribution to the model according to the permutation test. When the effect of location (regions) has been partialled out the main separation occurred according to degradation status with natural stands having higher levels of base-rock related substances. Variance partitioning also showed a strong site effect, comparable in explanatory potential to the soil variables.

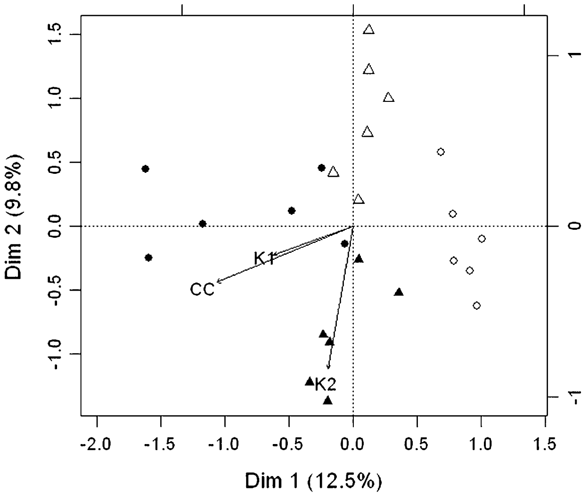

Fig. 2 Segregation of natural stands from degraded ones according to soil variables selected by forward selection procedure in redundancy analysis. Symbols and abbreviations as in Fig. 1

Relationships between soil properties and vegetation degradation based on fine-scale spatial structure of the plant community

According to the simultaneous analyses of soil and vegetation data based on stand-scale spatial structure by PCA and RDA, samples formed two major groups (Figs. 3 and 4). Both analyses resulted in the separation of natural and disturbed stands. The projection of soil variables onto the results of the PCA revealed that the first axis was negatively correlated with the bulk density gradient, with increasing concentration of calcium carbonate, potassium and ammonium nitrogen. This direction was coupled with natural stands. At the same time, the first axis and thus the location of degraded stands was positively correlated with penetration depth, as well as with the increasing content of soil organic matter, nitrate-nitrogen and available phosphorus.

The model resulting from redundancy analysis and subsequent variable selection contained only one soil-related variable, bulk density, which was also significant (Fig. 4). It was apparent that natural stands appeared in a more compact group along the revealed gradient than degraded ones, thus showing less

Table 2 Statistical summary of the RDA models. Explained variances per axes refer to the species-environment relationship. There was only one soil parameter retained in the reduced model for structural descriptors, therefore only one axis' details are shown. Significance has been tested using permutation tests (anova.cca function in the vegan package of R statistical environment, also recommended for RDA). As sites were included as conditioning variables and soil variables as constraints, it was possible to compare the proportions of variance explained by the different variable sets

		Abundance data	Structural descriptors
Validity of the model			
Significance of the model (p-value)		0.005	0.005
Axis 1	Variance explained (%)	12.540	25.430
	Significance (p-value)	0.005	0.01
Axis 2	Variance explained (%)	9.829	
	Significance (p-value)	0.005	
Axis 3	Variance explained (%)	4.418	
	Significance (p-value)	0.015	
Variables (p-value)		potassium in the upper layer (0.04), potassium in the lower layer(0.01), calcium carbonate (0.01)	bulk density (0.03)
Variance partitioning			
Proportion explained (Adjusted R^2)	site effect	0.085	−0.016
	joint effect	0.048	−0.027
	soil variables	0.132	0.228
	residuals	0.735	0.816

variation in bulk density. Variance partitioning has shown that site identity has no effect in this setting (Adjusted R^2 below 0; Table 2).

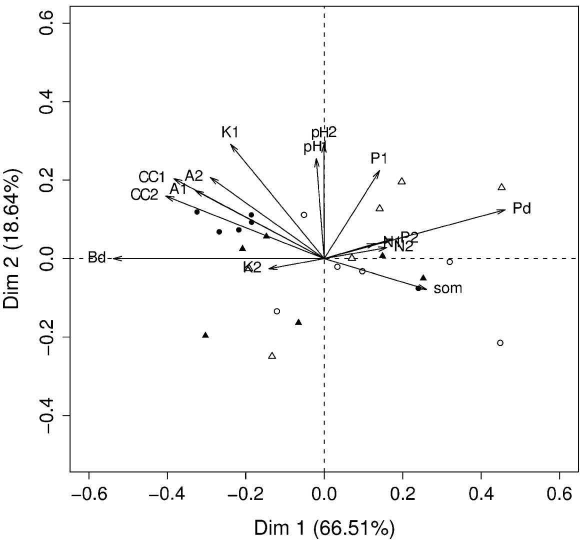

Fig. 3 Result of the PCA of the stands based on fine-scale community structure with soil data displayed as supplementary variables. Symbols and abbreviations as in Fig 1

Discussion

It has been long known that specific species and plant communities can be linked to specific soil attributes (Goodall 1989–2005; Maccherini 2006a,b; Bohlman et al. 2008). Our results have revealed that soil consistently mirrors even slight degradation of vegetation, independently of whether vegetation is characterized by abundance or structure. Severe vegetation degradation has already been shown to be accompanied by soil changes (Müller et al. 2004; Myklestad 2004; Li et al. 2009, but Lindell et al. 2010), but has not been shown for so low level degradation as in our case, where both states of our stands can still be regarded as belonging to the same plant association. Elberling et al. (2008) have shown that variation in soil characteristics within a plant community can be as large as those between communities. Our study offers an explanation for that by demonstrating that soil conditions differ within the same community according to degradation stages. Furthermore, our study has indirectly shown that this variance in soil conditions is characteristic to natural stands, since more degraded stands were closer in the

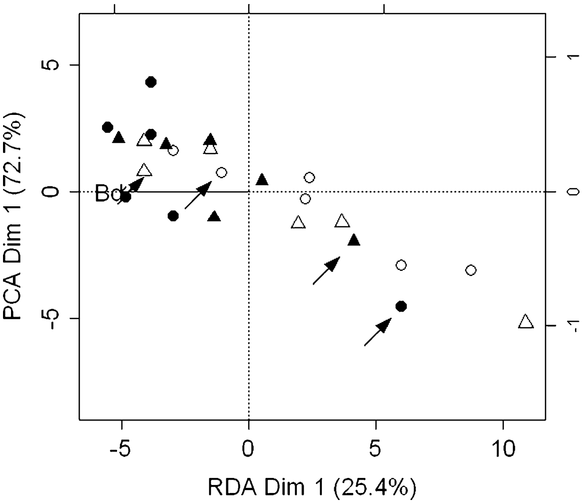

Fig. 4 RDA analysis of vegetation structure and soil. Previous vegetation analysis (Virágh et al. 2008) revealed that two stands within degraded ones and two within natural ones as assessed a priori, have vegetation structural characteristics typical to the other status. To keep consistence these are marked according to their a priori classification, but we added arrows pointing towards the symbols representing these, so that their apparent mislocation along the degraded-natural gradient is cleared. If we take the a posteriori, vegetation analysis-based classification for them, degraded and natural stands are even better differentiated. Symbols and abbreviations as in Fig. 1

virtual space formed by explanatory variables both regarding species composition and soil parameters, although interestingly this did not apply to vegetation structure. A homogenisation effect of degradation is well known in plant and animal communities (McKinney and Lockwood 1999; Lougheed et al. 2008), and recently a few studies have observed a similar pattern in soils, too (Wiesmeier et al. 2009; Lin et al. 2010).

Site effects were much stronger, comparable to the explanatory power of soil variables when abundance relationships were studied. This can be seen first of all on PCA ordinations, where the first axis separates the sites, when abundance patterns are studied, secondly in the results of variance partitioning. On the contrary, there is no such separation for structural descriptors. The fact that the relationship between plant abundance patterns and soil variables changes with geographic location is well-known from previous literature as well (Hájková et al. 2007; van Dobben and de Vries 2010). Kalusová et al. (2009) have even found that site-related factors explain more from the variance in species abundances than soil parameters even within one region. The response as assessed by the structural descriptors did not depend on species identities, which allows direct comparison even among sites that do not share species at all (Bartha et al. 1998; Bartha 2008). This is also reflected in our results with structural vegetation descriptors: site identity did not influence ordination and therefore variance partitioning was actually not necessary. However, this structural vegetation assessment has never been used in soil-vegetation studies before. According to our results it is a promising tool for investigations of soil-vegetation patterns together over biogeographic regions as well.

Ordination plots (PCA) with all the soil variables added, show similar pattern for both kinds of vegetation descriptors, while the soil variables that were retained in the models after variable selections (in RDA) differ. One typical pattern was associated with the influence of base rock on the soil, which also provided the significant explanatory variables for the abundance-related separation of stands. Substances coming from the base rock ($CaCO_3$ and potassium) were associated with natural stands, while increased amount of nutrients in the soil was linked to degraded stages. Clay and calcareous loess is naturally rich in calcium carbonate and potassium (Mengel and Rahmatullah 1998); therefore it is reasonable that their presence indicates natural stands in our case. This is also the reason for pH increasing towards natural stands. Indeed, calcareous grasslands are often species rich in the temperate zone (Marrs 1993; Basnou et al. 2009). Furthermore Critchley et al. (2002) have shown that species richness is higher if less nitrogen and phosphorus is present in their soil. Janssens et al. (1998), for example, reported that increased available potassium content is related to greater diversity in grasslands. A higher amount of other base-rock related cations in the soil is reported to be coupled with higher species diversity also (Amorim and Batalha 2008). However, there is a difference whether the cations come from the substrate, to which the community is adapted, or from fertilisation. In the latter case an increased level of potassium is often accompanied with degradation (Critchley et al. 2002; Spiegelberger et al. 2010).

The two physical parameters, penetration depth and bulk density pointed to opposite directions in the ordination space (PCA), which is reasonable since they measure soil structure from opposite points of view. The former also proved to be the sole significant explanatory variable of degradation, when assessed with structural descriptors. Bulk density was always greater and penetration depth was lower in natural stands, and thus these appeared to have more compact soils (Arshad et al. 1996, Lal 1994). Such a pattern is not typical in previous studies; increased bulk density and lower penetration depth have usually been associated with degradation (van Haveren 1983, Pei et al. 2008; Stavi et al. 2008). However, the cited papers deal with degradation due to grazing, where trampling makes soils under more heavily used pastures more compact. In our case, in one of the regions, both kinds of stands have been exposed to grazing in the past, while none were grazed in the other region. Therefore, differences in bulk density after the removal of site identity have to be the result of other effects. In our case, past and mild land use, as well as the use of the surrounding arable fields characterise degraded locations. It might be the encroachment of tall forbs as weeds and occasional human disturbances, which loosen up the soil at these sites and then result in the lower bulk density of the soil. At the same time, increased bulk density might (further) favour the establishment of weeds that have a wider tolerance than species of the original community.

Vegetation structure seems to reflect soil structure, rather than chemistry, since the only significant variable determining the division between natural and degraded stands was bulk density. It is again a marked difference compared to the case when vegetation was assessed by species abundances. Interestingly, it was exactly bulk density, where larger within-community variation than variation between communities has been observed (Elberling et al. 2008). Our results imply that structural differences among stands of the same community, which are often present (Bartha 2008; Virágh et al. 2008), can potentially explain such variation.

Conclusions

Even slight vegetation degradation was found to be accompanied by characteristic changes in the soil independently of the approach used to assess vegetation character. However, differences in the nature of the relationship according to assessment type were also discernible. When abundance was used as vegetation descriptor site differences were important, while they had no effect when structural descriptors were used. There was also a difference in the identity of significant explanatory variables. Higher levels of base-rock related soil variables differentiated natural stands from degraded ones when abundance was used, while a structural soil property in the case of structural vegetation descriptors. Therefore, we recommend considering structural characterisation of vegetation in studies of vegetation-soil relationships, because this is not sensitive to biogeographic differences, but is more sensitive to minor differences in vegetation status. Furthermore, results also imply that it probably reflects differences in soil structure better than species composition.

Acknowledgement We thank all our PhD students and assistants for their valuable help during data collection in the field. This project is supported by the Hungarian Research Fund (OTKA) grant no. K-62338.

References

Amorim PK, Batalha MA (2008) Soil chemical factors and grassland species density. Braz J Biol 68:279–285

Arshad MA, Lowery B, Grossman B (1996) Physical test for monitoring soil quality. In: Jones AJ, Doran JW (eds) Methods for assessing soil quality. SSSA, Madison, Wisconsin, USA, pp 123–141

Bartha S (2008) Beyond trivial relationships: on the hidden aspects of biodiversity. Folia Geobot 43:371–382

Bartha S, Campetella G, Canullo R, Bódis J, Mucina L (2004) On the importance of fine-scale spatial complexity in vegetation restoration. Int J Ecol Environ Sci 30:101–116

Bartha S, Czárán T, Podani J (1998) Exploring plant community dynamics in abstract coenostate spaces. Abstr Bot 22:49–66

Basnou C, Pino J, Smilauer P (2009) Effect of grazing on grasslands in the Western Romanian Carpathians depends on the bedrock type. Preslia 81:91–104

Bobbink R, Willems JH (1987) Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands: a threat to a species-rich ecosystem. Biol Conserv 40:301–314

Bobbink R, Willems JH (1992) Restoration management of abandoned chalk grassland in the Netherlands. Biol Divers Conserv 57:1–21

Bohlman SA, Laurance WF, Laurance SG, Nascimento HEM, Fearnside PM, Andrade A (2008) Importance of soil, topography and geographic distance in structuring central Amazonian tree communities. J Veg Sci 19:863–874

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73:1045–1055

Bremmer JM (1965) Inorganic forms of nitrogen. In: Black CA (ed) Methods of Soil Analysis. Agron 9:1179–1237

Campbell DJ, Hunter R (1986) Drop-cone penetration in situ and on minimally disturbed soil cores. J Soil Sci 37:153–163

Campetella G, Canullo R, Bartha S (2004) Coenostate descriptors and spatial dependence in vegetation – derived variables in monitoring forest dynamics and assembly rules. Community Ecol 5:105–114

Cheng X, An S, Chen J, Li B, Liu Y, Liu S (2007) Spatial relationships among species, above-ground biomass, N, and P in degraded grasslands in Ordos Plateau, northwestern China. J Arid Environ 68:62–667

Costa FR, Magnusson CWE, Luizão RC (2005) Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. J Ecol 93:863–878

Critchley CNR, Chambers BJ, Fowlert JA, Sanderson RA, Bhogal A, Rose SC (2002) Association between lowland grassland plant communities and soil properties. Biol Conserv 105:199–215

Diest A (1963) Soil test correlation studies on New Jersey soils: 2. A modified ammonium-lactate-acetic-acid method for measuring soil nutrients. Soil Sci 93:337–341

Elberling B, Tamstorf MP, Michelsen A, Arndal MF, Sigsgaard C, Illeris L, Bay C, Hansen BU, Christensen TR, Hansen ES, Jakobsen BH, Beyens L (2008) Soil and plant community-characteristics and dynamics at Zackenberg. Adv Ecol Res 40:223–248

Fekete G, Virágh K, Aszalós R, Orlóci L (1998) Landscape and coenological differentiation in *Brachypodium pinnatum* grassland. Coenoses 13:39–53

Godwin RJ, Warner NL, Smith DLO (1991) The development of a dynamic drop-cone device for the assessment of soil strength and the effects of machinery traffic. J Agric Eng Res 48:123–131

Goodall DW (ed) (1989–2005) Ecosystems of the World. Book Series, Elsevier

Gough L, Osenberg CW, Gross KL, Collins SL (2000) Fertilization effects on species density and primary productivity in herbaceous plant communities. Oikos 89:428–439

Hájková P, Hájek M, Apostolova I, Zelený D, Dítě D (2007) Shifts in the ecological behaviour of plant species between two distant regions: evidence from the base richness gradient in mires. J Biogeogr 35:282–294

Harrison KA, Bargett RD (2010) Influence of plant species and soil conditions on plant-soil feedback in mixed grassland communities. J Ecol 98:384–395

Herrick JE, Jones TJ (2002) A dynamic cone penetrometer for measuring soil penetration resistance. Soil Sci Soc Am J 66:1320–1324

Horváth A (2010) Validation of description of the xeromesophilous loess grassland association, *Euphorbio pannonicae – Brachypodietum pinnati*. Acta Bot Hung 52:103–122

Houba VJG, Novozamsky L, Lexmond TM, van der Lee JJ (1990) Applicability of 0.01 M CaCl 2 as a single extraction solution for the assessment of the nutrient status of soils and other diagnostic purposes. Commun Soil Sci Plant Anal 21:2280–2290

Husson F, Josse J, Le S, Mazet J (2010). FactoMineR: Multivariate Exploratory Data Analysis and Data Mining with R. R package version 1.14. http://CRAN.R-project.org/package=FactoMineR

Janssens F, Peters A, Tallowin JRB, Bakker JP, Bekker RM, Fillat F, Oomes MJM (1998) Relationship between soil chemical factors and grassland diversity. Plant Soil 202:69–78

Juhász-Nagy P (1976) Spatial dependence of plant populations. Part 1. Equivalence analysis (an outline for a new model). Acta Bot Acad Sci Hung 22:61–78

Juhász-Nagy P (1984) Spatial dependence of plant populations. Part 2. A family of new models. Acta Bot Acad Sci Hung 30:363–402

Juhász-Nagy P (1993) Notes on compositional diversity. Hidrobiologia 249:173–182

Juhász-Nagy P, Podani J (1983) Information theory methods for the study of spatial processes in succession. Vegetatio 51:129–140

Kalusová V, Le Duc MG, Gilbert JC, Lawson CS, Gowing DJG, Marrs RH (2009) Determining the important environmental variables controlling plant species community composition in mesotrophic grasslands in Great Britain. Appl Veg Sci 12:459–471

Lal R (1994) Soil Erosion Research Methods. Soil and Water Conservation Society. CRC Press, Boca Raton, Florida, USA

Laurance SGW, Laurance WF, Andrade A, Fearnside PM, Harms KE, Vincentini A, Luizao RCC (2010) Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. J Veg Sci 21:96–106

Lepš J, Šmilauer P (2003) Multivariate Analysis of Ecological data using *CANOCO.* Cambridge Univ Press 269 pp.

Li FR, Zhao WZ, Liu JL, Huang ZG (2009) Degraded vegetation and wind erosion influence soil carbon nitrogen and phosphorus accumulation in sandy grasslands. Plant Soil 317:79–92

Li WQ, Liu XJ, Khan MA, Gul B (2008) Relationship between soil characteristics and halophytic vegetation in coastal region of North China. Pak J Bot 40:1081–1090

Lin Y, Hong M, Han G, Zhao M, Bai Y, Chang SX (2010) Grazing intensity affected spatial patterns of vegetation and soil fertility in a desert steppe. Agric Ecosyst Environ 138:282–292

Lindell L, Astrom M, Oberg T (2010) Land-use versus natural controls on soil fertility in the Subandean Amazon, Peru. Sci Total Environ 408:965–975

Lougheed VL, Mcintosh MD, Parker CA, Stevenson RJ (2008) Wetland degradation leads to homogenization of the biota at local and landscape scales. Freshw Biol 53:2402–2413

Maccherini S (2006a) Small-scale spatial structure in a remnant calcareous grassland. Belg J Bot 139:103–144

Maccherini S (2006b) Factors associated with species richness in a remnant calcareous grassland. Grassland Sci 52:181–184

Marrs RH (1993) Soil fertility and nature conservation in Europe: Theoretical considerations and practical management solutions. Adv Ecol Res 24:241–300

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

Mengel K, Rahmatullah HD (1998) Release of potassium from the silt and sand fraction of loess-derived soils. Soil Sci 163:805–813

Moore PD, Chapman SB (eds) (1986) Methods in Plant Ecology. Blackwell Sci Publ, Oxford, p 589

Morales-Sillero A, Fernandet JE, Ordovás J, Suárez MP, Pérez JA, Linán J, López EP, Girón I, Troncoso A (2009) Plant-soil interactions in a fertigated 'Manzanilla de Sevilla olive orchard. Plant Soil 319:147–162

Müller MM, Guimaraes MF, Desjardins TC, Mitja D (2004) The relationship between pasture degradation and soil properties in the Brazilian amazon: a case study. Agric Ecosyst Environ 103:279–288

Myklestad A (2004) Soil, site, management components of variation in species composition of agricultural grasslands in western Norway. Grass Forage Sci 59:136–143

Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2011) vegan: Community Ecology Package. R package version 1.17-6. http://CRAN.R-project.org/package=vegan

Pei S, Fu H, Wan C (2008) Changes in soil properties and vegetation exclosure and grazing in degraded Alxa desert steppe of Inner Mongolia, China. Agric Ecosyst Environ 124:33–39

Pohl M, Alig D, Körner C, Rixen C (2009) Higher plant diversity enhances soil stability in disturbed alpine ecosystems. Plant Soil 324:91–102

R Development Core Team (2008) A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0. URL http://www.R-project.org.

Romme WH, Allen CD, Bailey JD, Baker WL, Bestelmeyer BT, Brown PM, Eisenhart KS, Floyd ML, Huffman DW, Jacobs BF, Miller RF, Muldavin EH, Swetnam TW, Tausch RJ, Weisberg PJ (2009) Historical and modern disturbance regimes, stand structures, and landscape dynamics in Piñon–Juniper vegetation of the western United States. Rangeland Ecol Manage 62:203–222

Schafer JL, Mack MC (2010) Short-term effects of fire on soil and plant nutrients in palmetto flatwoods. Plant Soil 334:433–447

Somodi I, Botta-Dukát Z (2004) Determinants of floating island vegetation and succession in a recently flooded shallow lake, Kis-Balaton (Hungary). Aquat Bot 79:357–366

Sparks DL (1996) Methods of Soil Analysis. Part 3. Chemical Methods. SSSA Book Ser 5, Madison, Wisconsin, USA, 1358 p

Spiegelberger T, Deleglise C, DeDanieli S, Bernard-Brunet C (2010) Resilience of acid subalpine grassland to short-term liming and fertilisation. Agric Ecosyst Environ 137:158–162

Standovár T, Ódor P, Aszalós R, Gálhidy L (2006) Sensitivity of ground layer vegetation diversity descriptors in indicating forest naturalness. Community Ecol 7:199–209

Stavi I, Ungar ED, Lavee H, Sarah P (2008) Surface microtopography and soil penetration resistance associated with shrub patches in a semiarid rangeland. Geomorphology 94:69–78

Ter Braak CJF, Šmilauer P (1998) CANOCO Reference Manual and User's Guide to Canoco for Windows. Center for Biometry, Wageningen, 351 pp

Tutin TG et al (eds) (2001) Flora Europaea. CD-version. Cambridge Univ Press, Cambridge

Van Dobben H, de Vries W (2010) Relation between forest vegetation, atmospheric deposition and site conditions at regional and European scales. Environ Pollut 158:921–93

Van Haveren BP (1983) Soil bulk density as influenced by grazing intensity and soil types on a shortgrass prairie sit. J Range Manage 36:586–588

Virágh K, Horváth A, Bartha S, Somodi I (2008) A multivariate methodological approach for monitoring the effectiveness of grassland management. Community Ecol 9:237–247

Walker LR, Wardle DA, Bardgett RD, Clarkson BD (2010) The use of chronosequences in studies of ecological succession and soil development. J Ecol 98:725–736

Wiesmeier M, Steffens M, Kölbl A, Kögel-Knabner I (2009) Degradation and small-scale spatial homogenization of topsoils in intensively-grazed steppes of Northern China. Soil Tillage Res 104:299–310