Original scientific article
Received: 2010-05-21

UDC 581.52:547.4(497.4)

RELATION BETWEEN CSR FUNCTIONAL SIGNATURES OF DRY GRASSLANDS FROM TWO CONTRASTING GEOLOGICAL SUBSTRATES

Sonja ŠKORNIK
Department of Biology, Faculty of Natural Sciences and Mathematics, University of Maribor, SI-2000 Maribor, Koroška 160, Slovenia
E-mail: sonja.skornik@uni-mb.si

Klavdija HARTMAN
Činžat 17, SI-2343 Fala, Slovenia

Mitja KALIGARIČ
Department of Biology, Faculty of Natural Sciences and Mathematics, University of Maribor, SI-2000 Maribor, Koroška 160, Slovenia

ABSTRACT

The paper presents floristic and functional comparison of two adjacent and structurally similar plant communities – calcareous (Bromion erecti) *and silicicolous* (Nardo-Agrostion tenuis) *dry grasslands. For functional comparison Grime's CSR triangle theory of plant strategies was used. The analysis of species composition showed great differences between both dry grassland types. Higher relative proportions of S component and lower relative proportions of C components in silicicolous grasslands suggest that those habitats generally experience higher intensities of stress when compared to calcareous grasslands, presumably owing to low resource availability on high-acidic sites and also due to their occurrence in higher altitudes.*

Key words: calcareous dry grasslands, silicicolous dry grasslands, species composition, plant functional types, plant traits, Slovenia

RELAZIONE TRA SIGLE FUNZIONALI CSR DI PASCOLI ARIDI SU DUE SUBSTRATI GEOLOGICI CONTRASTANTI

SINTESI

L'articolo presenta la comparazione floristica e funzionale fra due comunità vegetali adiacenti e strutturalmente simili – calcarea (Bromion erecti) *e silicea* (Nardo-Agrostion tenuis) *di pascoli aridi. Per la comparazione funzionale è stato usato il modello CSR di Grime, inerente alle strategie ecologiche delle piante. L'analisi della composizione delle specie ha evidenziato notevoli differenze fra i due tipi di pascoli aridi. Maggiori proporzioni relative della componente S e minori proporzioni della componente C nei pascoli aridi silicei suggeriscono che tali habitat generalmente sono sottoposti a maggiori intensità di stress in confronto ai pascoli aridi calcarei. Tale risultato presumibilmente è collegato alla minore disponibilità di risorse in siti ad alta acidità e al fatto che tali pascoli si trovano ad altitudini elevate.*

Parole chiave: pascoli aridi calcarei, pascoli aridi silicei, composizione di specie, tipi funzionali vegetali, caratteristiche morfologiche vegetali, Slovenia

INTRODUCTION

The traditional approach to vegetation classification is taxonomic in nature and usually performed at the species level (Duckworth *et al.*, 2000). On a large scale, predictions based on plant species are geographically bound (Woodward & Cramer, 1996). On a small scale, species are in some cases so widely spread and variable that by describing communities by species composition we may not perceive relevant patterns occurring below the resolving power of species (Diaz *et al.*, 1992). Consequently, classifying plant species according to their higher taxonomical level has strong limitations when it comes to answering important ecological questions at the scale of ecosystems, landscapes or biomes (Keddy, 1992; Körner, 1993). A promising way for answering such questions, as well as various other ecological questions, is by classifying plant species by their shared biological characteristics that relate to function, rather than by phylogeny (Grime *et al.*, 1988; Lavorel *et al.*, 1997; Diaz *et al.*, 2002). These alternative classes are often referred to as plant functional types or groups (Leishman & Westoby, 1992; Grime *et al.*, 1988; Gitay & Noble, 1997). Plant functional types can be defined as groups of plant species sharing similar functioning at the organismic level, similar responses to environmental factors (*e.g.,* temperature, water availability, nutrients, fire and grazing), and/or similar roles in (or effects on) ecosystems or biomes (*e.g.,* productivity, nutrient cycling, flammability and resilience) (Walker, 1992; Chapin *et al.*, 1996; Nobble & Gitay, 1996; Diaz & Cabido, 1997; Lavorel *et al.*, 1997; Grime, 2001). With plant functional types, comparisons between communities of widely differing composition can be facilitated (Diaz *et al.,* 2004).

The underlying bases for schemes of plant functional types can vary widely (Ramenskiy, 1938; Hermy & Stieperaere, 1985; Grime, 2001). One of three-type schemes, the so-called "CSR plant strategy theory" (Grime, 1974, 1977, 1979, 2001) is particularly efficient in the balance between the power of its predictions and the simplicity of its assumptions (Hunt *et al.*, 2004). Grime (1974, 1977, 1979, 2001) developed a classification based on how plants deal with two groups of external environmental factors, stress and disturbance. This scheme results in three primary plant strategies: competitors (C), stress-tolerators (S), and ruderals (R) and several intermediate strategies. The position of any species can be displayed upon a triangular ordination diagram (Grime, 1974, 2001; Hodgson *et al.*, 1999). Each strategy is characterized by a distinct set of ecological, morphological and physiological traits and is found in species occupying habitats of a particular kind (Grime *et al.*, 1988). Hodgson *et al.* (1999) developed a methodology that classifies unknown herbaceous subject based on validated "soft" traits (*i.e.* relatively undemanding), allowing practical ordination of wild plants within CSR space. The position in CSR diagram can be determined also for an entire vegetation sample (relevé). Hunt *et al.* (2004) presented a quantitative tool which facilitates the reduction of herbaceous plant communities to collections of functional types. The whole community is given a "functional signature", a three-part numerical index which concisely represents the balance between the different functional attributes that are present among the component species (Hunt *et al.*, 2004). The integrative power of the CSR signature is useful in comparative studies involving widely differing samples (Hunt *et al.*, 2004). Although Grime's CSR triangle theory has been often criticized (Tilman, 1988; Silvertown *et al.*, 1992; Wilson & Lee, 2000), Grime's ideas remain fundamental to the development of functional classifications and functional interpretation of plant communities (Hills *et al.,* 1994; Caccianiga *et al.*, 2006; Pipenbaher *et al.*, 2008; Zelnik & Čarni, 2008).

The aim of the present study was to determine whether two contrasting geological substrates – calcareous and silicicolous, affect the CSR functional signatures of related grasslands, being floristically substantially distinct. We actually compared species composition and plant life strategies as defined by Grime (1974) of two adjacent and structurally-similar plant communities on acidic and calcareous soils from the central part of Slovenia – acidic Matgrass (*Nardus stricta*) grasslands and species-rich calcareous grasslands. We applied the method of Hodgson *et al.* (1999) to allocate CSR plant functional types and the approach of Hunt *et al.* (2004) to derive a functional signature for the researched grasslands communities. These vegetation types were created by traditional, infrequent low intensity grazing or mowing with no external inputs (fertilizers) in the past (Škornik, 2003; Kaligarič *et al.*, 2006). They represent grasslands of moderate productivity and despite contrasting geological substrates both vegetation types represent habitats subject to a similar combination of intermediate level of disturbance and stress due to nutrient poor and shallow rocky soils which experience desiccation during the summer. We hypothesized that despite wide differences in plant species composition there are no significant differences in functional signatures between calcareous and silicicolous grassland types with respect to C, S and R components, since they both represent habitats experiencing nearly comparable effects of climate and land-use.

MATERIALS AND METHODS

Study area

The studied calcareous semi-dry grasslands appear only in small fragments in the hilly region of pre-Alpine and pre-Pannonian region and on low Dinaric and pre-

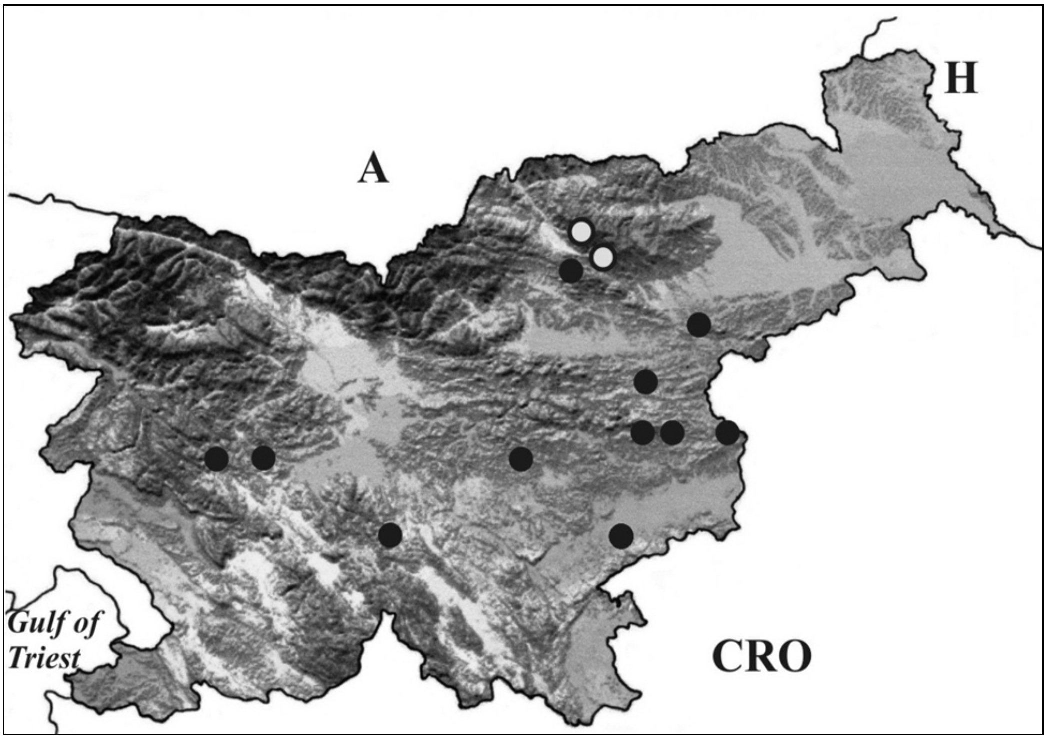

Fig. 1: Map of Slovenia with locations of the collected relevés of calcareous (●) and silicicolous (○) dry grasslands.
Sl. 1: Karta Slovenije z lokalitetami popisov suhih travnikov na apnencih (●) in silikatih (○).

Dinaric karst plateau at ca. 500-1100 m a.s.l. (Fig. 1). The geological substrate is made of calcareous limestone and dolomite. The climate is continental with mild to hot summers and cold winters. Mean annual temperature is between 6 and 10.5°C. The average annual precipitation is between 1000 and 1300 mm. The relevés of studied calcareous semi-dry grasslands belong to species-rich meadows from the *Bromion erecti* alliance described as association *Scabioso hladnikianae-Caricetum humilis* (Škornik, 2001). These grasslands are distributed over exposed sunny and dry areas and are therefore rich in xero-thermophilous and basiphilous species.

The silicicolous Matgrass grasslands were studied on the summit areas of Pohorje Mountains (NE Slovenia) (Fig. 1) at altitudes at ca. 1500 m a.s.l. We analysed relevés of association *Homogyno alpinae-Nardetum* (alliance *Nardo-Agrostion tenuis*, order *Nardetalia*) (Kaligarič & Škornik, 2002). Pohorje, the most dominant mountain range in the NE Slovenia, is situated at the south-easternmost edge of the Central (non-carbonate) Alps. The main characteristic of these grasslands are acid soils (pH less than 4.0), the result of the non-carbonate geological bedrock, predominantly metamorphic rocks and granodhiorythic lacolith (Hinterlechner-Ravnik, 1995). The study area has the montane climate with fresh summers and cold winters. The average temperature in the coldest month is below –3°C and in the warmest month above 10°C. The average annual precipitation is approx. 1336 mm (Ribniška koča, 1530m) (Furlan, 1980). These grasslands occur mainly on flat plains and gentle sloping ridges with very dry and shallow soils, poor with minerals and with low pH values (Kaligarič & Škornik, 2002). They are rich in species designated as xerophilous and acidophilous species.

Vegetation survey

We analysed 30 relevés of dry grasslands on calcareous bedrock – association *Scabioso hladnikianae-Caricetum humilis* (Škornik, 2001) and 32 vegetation relevés of dry grasslands on silicicolous bedrock – association *Homogyno alpinae-Nardetum* (Kaligarič & Škornik, 2002). Relevés were collected using standard procedure of the sigmatistic method (Braun-Blanquet, 1964; Westhoff & van der Maarel, 1973; Dierschke, 1994).

Allocating a CSR plant functional type to plant species and vegetation samples (relevés)

The CSR scheme takes into account a number of different plant traits (Hodgson *et al.*, 1999). To determine one of 19 CSR functional types for 122 plant species recorded in 62 analysed vegetation relevés we used a rapid method for attribution of CSR type from simple measurements and data published by Hodgson *et al.* (1999). We used the following plant traits: canopy height, leaf dry matter content, flowering period, flowering start, lateral spread, leaf dry weight, specific leaf area. Traits were chosen from our own database (protocol standardized by Cornelissen *et al.*, 2003). Calculations of CSR coordinates were made by entering these data into the spreadsheets of Hodgson *et al.* (1999), made available for this purpose at www.ex.ac.uk/~rh203/allocating_csr.html. For 21 plant species we used data from a look-up table with CSR types for 1000 European species (source J. G. Hodgson, UCPE Sheffield).

The relative proportions of CSR functional types for our 62 samples (relevés) of vegetation were calculated and plotted in CSR triangle by using spreadsheet-based tools of Hunt *et al.* (2004), available at www.people.exeter.ac.uk/rh203/allocating_csr.html.

To test differences in relative proportions of C-, S- and R-strategists among relevés of calcareous and silicicolous dry grasslands, we used a *Student's* t-test for independent samples (SPSS Inc., 2006), since the data were sufficiently normally distributed (Shapiro-Wilks and Lilliefors tests).

Nomenclature

Taxonomic nomenclature follows Martinčič *et al.* (2007), syntaxonomic nomenclature follows Mucina *et al.* (1993), Grabherr & Mucina (1993) and Škornik (2003).

RESULTS

The total number of vascular plant species recorded in 62 relevés of studied grassland communities was 143 with 105 in the calcareous (mean=45±6.8 per plot, N=30) and 45 (mean=16±3.8 per plot, N=32) in the silicicolous grasslands. There are only 7 common species, namely *Antennaria dioica, Anthoxanthum odoratum, Cruciata glabra, Gymnadenia conopsea, Luzula campestris, Potentilla erecta* and *Veronica chamaedrys*, 98 exclusive to the calcareous and 38 exclusive to the silicicolous semi-dry grasslands. All species are listed in Appendix 1.

Characteristic of calcareous semi-dry grasslands are particularly many calciphilous and xerophilous species, such as *Acinos alpinus, Anthericum ramosum, Bromopsis erecta, Centaurea scabiosa* subsp. *fritschii, Globularia punctata, Helianthemum ovatum* and *Koeleria pyramidata,* which are absent on non-carbonate soil. In silicicolous grasslands calcifuge species which can tolerate soil with lower pH values appear, such as *Arnica montana, Calluna vulgaris, Carex pilulifera, Festuca rubra, Hieracium pilosella, Nardus stricta* and *Ranunculus acris.*

Ordination of species within CSR space (Tab. 1) demonstrate that CR, SC, CSR and the combination of SC and CSR types are prevalent strategies of plant species on both calcareous and silicicolous semi-dry grasslands. The most frequent are competitive-ruderals (CR), which were especially strongly represented in the species composition of silicicolous semi-dry grasslands (33.34%). Examples of competitive-ruderals are species *Agrostis capillaris, Carlina acaulis, Cirsium pannonicum, Linum catharticum, Plantago media, Rhinanthus glacialis* and *Stellaria graminea*. Stress-tolerant competitors (SC) included some grasses, sedges and rushes, *e.g. Carex flacca, Deschampsia caespitosa, Luzula luzuloides* and *Molinia caerulea*. CSR strategists include small geophytes (*e.g. Orchis tridentata, Orchis ustulata* and *Primula veris*), small deep-rooted forbs with rosettes (*e.g. Antennaria dioica, Plantago lanceolata, Scabiosa columbaria, Silene vulgaris*) and small sedges like *Carex ornithopoda* (Append. 1).

Tab. 1: CSR strategies of 143 plant species recorded in 62 relevés of dry grasslands from calcareous (30 relevés) and silicicolous (32 relevés) geological substrates. Values are percentage frequencies.
Tab. 1: CSR strategije 143 rastlinskih vrst suhih travnikov na karbonatni (30 popisov) in silikatni (32 popisov) geološki podlagi. Vrednosti v tabeli ustrezajo frekvencam (%) pojavljanja vrst.

	Calcareous	**Silicicolous**
N of relevés	30	32
N of plant species	105	45
CSR plant strategy		
C	2.9	0.0
S	1.0	0.0
R	0.0	0.0
CR	**19.1**	**33.3**
SR	1.0	0.0
SC	**17.1**	**11.1**
CSR	**17.1**	**8.9**
C/CR	4.8	2.2
C/SC	3.8	2.2
C/CSR	3.8	0.0
CR/CSR	1.9	4.4
R/CR	2.9	4.4
R/CSR	0.0	0.0
R/SR	1.0	0.0
SR/CSR	4.8	2.2
SC/CSR	5.7	**15.6**
S/SC	5.7	6.7
S/CSR	5.7	6.7
S/SR	1.9	2.2

The positions of calculated functional signatures for all 62 relevés of studied grasslands in CSR space are presented in Figure 2. Relevés are arranged on the right side of the triangle along the line, where stress and competition in various equilibria are the most important determinants of the vegetation.

When calculating functional signatures, we considered the percentage of abundance of each plant species in relevé. Differences in functional signatures within the samples (relevés) of both vegetation types are due to fluctuations in abundance of dominant species which can be linked to differences in soil characteristics of microhabitat or to disturbance abundance (Fig. 2). Relevés of calcareous grassland positioned in the upper part of the triangle represent less-managed grasslands that exhibit conditions favourable to the species with stressed C component, such as *Brachypodium pinnatum, Centaurea scabiosa* subsp. *fritschii* and *Peucedanum oreoselinum.* The relative importance of S-coordinate in the part of relevés of silicicolous grasslands was revealed due to the strong dominance of stress-tolerant grass species *Nardus stricta* in those vegetation samples.

The comparison of relative proportions of C, S and R components among relevés showed significantly (P <0.0001) higher relative proportions of S component (mean=0.52, N=32) in silicicolous grasslands than in calcareous grasslands (mean=0.37, N=30). On the other hand, calcareous grasslands had significantly (P <0.0001) higher relative proportions of C component (mean=0.46, N=30) than acid grasslands (mean=0.31, N=32).

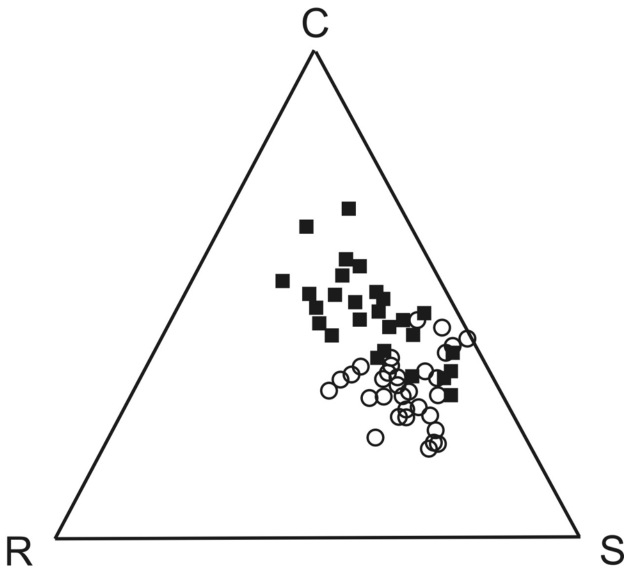

Fig. 2: CSR ordination of relevés (N=62, 143 species) of dry grasslands from calcareous and silicicolous geological substrates. Legend: ■ – calcareous dry grasslands; O – silicicolous dry grasslands.
Sl. 2: CSR ordinacija popisov (N=62, 143 vrst) suhih travnikov na karbonatni in silikatni geološki podlagi. Legenda: ■ – popisi karbonatnih suhih travnikov ; O – popisi silikatnih suhih travnikov.

DISCUSSION

As expected and observed for a long time (*e.g.,* Gigon, 1987, Grime, 1979; Pärtel, 2002), great floristic differences between the calcareous and non-calcareous (silicolous) grasslands were found. These habitats have only a few common species and many species related to either basic or acidic soil pH. It is generally accepted that the main reason why some substrates host different plant species than others lies in chemical processes and factors rather than in physical ones (temperature, moisture, etc.) (Kinzel, 1983; Gigon, 1987).

The calcareous grasslands are characterized by high species richness, typical of these semi-natural grasslands (*Bromion erecti*) in extensive use, which are among the most species-rich habitats in Europe (Willems *et al.*, 1993). Pärtel (2002) and Ewald (2003) suggest that the relationship between local species density and soil pH is determined by regional species pool size (Zobel *et al.*, 1998), which in turn reflects the relative abundance of soil types during the evolutionary history of the flora. Ewald (2003) observed that calcareous sites in Central Europe have higher species density and larger species pool than acidic sites, and argues that this is due to a Pleistocene bottleneck for acidophiles. Peet *et al.* (2003) contradict the assertion of Pärtel (2002) and Ewald (2003). They conclude that richness on higher pH sites is a result of generally more favorable conditions for plant growth and/or establishment. It is known that more base-rich sites are generally more invasible *(e.g.*, Davis *et al.*, 2000; Brown & Peet, 2003), presumably owing to greater resource availability on high-base sites. Under extreme acidity, the nutrient cations are so mobile that they are easily leached into groundwater (Gurevitch *et al.*, 2002).

CSR classification of all species recorded (Tab. 1) expresses the response on stress and disturbance in the studied grasslands. The three primary C-, S-, and R-strategists represent extremes in the range of conditions available to plants (Grime, 2001) and are therefore very rare in grasslands we have researched. Namely, these are habitats experiencing intermediate intensities of stress and disturbance and in such circumstances the vegetation usually includes many species with strategies intermediate between those of the competitor, the stress-tolerator, and the ruderal (Grime, 2001). For the investigated unfertilised dry grasslands, effect of disturbance is mainly due to the mowing once a year (or even every second year) and occasional grazing (Kaligarič & Škornik, 2002; Škornik *et al.*, 2006). Although these disturbances are severe, they occur infrequently and prevent dominance by competitors. The competitive nature of species in the present study is restricted also by moderate stress conditions, due to nutrient-deficient and shallow soils which experience desiccation during summer. Many species within competitive-ruderals and stress-tolerant competitors *(e.g. Agrostis capillaries, Carex flacca, Deschampsia caespitosa, Molinia caerulea)* are perennials showing capacity for rapid lateral vegetative spread and for efficient colonisation of temporary gaps (Lovett-Doust, 1981).

According to Hunt *et al.* (2004), the integrative power of the functional signatures within the context of the CSR system of plant functional types is especially useful in comparative studies of widely differing samples. We hypothesized that despite very different floristic composition there will be no significant differences in functional signatures between relevés of silicicolous and calcareous dry grasslands. Our results do not support our hypotheses, however, they agree with the observations that more base-rich sites are less stressful for plants. We can observe some relevés, which showed similar values of functional signatures (Fig. 2). These were samples of calcareous grasslands characterised by severe level of stress due to extremely shallow dry soil and less-managed or even unmanaged samples of silicicolous dry grasslands. Species which were abundant in these habitats were stress-tolerant competitors (SC, S/SC). Examples are *Carex humilis, Koeleria pyramidata, Leontodon incanus, Hippocrepis comosa* and *Dianthus carthusianorum,* all species which were abundant in calcareous grasslands. The predominant stress-tolerant competitors in the case of overlapping acidic dry grasslands were members of the Ericaceae: *Calluna vulgaris*, *Vaccinium myrtillus* and *V. vitis-idaea*. In Europe and North America these sclerophyllous shrubs species are very common and associated with nutrient-deficient acidic soils if management regimes allow the development of woody vegetation (Grime, 2001). Beside the soil chemistry, the altitudinal distribution of sample grasslands should not be neglected as well; the silicicolous grasslands were sampled in higher altitudes, where growing period is shorter and climatic conditions are sharper. These require plant strategies closer to S strategy, which was actually confirmed within the present study.

In conclusion, although some authors have expressed doubts concerning the predictive power of CSR theory (Wilson & Lee, 2000), we have demonstrated its usefulness in comparative analysis of plant communities of widely differing species composition.

PRIMERJAVA CSR FUNKCIONALNIH OZNAK SUHIH TRAVIŠČ Z DVEH RAZLIČNIH GEOLOŠKIH PODLAG

Sonja ŠKORNIK
Oddelek za biologijo, Fakulteta za naravoslovje in matematiko, Univerza v Mariboru, SI-2000 Maribor, Koroška 160
E-mail: sonja.skornik@uni-mb.si

Klavdija HARTMAN
Činžat 17, SI-2343 Fala

Mitja KALIGARIČ
Oddelek za biologijo, Fakulteta za naravoslovje in matematiko, Univerza v Mariboru, SI-2000 Maribor, Koroška 160

POVZETEK

Z našo študijo smo želeli odgovoriti na vprašanje, ali različna podlaga – karbonatna in ne-karbonatna silikatna vpliva na razlike v CSR funkcionalni oznaki dveh po strukturi podobnih rastlinskih združb. Za funkcionalno primerjavo smo uporabili Grime-ov model CSR ekoloških strategij rastlin. Proučevani suhi travniki predstavljajo antropogeni habitat, ki je nastal kot posledica dolgotrajne tradicionalne ekstenzivne paše oz. košnje. To so travišča z zmerno produkcijo, ki so kljub kontrastni geološki podlagi podvržena primerljivi kombinaciji zmerne motnje ter stresa. Slednji je predvsem posledica pomanjkanja hranil v tleh ter vodnega stresa zaradi plitkih kamnitih tal, ki se v poletnih mesecih pogosto izsušijo. Tako smo postavili hipotezo, da kljub zelo različni floristični sestavi ne bomo našli statistično značilnih razlik v funkcionalnih oznakah za oba tipa vegetacije. Analizirali smo 30 fitocenoloških popisov suhih travnikov na karbonatih (asoc. Scabioso hladnikianae-Caricetum humilis, *zveza* Bromion erecti) *ter 32 fitocenoloških popisov silikatnih suhih travnikov (asoc.* Homogyno alpinae-Nardetum, *zveza* Nardo-Agrostion tenuis). *Na osnovi primerjave floristične sestave smo potrdili, da se suhi travniki na karbonatni in silikatni geološki podlagi med sabo* *zelo razlikujejo, saj se od zabeleženih skupno 142 vrst, samo 7 rastlinskih vrst pojavlja tako na silikatnih kot tudi na karbonatnih travnikih. Primerjavo tipov CSR ekoloških strategij smo izvedli na osnovi frekvenc (v %) pojavljanja vrst v skupinah popisov. Pokazala je, da je sestava CSR tipov ekoloških strategij na obeh tipih suhih travnikov zelo podobna. Na obeh traviščih prevladujejo vrste s t.i. sekundarnimi CSR ekološkimi strategijami C-R, C-S in CSR, značilne za vrste podvržene zmernemu stresu in motnji. Pri izračunavanju funkcionalih oznak popisov upoštevamo ne samo prisotnost/odsotnost temveč tudi pokrovnost vrst v popisih. Primerjava razporeditve funkcionalnih oznak popisov v CSR trikotniku je tako pokazala, da imata na proučevana suha travišča najpomembnejši vpliv stres in kompeticija v različnih razmerjih. Razlike v funkcionalnih oznakah med popisi znotraj posameznega tipa suhih travnikov se pojavljajo zaradi nihanja v pogostnosti dominantnih vrst, ki so posledica razlik v talnih razmerah ter stopnjah motnje. Kljub temu, da so si funkcionalne oznake nekaterih popisov iz različnih geoloških podlag zelo podobne, pa so statistične analize pokazale statistično značilne večje relativne deleže komponente S in manjše relativne deleže komponente C v popisih silikatnih travnikov. Naši rezultati tako ne podpirajo naše hipoteze, v kateri smo predvideli, da ne bomo našli statistično značilnih razlik v funkcionalnih oznakah za oba tipa vegetacije. Zato pa lahko naše izsledke uporabimo za potrditev domneve o bolj stresnih razmerah na rastiščih z nižjimi pH vrednostmi tal. Ta domneva namreč predstavlja enega izmed najpogostejših odgovorov, ki ga različni raziskovalci ponujajo na zelo znano vprašanje v ekologiji rastlin, zakaj obstaja toliko večja vrstna pestrost na tleh z višjimi vrednostmi pH v primerjavi s tlemi z nižjimi pH vrednostmi.*

Ključne besede: karbonatni suhi travniki, silikatni suhi travniki, vrstna sestava, funkcionalni tipi rastlin, morfološke poteze rastlin, Slovenija

REFERENCES

Braun-Blanquet, J. (1964): Pflanzensoziologie. Grundzüge der Vegetationskunde. Springer Verlag, Wien, 865 p.

Brown, R. L. & R. K. Peet (2003): Diversity and invasibility of southern Appalachian plant communities. Ecology, 84, 32–39.

Caccianiga, M., A. Luzzaro, S. Pierce, R. M. Ceriani & B. Cerabolini (2006): The functional basis of a primary succession resolved by CSR classification. Oikos, 112, 10–20.

Chapin, F. S. I., M. S. Bret-Harte, S. E. Hobbie & H. Zhong (1996): Plant functional types as predictors of transient responses of arctic vegetation to global change. J. Veg. Sci., 7, 347–358.

Cornelissen, J. H. C., S. Lavorel, E. Gernier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas & H. Poorter (2003): A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot., 51, 335–380.

Davis, M. A., J. P. Grime & K. Thompson (2000): Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol., 88, 528–534.

Diaz, S. & M. Cabido (1997): Plant functional types and ecosystem function in relation to global change. J. Veg. Sci., 8, 63–474.

Diaz, S., A. Acosta & M. Cabido (1992): Morphological analysis of herbaceous communities under different grazing regimes. J. Veg. Sci., 3, 689–696.

Diaz, S., S. McIntyre, S. Lavorel & J. G. Pausas (2002): Does hairiness matter in Harare? Resolving controversy in global comparisons of plant trait responses to ecosystem disturbance. New Phytol., 154, 7–9.

Diaz, S., J. G. Hodgson, K. Thomspon et al. (2004): The plant traits that drive ecosystems: evidence from three continents. J. Veg. Sci., 15, 295–304.

Dierschke, H. (1994): Pflanzensoziologie: Grundlage und Methode. Ulmer, Stuttgart, 864 p.

Furlan, D. (1980): Klimatski prikaz Severovzhodne Slovenije. HMZS, Ljubljana.

Duckworth, J., M. Kent & P. M. Ramsay (2000): Plant functional types: an alternative to taxonomic plant community description in biogeography? Prog. Phys. Geog., 24, 515–542.

Ewald, J. (2003): The calcareous riddle: why are there so many calciphilous species in the central Europaean flora? Folia Geobot., 38, 357–366.

Gigon, A. (1987): A hierarchic approach in causal ecosystem analysis: the calcifuge-calcicole problem in Alpine grasslands. Ecol. Stud., 61, 228–244.

Gitay, H. & I. R. Noble (1997): What are plant functional types and how should we seek them? In: Smith, T. M, H. H. Shugart & F. I. Woodwart (eds.): Plant functional types. Cambridge University Press, Cambridge, pp. 3–19.

Grabherr, G. & L. Mucina (eds.) (1993): Die Planzengesellschaften Österreichs. Teil II. Natürliche waldfreie Vegetation. Gustav Fischer Verlag Jena, Stuttgart, New York, 523 p.

Grime, J. P. (1974): Vegetation classification by reference to strategies. Nature, 250, 26–31.

Grime, J. P. (1977): Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat., 111, 1169–1194.

Grime, J. P. (1979): Plant strategies and vegetation processes. Wiley.

Grime, J. P. (2001): Plant strategies, vegetation processes, and ecosystem properties. John Wiley & Sons, Chichester, 222 p.

Grime, J. P., J. G. Hodgson & R. Hunt (1988): Comparative plant ecology: a functional approach to common British species. Unwin Hyman Ltd., London, 742 p.

Gurevitch, J., S. M. Scheiner & G. A. Fox (2002): The ecology of plants. 2nd Ed. Sinauer Associates, Sunderland, MA, 523 p.

Hermy, M. & H. Stieperaere (1985): Capitalists and proletarians (MacLeod, 1894): an early theory of plant strategies. Oikos, 44, 43–49.

Hills, J. M., K. J. Murphy, I. D. Pulford & T. H. Flowers (1994): A method for classifying Europaean riverrine wetland ecosystems using functional vegetation groups. Funct. Ecol. 8, 242–252.

Hinterlechner-Ravnik, A. (1995): O geologiji Pohorja. Proteus, 57, 334–339.

Hodgson, J. G., P. J. Wilson, R. Hunt, J. P. Grime & K. Thompson (1999): Allocating C-S-R plant functional types: a soft approach to a hard problem. Oikos, 85, 282–294.

Hunt, R., J. G. Hodgson, K. Thompson, P. Bungener, N. P. Dunnett & A. P. Askew (2004): A new practical tool for deriving a functional signature for herbaceous vegetation. Appl. Veg. Sci., 7, 163–170.

Kaligarič, M. & S. Škornik (2002): Contribution to the knowledge of the dry grassland vegetation on the highland areas of the Pohorje Mountain (Slovenia). Annales, Ser. Hist. Nat., 12(1), 53–60.

Kaligarič, M., M. Culiberg & B. Kramberger (2006): Recent vegetation history of the North Adriatic grasslands: expansion and decay of an anthropogenic habitat. Folia Geobot., 41, 241–258.

Keddy, P. A. (1992): A pragmatic approach to functional ecology. Funct. Ecol., 6, 621–626.

Kinzel, H. (1983): Influence of limestone, silicates and soil pH on vegetation. In: Lange, O. L., P. S. Nobel, C. B. Osmond & H. Ziegler (eds.): Physiological Plant Ecology. III. Responses to the Chemical and Biological Environment. Encyclopedia of Plant Physiology, New Series, Vol. 12C. Springer Verlag, Berlin, Heidelberg, pp. 201–244.

Körner, C. (1993): Scaling from species to vegetation: the usefulness of functional groups. In: Schulze, E. D. & H. A. Mooney (eds.): Biodiversity and Ecosystem Function. Ecological Studies. Springer Verlag, Berlin, pp. 116–140.

Lavorel, S., S. McIntyre, J. Landsberg & T. D. A. Forbes (1997): Plant functional classification: from general groups to specific groups based on response to disturbance. Trends Ecol. Evol., 12, 474–478.

Leishman, M. R. & M. Westoby (1992): Classifying plants into groups on the basis of associations of individual traits – evidence from Australian semi-arid woodlands. J. Ecol., 80, 417–424.

Lovett-Doust, L. (1981): Population dynamics and local specialisation in a clonal perennial (*Ranunculus repens*). I. The dinamics of ramets in contrasting habitats. J. Ecol., 69, 743–755.

Martinčič, A., T. Wraber, N. Jogan, A. Podobnik, B. Turk & B. Vreš (2007): Mala flora Slovenije. Kjuč za določanje praprotnic in semenk. Tehniška založba Slovenije, Ljubljana, 967 str.

Mucina, L., G. Grabherr & T. Ellmauer (eds.) (1993): Die Pflanzengesellschaften Österreichs. Teil I. Anthropogene Vegetation. Gustav Fischer Verlag, Jena, 578 p.

Noble, I. R. & H. Gitay (1996): A functional classification for predicting the dynamics of landscapes. J. Veg. Sci., 7, 329–336.

Pärtel, M. (2002): Local plant diversity patterns and evolutionary history at the regional scale. Ecology, 83, 2361–2366.

Peet, R. K., J. D. Fridley & J. M. Gramling (2003): Variation in species richness and species pool size across a pH gradient in forests of the Southern Blue Ridge Mountains. Folia Geobot., 38, 391–401.

Pipenbaher, N., M. Kaligarič, S. Škornik (2008): Functional comparison of the sub-Mediterranean illyrian meadows from two distinctive geological substrates. Annales, Ser. Hist. Nat., 18(2), 247–258.

Ramenskiy, L. G. (1938): Introduction to the geobotanical study of complex vegetations. Selkozgiz, Moscow, RU.

Silvertown, J., M. Franco & K. McConway (1992): A demographic interpretation of Grime's triangle. Funct. Ecol., 6, 130–136.

SPSS inc. (2006): SPSS Base 15.0 User's Guide. SPSS Inc., Chicago, IL.

Škornik, S. (2001): A contribution to the knowledge of dry grassland vegetation of the *Brometalia erecti* Koch 1926 order in Slovenia. Acta Biol. Slov., 44, 29–43.

Škornik, S. (2003): Suha travišča reda Brometalia erecti Koch 1926 na Goričkem (SV Slovenija). Hacquetia, 2, 71–90.

Škornik, S., M. Lončar & M. Kaligarič (2006): Vegetation of silicicolous grasslands of the highlands of North-Eastern Slovenia. Hacquetia, 5, 193–211.

Tilman, D. (1988): Plant strategies and the dynamics and structure of plant communities. Princeton University Press, 360 p.

Walker, B. H. (1992): Biodiversity and ecological redundancy. Conserv. Biol., 6, 18–23.

Westhoff, V. & E. van der Maarel (1973): The Braun-Blanquet approach. Handb.Veg. Sci., 5, 156–172.
Willems, J. H., R. K. Peet & L. Bik (1993): Changes in chalk-grassland structure and species richness resulting from selective nutrient addition. J. Veg. Sci., 4**,** 203–212.
Willson, J. B. & W. G. Lee (2000): C-S-R triangle theory: community-level predictions, tests, evaluation of criticisms, and relation to other theories. Oikos, 91, 77–96.
Woodward, F. I. & W. Cramer (1996): Plant functional types and climatic changes: Introduction. J. Veg. Sci., 7, 306–308.
Zelnik, I. & A. Čarni (2008): Distribution of plant communities, ecological strategy types and diversity along a moisture gradient. Community Ecol., 9, 1–9.
Zobel, M., M. Van der Maarel & C. Dupré (1998): Species pool: the concept, its determination and significance for community restoration. Appl. Veg. Sci., 1, 55–66.

Appendix 1: A list of 143 plant species recorded in 62 relevés of dry grasslands from calcareous (30 relevés) and silicicolous (32 relevés) geological substrates. Species values are percentage frequencies.
(*) Data from look-up table with CSR types for 1000 European species (source J. G. Hodgson, UCPE Sheffield).
Priloga 1: Seznam 143 rastlinskih vrst zabeleženih v 62 popisih suhih travišč na apnenčasti (30 popisov) in silikatni (32 popisov) geološki podlagi. Vrednosti ustrezajo frekvencam pojavljanja vrst v skupinah popisov
(*) Podatki, ki smo jih povzeli iz tabele s CSR tipi za 1000 vrst Evropske flore (vir J. G. Hodgson, UCPE Sheffield).

Species	**CSR plant strategy**	**Calcareous**	**Silicicolous**
Acinos alpinus	CSR*	70	.
Agrostis capillaris	CR	.	9
Anacamptis pyramidalis	R/CR	20	.
Anemone nemorosa	C/SC	.	19
Antennaria dioica	CSR*	17	25
Anthericum ramosum	C/CR	57	.
Anthoxanthum odoratum	SR/CSR	20	16
Anthyllis vulneraria	CR	80	.
Arnica montana	CR	.	97
Arrhenatherum elatius	C/CSR	13	.
Asperula cynanchica	SR/CSR	63	.
Avenella flexuosa	SC/CSR	.	63
Avenochloa pubescens	CR	13	.
Betonica officinalis	C/CR	13	.
Brachypodium rupestre	C	100	.
Briza media	SC/CSR	80	.
Bromopsis erecta agg.	C/CSR	83	.
Buphthalmum salicifolium	CR	93	.
Calluna vulgaris	SC	.	78
Campanula barbata	CR	.	75
Carex caryophyllea	S	87	.
Carex flacca	SC	60	.
Carex humilis	S/SC	50	.
Carex montana	S/SC	70	.
Carex ornithopoda	CSR*	27	.
Carex pilulifera	SC/CSR	.	34
Carlina acaulis	CR	67	.
Carlina vulgaris	CR	13	.
Centaurea pannonica	CR	10	.
Centaurea jacea subsp. *jacea*	SC/CSR	30	.
Centaurea scabiosa subsp. *fritschii*	C/CR	90	.
Centaurea triumfettii	CR	20	.

Species	**CSR plant strategy**	**Calcareous**	**Silicicolous**
Chamaecytisus supinus	SC/CSR	33	.
Chamaespartium sagittale	S/CSR	10	.
Cirsium pannonicum	CR	70	.
Cruciata glabra	S/SC	23	13
Dactylis glomerata	C/CSR	50	
Deschampsia caespitosa	SC	.	16
Dianthus carthusianorum	SC	63	.
Dorycnium germanicum	CR/CSR	17	.
Euphorbia cyparissias	CSR	60	.
Euphorbia verrucosa	S/SC	63	.
Euphrasia stricta	CR/CSR	.	6
Festuca rubra agg.	CSR	.	50
Festuca rupicola	S/CSR	87	.
Galium mollugo	C/CSR	13	.
Galium verum	SC/CSR	40	.
Genista januensis	CS*	77	.
Gentiana cruciata	CR	.	19
Gentiana pannonica	CR	.	22
Gentiana utriculosa	SR/CSR	20	.
Gentiana verna subsp. *tergestina*	SC	20	.
Gentianella germanica	CSR*	20	.
Geranium sanguineum	C/SC	33	.
Globularia cordifolia	SC	10	.
Globularia punctata	C/SC	80	.
Gymnadenia conopsea	S/SR*	40	44
Helianthemum ovatum	SR/CSR	93	.
Hieracium aurantiacum	CR	.	28
Hieracium bauhinii	C/CR	30	.
Hieracium laeviculae	CR	.	41
Hieracium pilosella	SC	17	.
Hippocrepis comosa	SC	73	.
Homogyne alpina	CR	.	47
Hypericum montanum	SC/CSR	.	6
Hypericum perforatum	SC	.	13
Hypochoeris maculata	C/CR	53	.
Hypochoeris uniflora	CR	.	25
Inula salicina	CS*	17	.
Knautia drymeia	CR	50	.
Koeleria pyramidata	S/SC	100	.
Laserpitium siler	C/SC	23	.
Leontodon helveticus	R/CR	.	47
Leontodon hispidus subsp. *danubialis*	CR	37	.
Leontodon incanus	SC	73	.
Leucanthemum vulgare	C*	40	.
Leucanthemum ircutianum	CR	.	9
Lilium martagon	CSR*	10	.
Linum catharticum	CR	67	.
Linum viscosum	CS*	10	.
Lotus corniculatus	SC/CSR	77	.
Luzula campestris	S/CSR	17	41

Species	CSR plant strategy	Calcareous	Silicicolous
Luzula luzuloides	SC	.	41
Luzula pilosa	SC/CSR	.	44
Luzula sylvatica	SC/CSR	.	38
Lychnis flos-cuculi	CR	.	38
Medicago lupulina	R/SR	17	
Melampyrum pratense	CR/CSR	.	75
Molinia caerulea	SC	.	6
Nardus stricta	S/CSR	.	100
Orchis morio	S/SR	13	.
Orchis tridentata	CSR*	33	.
Orchis ustulata	CSR*	23	.
Peucedanum cervaria	C	10	.
Peucedanum oreoselinum	C/SC	83	.
Phyteuma orbiculare	SC	30	.
Phyteuma spicatum	C/CR	.	6
Pimpinella saxifraga	CR	47	.
Plantago lanceolata	CSR	83	.
Plantago media	CR	90	.
Platanthera bifolia	R/CR	10	.
Polygala chamaebuxus	CS*	23	.
Polygala comosa	S/SC	90	.
Polygala vulgaris	SC/CSR	13	6
Polygonatum odoratum	CR	13	.
Potentilla erecta	S/CSR	27	100
Primula vulgaris	CSR*	33	.
Prunella grandiflora	CR/CSR	43	.
Prunella laciniata	CR	27	.
Prunella vulgaris	R/CR	17	.
Pseudorchis albida	R/CR	.	13
Pulsatilla grandis	CSR*	10	.
Ranunculus acris	CSR	.	9
Ranunculus bulbosus	SR	43	.
Ranunculus nemorosus	CR	33	.
Rhinanthus glacialis	CR	57	.
Rhinanthus minor	SR/CSR	10	.
Rhinanthus pulcher	CR	.	6
Salvia pratensis	CR	50	.
Sanguisorba minor	SC	97	.
Scabiosa columbaria	CSR*	17	.
Scabiosa hladnikiana	CR	53	.
Scabiosa triandra	CR	63	.
Silene nutans	S/CSR	40	.
Silene vulgaris	CSR*	20	.
Solidago virgaurea	CR	.	59
Stachys recta	SC	37	.
Stellaria graminea	CR	.	6
Teucrium chamaedrys	SC/CSR	.	6
Thalictrum minus	S/CSR	13	.
Thesium bavarum	CSR*	60	.

Species	**CSR plant strategy**	**Calcareous**	**Silicicolous**
Thlaspi praecox	SC	33	.
Thymus pulegioides	SC/CSR	60	.
Tofieldia calyculata	CS*	13	.
Trifolium montanum	SC	83	.
Trifolium pratense	CSR	17	.
Vaccinium myrtillus	S/SC	.	66
Vaccinium vitis-idaea	S/SC	.	69
Veratrum album subsp. *album*	CR	.	50
Veronica chamaedrys	CSR	10	6
Veronica jacquinii	SC	63	.
Viola canina	CSR*	13	.