

## Preface

Ecological research is gaining more and more importance in the twenty-first century. The demand for existing, integrated knowledge is also increasing so that results could be utilised by the European Union and other organisations, like the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) convened by UNEP. It is mainly the result of many years of preparation by the Institute of Ecology and Botany of HAS that the European Platform for Biodiversity Research Strategy convention became part of the official expert's meetings of the Hungarian EU presidency.

The Institute of Ecology and Botany (IEB HAS) as one of the leading institutions of ecological research concerning the Pannonian Biogeographical Region, started to improve its research profile in 2011. In order to strengthen the Danube research, the Hungarian Academy of Sciences appointed a former department of IEB HAS into an independent Danube Research Institute. The remaining institution with a mainly plant ecological profile pursued a development strategy of four directions. These are the following:

- functional ecological research based on experiments and modelling ;
- study of ecosystem services in the Pannonian Biogeographical Region; study of ecological impacts of climate change;
- linking supra- and infra-individual research through the development of plant chemical and soil microbiological laboratory;
- organisation of existing ecological data into a knowledge base accessible for the international e-infrastructure.

The goal of publishing these current selection of our results is to demonstrate the latest research topics of IEB HAS for a broader professional and interested audience. In this third booklet of our series mainly (but not exclusively) the results of our young scientists, PhD students or postdocs are included. The booklet series serves environmental education and awareness raising by publishing scientific papers in a more comprehensive and short language.

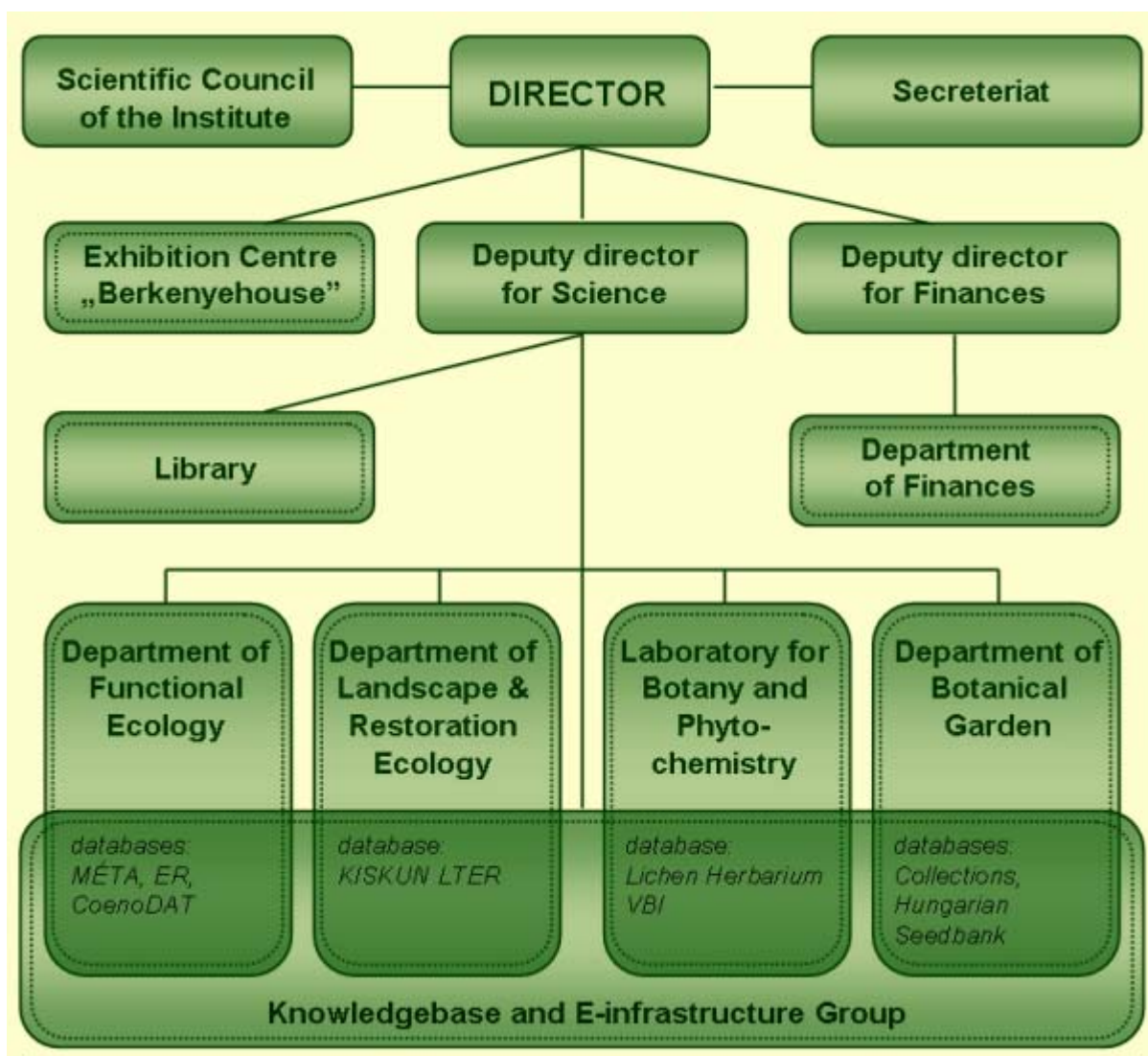
We hope that this booklet facilitates the dissemination of knowledge on the research and development directions of IEB HAS for the participants of the European Platform of Biodiversity Research Strategy conference and other interested stakeholders in order to improve the understanding of the ecological background of sustainable ecosystems services.

Vácrátót, April, 2011

dr. Katalin Mázsa, editor

dr. Katalin Török, director of IEB

Organisation structure of IEB HAS and connections between divisions, including the main databases:



# The role of IEB in the expert programme of the Hungarian EU presidency

KATALIN TÖRÖK<sup>1</sup>, director

## Abstract

A joint planning for the Hungarian EU presidency started already some years ago, based on the long collaboration between the official nature conservation authorities and the Institute of Ecology and Botany (IEB). The activities included support in the tasks related to the presidency and the organisation of joint meetings. Several colleagues from the Institute have been involved in the reviewing of expert documents. The presidency conference of the EPBRS (*European Platform for Biodiversity Research Strategy*) was organised with the Ministry of Rural Development. IEB even had a major role in the expert programme of the European Nature Directors Meeting. Both conferences are organized in the first half of 2011.

## Introduction

The tasks related to the conservation, management and reporting on nature for a European Union member state cannot be fully satisfied with the exclusive participation of the official nature conservation apparatus. IEB and its researcher staff have provided important expert background for several decades for the governments. This support included among others, the designation of national parks, the identification of listed species and habitats of the Pannonian eco-region, reporting obligations in relation to the NATURA 2000 network, the design and implementation of the biodiversity monitoring system. The daily, mutually beneficial relationship with the staff of nature conservation institutions and national parks has paved the road to our role in the organisation of the presidency. Brainstorming started already in the early planning phase (2008) on how to include the EPBRS meeting into the official programme of the presidency, as it was the tradition before, in order to ensure to a certain extent the financial background of the conference. Our ideas and priorities have been acknowledged, so ecosystem services and biological invasion became the topic of the meeting. The presidency was preceded by the review and preparation of a number of EU level documents where IEB had a significant role.

## Expert support

Several European programs and reports dealing with biodiversity were prepared in 2010, which have been reviewed and finalized by invited experts. IEB has been invited by the European Environment Agency to the consultation of the 2010 EU biodiversity status review (*EU 2010 Biodiversity Baseline Report*). This review not only assesses the status of biodiversity, but also suggests a plan of action. Our participation opened the opportunity to influence the biodiversity strategy of the EU until 2020. We acknowledge that the report is the work of qualified experts, and that by gaining access to the reports before publication, we also got an advantage in writing research applications. The report concludes that biodiversity is declining steadily, which is detrimental to the natural capital influencing human quality of life. Therefore, new, more stringent goals are set for a further period, the year 2020 marked as the halting of biodiversity loss and the restoration of at least 15% of the degraded areas.

---

<sup>1</sup> igazgato@botanika.hu

The other important line of work is the activity related to the Convention on Biological Diversity (CBD). An important part of preparing for the meetings is the drafting of a single European standpoint. IEB experts had a voice in the drafting procedure, most expressed for the Hungarian EU presidency. The International Year of Biodiversity (2010<sup>2</sup>) was an important milestone in setting priorities. It is widely accepted that targets have not been met, since the loss of biodiversity has not been halted, neither at global nor at local level. Thus, further work to develop the goals will be a major task of the Parties of the Convention. IEB researchers also took part in reviewing the drafts on target setting.

Two of our researchers participated in the ad-hoc expert groups of the Convention as national experts, where the link between climate change and biodiversity, and biological invasions were the topics. Their professional support and suggestions improved the valuation of Hungarian contribution and raised the Institute's professional reputation. However, the participation required a significant work load, which does not appear directly in publications.

### **EPBRS Conference**

As a result of a long-term preparatory work by IEB, the European Platform for Biodiversity Research Strategy convention became part of the official expert meetings of the Hungarian EU presidency. The supporting statement of the Biology Section of the Hungarian Academy of Sciences had a major part in this to happen. One of the two Presidency events of official nature conservancy was fully organized by IEB, and we had a significant role even in the other one. We determined the topic of the EPBRS Conference to be “*Research priorities to sustain ecosystem services*”. In cooperation with the international Steering Committee of EPBRS, we developed the program and invited plenary speakers. Along with the IEB staff, a department head of the Ministry of Rural Development was also involved in the Organising Committee.

The conference was held with governmental support at Stefánia Palace, in one of the official meeting venues of the Presidency. First, plenary speakers introduced the topic at the professional program, and then three working groups drafted research priorities. The Hungarian EPBRS meeting was the last, after 10 years to be organised along the regular arrangement. Therefore this meeting can be considered as a landmark. The Steering Committee discussed the future of EPBRS and the possible reorganisation of its activity for a full day during the meeting, further clarifying the role of EPBRS in the changed international environment.

### **Nature Conservation Directors Meeting**

The comments and suggestion of the experts of IEB have been included in the program of this meeting as well, organised by the Ministry of Rural Development. Along the traditions of the Presidency meetings, the national interests dominated the choice of topics. Thus, ecosystem services, wetlands and biological invasion were selected as main themes. A publication of a standpoint on these issues is foreseen; the role of IEB staff in the drafting is acknowledged. A plenary report will be provided about the results of the EPBRS conference, and in addition, a researcher from IEB will give an oral presentation on the topic of ethnoecology.

---

<sup>2</sup> <http://www.cbd.int/2010/welcome/>

The official organisers accepted our proposal to improve the science-policy interface by bringing the biodiversity-knowledge project into focus (biodiversity-knowledge network<sup>3</sup>). The theme also holds opportunity for decision makers to discuss issues of interest, to assess needs, and formulate questions at national and EU levels. This activity can serve the requirements of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES<sup>4</sup>), which is under development.

---

<sup>3</sup> <http://biodiversityknowledge.eu/>

<sup>4</sup> <http://www.ipbes.net/>

# Community differentiation in dry perennial sand grasslands along an aridity gradient.

SÁNDOR BARTHA<sup>1</sup>, GIANDIEGO CAMPETELLA<sup>2</sup>, MIKLÓS KERTÉSZ, GYÖRGY KRÖEL-DULAY,  
TAMÁS RÉDEI, KLÁRA VIRÁGH, GÁBOR FEKETE AND EDIT KOVÁCS-LÁNG

## Abstract

Spatial variability of species composition was studied in perennial sand grasslands in Hungary at multiple (regional, landscape and stand) scales. Three sites were compared along an aridity gradient. Existing differences in climate along this ca. 200 km gradient correspond to regional climate changes predicted for the next 20-30 years. We found a decreasing trend of beta diversity (which represents the spatial complexity), with increasing aridity at fine scale, and on the contrary, an increasing trend at landscape scale. We conclude that the major trend of the vegetation differentiation due to aridity is the decrease of compositional variability at fine-scale accompanied by a coarse-scale diversification.

## Introduction

Theory suggests that ecosystem level adaptation, efficiency and stability depend strongly on the spatial complexity of ecosystems (WALKER et al. 1981, GUNDERSON and PRITCHARD 2002). Spatial complexity is often represented by beta diversity, i.e. by the variation of species composition among sites. Recently increasing attempts have been made to measure beta diversity at landscape or macroecological scales. Beta diversity changes with altitude (SANG 2009), with succession (HOGEWEG et al. 1985, DEL MORAL 2007) and with vegetation degradation (CHANETON et al. 2002, KÉFI et al. 2007). Consequently, it can be a sensible indicator of climate change and man-induced desertification (BESTELMEYER et al. 2006, KÉFI et al. 2007).

Perennial sand grassland is a component of the remnant natural forest-steppe vegetation of the Hungarian Plain (FEKETE 1992). This vegetation type is expected to respond to climate change in a sensitive way (KOVÁCS-LÁNG et al. 2008). Regional climate change scenarios predict a decrease in growing season precipitation and an increase in growing season temperature for the Carpathian Basin during the next decades (BARTOLY et al. 2007). Existing differences in climate along a ca. 200 km north-west to south-east gradient in Hungary (BORHIDI 1993, KUN 2001) correspond to regional climate changes predicted for the next 20-30 years. Sand grasslands occur along this gradient. Therefore, assessing their large-scale variability along the current climate gradient may help to forecast future differentiation of this vegetation type in the region. Landuse effects can accelerate vegetation processes driven by climatic changes. Sand grasslands are especially sensitive to disturbance and they are threatened by man-induced desertification (FEKETE 1992). Therefore, there is an urgent need to develop effective indicators for early warning about desertification processes.

In a recent study, KOVÁCS-LÁNG et al. (2000) found decreasing alpha diversity, plant cover and proportion of forest species, and increasing proportion of sand grassland specialists and annuals of continental and submediterranean character along the 200 km north-west to south-

---

<sup>1</sup> sanyi@botanika.hu

<sup>2</sup> Department of Environmental Science, Botany and Ecology section, Camerino University, via Pontoni 5, 62032 Camerino, Italy.

east gradient in Hungary. Here, we further explore the vegetation differentiation along this aridity gradient by extending our study to the patterns of beta diversity.

## Methods

Within the forest steppe biome in Hungary, three study sites: Gönyű (47°43'N, 17°49'E), Csévharaszt (47°17'N, 19°24'E) and Fülöpháza (46°53'N, 19°23'E) have been chosen along an aridity gradient. The climate is temperate. Mean annual precipitation along the gradient varies between 565 mm and 535 mm. The mean annual temperature varies between 10.07 °C in the north-west and 10.33 °C in the south-east. There are strong seasonal and daily fluctuations in temperature and air humidity and uneven temporal distribution in precipitation. The climate at Fülöpháza is slightly more arid. The relative frequency of droughts and the temporal variability of climatic features expressed by the frequency distribution of precipitation curve types show clear trends and a significant increase in aridity from Gönyű to Fülöpháza (KUN 2001, KOVÁCS-LÁNG et al. 2008).

Six stands of *Festucetum vaginatae* grasslands were selected at each site for representing the coarse-scale within-site heterogeneity. For fine-scale heterogeneity sampling, presences of plant species were recorded along 52 m long circular belt transect of 1040 units of 0.05 m x 0.05 m contiguous microquadrats. The sampling was performed in late spring, during the phenological optimum of the vegetation. Beta diversity indices were calculated at two scales: at fine within-stands and at coarse between-stand scales (for more details see BARTHA et al. 2011).

Various beta diversity measures were used (Anderson et al. 2010). Whittaker  $\beta_W = \gamma/\alpha$ , where  $\gamma$  is the total number of species in the sampled vegetation patch and  $\alpha$  is the average number of species recorded in the smaller sampling units (Beta(1/0)).  $\beta_{\text{Shannon}} = H_\gamma/H_\alpha$  includes also relative abundance information (Beta (Shannon)). Beta diversity as the spatial turnover of species composition was represented by the mean 1-Sørensen index (for presence-absence data) and by the mean Bray-Curtis index (for abundance data). We calculated also the maximum number of the realized species combinations (NRC) (JUHÁSZ-NAGY and PODANI 1983) to represent beta diversity at fine scales. As an alternative measure of the coarse-scale beta diversity, we calculated the between-stand relative variance (CV%) of max. NRC. Beta diversity indices were calculated by the PRIMPRO (BARTHA et al. 1998) and SYN-TAX 5.0 (PODANI 1993) software packages. Differences between sites were analysed using one-way ANOVA and with post hoc tests using LSD statistics. Overall trend along the gradient was evaluated by Spearman rank correlation. Homogeneity of variance was tested by Levene statistic (Statistica 7.0, StatSoft Inc., Tulsa, OK, USA).

## Results

There were significant differences in beta diversity between sites at both scales (**Table 1**). At coarse scale, the highest beta diversity appeared at Fülöpháza. The opposite trend was found at fine spatial scales with the highest beta diversity at Gönyű and the lowest at Fülöpháza.

The maximum number of realized species combinations (max. NRC) showed decreasing trend along the aridity gradient (**Figure 1a**). We found the highest max. NRC at Gönyű (one-way ANOVA,  $F=8.844$ ,  $p<0.003$ ) and an overall decreasing trend with increasing aridity (the Spearman rank correlation was  $-0.734$ ,  $p<0.01$ ,  $N=18$ ). Between-stand relative variance of maximum NRC increased from Gönyű to Fülöpháza (Levene statistics,  $p<0.02$ ) (**Figure 1b**).

Beta-diversity descriptors	Mean					Variance					
	N	Gönyü	Csévharaszt	Fülöpháza	F	One-Way ANOVA Sig.	All Sites Spearman correlation Sig.	Gönyü	Csévharaszt	Fülöpháza	Levene statistic (homog. of var.) Sig.
<b>Fine scale (20 cm)</b>											
Beta(1/0)	18	6.803a	6.230a	5.950a	0,501	0,616	-0,376	0,782	1,608	4,411	0,406
Beta(Shannon)	18	<b>5.850a</b>	3.399b	2.891b	20,496	<b>0,000</b>	<b>-0.787(**)</b>	0,412	1,169	0,618	0,276
Sorensen	18	<b>0.607a</b>	0.509b	0.438b	6,539	<b>0,009</b>	<b>-0.669(**)</b>	0,002	0,008	0,010	0,080
Bray-Curtis	18	<b>0.676a</b>	0.571ab	<b>0.497b</b>	4,187	<b>0,036</b>	<b>-0.616(**)</b>	0,002	0,012	0,020	0,079
<b>Coarse scale (stands)</b>											
Beta(1/0)	18	2.010a	2.208a	2.373a	1,050	0,374	0,236	0,067	0,087	0,413	0,051
Beta(Shannon)	18	1.505a	1.421a	<b>3.014b</b>	3,653	<b>0,048</b>	0,275	0.064a	0.209a	<b>3.683b</b>	<b>0,000</b>
Sorensen	45	0.327a	0.357a	<b>0.484b</b>	22,564	<b>0,000</b>	<b>0.645(**)</b>	0,003	0,003	0,009	0,145
Bray-Curtis	45	0.347a	0.368a	<b>0.566b</b>	21,911	<b>0,000</b>	<b>0.595(**)</b>	0.004a	0.002a	<b>0.023b</b>	<b>0,000</b>

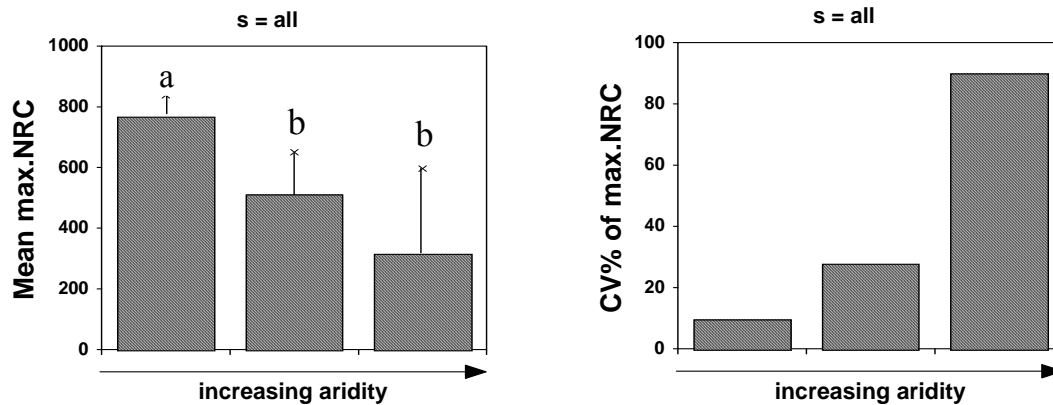
**Table 1.** Differences in beta diversity measures along the aridity gradient

Gönyü n=6, Csévharaszt n=6, Fülöpháza n=6. Not significant differences at P=0.05 based on One-Way ANOVA, post hoc tests were accomplished according to LSD statistic.

Means followed by the same letters within a row mean that means are not significantly different.

Homogeneity of variance was tested by Levene statistic for each pairs of stations. Significant different values are marked in bold.

Spearman correlation of each variable respect to the type of station (following such order: Gönyü n=1, Csévharaszt n=2, Fülöpháza n=3) are reported. P < 0.05 (\*); P < 0.01 (\*\*). Significant different values are marked in bold.



**Figure 1.**

**a,** The number of realized species combinations (NRC) representing beta diversity (spatial variability) in the sand grassland vegetation along an aridity gradient. Data from three sites (Gönyű, Csévharaszt, and Fülöpháza) represent the gradient from the mesic to the arid direction. At each site, the means (columns) represent the spatial variability at patch scale, and the standard deviations (small bars) represent the spatial variability at landscape scale. Mean values marked by different letters mean significant differences ( $p < 0.05$ ).

**b,** Relative variability (coefficient of variation) of beta diversity of the sand grassland vegetation along an aridity gradient, expressed by the CV% of maximum number of realized species combinations. The columns represent the landscape-scale spatial variability within a site.

## Discussion

There is only minor change in mean annual precipitation along the studied 200 km gradient. However, analysing compositional heterogeneity with various beta diversity measures along this gradient, we found a significant decrease of beta diversity at fine within-stand scale, and a significant increase of beta diversity at landscape scale. These changes are similar to the trends found during community degradation in other systems (BARTHA et al. 2004) and opposite to the patterns reported from successional communities (JUHÁSZ-NAGY and PODANI 1983, HOGEWEG et al 1985, BARTHA 1991).

While the dynamical consequences of the spatial differentiation in sand grassland vegetation need experimental approaches and long-term observations, our present study provides direct evidence that “sociological coordination” of vegetation (i.e., the relative structural and compositional invariability of plant communities) decreases with increasing aridity. The term “sociological coordination” was addressed by FEKETE (1992) who compared climatically zonal communities and edaphic communities in the temperate forest steppe zone. He found higher landscape-scale sociological coordination between stands of the climatically zonal communities than between stands of the azonal one. Based on the relative variance (CV%) of NRC, our results demonstrate that “sociological coordination” in sand grasslands decreases with increasing aridity and probably will decrease due to global changes

Decreasing fine-scale compositional heterogeneity involves decreasing resilience (MCNAUGHTON 1988; GUNDERSON and PRITCHARD 2002). In a previous permanent plot study, we found considerably (5 times) higher relative interannual variability of fine-scale structural complexity at Fülöpháza than at Csévharaszt (BARTHA et al 2008). In the present study, CV% of max. NRC showed consistent increase from Gönyű to Fülöpháza. We suppose that this increase of the coarse-scale spatial heterogeneity is related to the temporal heterogeneity of vegetation. The increasing interannual variability in vegetation induced by

climatic or land-use changes at fine scale, finally result in increased spatial heterogeneity at landscape scale.

Our present study provides evidence of scale-dependent changes of beta diversity in sand grassland communities with increasing aridity. More comparative studies are needed to explore the fine-scale and coarse-scale structural variability in various vegetation types and to understand the functional aspects of this variability together with the possible consequences on ecosystem services in changing landscapes.

## Acknowledgements

This study is part of the KISKUN Long Term Ecological Research Programme. We thank Edit Molnár, Barbara Lhotsky, István Hahn, Szilárd Bokros, Réka Aszalós, András Kun, Péter Ittész, and Wylie Harris for assistance during the field work. We acknowledge the general support of the Kiskunság National Park and the Duna-Ipoly National Park. The research was supported by the Hungarian National Science Foundation (OTKA K 72561 and T 21166).

## References

- ANDERSON M.J., CRIST T.O., CHASE J.M., VELLEND M., INOUE B.D., FREESTONE A.L., SANDERS N.J., CORNELL H.V., COMITA L.S, DAVIES K.F., HARRISON S.P., NATHAN J. B. KRAFT N.J.B., JAMES C. STEGEN J.C. and SWENSON N.G. 2011: Navigating the multiple meanings of diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14: 19-28.
- BARTHA S. 1991: *Diversity processes during revegetation on dumps from strip coal-mining*. Monograph Symposium "Biological Diversity", Madrid, 1989. pp. 180-181.
- BARTHA S., CZÁRÁN T., PODANI J. 1998: Exploring plant community dynamics in abstract coenostate spaces. *Abstracta Botanica* 22: 49-66.
- BARTHA S., CAMPETELLA G., CANULLO R., BÓDIS J., MUCINA L. 2004: On the importance of fine-scale spatial complexity in vegetation restoration. *International Journal of Ecology and Environmental Sciences* 30: 101-116.
- BARTHA S., CAMPETELLA G., RUPRECHT E., KUN A., HÁZI J., HORVÁTH A., VIRÁGH K., MOLNÁR ZS. 2008: Will inter-annual variability in sand grassland communities increase with climate change? *Community Ecology* 9(Suppl): 13-21.
- BARTHA S., CAMPETELLA G., KERTÉSZ M., HAHN I. KRÖEL-DULAY Gy., RÉDEI T. KUN A, VIRÁGH K., FEKETE G., KOVÁCS-LÁNG E. 2011. Beta diversity and community differentiation in dry perennial sand grasslands. *Annali di Botanica* (in press)
- BARTHOLY J., PONGRÁCZ R., GELYBÓ GY. 2007: Regional climate change expected in Hungary for 2071-2100. *Applied Ecology and Environmental Research* 5: 1-17.
- BESTELMEYER B.T., BROWN J. R., HAVSTAD K. M., FREDRICKSON E. L. 2006: A holistic view of an arid ecosystem: a synthesis of research and its applications. In: HAVSTAD K., HUENNEKE L. F., SCHLESINGER W. H. (eds.), *Structure and Function of Chihuahuan Desert Ecosystem. The Jornada Basin Long-Term Ecological Research Site*. Oxford University Press, Oxford, pp. 236-245.
- BORHIDI A. 1993: Characteristics of the climate of the Danube-Tisza Mid-region. In: SZUJKÓ LACZA J., KOVÁTS D. (eds.), *The Flora of the Kiskunság National Park. In the Danube-Tisza Mid-Region of Hungary* (Vol. I. The flowering plants.). Budapest, Magyar Természettudományi Múzeum, pp. 9-20.
- CHANETON E. J., PERELMAN B., OMACINI M., LEÓN J. C. 2002: Grazing, environmental heterogeneity, and alien plant invasion in temperate Pampa grasslands. *Biological Invasions* 4: 7-24.

- DEL MORAL R. 2007: Limits to convergence of vegetation during early primary succession. *Journal of Vegetation Science* 18: 479–488.
- FEKETE G. 1992: The holistic view of succession reconsidered. *Coenoses* 7: 21-29.
- GUNDERSON L. H. and PRITCHARD JR. L. (eds.) 2002: *Resilience and the behaviour of large-scale systems*. Island Oress, Washington.
- HOGEWEG P., HESPER B., VAN SCHAIK C. P., BEEFTINK W. G. 1985: Patterns in vegetation succession, an ecomorphological study. In: WHITE J. (ed.): *The population structure of vegetation*. Dr. W. Junk Publ., Dordrecht, pp. 637-666.
- JUHÁSZ-NAGY P., PODANI J. 1983: Information theory methods for the study of spatial processes and succession. *Vegetatio* 51: 129-140.
- KÉFI S., RIETKERK M., ALADOS L. C., PUEYO Y., PAPANASTASIS V. P., ELAICH A., DE RUITER P. C., 2007: Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449: 213-217.
- KOVÁCS-LÁNG E., BARTHA S., KRÖEL-DULAY GY., KERTÉSZ M., FEKETE G., MIKA J., RÉDEI T., RAJKAI K., HAHN I. 2000: Changes in the composition of sand grasslands along a climatic gradient in Hungary and implications for climate change. *Phytocoenologia* 30: 385-407.
- KOVÁCS-LÁNG E., MOLNÁR E., KRÖEL-DULAY GY., BARABÁS, S. (eds.) 2008: *The KISKUN LTER, Long-term ecological research in the Kiskunság, Hungary*. Vácrátót, Institute of Ecology and Botany, H.A.S.
- KUN A. 2001: Analysis of precipitation year types and their regional frequency distributions in the Danube-Tisza Mid-Region, Hungary. *Acta Botanica Hungarica* 43: 175-187.
- MCNAUGHTON S. J. 1988: Diversity and stability. *Nature* 333: 204-205.
- PODANI J. 1993: *SYN-TAXpc. Version 5.0. User's guide*. Scientia Publishing, Budapest.
- SANG W. 2009: Plant diversity patterns and their relationships with soil and climatic factors along an altitudinal gradient in the middle Tianshan Mountain area, Xinjiang, China. *Ecological Research* 24: 303-314.
- WALKER B.H., LUDWIG D., HOLLING C. S., PETERMAN R. M. 1981: Stability of semi-arid savanna grazing systems. *Journal of Ecology* 69: 473-498.

# Regeneration of sandy old-fields - a new method to assess recovery success

ANIKÓ CSECSERITS<sup>1</sup>, BÁLINT CZÚCZ, MELINDA HALASSY, GYÖRGY KRÖEL-DULAY, TAMÁS RÉDEI, REBEKA SZABÓ AND KATALIN SZITÁR

## Abstract

Abandoned agricultural fields are potential sites for the regeneration of semi-natural vegetation, and the newly developed vegetation can counteract biodiversity loss. We studied the vegetation of 161 old-fields in the Kiskunság, central Hungary. Old-fields were categorized into three age groups based on historical aerial photographs: fields abandoned 1-7, 8-20, and 21-57 years ago. The recovery success on old-fields was assessed by using potential target communities (open and closed grasslands and forest) as references. Species richness and cover of characteristic species of natural habitats were used as regeneration indicators. In our paper we present a new selection method for defining species groups and the results of the comparison based on these species groups.

## Introduction

Regeneration success following land abandonment depends on various factors and the resulting communities may or may not resemble to potential natural vegetation. Biogeographic zone, vegetation type, biotic and abiotic site conditions, surrounding landscape, previous land use have all been shown to affect recovery (PRACH and REHOUNKOVA 2006, COUSINE and AGGEMYR 2008). Secondary vegetation often exhibits a dual character: having some features and components from the target community but also others, often alien species, that differentiate them. A recent concept of “novel ecosystems” suggests that such new – often stable – combinations of species are becoming more and more frequent due to mixture of floras, altered disturbance regime and environmental conditions including climate change that create “no-analog” site conditions (HOBBS et al. 2006, WILLIAMS et al. 2007, HOBBS et al. 2009).

The evaluation of vegetation developed on abandoned fields can be done by various methods. The use of chronosequences (stands abandoned at different times) is a widely used approach, even if its limitations are acknowledged (PICKETT 1989, WALKER et al. 2010). Another method frequently used in evaluating restoration projects is the comparison of secondary vegetation with target vegetation (ARONSON et al. 1995, BLOCK et al. 2001). The combination of these two approaches, however, is rarely done (e.g. RUPRECHT 2006, ÖSTER et al. 2009).

The choice of appropriate target is always an issue, since it may not always be clear what the potential vegetation of a particular site may be at present (BAKKER et al. 2000, SUDING & GROSS 2006). Thus, a comparison with multiple possible target communities would be a desirable approach, but is rarely done (e.g. FAGAN et al. 2008).

The comparison is made frequently on the basis of species richness, but it can be overly simplifying. We can use the spectra of environmental indicator values, however in case of not yet stabilized communities, it can be misleading. An other approach is the study of the presence and dominance of species groups characteristic to natural habitats. In our study, we defined these species groups on the basis of a regional field survey.

---

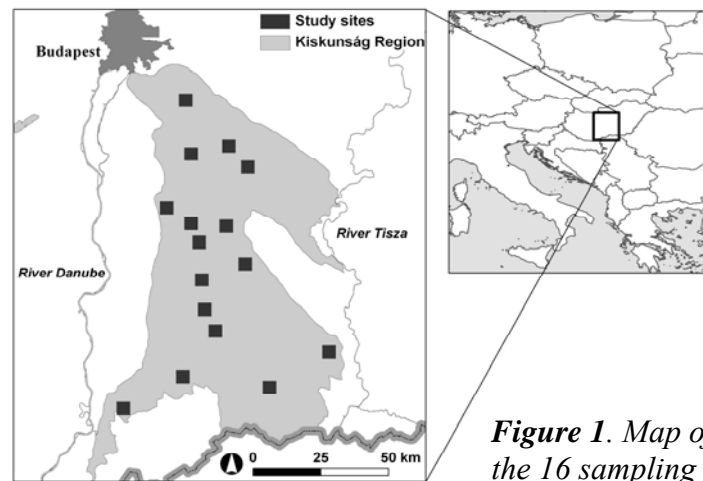
<sup>1</sup> aniko@botanika.hu

The overall aim of our study was to investigate old-field succession at the regional scale in the Kiskunság along a chronosequence, and evaluate regeneration success by comparing old-field vegetation with multiple target communities including grassland and forest elements of the zonal forest steppe mosaic and agricultural fields as starting phase of recovery.

## Methods

### Data collection

We used the field site network of the KISKUN-LTER program representing the variability in regional land-use types (RÉDEI et al. 2008; **Figure 1**). Within each study site, we sampled 3 separate stands of 11 habitat types, if they were present. In a total of 507 plots, 20 m × 20 m in size, we estimated the aboveground percentage cover of vascular plant species. Vegetation surveys were carried out between 2006 and 2008.



*Figure 1. Map of the study area with the 16 sampling sites.*

Old-fields were categorized into three age groups based on historical aerial photographs: old-fields abandoned 1-7 years ago (O1), old-fields abandoned 8-20 years ago (O2), and old-fields abandoned 21-57 years ago (O3). Abandonment of old-fields was defined as the cessation of ploughing, though occasional grazing or mowing may occur. Nevertheless, we hypothesized that the impact of elapsed time since abandonment would greatly exceed the impact of random grazing and mowing.

To represent the starting point of the secondary succession, we used relevés made in different agricultural habitats (A). Our potential target communities were open grassland (GO), closed grassland (GC), open woodland (FO), closed woodland (FC). For forest plantations, we sampled black locust (PR), black and Scots pine (PP) and non-native poplar (PE) plantations (**Table 1**). For more detail see CSECSERITS et al. (in press).

### Data analysis

Characteristic species of natural habitats were selected by determining the fidelity of species to natural habitats with Fisher-exact test (CHYTRY et al. 2002) in the Juice programme (TICHY 2002) using the relevés of A, PR, PP, PE, GO, GC, FC habitats. Species faithful to natural habitats at  $p=0.01$  level of significance were regarded as characteristic. Characteristic species of GO, GC and FC, FO were defined on the basis of the fidelity of species to GO, GC and FC, FO respectively by using the relevés of natural habitats only. Differences in species richness

and cover of species groups (characteristic species of natural habitats, of GO, GC and FC and neophytes – species introduced in Europe after the discovery of America (MIHÁLY and BOTTA-DUKÁT 2004) - among habitats were examined using Kruskal-Wallis test and Dunn post-hoc tests.

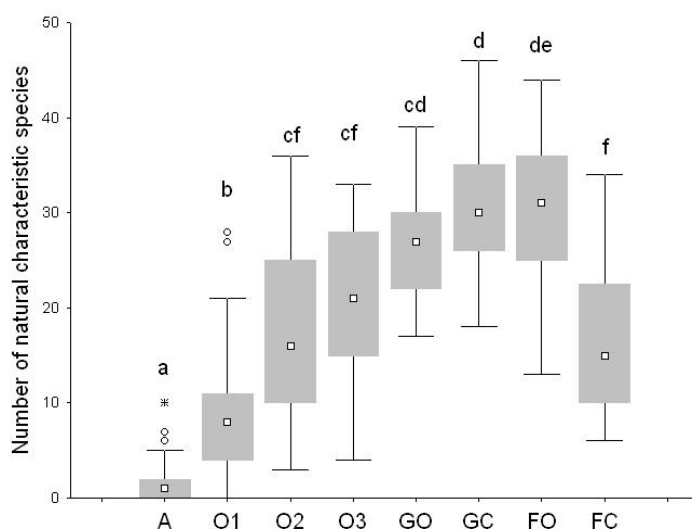
Name of habitat	Abb.	Number of relevés	Dominant species or description
Agricultural	A	75	Fields, vineyards and orchards
Old-field	O1	57	
Old-field	O2	53	
Old-field	O3	51	
Open grassland	GO	41	<i>Festuca vaginata</i> , <i>Stipa borysthenica</i>
Closed grassland	GC	46	<i>Festuca wagnerii</i> , <i>Stipa capillata</i> , <i>Bothriocloa ischaemum</i>
Open forest	FO	38	<i>Quercus robur</i> , <i>Populus alba</i> , <i>Juniperus communis</i>
Closed forest	FC	36	<i>Quercus robur</i> , <i>Populus alba</i>
Black locust plantation	PR	44	<i>Robinia pseudo-acacia</i>
Pinus plantation	PP	47	<i>Pinus nigra</i> , <i>Pinus sylvestris</i>
Non-native poplar plantation	PE	19	<i>Populus x euamericana</i>

**Table 1.** Number and description of the studied habitats. Abb.: abbreviation of the habitat.

## Results

We found 105 species significantly confined to natural habitats. Out of these species, 28 were characteristic to GO, 32 species to GC and 23 to FC. In old-field relevés we detected 85 characteristic species of natural habitats, 27 GO, 29 GC and 11 FC species (CSECSERITS et al. 2011 in press). As there were so few species faithful specifically to FO, we did not use this species group in the further analysis.

The species number of *characteristic species of natural habitats* was significantly higher in O2 and O3 than in O1. The number of such species found in O2 and O3 was not significantly different from the species number of open grasslands and closed forests, but it was lower than that of closed grasslands and open forests (**Figure 2**). The cover of *characteristic species of natural habitats* in O1 was significantly lower than in O2 and O3. In O2 and O3, the cover of these species achieved the level of that in open grasslands, but it was lower than in other natural habitats.

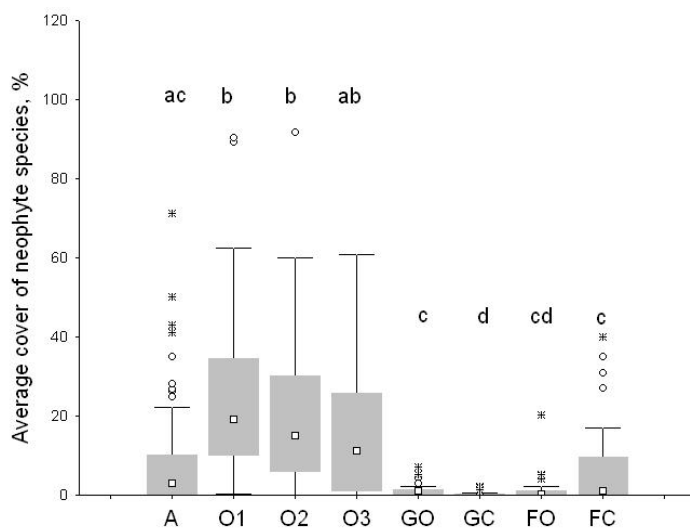


**Figure 2.** Species number of characteristic species of natural habitats. Habitat types with the same letter are not statistically different ( $p < 0.05$ ; Kruskal-Wallis test and Dunn post hoc test). Empty squares are medians, boxes are quartiles, whiskers are non-outlier minimum and maximum values,  $\circ$  outliers, \*extreme values. For abbreviations see table 1.

We found that O2 and O3 supported as many *open grassland species* as closed grasslands and open forests did, moreover in O3 it was as high as in open grasslands. Considering the cover of this species group, O2 and O3 did not differ significantly from closed grassland and open forests and in O3 it was as high as in open grasslands.

There were fewer *closed grassland species* in O1 than in O2 and O3. The species number of these species in O2 and O3 did not differ from that in open grasslands and open forests, but in closed grasslands it was significantly higher. The cover of *closed grassland species* showed a similar trend: it was significantly lower in O1 than in O2 and O3. The cover of this species group in O1 did not differ from what we found in open grasslands and in forests. In O2 and O3, this species group reached higher cover than in open grasslands, but was significantly lower than in closed grasslands. The number of *forest species* in O2 and O3 was as low as in open and closed grasslands.

The relevés of old-fields contained 34 neophyte species, while 21 neophyte species appeared in the relevés of natural habitats. In old-fields, the most frequent neophyte species were *Ambrosia artemisiifolia* (frequency: 80.7%, mean cover: 5%), *Conyza canadensis* (frequency: 80.1%, mean cover: 1.73 %) and *Asclepias syriaca* (frequency: 79.5 %, mean cover: 12.14 %). The number of neophyte species was significantly higher in O1 and O2 than in natural habitats. In O3 it was equal to open grassland and forests. The cover of neophyte species was significantly higher in every age group of old-fields than in natural habitats (**Figure 3**).



**Figure 3.** Average cover of neophyte species. Habitat types with the same letter are not statistically different ( $p < 0.05$ ; Kruskal-Wallis test and Dunn post hoc test). Empty squares are medians, boxes are quartiles, whiskers are non-outlier minimum and maximum values,  $\circ$  outliers, \*extreme values. For abbreviations see table 1.

## Discussion

Species richness is a widely used but often criticised measure of regeneration success, because it does not take species identity into account. The richness of habitat specialist species is a more reliable indicator (BAKKER 2008). Determining fidelity of species characteristic to different semi-natural habitats on the basis of a regional survey enabled us to define species groups reflecting present habitat preference. This approach can be used in other regions and our species list can be used in other projects dealing with regeneration or restoration in the region.

In our case, 80% of species characteristic to semi-natural habitats were capable of colonizing old-fields in a few decades, which is compared with other studies a good result. Studies that reported less successful vegetation recovery on old-fields suggest that the main reason of failure is propagule limitation, which is due to either habitat fragmentation or the regional rarity of some species. The Kiskunság still exhibits significant quantities of semi-natural

grassland habitats which can serve as regeneration sources (MOLNÁR et al. 2007, CZÚCZ et al. 2011).

We found that open and closed grassland species are much more successful in establishing, as well as in spreading on old-fields compared to forest species. There may be several reasons for the poor establishment of forest species: the region is located in the forest-steppe zone; there are much fewer natural forest fragments left compared to grasslands (BÍRÓ et al. 2008, BÍRÓ & MOLNÁR 2009) suggesting a stronger propagule limitation for forest species and the regional decline of ground water table is more favourable for the drought-tolerant grassland species.



**Figure 4.** A typical old-field in the Kiskunság with the dominant native grass: sandy federgrass (*Stipa borysthenica*) and with the non-native milkweed (*Asclepias syriaca*).

The vegetation of the studied old-fields are similar to the grassland, however the cover of neophyte species is larger than in semi-natural habitats. This new and through the studied time-scale stabile combination of species can be considered as appearance of a new community (HOBBS et al. 2006) which can have nature conservation values.

## References

- ARONSON J., DHILLION S., LE FLOC'H E. 1995: On the need to select an ecosystem of reference, however imperfect: a reply to Pickett and Parker. *Restoration Ecology* 3: 1-3.
- BAKKER J. D. 2008: Increasing the utility of Indicator Species Analysis. *Journal of Applied Ecology* 45: 1829-1835.
- BAKKER J. P., GROOTJANS A. P., HERMY M., POSCHLOD P. 2000: How to define targets for ecological restoration? Introduction. *Applied Vegetation Science* 3: 3-6.
- BÍRÓ M., RÉVÉSZ A., MOLNÁR ZS., HORVÁTH F., CZÚCZ B. 2008.: Regional habitat pattern of the Duna-Tisza köze in Hungary II. The sand, the steppe and the riverine vegetation; degraded and ruined habitats. *Acta Botanica Hungarica* 50:21-62.
- BÍRÓ M., MOLNÁR ZS. 2009: Az Alföld erdei a folyószabályozások és az alföldfásítás előtti évszázadban. In: KÁZMÉR M. (szerk): *Az elmúlt 500 év környezeti eseményei történelmi és természettudományi források tükrében*. Hantken kiadó, Budapest, pp. 169-206.

- BLOCK W. M., FRANKLIN A. B., WARD J. P. JR., GANEY J. L., WHITE G. C. 2001: Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restoration Ecology* 9, 293–303.
- CHYTRY M., TICHY L., HOLT J., BOTTA-DUKÁT Z. 2002: Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science* 13: 79-90.
- COUSINE S. A. O., AGGEMYR E. 2008: The influence of field shape, area and surrounding landscape on plant species richness in grazed ex-fields. *Biological Conservation* 141: 126-135.
- CZÚCZ B., CSECSERITS A., HORVÁTH F., SZABÓ R., BOTTA-DUKÁT Z. HORVÁTH F., MOLNÁR ZS. 2011: Estimating the climatic adaptive capacity of natural ecosystems with landscape connectivity and diversity indicators. *Journal of Vegetation Science* (in press)
- CSECSERITS A., CZÚCZ B., HALASSY M., KRÖEL-DULAY GY., RÉDEI T., SZABÓ R., SZITÁR K., TÖRÖK K. Regeneration of sandy old-fields in the forest-steppe region of Hungary. *Plant Biosystems*: (under revision).
- FAGAN K. C., PYWELL R. F., BULLOCK J. M., MARRS R. H. 2008: Do restored calcareous grassland on former arable fields resemble ancient targets? The effect of time, methods and environment on outcomes. *Journal of Applied Ecology* 45: 1293-1303.
- HOBBS R. J., ARICO S., ARONSON J., BARON J. S., BRIDGEWATER P., CRAMER V. A., EPSTEIN P. R., EWEL J. J., KLINK C. A., LUGO A. E., NORTON D., OJIMA D., RICHARDSON D. M., SANDERSON E. W., VALLADARES F., VILÀ M., ZAMORA R., ZOBEL M. 2006: Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15: 1-7.
- HOBBS R. J., HIGGS E., HARRIS J. A. 2009: Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution* 24: 599-605.
- MIHÁLY B., BOTTA-DUKÁT Z. (szerk.) 2004: *Biológiai inváziók Magyarországon. Özönnövények* (Biological invasion in Hungary. Invasive plants). Természetbúvár Alapítvány Kiadó, Budapest.
- MOLNÁR ZS., BIRÓ M., BÖLÖNI J., HORVÁTH F. 2008: Distribution of the (semi-)natural habitats in Hungary I. Marshes and grasslands. *Acta Botanica Hungarica* 50 (suppl.): 59-106.
- ÖSTER M., ASK K., RÖMERMANN C., TACKENBERG O., ERIKSSON O. 2009: Plant colonization of ex-arable fields from adjacent species-rich grasslands: The importance of dispersal vs. recruitment ability. *Agriculture, Ecosystems & Environment* 130: 93-99.
- PICKETT S. T. A. 1989: Space-for-time substitution as an alternative to long-term studies. In: LIKENS, G.E. (szerk.) *Long-term Studies in Ecology: Approaches and Alternatives*. Springer, New York. pp. 110-135.
- PRACH K., REHOUNKOVÁ K. 2006: Vegetation succession over broad geographical scales: which factors determine the patterns? *Preslia* 78: 469-480.
- RÉDEI T., KRÖEL-DULAY GY., BARABÁS S., LELLEI-KOVÁCS E., SZABÓ R., TÖRÖK K. 2008: A network of long-term ecological and socio-economic research sites to study the effects of land use change. In: KOVÁCS-LÁNG E, MOLNÁR E, KRÖEL-DULAY GY, BARABÁS S. (szerk.): *The KISKUN LTER: Long-term ecological research in the Kiskunság*. Institute of Ecology and Botany of the Hungarian Academy of Sciences (IEB HAS), Vácrátót pp. 15-19.
- RUPRECHT E. 2006: Successfully recovered grassland: a promising example from Romanian old-fields. *Restoration Ecology* 14: 473-480.
- SUDING K. N., GROSS K. L. 2006: The dynamic nature of ecological systems: multiple states and restoration trajectories In: FALK D. A., PALMER M. A., ZEDLER J. B. (eds.) *Foundations of restoration ecology*. Society for Ecological Restoration International, Island Press, pp. 190- 209. Washington, DC: Island Press
- TICHY L. 2002: JUICE, software for vegetation classification. *Journal of Vegetation Science* 13: 451-453.
- WALKER L. R., WARDLE D. A., BARDGETT R. D., CLARKSON B. D. 2010: The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology* 98: 725-736.
- WILLIAMS J. W., JACKSON S. T. 2007: Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5: 475–482.

# Grazing effects on the spread of fire in open sand grassland

GÁBOR ÓNODI<sup>1</sup>, MIKLÓS KERTÉSZ, ZOLTÁN BOTTA-DUKÁT AND VILMOS ALTBÄCKER<sup>2</sup>

## Abstract

We studied the effects of sheep and rabbit grazing on the spread of induced fire on an open sand grassland community in the Hungarian Plain. Patches of open sand grassland were grazed by sheep in April and by sheep and rabbit in May of 2003. Half of each patch was burned in July. Canopy cover of the litter and vascular plant species, species number, plant height, burnt area and the speed of fire-spread were estimated in one by one meter quadrates. Burnt area was significantly smaller with late sheep grazing, while the speed of fire-spread decreased significantly due to rabbit grazing compared to that of the control. Plant height was significantly decreased by early and late sheep grazing, while rabbit grazing resulted in significantly lower canopy cover values of vascular plants compared to the control.

## Introduction

Grazing and fire regimes are the most important large scale disturbances on semiarid and arid grassland communities (VAN LANGEVELDE et al. 2003, GHERMANDI et al. 2004, FELDMAN and LEWIS 2005). In most cases, fire and herbivory are independently investigated. However, there is very little research on how these two agents influence the function of each other (ARCHIBALD et al 2005). In our study, we intended to look deeper into how herbivory affects fire-spread of an open semiarid sand grassland community.

Herbivore density has decreased in the Kiskunság National Park since the beginning of the 1990s (KATONA et al. 2004). One important cause for this was the decline in stock density of cattle and sheep in Hungary. Additionally, the abundance of rabbit decreased dramatically in 1994 and 1995 due to a combination of myxomatosis and hemorrhagic disease, followed by an exceptionally long snow cover that winter. We assumed that decreased herbivory increases the extent of both anthropogenic and naturally ignited wildfires.

In this paper, we present a field experiment conducted on a forest-steppe mosaic of open sand grassland and *Juniperus-Populus* woody patches in the Kiskunság National Park. We wanted to know whether moderate rabbit and sheep grazing could affect the spread of fire in this open grassland community as has been demonstrated with persistent heavy grazing in denser communities (ARCHIBALD et al. 2005). We conducted our experiment on the grassland patches which play a substantial role in transmitting fire among the woody patches of the *Juniperus-Populus* community in the forest-steppe vegetation.

## Material and Methods

Our study site lies on the Hungarian Plain, in the outskirts of Orgovány (N46°47.369, E19°26.829), on a forest-steppe area, which is one of the westernmost extensions of the forest-steppe zone in Europe (KOVÁCS-LÁNG et al. 2000). The area is part of the Kiskunság National Park. The study site is a mosaic of open sand grassland and woody patches of

---

<sup>1</sup> gabor.onodi@botanika.hu

<sup>2</sup> Department of Ethology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/c

*Juniperus communis* (L.), *Populus alba* (L.), and *Populus nigra* (L), based on the nomenclature of SIMON (2000).

We conducted the experiment in 2003, in an extreme dry year. The size of the study site was one hectare. Within the study site, we marked 10 blocks of the open sand grassland among the woody patches. Each block consisted of four differently treated grassland patches, namely, an ungrazed control plot, an early sheep grazed (middle of April), a late sheep grazed (end of May), and a rabbit grazed (end of May) plot. Each patch consisted of 1 m x 1 m quadrates. The patches were fenced during the grazing period which lasted until the sheep or rabbit (one animal per patch) reduced the original vegetation cover to 50% (estimated visually) through plant removal and trampling. We performed the burning treatment in July for all blocks on the same day. We burned half of each patch, including two of the four quadrates. There remained two unburned quadrates in each patch to examine regeneration following the grazing treatments.

We took samples three times in 2003. Sampling periods were before the grazing treatments in April, before the burning treatment in July, and after the burning treatment in September. We estimated the effects of treatments and sampling date on the species number, on the canopy cover of the vascular plants, and on the litter, using a three-way repeated measure ANOVA. Treatments (grazing, burning) were fixed factors, while the third factor (the block) was random. We analyzed the effects of grazing on plant height, burnt area, and speed of fire-spread by two-way ANOVA with one fixed factor (grazing) and one random factor (block). After both ANOVA analyses, pairwise comparisons by Tukey's HSD tests were carried out.

## Results

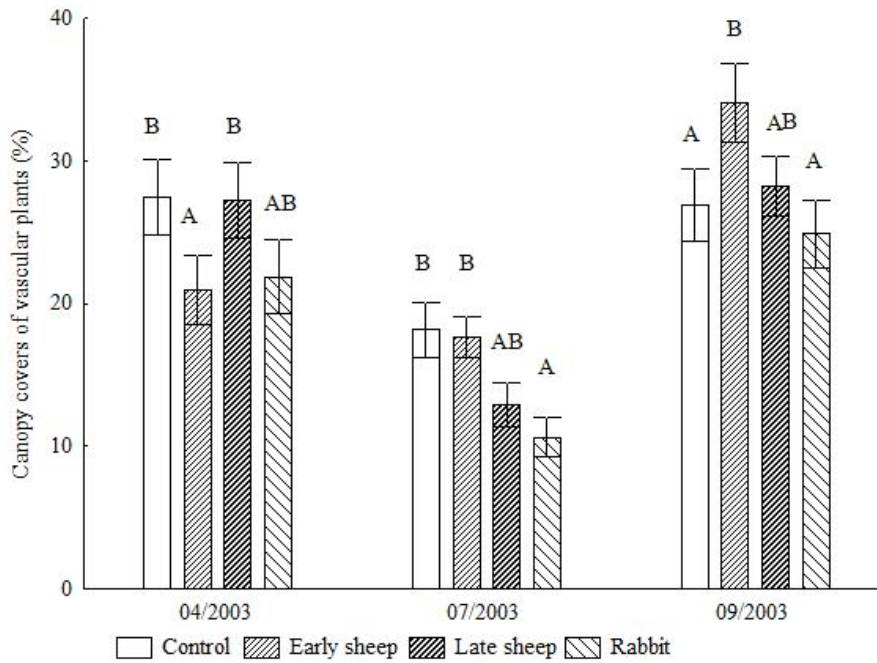
Canopy cover of litter increased between April and July in the case of the grazing control quadrates, while it did not change in relation to the three grazed treatment types.

Canopy cover of vascular plants (**Figure 1.**) decreased between April and July, however, there was no change in the case of early sheep grazing. Consequently, in July before the burning treatment we found no difference between grazing control and early sheep grazing, while rabbit grazing decreased the canopy cover compared to both the control and the early sheep grazing. Late sheep grazing resulted in non-significantly lower canopy values. Canopy cover of vascular plants increased from July to September in all grazing treatments. Early sheep grazing resulted in higher values compared to the control in September.

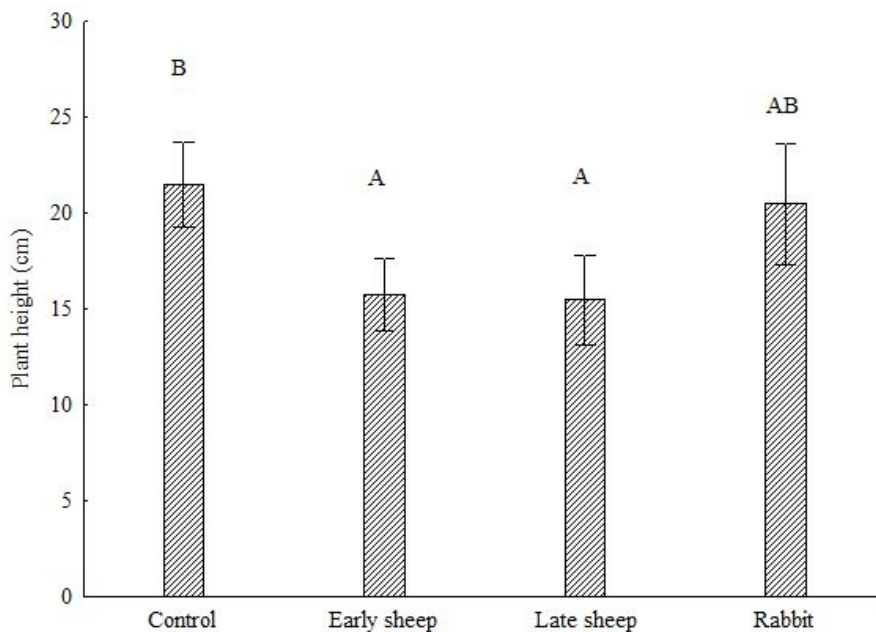
Plant height was lower in the grazed quadrates due to the early and late sheep grazing compared to the control, while rabbit grazing resulted in intermediate values (**Figure 2.**).

Burnt area was smaller in the case of late sheep grazing compared to that of the early sheep grazing and the control, while rabbit grazing insignificantly decreased the extent of fire (**Figure 3.**). The speed of fire-spread decreased due to rabbit grazing compared to the control (**Figure 4.**).

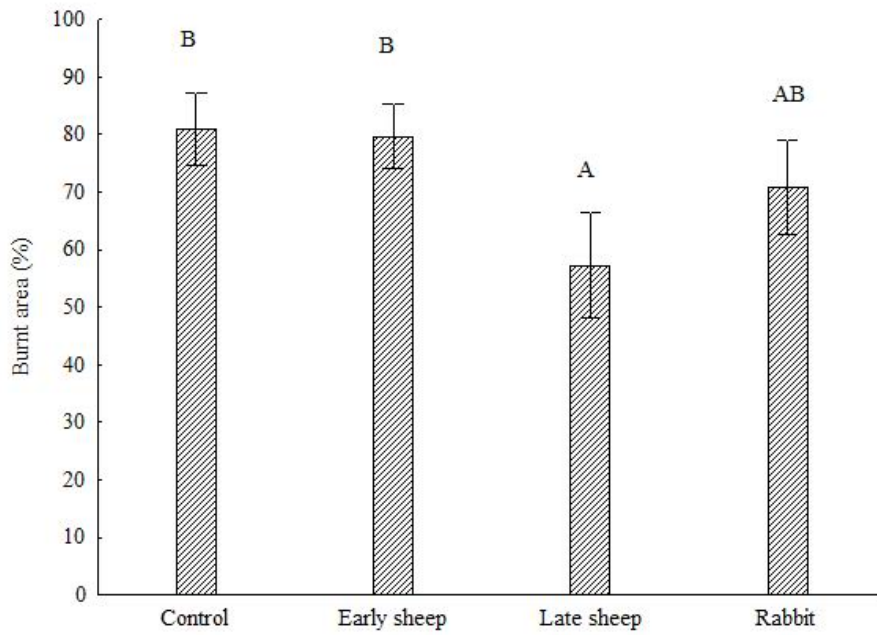
Species number was not affected by the grazing treatments.



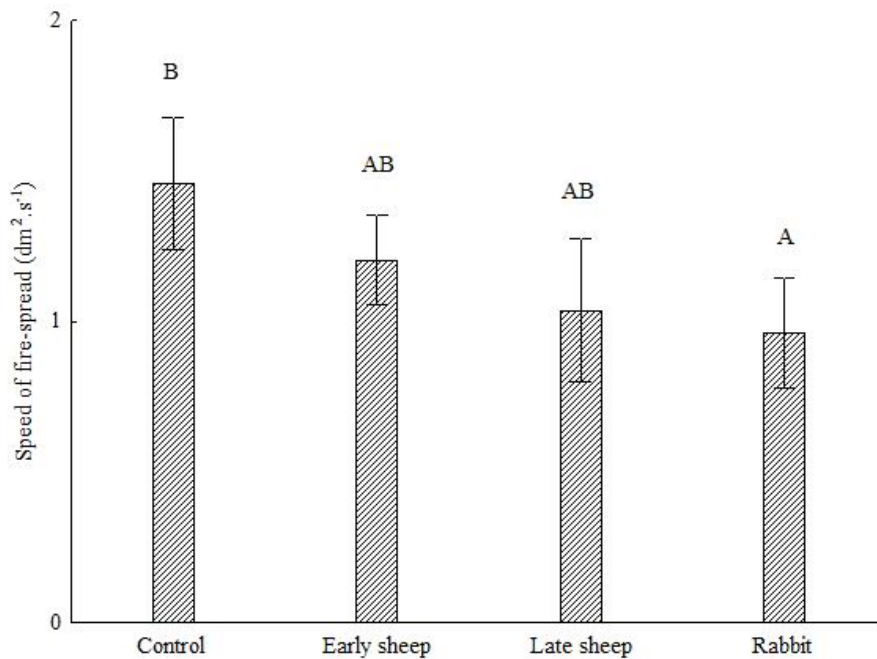
**Figure 1.** Canopy covers of the vascular plants (mean  $\pm$  SE) for the four types of grazing treatments at the sampling dates, before the grazing treatment in April, before the burning treatment in July and two months after the burning in September. Columns in the same cluster followed by the same letter are not significantly different according to Tukey's HSD test.



**Figure 2.** Plant height (mean  $\pm$  SE) for the four types of grazing treatments prior to the burning treatment in July. Columns in the same cluster followed by the same letter are not significantly different according to Tukey's HSD test.



**Figure 3.** The extension of the fire (mean  $\pm$  SE) for the four types of grazing treatments in July. Columns in the same cluster followed by the same letter are not significantly different according to Tukey's HSD test.



**Figure 4.** The speed of fire-spread (mean  $\pm$  SE) for the four types of grazing treatments in July. Columns in the same cluster followed by the same letter are not significantly different according to Tukey's HSD test.

## Discussion

We found that the effect of sheep grazing on the extension of fire depends upon the timing of the grazing treatments. According to our expectation, sheep grazing in late spring decreased the extension of fire during the mid-summer drought on the open sand grassland, while despite our preliminary assumption, sheep grazing in April had no effects on fire-spread. The reason for this is that the vegetation of the patches grazed in April had enough time to regenerate before July, thus the canopy cover of the vegetation was similar to the control prior to the burning treatment. The green vegetation of the patches grazed in late spring, either by sheep or by rabbit, did not regenerate by July, but was regenerated by September. On the prairie, long-term heavy grazing has a negative effect on fire-spread, because it breaks up the homogenous grass layer (GOSZ and GOSZ 1996, ARCHIBALD et al. 2005). We found that even moderate grazing causes decreased fire-spread on open sand grasslands.

However, species identity is also important in the case of fire-spread, because only rabbit grazing decreased significantly the speed of fire-spread, and only sheep grazing in May decreased significantly the extension of fire. These two animals have different grazing habits. Sheep eat the top of the vegetation, while rabbits consume the interior portions of it. Accordingly, sheep grazing resulted in a stronger decrease in plant height, while rabbit grazing more strongly decreased canopy cover of vascular plants. Our results show that both the amount of combustible biomass (canopy cover of vascular plant and litter) and the structure of the vegetation (height) play a role in the spread of fire (speed of fire spread and burnt area).

We suggest that the accumulation of litter (due to decreased herbivory on the sand grassland patches) might affect the structure of the whole forest-steppe habitat, because an enhanced litter layer on the open grassland can transmit fire among the woody patches. Therefore, in the absence of large herbivores spread of fire may increase in the *Juniperus-Populus* forest-steppe where woody patches are surrounded by a matrix of open sand grasslands. Woody patches play an important role in sustaining biodiversity, although most of the endemic and other protected species live on the sand grasslands. This is because they increase habitat diversity by producing shaded and more humus-rich habitat-patches, which results in the remarkable species richness characteristic of the Sand Ridge vegetation. Fire damages this pattern of the vegetation. According to our long term observations on the Kiskunság, *Juniperus communis* is not able to regenerate after fire; it is replaced by resprouter trees, such as the invasive *Robinia pseudo-acacia* or *Populus* species. Therefore, fire may affect the vegetation, not only in the short-term, but can cause long-term compositional changes, which has a greater effect on the grassland than burning itself.

## Acknowledgements

We are grateful to Katalin Csatádi, István Németh and Olivér Váczi for their contribution to the field work. We thank the Kiskunság National Park (Hungary) for the support of our field experiments. This study was funded by the Hungarian Scientific Research Found (OTKA T 29703) and by the National Research and Development Program (NKFP 3B-0008/2002).

## References

- ARCHIBALD, S., BOND, W. J., STOCK, W. D., FAIRBANKS, D. H. K. 2005: Shaping the landscape: fire-grazer interactions in an African savanna. *Ecological Applications* 15: 96-109.

- FELDMAN, S. R., LEWIS, J. P. 2005: Effects of fire on the structure and diversity of a *Spartina argentinensis* tall grassland. *Applied Vegetation Science* 8: 77-84.
- GHERMANDI, L., GUTHMANN, N., BRAN, D. 2004: Early post-fire succession in northwestern Patagonia grasslands. *Journal of Vegetation Science* 15: 67-76.
- GOSZ, R. J., GOSZ, J. R. 1996: Species interactions on the biome transition zone in New Mexico: response of blue gramma (*Bouteloua gracilis*) and black gramma (*Bouteloua eripoda*) to fire and herbivory. *Journal of Arid Environments*. 34: 101-114.
- KATONA, K., BÍRÓ, ZS., HAHN, I., KERTÉSZ, M., ALTBÄCKER, V. 2004: Abundance of European hares in a lowland area, Hungary: a long term ecological study in the period of the rabbit extinction. *Folia Zoologica* 53: 255-268.
- KOVÁCS-LÁNG E., KRÖEL-DULAY GY., KERTÉSZ M., FEKETE G., BARTHA S., MIKA J., DOBI-WANTUCH I., RÉDEI T., RAJKAI K., HAHN, I. 2000: Changes in the composition of sand grasslands along a climatic gradient in Hungary and implications for climate change. *Phytocoenologia* 30: 385-407.
- SIMON T. (szerk.) 2000: *A magyarországi edényes flóra határozója*. [Identification guide of hungarian vascular flora.] Nemzeti Tankönyvkiadó, Budapest.
- VAN LANGEVELDE, F., VAN VIJVER, C. A. D. M., KUMAR, L., VAN KOPPEL, J., RIDDER, N., VAN ANDEL, J., SKIDMORE, A. K., HEARNE, J. W., STROOSNIJDER, L., BOND, W. J., PRINS, H. H. T., RIETKERK, M. 2003: Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84: 337-350.

# Respiration of the sandy soil of Kiskunság in the light of climate change

ESZTER LELLEI-KOVÁCS<sup>1</sup>, EDIT KOVÁCS-LÁNG, ZOLTÁN BOTTA-DUKÁT, TIBOR KALAPOS,  
GYÖRGY KRÖEL-DULAY

## Abstract

In the Kiskunság, near Fülöpháza, we established a climate simulation experiment in 2001, where passive nighttime warming and a decrease in precipitation in the vegetation period were simulated. In present work the results of our six-year study on soil respiration in this experimental site are reported.

## Introduction

Soil respiration is an important part of the atmosphere-ecosystem interactions, while it accounts for the second largest carbon flux between ecosystem and atmosphere. Therefore, responses of soil respiration to climate change have considerable impacts on climate predictions. Our knowledge, however, on the carbon balance of arid and semiarid ecosystems with transient type of vegetation is very limited. Transient climate zones of terrestrial ecosystems are supposedly highly sensitive to climate change. On the other hand, such ecosystems are usually exposed to frequent climatic or weather fluctuations, therefore they could possess higher adaptive capacity to fluctuations of this sort. For this paradox, the functioning of these habitats can be understood only in long-term studies.

Soil respiration, as an indicator of soil biological activity, is strongly influenced by temperature and soil moisture. By climate predictions further warming, and in the vegetation period enhanced drought is expected in Hungary for the next period (MIKA 2003). Near Fülöpháza, in a sandy forest-steppe patch with white poplar sprouts, we have launched a climate simulation experiment in the frame of the EU FP5 VULCAN project, applying passive nighttime warming and rain exclusion in the peak vegetation period (BEIER et al. 2004). Since 2003, we have been investigating soil respiration within this experiment, to estimate ecosystem responses to changing climatic conditions (LELLEI-KOVÁCS et al. 2008). We monthly measure soil respiration and soil surface temperature by infrared gas analyser, while monthly soil moisture is measured by TDR handheld device.

In this study we aimed at the quantification of 1) soil respiration rate in the semiarid temperate sand forest-steppe ecosystem; 2) the daily, seasonal and yearly courses of the intensity of CO<sub>2</sub> emission from the soil; and 3) the magnitude of the effects of heat and drought treatments applied in accordance with forecasted changes in climate.

## Variability of environmental factors affecting soil respiration

Weather of the studied six year between 2003 and 2008 varied highly, offering a good opportunity to compare weather and soil respiration rates between years. The highest interannual variability appeared in the amount of precipitation between April and June (in the peak vegetation period). Soil temperature changed significantly with months, time of the day and years, often exceeding 50°C in summer, while the lowest values were recorded around 0°C at the beginning (in March) or at the end (in November) of the growing season.

---

<sup>1</sup> eszter@botanika.hu

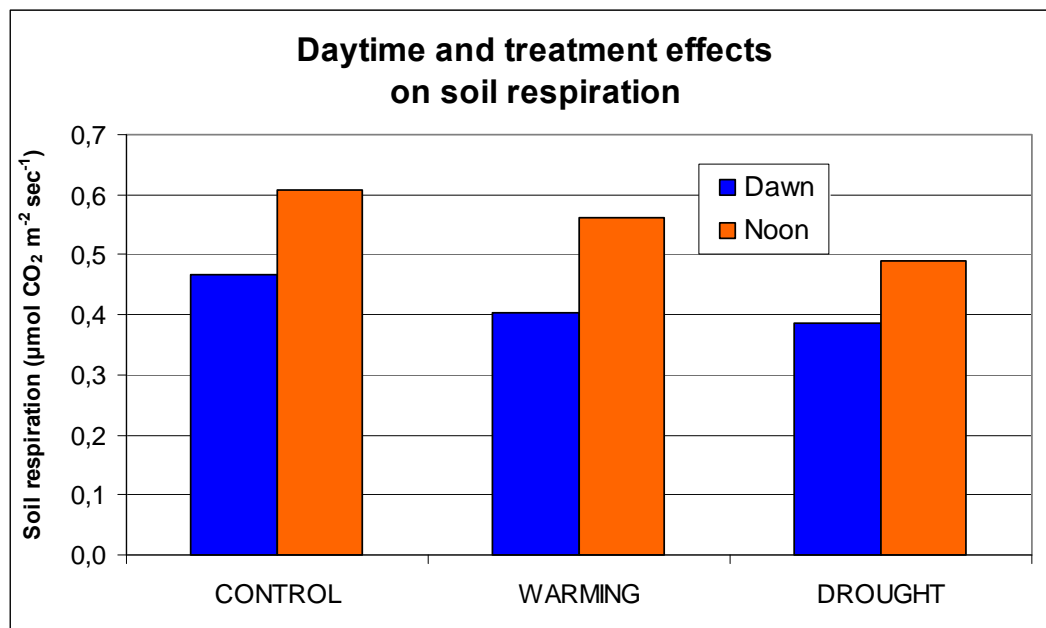
Between 2003 and 2008 passive nighttime warming reduced cooling down at 1.7°C on soil surface at dawn, while this difference totally disappeared by noon. Volumetric soil moisture content of the sandy soil of high infiltration rate and low water holding capacity ranged from 0.0 to 14.4% during the six years. Warming treatment and drought treatment decreased soil moisture content during the year with an average of 0.5 and 1.0 vol%, respectively. Directly under the drought treatment, this reduction reached 2.3 vol%.

### Effects of years, months and daytime on soil CO<sub>2</sub> efflux

During the six years of the field experiment soil respiration rate was very low, between 0.09 and 1.94  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . Mean soil respiration rate varied significantly with years, months and time of the day. The seasonal course of soil respiration showed clear temperature limitation in winter and moisture limitation in summer, in all treatments. During the day significantly (about 54%) lower values are characteristic at dawn than those at midday.

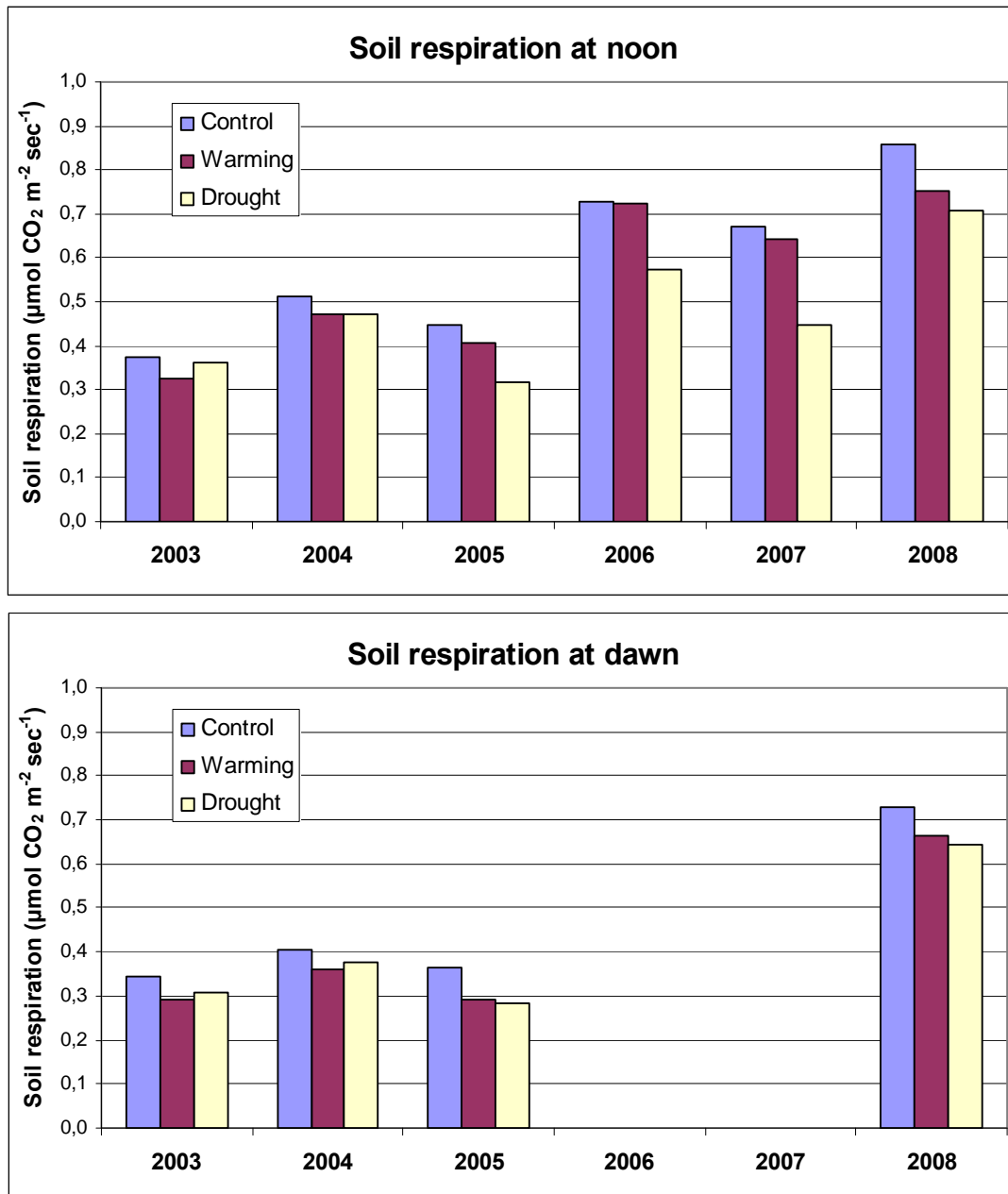
### Effects of heat or drought treatments on soil CO<sub>2</sub> efflux

Surprisingly, both warming and drought treatment had decreasing effects on soil respiration (**Figure 1**). Only the extent of the effects was depending on the given part of the day. At dawn, soil respiration was decreased by both warming and drought treatment at 13% to control, while at daytime, warming and drought treatment decreased soil respiration at 8% and 20%, respectively.



**Figure 1.** Impacts of daytime and treatments on soil respiration

Investigating the individual years separately, a more detailed pattern emerges (**Figure 2**). During the exceptionally dry and hot 2003 not only the drought treatment, but also the control suffered severe drought. Soil respiration differed not significantly between the treatments in this year. Also in the relatively cool and rainy 2004, soil respiration responded neither to the heat nor to the drought treatments in the studied period despite the relatively large amount of precipitation excluded in drought treatment. Between 2005 and 2008, however, drought treatment decreased daytime soil respiration significantly, at least in the treatment period.



*Figure 2. Annual averages of soil respiration values at dawn and at noon*

## Conclusions

Soil respiration is controlled by numerous environmental factors as temperature, soil water content, substrate availability, vegetation pattern, and by the spatial and temporal variation of each of them. Our six-year study was conducted in a spatially heterogenous vegetation, in a patch of the forest-steppe mosaic, within various temperature and moisture conditions, which is characteristic for the climate of the Pannonian region and also derives from the physical characteristics of the sandy substrate. Measured soil respiration rates in this temperate semiarid vegetation were rather low, related to other temperate grasslands or shrublands. These data, however, are understandable considering the extreme environmental conditions and very low organic matter content of the soil. Since microbial activity is closely associated

with the surface of roots in this system, the heterotrophic (mostly bacterial and fungal) and autotrophic (root) respiration cannot be separated. Under such extreme conditions, soil respiration rate can be one or two orders of magnitude lower than that in soils of higher biological activity.

In the Pannonian forest-steppe, soil respiration displays a characteristic, annually repeated seasonal course. Seasonal course of soil respiration, however, may be controlled not only by temperature but also seems to be closely associated with water availability and the seasonal activity pattern of vegetation, reaching its peak in spring and autumn and having a summer water-limited and a winter temperature-limited period.

Contrary to expectations, nocturnal warming did not enhance soil respiration relative to control in our six-year experiment, although soil surface at dawn was tempered by an average of 1.6°C as a consequence of nocturnal sheltering, what should create more beneficial temperature conditions for soil respiration. Heat treatment, however, had an indirect effect as well, i.e., decreasing the soil moisture content of the topsoil relative to control, and this could outweigh the expected positive effect of the rising temperature on soil respiration. The simultaneous drying effect of the heat treatment could be caused by the exclusion of dewfall by the roofs covering the plots at night, and on the other hand, from the presumed reduction in water vapor condensation and underground dew formation. The latter is a direct consequence of the restrained cooling down of the soil surface. Higher evaporation rate at night due to higher temperature on the treated plots could also contribute to the lower water content of the soil.

The degree of the changes in soil respiration due to treatments, however, was different in the different years. Weather extremities (severe drought and hot spring in 2003, and unusually high rainfall in 2004) damped the effects of treatments of the given extent while in the more or less average years of 2005 and 2006 treatment effects were more pronounced. It seems that rather the relative, than the absolute amount of excluded precipitation determines the significance of the treatment effects. Supposedly, to reach a significant effect, at least the half amount of the total precipitation should be excluded, on the other hand, the extreme water condition of the control may have also an important role. This also draws attention to the importance of the effects of weather extremities during climate change.

## **Acknowledgements**

We would like to acknowledge the support of the following research grants: EU FP5 VULCAN project (EVK2-CT-2000-00094), NKFP 3B-0008/2002 grant from the Hungarian Government.

## **References**

- BEIER C., EMMETT B., GUNDERSEN P., TIETEMA A., PEÑUELAS J., ESTIARTE M., GORDON C., GORISSEN A., LLORENS L., RODA F., WILLIAMS D. 2004: Novel approaches to study climate change effects on terrestrial ecosystems in the field: drought and passive nighttime warming. *Ecosystems* 7: 583-597.
- LELLEI-KOVÁCS E., KOVÁCS-LÁNG E., KALÁPOS T., BOTTA-DUKÁT Z., BARABÁS S., BEIER C. 2008: Experimental warming does not enhance soil respiration in a semiarid temperate forest-steppe ecosystem. *Community Ecology* 9: 29-37.
- MIKA J. 2003: Regionális éghajlati forgatókönyvek: tények és kétségek. (Regional climatic scenarios: facts and doubts.) In: CSETE L. (ed.): "Agro-21" *Füzetek* 32: 11-24.

# Long-term vegetation degradation in Hungarian rock grassland communities

KATALIN SZITÁR<sup>1</sup> AND KATALIN TÖRÖK

## Abstract

We demonstrate a possible application of large historical vegetation data sets as reference to detect trends in natural state of the vegetation. Phytosociological relevés re-sampled after 3-6 decades were used to detect and interpret long-term plant compositional changes of seven rock grassland associations in Hungary. Data analyses were designed to minimise the negative effects arising from the application of historical information.

Detrended correspondence analysis shows a uniform displacement of plot averages in the ordination space in six communities. Occurrences of species typical to rock grassland associations decreased significantly. Natural pioneers, disturbance-tolerant and weed species increased in number. Nevertheless, their amount is relatively low and natural constituents of the communities still dominate, therefore the detected changes can be described as a minor degradation.

## Introduction

In Europe, large phytosociological data sets were gathered from the early 20<sup>th</sup> century on (DENGLER et al. 2011). The difficulty in using these data for assessing the change in the natural state is that these were not gathered with the intention to serve as state references (BOTTA-DUKÁT et al. 2007). Their use is often criticised because of inconsistency in sampling methodologies, imprecise localization of the plots (WILLIAMS et al. 2005), differences in species abundance estimates (WILD et al. 2004). These problems can be minimised if the 'corresponding quadrat' concept (PERSSON 1980) is applied.

Rock grassland communities are considered to have a rather stable species composition (TÖRÖK and ZÓLYOMI 1998, RÉDEI et al. 2003) and thus are suitable for testing the sensitivity of the approach (**Figure 1**). Historical phytosociological relevés of seven rock grassland communities of European importance were resampled after 30-60 years in Hungary. The aim of the study was to detect and interpret long-term vascular plant composition changes of rock grassland associations.

## Methods

Seven associations of rock grasslands were included in the present analysis representing the diversity of Hungarian rock grasslands on three main substrate types: dolomite, limestone and silicate. **Table 1.** shows details of the phytosociological relevés of Tibor Simon, András Horánszky, Bálint Zólyomi, and Júlia Szujkó-Lacza, recorded between 1931 and 1961 and served as historical references for resampling.

---

<sup>1</sup> szitar@botanika.hu

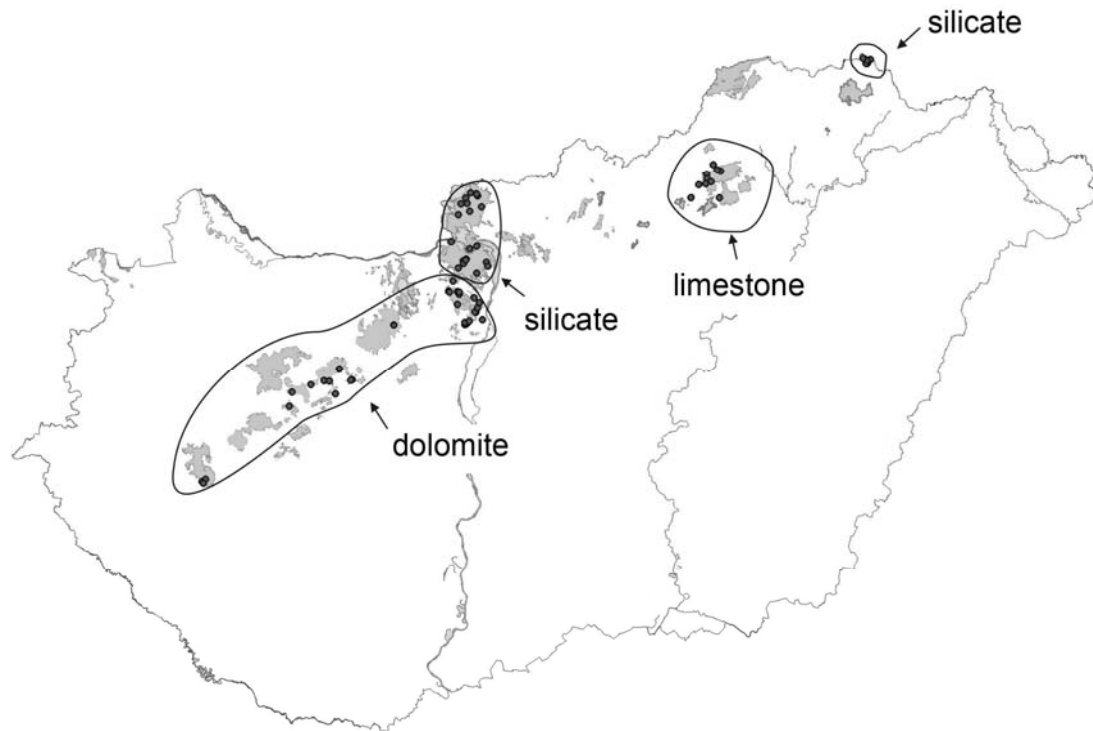


**Figure 1** (a) Species rich stand of *Minuartio-Festucetum pseudodalmaticae* on the Castle Hill of Füžér, Zempléni Mts. (b) Strictly protected *Primula auricula* in dolomite rock grassland.

Association	Abbrev.	Time	Mountains	Rock type	Number of plots	Author and reference
Minuartio-Festucetum pseudodalmaticae (Mikyška 1933/ Klika 1938)	MF	1958-61	Zempléni Mts.	silicate	5	SIMON (1977)
Poetium scabrae (Zólyomi 1936)	PP	1954-60	Börzsöny Mts.	silicate	11	SZUIKÓ-LACZA (1961)
Potentillo-Festucetum pseudodalmaticae (Majovsky 1955)	PF	1953-56	Visegrádi Mts.	silicate	12	Horánszky (TÖRÖK et al. 1994)
Campanulo divergentiformis-Festucetum pallentis (Zólyomi 1958)	CF	1931-32	Bükk Mts.	limestone	9	Zólyomi (TÖRÖK and ZÓLYOMI 1998)
Seslerietum sadlerianae (Soó ex Zólyomi 1936)	SS	1933-35	Budai Mts.	dolomite	5	Zólyomi (TÖRÖK and ZÓLYOMI 1998)
Festuco pallentis-Brometum pannonicum (Zólyomi 1958)	FB	1932-41	Budai, Keszthelyi, Bakony and Vértes Mts.	dolomite	14	Zólyomi (TÖRÖK and ZÓLYOMI 1998)
Seselio leucospermi-Festucetum pallentis (Zólyomi /1936/ 1958)	SF	1933-41	Budai, Keszthelyi and Bakony Mts.	dolomite	15	Zólyomi (TÖRÖK and ZÓLYOMI 1998)

**Table 1.** Historical phytosociological relevé data: association type, abbreviation, time and place of sampling, substrate type, number of plots, and author of historic samples used in the study.

Altogether 151 plots at 71 sites have been resampled in the Hungarian Northern- and the Trans-Danubian Mountains between 1990 and 1994 (**Figure 2**). Since no permanent plots were marked during the first sampling period, plots were reinvestigated carefully according to the historical description of locality, aspect, slope, elevation, vegetation period, plot size (either 16 or 25 m<sup>2</sup>) and earlier species lists. Re-investigated plot data are unpublished, except for the *Potentillo-Festucetum pseudodalmaticae* (PF) from the Visegrád Mts. (TÖRÖK et al. 1994).



**Figure 2.** Map of Hungary with the sampled rock grassland sites (black dots). Natura 2000 sites of the 'Rupicolous pannonic grasslands (*Stipo-Festucetalia pallentis*)' habitat (code 6190) are indicated by grey polygons.

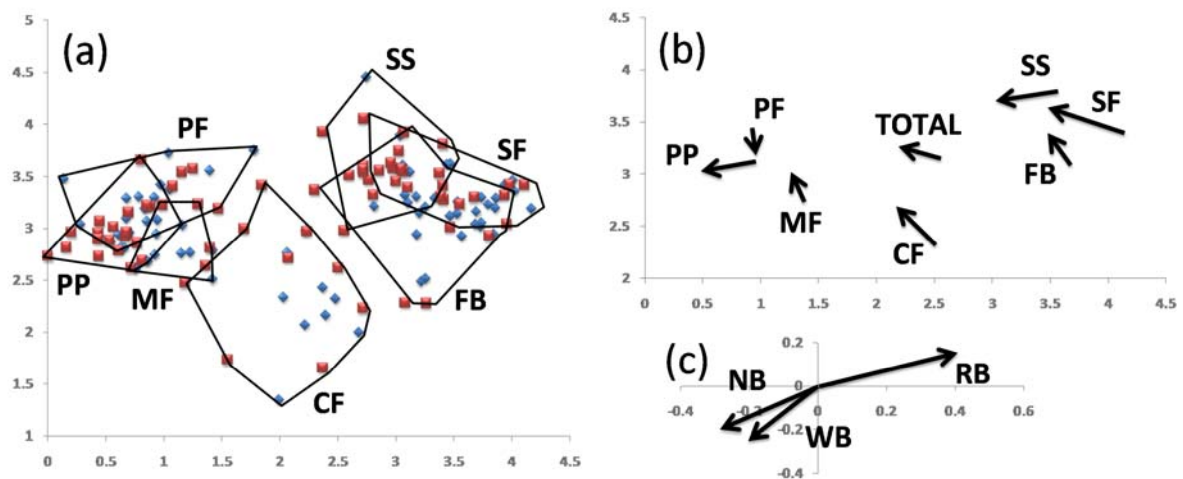
During the first sampling period cover estimation underwent a methodological development, therefore only binary data were used for this study. Jaccard similarity index was used as a measure of compositional similarity to compare plots from the two time periods (JACCARD 1912). The most similar plot pairs were selected for each site to avoid the overestimation of changes and used for further analyses (71 plot pairs with altogether 444 species).

General compositional changes were examined by detrended correspondence analysis (DCA) using CANOCO 4.5 (TER BRAAK and ŠMILAUER 2002). The results of vegetation change were interpreted with different species attributes. Ecological indicator values of Borhidi express ecological preferences of plant species for soil reaction (RB), nitrogen (NB) and soil moisture (WB) in ordinal scales, running from 1 to 9 (12 for moisture). They correspond to Ellenberg's respective indicator values (ELLENBERG et al. 1992) adapted to the Hungarian flora. The mean indicator values (calculated as a mean value of those species present in the plot) were used as supplementary variables to estimate changes in site conditions. The significance of changes in absolute frequency of Raunkiaer life form categories (RAUNKIAER 1934) and social behaviour types (SBT) of BORHIDI (1995) was tested by paired t-test. SBT categories were used to estimate the naturalness of communities: competitors (C; dominant perennial species of natural communities), specialists (S; stenotolerant species of low competitiveness) and generalists (G; species of wide ecological tolerance) represent the natural constituents of

communities. Natural pioneers (NP; species of initial stages of succession series) and disturbance tolerants (DT; pioneer elements of secondary succession) indicate natural disturbances, whereas weeds, alien species and ruderal competitors (W) indicate degradation processes. As changes in species attributes were consistent among associations, we present the results averaged across association types.

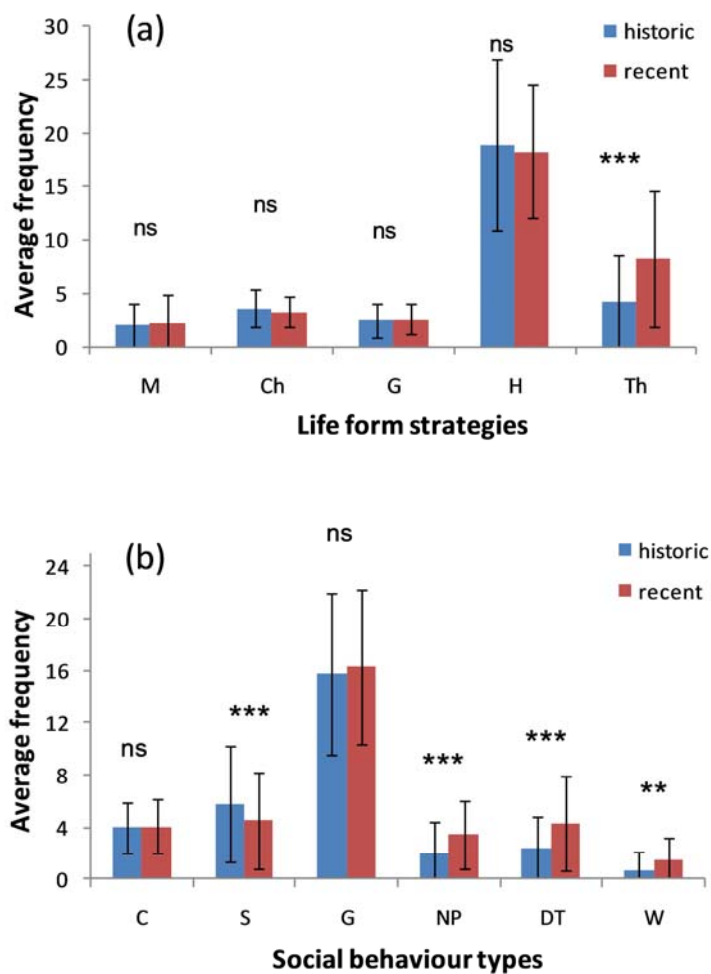
## Results and Discussion

The investigated seven rock grassland associations underwent vascular plant species composition changes according to the uniform displacement of plot averages for six associations along the first axis in the ordination diagram (**Figure 3**). Considering the wide geographical distribution of the plots (maximum distance about 300 km), this change seems to indicate similar trends of vegetation change and can be attributed to general pressures operating at the large scale rather than to diverse local impacts (TÖRÖK and SZITÁR 2010).



**Figure 3.** DCA diagram based on the presence/absence data (total inertia: 15.86; Axis 1 eigenvalue: 0.56, axis length: 4.212, Axis 2 eigenvalue: 0.37, axis length: 4.461). (a) Polygons enclose plots of different community types for both sampling periods. Blue symbols represent historic, red symbols represent recent plots. (b) Arrows illustrates the displacement of the associations in the ordination space between the two time periods based on the average scores of plots on the first and second ordination axes. (c) Arrows represents biplot scores of mean indicator values of Borhidi, as supplementary environmental variables on the first and second DCA axes. Abbreviations see in Table 1 and in the text. Total – total average.

The first and the second axes are negatively correlated with mean NB ( $r = -0.49$  and  $-0.60$  respectively) and WB indicator values ( $r = -0.44$  and  $-0.50$ ) and positively correlated with RB values ( $r = 0.85$  and  $0.45$ ). The changes of WB indicator values show that the share of species of less extreme dry habitat decreased in time. The shift of mean NB values may suggest that nitrogen deposition occurred in the last 60 years (national average N deposition was  $6-10 \text{ kg ha}^{-1} \text{ yr}^{-1}$  in 2000 according to BOZÓ 2004). The effects of dung of overpopulated mouflon herds can be another reason for the changes towards mesotrophic conditions indicated by vegetation changes (CHYTRÝ and DANIHELKA 1993, HOBBS 1996).



**Figure 4.** (a) Frequency changes in Raunkiaer life forms (+/- SD) between the two sampling periods. Abbreviations: M: trees and shrubs; Ch: dwarf shrubs; G: geophytes; H: hemicryptophytes; Th: annuals and biannuals. (b) Change in the occurrence (+/- SD) of the Social Behaviour Types between 1931-61 and 1991-94. Abbreviations see in the text. Significant differences based on *t*-tests between historical / recent data are indicated by \* ( $p < 0.05$ ), \*\* ( $0.001 < p < 0.05$ ) and \*\*\* ( $p < 0.001$ ), ns = non significant.

The study of life forms revealed the loss of dwarf shrub species and the arrival of annuals (**Figure 4a**), which is considered a sign of degradation in several perennial grassland communities (RUPRECHT and BOTTA-DUKÁT 2000, PODANI et al. 2005). It is assumed that physical soil disturbance and trampling by grazing animals induce the establishment of annuals at temporarily open soil surfaces. A 7.5 fold increase in mouflon stock and a 5 fold increase in red deer and roe deer stocks between 1960 and 2000 according to the National Game Database (CSÁNYI 2001) support this hypothesis. SBT values reflect the different functional role of species in the grassland. The distribution of behaviour types has changed significantly during the last 30-60 years in favour of pioneers, disturbance-tolerants and weeds (**Figure 4b**). Nevertheless, their amount is relatively low and natural constituents of the communities still dominate, therefore the detected changes can be described as a minor degradation.

## References

- BORHIDI A. 1995: Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian flora. *Acta Botanica Hungarica* 39: 97-181.
- BOTTA-DUKÁT Z., KOVÁCS-LÁNG E., RÉDEI T., KERTÉSZ M., GARADNAI J. 2007: Statistical and biological consequences of preferential sampling in phytosociology: theoretical considerations and a case study. *Folia Geobotanica* 42: 141-152.

- BOZÓ L. 2004: Regionális levegőkörnyezeti terhelés: hatások és várható tendenciák Magyarországon. Környezetállapot értékelés Program. *Munkacsoport tanulmányok 2003-2004*.
- CHYTRÝ M., DANIHELKA J. 1993: Long-term changes in the field layer of oak and oak-hornbeam forests under the impact of deer and mouflon. *Folia Geobotanica & Phytotaxonomica* 28: 225-245.
- CSÁNYI S. 2001: National Game Database. Gödöllő (forrás: [www.vvt.gau.hu](http://www.vvt.gau.hu))
- DENGLER J., JANSEN F., GLÖCKLER F., PEET R. K., DE CÁCERES M., CHYTRÝ M., EWALD J., OLDELAND J., FINCKH M., LOPEZ-GONZALEZ G., MUCINA L., RODWELL J. S., SCHAMINÉE J. H. J., SPENCER N. 2011: The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *Journal of Vegetation Science* 22: (in press).
- ELLENBERG H., WEBER H.E., DÜLL R., WIRTH V., WERNER W., PAULISSEN D. 1992: Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18: 1-248.
- HOBBS N.T. 1996: Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60: 695–713.
- JACCARD J. G. M. 1912: The distribution of the flora of the alpine zone. *New Phytologist* 11: 37–50.
- PERSSON S. 1980: Succession in a south Swedish deciduous wood: a numerical approach. *Vegetatio* 43: 103-122.
- PODANI J., CSONTOS P., TAMÁS J., MIKLÓS I. 2005: A new multivariate approach to studying temporal changes of vegetation. *Plant Ecology* 181: 85-100.
- RAUNKIAER, C. 1934: *Life forms of plants and Statistical Plant Geography*. Clarendon Press, Oxford, 632 pp.
- RÉDEI T., BOTTA-DUKÁT Z., CSIKY J., KUN A., TÓTH T. 2003: On the possible role of local effects on the species richness of acidic and calcareous rock grasslands in northern Hungary. *Folia Geobotanica* 38: 453-467.
- RUPRECHT E., BOTTA-DUKÁT, Z. 2000: Long-term vegetation textural changes of three fen communities near Cluj-Napoca (Romania). *Acta Botanica Hungarica* 42: 265-284.
- SIMON T. 1977: *Vegetationsuntersuchungen im Zempléner Gebirge*. Akadémiai Kiadó, Budapest, 351 pp.
- SZUJKÓ-LACZA J. 1961: Die Trockenrasen und der Andesit-Kalkwald im Börzsönygebirge. *Annales Historico-naturales Musei Nationalis Hungarici* 53: 225-240.
- TER BRAAK C. J. F., ŠMILAUER P. 2002: *CANOCO reference manual and CanoDraw for Windows user's guide*. Biometris, Wageningen and České Budějovice, 500 pp.
- TÖRÖK K., HORÁNSZKY A., KÓSA G. 1994: Long-term changes of species composition in an andesite grassland community of the Visegrád Mts., Hungary. *Abstracta Botanica* 18: 13-27.
- TÖRÖK K., SZITÁR K. 2010: Long-term changes of rock grassland communities in Hungary. *Community Ecology*. 11:68-76.
- TÖRÖK K., ZÓLYOMI B. 1998: Synbotanical research of rock grasslands. Syntaxonomic revision on five rock grassland communities of the Carpathian Basin. In: CSONTOS, P. (ed.). *Synbotanical research of rock grasslands*. Scientia Kiadó, Budapest, pp. 109-132.
- WILD J., NEUHÄUSLOVÁ Z., SOFRON J. 2004: Changes of plant species composition in the Šumava spruce forests, SW Bohemia, since the 1970s. *Forest Ecology and Management* 187: 117-132.
- WILLIAMS N. S. G., MORGAN J. W., McDONNELL M. J., MCCARTHY M. A. 2005: Plant traits and local extinctions in natural grasslands along an urban-rural gradient. *Journal of Ecology* 93: 1203-1213.

# The effects of stand characteristics on the understorey in *Quercus petraea* and *Q. cerris* dominated forests

RÉKA ÁDÁM<sup>1</sup> AND JÁNOS BÖLÖNI

## Abstract

The shelterwood system used in Hungary has many effects on the composition and structure of the herb layer. The aim of our study was to identify the main variables that affect the occurrence of herbs and seedlings in Turkey oak-sessile oak (*Quercus cerris* and *Q. petraea*) stands. The study was carried out in the Bükk mountains, Hungary. 122 sampling plots were established in 50-150 year old oak forests, where we studied the species composition and structure of the understorey and overstorey. The occurrence of herbs was affected by canopy closure, the heterogeneity and patchiness of the stand, the slope and the east-west component of the aspect. The composition of saplings was significantly explained by the ratio of the two major oak species in the stand and the proximity of the adult plants. An important result for forest management was that sessile oaks were able to regenerate almost only where they were dominant in the overstorey.

## Introduction

The different types of forest use – harvesting, collecting fuel and litter, grazing, hunting – and the importation of alien species have significantly changed the species composition, the structure and the dynamics of our forests (BENGTSSON et al 2000). Forest species – a lot of them have low reproduction and dispersal capacity (HERMY et al 1999) – have to face the reduction and fragmentation of their habitat. In addition, species with good colonization capacity may gain advantage (BENGTSSON et al 2000), so the success of forest species decrease because of various reasons. 20 % of the Hungarian forests are protected, but a lot of these stands are managed with shelterwood system. (STANDOVÁR 2002). In the case of this type of forest management, the species of the understorey are stressed not only by the clear-cutting. The foresters often create stands with few tree species, homogenous structure and one age-group. Several structural component – which are typical in naturally developing forests – are absent in these stands.

In our study we assessed main factors that affect the occurrence of herb species and tree seedlings. Are some of the variables affecting understorey species composition typical of naturally developed forests?

## Methods

In our study we established 122 sampling plots, 500 m<sup>2</sup> in size, in 50-150 year old *Quercus petraea* and *Q. cerris* dominated stands in the south part of Bükk mountains, Hungary. Each plot consisted of 28 quadrats, 0.5 m<sup>2</sup> in size, where the species list of the understorey was recorded. Besides, we studied the species composition and structure of the shrub layer (in one quadrat, 100 m<sup>2</sup> in size and in four quadrats, 7-7 m<sup>2</sup> in size) and the overstorey (in the whole

---

<sup>1</sup> helleborus42@gmail.com

plot, 500 m<sup>2</sup> in size), the canopy closure and abiotic variables. For data analysis we used Redundancy Analysis (RDA) and Generalized Linear Model (GLM).

## Results and discussion

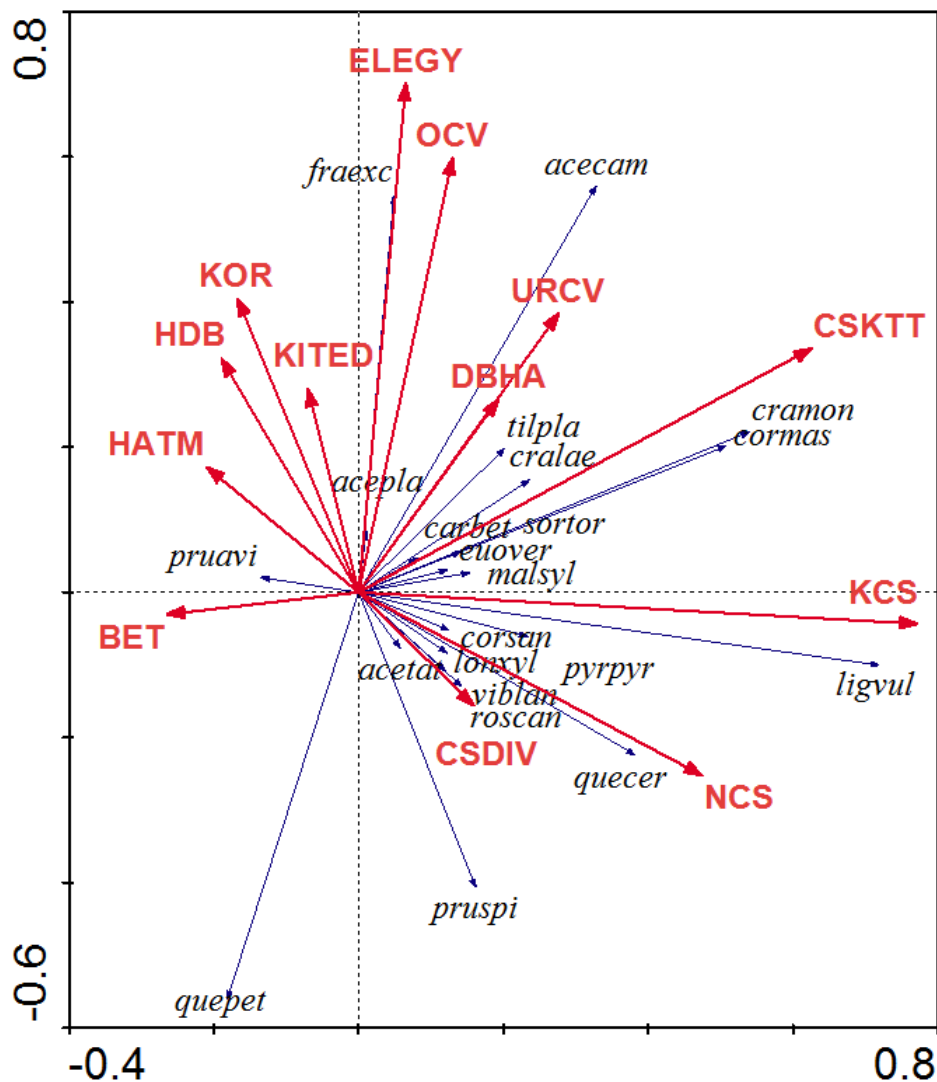
The structure of the overstorey had significant effects on the cover of the understorey. (**Table 1.**) The canopy of the young, slim trees are tightly closed, thus sunlight only reaches the ground layer partly. In addition, dense shrub layer can further reduce the amount of light, so the cover of the understorey is low. With the growth of the trees, self-thinning begins (in managed stands it is done by the foresters), and the overstorey opens up. A lower canopy layer can develop, which contains mainly compound species and grown-up shrubs, therefore spatial heterogeneity and species diversity increase. In these open, patchy stands more and more heterogeneous sunlight reaches the understorey, hence the cover increases (CSONTOS 1996). Interestingly, according to our results the east-west component of the aspect is an important variable, the understorey has greater cover on western slopes. (Although, in absence of Turkey-sessile oak stands in northern slopes, we couldn't examine them.).

<i>Variable</i>	<i>Sign</i>	<i>The variance ratio covered by the variables</i>	<i>F-value</i>
ncs	-	16.64 %	38.08 ***
kcs	+	11.06 %	25.30 ***
oatm	+	7.72 %	17.66 ***
zar	+	6.81 %	15.58 **
al	+	4.71 %	10.77 **
kitkn	+	2.81 %	6.42 *

**Table 1.** The significant variables that determine the cover of the understorey.

In the studied *Quercus petraea* – *Q. cerris* dominated forests different variables explained the occurrence of herbs and seedlings. There are variables in both groups which are typical for naturally developed forests, for example species-rich shrub layer, relatively high proportion of compound tree species, heterogeneous stand structure. These variables could be generated in managed forests too, assuming proper forest management.

The occurrence of herb species was defined by the canopy closure, tree-layer heterogeneity and patchiness, the slope and the east-west component of the aspect. The herb species could be categorized into two groups whose occurrence was defined by different variables. Those typical to xeric oak forests and the acidofrequent species mostly preferred the older, groved stands dominated by *Q. petraea* with few associate tree species, and with less dense shrub layer. The second group consisted of generalist and mesic forest species. These preferred taller stands – possibly on deeper soil – dominated by *Q. cerris* with more associate tree species.



**Figure 1.** The most significant variables that determine the occurrence of tree species in the understory.

**Abbreviations of the species' names:** *acecam* – *Acer campestre*, *aceplat* – *Acer platanoides*, *acetat* – *Acer tataricum*, *carbet* – *Carpinus betulus*, *cormas* – *Cornus mas*, *corstan* – *Cornus sanguinea*, *cralae* – *Crataegus laevigata*, *cramon* – *Crataegus monogyna*, *euover* – *Euonymus verrucosus*, *fraexc* – *Fraxinus excelsior*, *ligvul* – *Ligustrum vulgare*, *lonxyl* – *Lonicera xylostemum*, *malsyl* – *Malus sylvestris*, *pruavi* – *Prunus avium*, *pruspi* – *Prunus spinosa*, *pyrpyr* – *Pyrus pyraster*, *quecer* – *Quercus cerris*, *quepet* – *Quercus petraea*, *roscan* – *Rosa canina*, *sortor* – *Sorbus torminalis*, *tilpla* – *Tilia platyphyllos*, *viblan* – *Viburnum lantana*.

**Abbreviations of the variables:** *kor* – the age of the stand, *kitkn* – deviation from East, *kited* – deviation from North, *dbha* – the number of living trees per ha, *oatm* – the mean diameter of living trees, *ocv* – coefficient of variation of the diameter of living trees, *urcv* – coefficient of variation of the diameter of trees in dominant social status, *al* – the ratio of trees in the lower canopy layer, *elegy* – ratio of compound species, *csktt* – proportion of Turkey oaks within the oaks, *bet* – the ratio of unhealthy trees, *zar* – the mean openness of canopy, *hdb* – number of standing dead trees per ha, *hatm* – the average diameter of standing dead trees, *ncs* – the number of high shrubs (>1.3 m) per ha, *kcs* – the number of low shrubs per ha, *csdiv* – species diversity of shrubs.

The occurrence of seedling species was primarily defined by the characteristics of the shrub layer and the species composition of the overstorey (Figure 1). Interestingly, even anemochore species need proximity to the parent plant in order to regenerate. This

phenomenon is particularly relevant in the case of the barochor and zoochor sessile oak, which is an important species for forest management, but is very difficult to regenerate. According to our results the presence of sessile oak is not sufficient for successful regeneration, it has to be dominant in the overstorey. The other relevant stand characteristic that defines the appearance of tree seedlings and shrubs is the ratio of the two oak species in the overstorey. Most of the shrub species prefer stands with Turkey oak dominance. There are multiple explanations for these phenomena. It is possible that the shift in the ratio of the sessile and Turkey oaks is because of the improper forest management that disturbs the territory periodically, thus the shrubs can gain importance. Another theory involves the soil as a factor of the overstorey species composition. While turkey oak prefers soil with neutral pH in Hungary, sessile oak is more tolerant. Thus, as the soil becomes more acidic, the ratio of the two species shifts toward the sessile oak (GENCSI and VANCSURA 1992). According to field experiences, most shrub species dislike acidic soil as well. The third explanation is based on the different soil use of the two oak species (GENCSI and VANCSURA 1992). Sessile oaks take up more water thus drying the soil so that it becomes unfavourable for shrubs. (Further details: ADAM 2010.)

Summarizing our results we conclude that the age of the stand has a strong – though indirect – effect on the occurrence of the understorey species. The understorey composition that is typical of older, more naturally-developed forests is not impossible to attain in managed stands, especially with the appropriate management.

## References

- ADAM R. 2010: The effects of stand characteristics on the understorey in *Quercus petraea* and *Q. cerris* dominated forests. Thesis. Eötvös Loránd University.
- BENGTSSON J., NILSSON S. G., FRANC A., MENOZZI P. 2000: Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management* 132: 39-50.
- CSONTOS P. 1996: *Az aljnövényzet változásai cseres-tölgyes erdők regenerációs szukcessziójában*. Scientia Kiadó, Budapest, 122 pp.
- GENCSI L., VANCSURA R. 1992: *Dendrológia*. Mezőgazda Kiadó, Budapest, 728. pp.
- HERMY M., HONNAY O., FIRBANK L., GRASHOF-BOKDAM C., LAWESSON J. E. 1999: An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation* 91: 9-22.
- STANDOVÁR T. 2002: A természetes és a kezelt erdők főbb különbségei. *Erdészeti Lapok* 138 (1): 3-6.

# ***Salvia* species as potential essential oil sources in Hungary**

IMRE MÁTHÉ<sup>1,2</sup>, KATALIN VERES<sup>2</sup>, RITA ENGEL, KRISZTINA SZABÓ AND GÁBOR JANICSÁK

## **Abstract**

In the course of the evaluation of the species belonging to the Section *Salvia* of the genus *Salvia* (Family Lamiaceae) the essential oil content and the composition of the species have been investigated with special respect to their neurotoxic  $\alpha$ -, and  $\beta$ -thujone content. It could be established that from among the species *S. lavandulifolia* Vahl., *S. candelabru* Boiss., *S. tomentosa* Mill., (*S. grandiflora* Etlinger), *S. fruticosa* Mill., *S. ringens* Sibth. & Sm. only *S. tomentosa* had both beneficially high essential oil content and low or no thujone content. As it can be cultivated in the temperate climatic belt, in Hungary, *S. tomentosa* may be an alternative essential oil producing plant beside the *S. officinalis* L.

## **Introduction**

Lamiaceae family is one of the richest plant families in medicinal and aromatic plants of the Hungarian flora. The vast majority of Lamiaceae species prefers warmer climate than that exists in Hungary. It also holds true of the great majority of the genus *Salvia*. Despite this fact, the Mediterranean official sage (*S. officinalis* L.) can be cultivated well in Hungary among others for its exploitable high essential oil content. From among the approximately more than one thousand species of the *Salvia* genus only a few meet Hegnauer's definition on high essential oil containing species (namely the species bearing more than 0.5 % essential oil). (HEGNAUER 1966). *S. officinalis* fulfils Hegnauer's definition and can be cultivated successfully in Hungary. *S. officinalis* has several virtues. It is traditionally regarded as a panacea. Official sage has antispasmodic, antioxidant, (food preservative) effects. It is used to treat gastrointestinal disturbances, excessive perspiration, proposed for inflammation of the mucous membranes of the mouth and throat, etc. The drug is broadly used in perfume industry, oral hygiene. (BRUNETON 1999)

The essential oil fraction obtained from *S. officinalis* by steam distillation contains a significant proportion of the biologically active ingredients of the plant. Among the essential oil components, however, some ingredients, predominantly  $\alpha$ - and  $\beta$ -thujones (up to 60% of the oil) are of harmful effect to health, because of their neurotoxic properties (BRUNETON 1999). So, especially for oral usage thujone free or at least in thujone poor oils or oil containing plants, plant products would be preferable in many cases. Our purpose was to find a plant, having similar beneficial properties than the official sage has, but without high thujone content in its essential oil fraction. To achieve this end the following possibilities were given: 1). to evaluate other *Salvia* species including those native to Hungary, 2) to try to select thujone free plants from the official sage populations of various origin, 3) to screen the closely related species of *S. officinalis* for high essential oil content with low or no thujone content. In all cases the possibilities of domestication of the strange plants should be investigated, if we want to cultivate and exploit the plants in Hungary.

---

<sup>1</sup> MTA ÖBKI, Vácrátót, mathe@pharm.u-szeged.hu

<sup>2</sup> SZTE Farmakognóziái Intézet, Szeged

As far as the *Salvia* species, out of the members of the section *Salvia*, concerned including the species native to Hungary, a lot of studies have been performed by our research group. The *Salvia* species, native to Hungary are more different from the official sage in their properties including the relatively low essential oil content, so that they can not replace *S. officinalis* (MÁTHÉ et al. 1992, 1993). Consequently, we have to concentrate to the species of *Salvia* section. *S. officinalis* has been cultivated and used, without any problems, e.g. in the gardens as ornamental plant for a long time in Hungary. The other members of the *Salvia* section, however, had not been investigated and used in Hungary before.

## Materials and Methods

The plants that can not be found in the Hungarian flora were grown from seeds in our experimental field at Vácraót. The species of Section *Salvia* we have are as follows: beside *S. officinalis* L., *S. lavandulifolia* Vahl., *S. candelabrum* Boiss., *S. tomentosa* Mill., (*S. grandiflora* Etlinger), *S. fruticosa* Mill., *S. ringens* Sibth & Sm. Their seeds were obtained via the seed exchange program of botanical gardens. These plant stands have been serving our researches for several years and from time to time they were renewed by re-sowing. The plants were sampled for various purposes. The variation of oil content was measured in different times, e.g. during the vegetation period, in successive years, plants of different origin were compared with each others. The essential oil was obtained by steam distillation according to as the procedure is described in the actual Hungarian Pharmacopoea. (PH.HG. VIII. 2004). The content of essential oil was calculated in ml / 100 g (dry or fresh weight). The oil composition was determined by GC, GC/MS measurements. Details of our methods and procedures had been published earlier (DOBOS et al. 1997, MÁTHÉ et al. 1997).

## Discussion

Firstly the essential oils of the official sage (*S. officinalis*) samples were analysed. In the most cases more than 30 components were separated and the majority of them could be identified by GC and GC MS methods. From among the several studies **Table 1.** illustrates how the ratios of some of the main components can vary, if samples of various origin were analysed. On the bases of this table and also that of other investigations it has become clear that  $\alpha$ - and  $\beta$ -thujone occur in all samples in smaller or larger proportions. We have not found *S. officinalis* essential oil, free of thujones. Our data are in harmony with the results of other researchers (BRUNETON 1999, DOBOS et al. 1997, LAWRENCE 1992, MÁTHÉ et al. 1992, MÁTHÉ et al. 1993, NÉMETH et al. 2007).

	In Spring		In Autumn	
	Intervals	Means (X)	Intervals	Means (X)
1,8-cineol	3,8 – 10,1	6,8	3,6 – 12,1	7,6
$\alpha$ -tujone	15,8 – 38,7	27,3	21,4 – 47,0	34,2
$\beta$ -tujone	1,3 – 6,1	3,6	1,9 – 17,2	9,4
Camphor	1,7 – 7,3	4,5	11,2 – 23,5	16,8
$\beta$ -cariophyllene	2,7 – 14,7	8,6	1,8 – 6,7	4,2
$\alpha$ -humulene	4,6 – 14,1	9,3	2,2 – 6,5	4,3
guajol	6,7 – 19,9	13,3	3,5 – 6,4	5,0

**Table 1.** The variation of some main essential oil ingredients of *Salvia officinalis* samples (n=9). Remarks: Proportion of components in the percentage of the total oil fraction obtained by steam distillation

**Table 2.** demonstrates the variation of the content of essential oil of *S. officinalis*. Table 2. shows that the highest content of oil is in the generative phase of the plants, when the yield (1-1.5 %) fits that of the requirements of Ph.Hg. VIII. As it can be estimated the oil composition varies even in the vegetation period. On the bases of our experiments too *S. officinalis* can be cultivated well in Hungary it may provide high essential oil content but in all case with thujones in it.

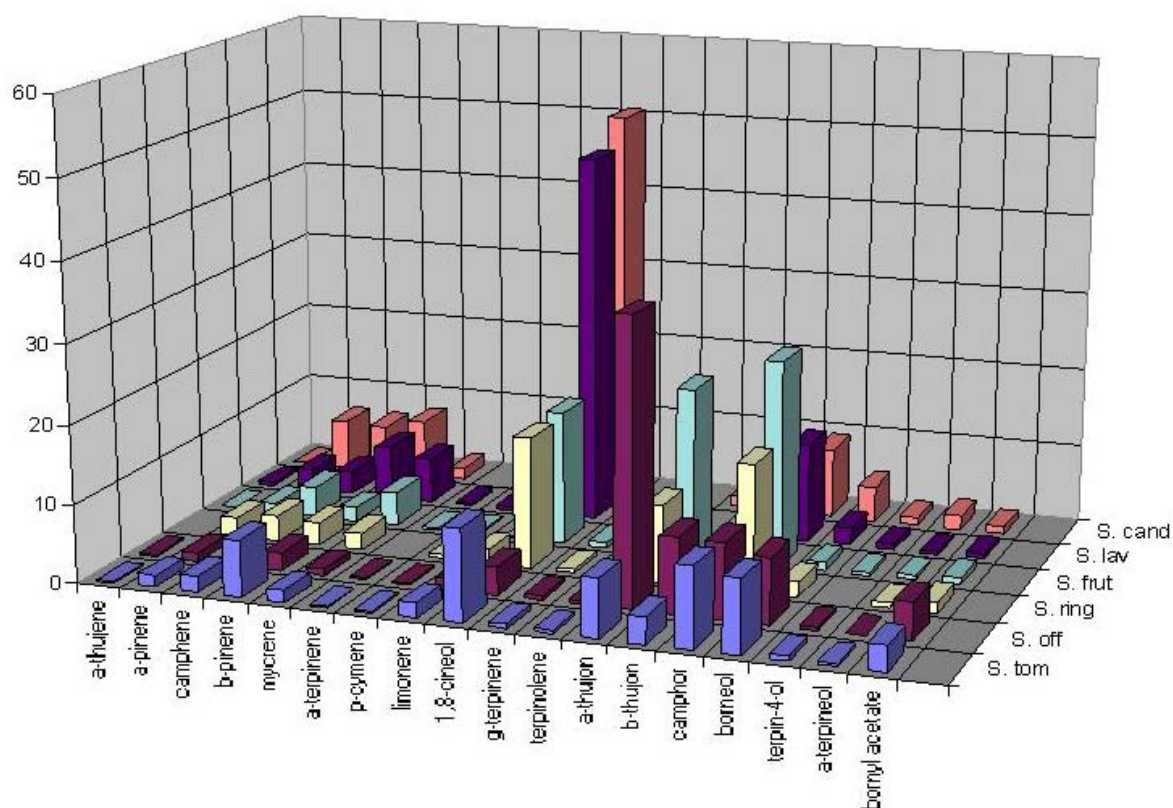
	Leaf	Generative Organs
April	0,88	
May	0,62	
June	0,81	
July	1,04	1,59
August	1,31	0,70
September	1,03	0,63
October	0,85	
November	0,83	

**Table 2.** Variation of the essential oil content (ml/100 g dry wt.) of *Salvia officinalis* during the vegetation period (MÁTHÉ et al. 1993)

As we have already pointed out, these species were introduced in successive years from seeds. They are perennial so the plants could be investigated several times in the past. (MÁTHÉ et al. 1993, 1997, MÁTHÉ és CSEDŐ 2007)1. **Table 3.** informs us about the average essential oil content of 7 *Salvia* species. It is obvious that *S. lavandulifolia* has the highest oil content. (Of course the cultivation and the conditions of harvest, processes of the species were similar, making the comparison possible!) *S. lavandulifolia* had no thujone content as it can be seen (**Figure 1**), as it could have been expected on the bases of scientific literature (BRUNETON 1999). This perennial plant fulfils our expectations (high oil content and without thujone) but in winter period at severe cold the plants died out. This West Mediterranean plant can not accept the continental climatic conditions predominantly the severe winters. As far as the other species concerned the oil content was more or less similar to that of *S. officinalis* with the exception of *S. ringens*. This plant contains essential oil only in traces. If the other species concerned out of *S. lavandulifolia*, all of them had thujone content. This holds true of *S. triloba* (*S. fruticosa*) which ought to have had cineole content as main ingredient of the oil (Bruneton 1999) but, instead of cineole, thujone and camphore were found as the chief ingredients of the essential oil. *S. tomentosa* samples however had low, in many cases, only in traces, thujone content. This plant keeps well in the winter period and has relatively high oil content like in its native Bulgarian habitats (GENOVA et al. 1998) and, what is more, it seems to provide as much phytomass as *S. officinalis*.

<i>S. lavandulifolia</i> Vahl.	0,89
<i>S. officinalis</i> L.	0,25
<i>S. tomentosa</i> Mill.	0,39
<i>S. candelabrum</i> Boiss.	0,25
<i>S. fruticosa</i> Mill.	0,46
<i>S. ringens</i> Sibth.	traces

**Table 3.** Essential oil content of some species of the section *Salvia* (ml / 100 g fresh wt.) (MÁTHÉ et al. 2007)



**Figure 1.** Proportion in percentages of monoterpenes in the essential oils of the species of section *Salvia*

**Figure1**, a column diagram, illustrates the proportions of individual components of the essential oils of some species of the Section *Salvia*. It shows that significant differences are among the species, but significant similarities can also be observed. In all, *S. tomentosa* can be proposed as alternative ‘sage drug’, beside *S. officinalis*. We have studied beside essential oils other types of biologically active ingredients (rosmarinic, caffeic, ursolic, oleanolic acids, flavonoids, etc.) of these species. They do not differ significantly from those of *S. officinalis* (JANICSÁK et al. 1999, 2006, 2007, 2010, MÁTHÉ 2002, 2007, MÁTHÉ et al. 2002, 2007, NIKOLOVA et al. 2006 ). This holds also true of their biological effects, among them, their antioxidant capacities (JANICSÁK et al. 2010, HOHMANN et al. 1999, HÁZNAGY-RADNAI et al. 2006, ZUPKO et al. 2001).

## Summary

*Salvia* species native to Hungary do not belong to the essential oil containing species. The most frequently used *S. officinalis* originated from the Balkan Peninsula, has high essential oil content but its high neurotoxic thujone content limits the internal application of its products. It has turned out that high thujone ( $\alpha$ -,  $\beta$ -thujone) content can not be reduced by selection of the sage samples of various origin. Thujone content will be in all cases high at least under Hungarian climatic conditions. From among the closely related species *S. lavandulifolia* proved to be the best plant both regarding its high essential oil production and with the lack of thujones in its oil. It has no thujone content but the perennial plant can not outlive the severe winter period. From among the other *Salvia* species, *S. tomentosa* Mill. has rather high essential oil production with no or very small amount of thujone in it. It seems to be well

cultivated in Hungary. We can grow its populations in our experimental field for several years without any difficulties. Consequently, *S. tomentosa* is worthy of further studies for a large scale production as an alternative or complementary species of *S. officinalis*.

### Acknowledgements

The authors express their thanks to the late Imre Máthé member of the HAS and the late Dr Vilmos V. Miklóssy for the establishment of the plant collections, for the identification of the species. We thank for the financial support to the National Scientific Research Grant (OTKA) (Project number: OTKA 43148)

### References

- BRUNETON J. 1999: *Pharmacognosy Phytochemistry Medicinal Plants*. 2nd edition. Intersept Ltd. Londres, Paris, New York, 1119 pp.
- DOBOS Á., NAGY G., GENOVA E. M., MÁTHÉ I., MIKLÓSSY V. V., JANICSÁK G. 1997: Comparative analysis of *Salvia officinalis* and *S. tomentosa* essential oils. In: FRANZ CH., MÁTHÉ Á., BUCHBAUER G. (eds.): *Essential Oils Basic and Applied Research Proceedings of the 27<sup>th</sup> International Symposium on Essential Oils*; 1996 September 8-11; Vienna, Austria pp. 241-243.
- GENOVA E., DOBOS Á., MÁTHÉ I. 1998: *Salvia tomentosa* Mill.- An interesting aromatic plant from the Bulgarian flora. *Lek. Sirov.* 47 (18): 25-32.
- HÁZNAGY-RADNAI E., CZIGLE SZ., ZUPKO I., FALKAY GY., MÁTHÉ I. 2006: Comparison of antioxidant activity in enzyme-independent system of six *Salvia* species. *Fitoterapia* 77: 521-524.
- HEGNAUER R. 1966: *Chemotaxonomie der Pflanzen*. Band 4. Birkhäuser Verlag, Basel. pp. 289-346.
- HOHMANN J., ZUPKÓ I., RÉDEI D., CSÁNYI M., FALKAY GY., MÁTHÉ I., JANICSÁK G., 1999: Protective effects of the aerial parts of *Salvia officinalis*, *Melissa officinalis* and *Lavandula angustifolia* and their constituents against enzyme-dependent and enzyme-independent lipid peroxidation. *Planta Medica* 65: 576-578.
- JANICSÁK G., VERES K., KAKASY A. Z., MÁTHÉ I. 2006: Study of the oleanolic and ursolic acid contents of some species of the Lamiaceae. *Biochemical Systematics and Ecology* 34: 392-396.
- JANICSÁK G., ZUPKO I., MÁTHÉ I., HOHMANN J. 2010: Comparative study of the antioxidant activities of eleven *Salvia* species. *Natural Product Communications* 5: 227-230.
- JANICSÁK G., MÁTHÉ I., MIKLÓSSY-VÁRI V., BLUNDEN G. 1999: Comparative studies of the rosmarinic and caffeic acid contents of Lamiaceae species. *Biochemical Systematics and Ecology* 27: 733-738.
- JANICSÁK G., VERES K., KAKASY A. Z., MÁTHÉ I. 2007: Az oleánol- és ursolsav előfordulása a Lamiaceae családban. *Revista de Medicina si Farmacie – Orvosi és Gyógyszerészeti Szemle* 53 (Supplement 4.): 189-195.
- LAWRENCE B. M. 1992: Chemical components of Labiatae oils and their exploitation. In: HARLEY R. M. AND REYNOLDS T. (eds.): *Advances in Labiatae Science*. The Royal Botanical Garden, Kew, U.K. pp. 399-436.
- MÁTHÉ I. 2002: A Lamiaceae család terpenoidjainak kemotaxonómiája – avagy egy OTKA pályázat utóélete és eredményessége tizenöt év távlatából. In: SALAMON-ALBERT É. (szerk.): *Magyar botanikai kutatások az ezredfordulón, Tanulmányok Borhidi Attila 70. születésnapja tiszteletére*. PTE Növénytani Tanszék, Pécs pp. 195-203.
- MÁTHÉ I. 1997: Some aspects of recent researches on *Lamiaceae* species in Hungary. *Arch*

*farm.* 5: 395-404.

- MÁTHÉ I. JR., MIKLÓSSY V. V., MÁTHÉ Á., BERNÁTH J., OLÁH L., BLUNDEN G., PATEL A. V. 1993: Essential oil content as chemotaxonomic marker for the genus *Salvia* with reference to its variation in *Salvia officinalis* L. *Acta Horticulturae* 330: 123-132.
- MÁTHÉ I. JR., OLÁH L., MÁTHÉ Á., MIKLÓSSY V. V., BERNÁTH J., BLUNDEN G., PATEL A. V., MÁTHÉ I. 1992: Changes in the essential oil production of *Salvia officinalis* under climatic conditions of the temperate belt. *Planta Medica* 58: 680.
- MÁTHÉ I., CSEDŐ K. 2007: Chemical differences and similarities in the family Lamiaceae. *Revista de Medicina si Farmacie – Orvosi és Gyógyszerészeti Szemle* 53 (Supplement 4.): 1-14.
- MÁTHÉ I., HOHMANN J., JANICSÁK G., NAGY G., RÉDEI D. 2007: A *Salvia officinalis* és néhány rokon faj biológiailag aktív anyagainak kémiai diverzitása. *Acta Pharmaceutica Hungarica* 77: 37-45.
- MÁTHÉ I., NAGY G., DOBOS Á., MIKLÓSSY V.V., JANICSÁK G. 1997: Comparative studies of the essential oils of some species of Sect. *Salvia*. In: FRANZ CH., MÁTHÉ Á., BUCHBAUER G. (eds.): *Essential Oils: Basic and Applied Research Proceedings of the 27<sup>th</sup> International Symposium on Essential Oils*; 1996 September 8-11; Vienna, Austria pp. 244-247.
- NÉMETH T. S., NÉMETH T., MÁTHÉ I., VERES K., FARKAS Á., PAPP N., HORVÁTH GY. 2008: Orvosi zsálya leveléből nyert illóolaj gázkromatográfiás vizsgálata. *Orvostudományi Értesítő* 81: 137-138.
- NIKOLOVA M., JANICSÁK G., GENOVA E., MÁTHÉ I. 2006: Comparative analysis of external flavonoids of Bulgarian and Hungarian samples of *Salvia* species. *Acta Botanica Hungarica* 48 (3-4): 361-367.
- PH.HG VIII. 2004: *Magyar Gyógyszerkönyv. 2.*, Medicina Könyvkiadó, Budapest. pp. 2350-2354.
- ZUPKÓ I., HOHMANN J., RÉDEI D., FALKAY GY., JANICSÁK G., MÁTHÉ I. 2001: Antioxidant activity of leaves of *Salvia* species in enzyme-dependent and enzyme-independent systems of lipid peroxidation and their phenolic constituents. *Planta Medica* 67: 366-368.

# Biological activities of secondary lichen metabolites

KATALIN MOLNÁR<sup>1</sup> AND EDIT FARKAS

## Abstract

Lichens produce a great variety of secondary metabolites and most of them are unique. These chemically diverse lichen substances accumulate on the outer surfaces of the hyphae. They have several biological activities, including photoprotection against intense radiation, as well as allelochemical, antiviral, antitumor, antibacterial, antiherbivore, antioxidant, antipyretic, and analgesic action. These compounds are also important factors in metal homeostasis and pollution tolerance of lichen thalli.

## Introduction

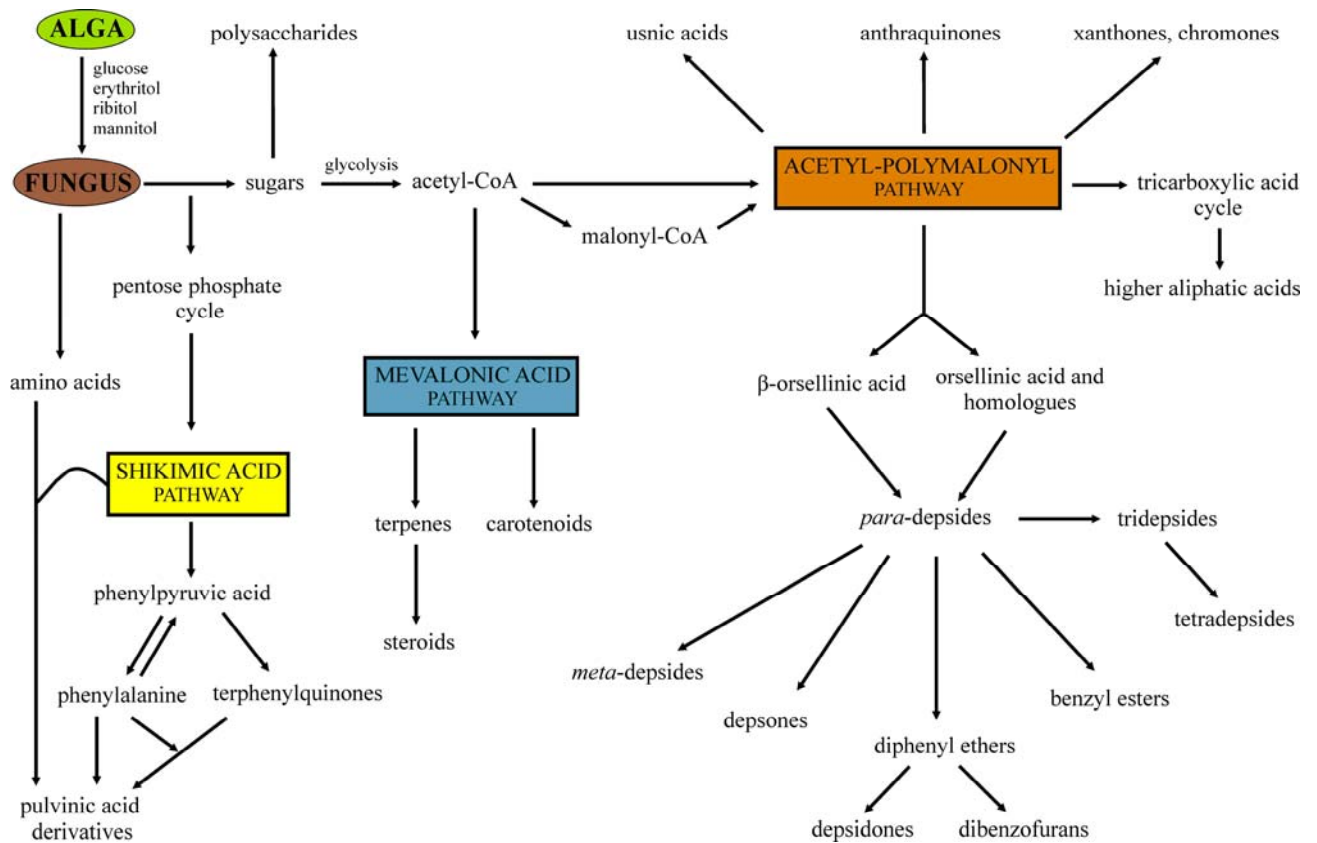
Our paper based on a detailed review (MOLNÁR and FARKAS 2010), and the complete list of references is shown in that paper.

Lichens produce a great number of various secondary metabolites, and most of them occur exclusively in these symbiotic organisms. They are produced by the mycobiont (ELIX 1996), and accumulate as extracellular tiny crystals on the outer surfaces of the hyphae. Approximately 1050 secondary compounds have been identified to date (STOCKER-WÖRGÖTTER 2008). Lichen products are restricted to specific areas of the thallus (FEIGE and LUMBSCH 1995, NYBAKKEN and GAUSLAA 2007), which correlate with the different functions of lichen metabolites. HYVÄRINEN et al. (2000) reported that the concentrations of secondary compounds in some lichen species are higher in reproductive structures than in the vegetative parts of the thallus. This pattern is concordant with the optimal defense theory, which states that the structures most important for fitness should be chemically better defended. The distribution patterns of secondary metabolites are usually taxon specific, and therefore have been widely used in lichen taxonomy and systematics (*e.g.*, CULBERSON 1969, HAWKSWORTH 1976, NYLANDER 1866). Lichen substances are classified by CULBERSON and ELIX (1989) according to their biosynthetic origins and chemical structural features. Most secondary lichen metabolites are derived from the acetyl-polymalonyl pathway, while others originate from the mevalonic acid and shikimic acid pathways (**Figure 1**).

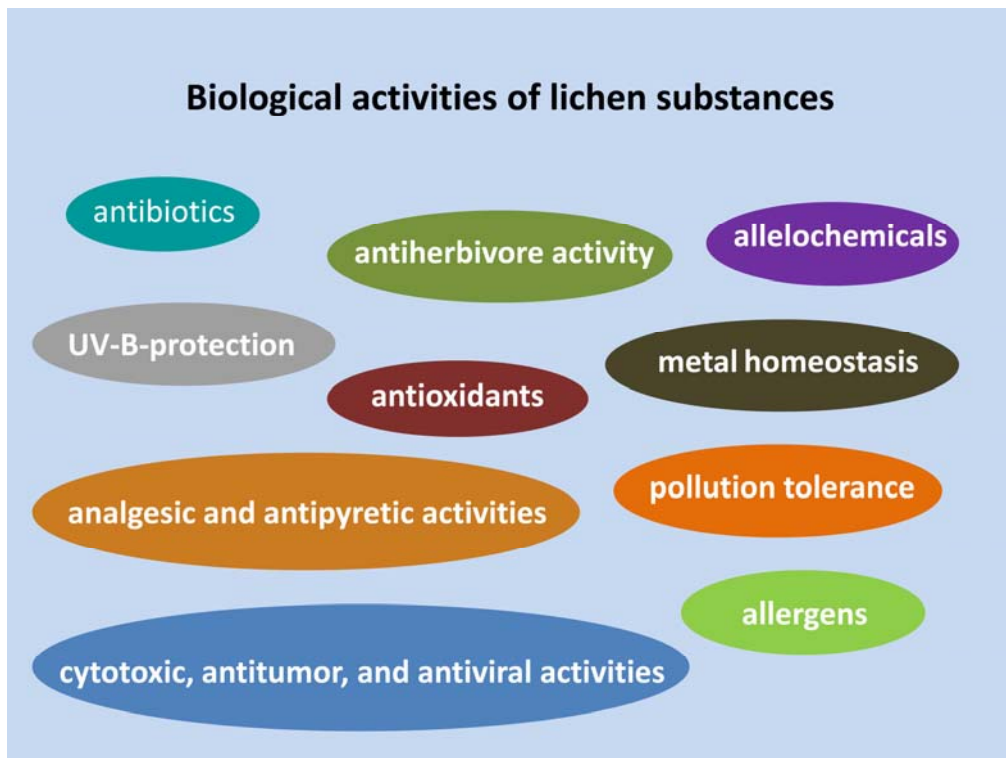
Due to experimental techniques, our knowledge of the biological activities (**Figure 2**) of these extracellular products has increased significantly in the last decades, and it was recently reviewed by the present authors (MOLNÁR and FARKAS 2010).

---

<sup>1</sup> kmcz100@gmail.com



**Figure 1.** Biosynthetic pathways of lichen secondary metabolites [modified from ELIX and STOCKER-WÖRGÖTTER (2008)].



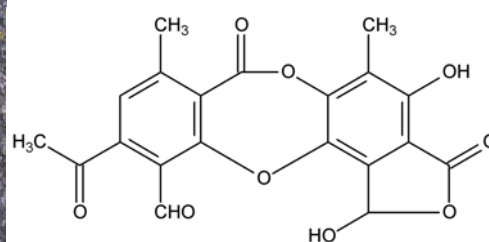
**Figure 2.** Lichen substances have several biological activities.

## Antioxidant activity

Free radicals play an important role in many chemical processes in the cells, but they are also associated with unwanted side effects, causing cell damage. Since synthetic antioxidants are often carcinogenic, finding natural substitutes is of great interest. Lichens have been found to contain a variety of secondary lichen substances, which are strong antioxidant compounds.

According to LUO et al. (2009), the extreme conditions in Antarctica increase oxidative stress, consequently, Antarctic lichens contain larger amounts of antioxidant substances and have higher antioxidant activity than tropical or temperate lichens.

AMO de PAZ et al. (2010) reported that methanol extracts of *Xanthoparmelia camtschadalis* and *X. conspersa* (**Figure 3.**), as well as their isolated lichen compounds (salazinic acid, stictic acid, and usnic acid) protected human astrocytes from hydrogen peroxide-induced damage. Astrocytes are the first line of defense in the brain against neurotoxicity of reactive oxygen species (ROS), thus salazinic acid, stictic acid, and usnic acid could act as antioxidant agents in those neurodegenerative disorders associated with oxidative damage (e.g., Alzheimer's disease and Parkinson's disease).



**Figure 3.** *Xanthoparmelia conspersa* contains the  $\beta$ -ornicinol depsidone stictic acid as major lichen compound in the medulla. This antioxidant lichen substance plays an important role in the protection against oxidative stress.

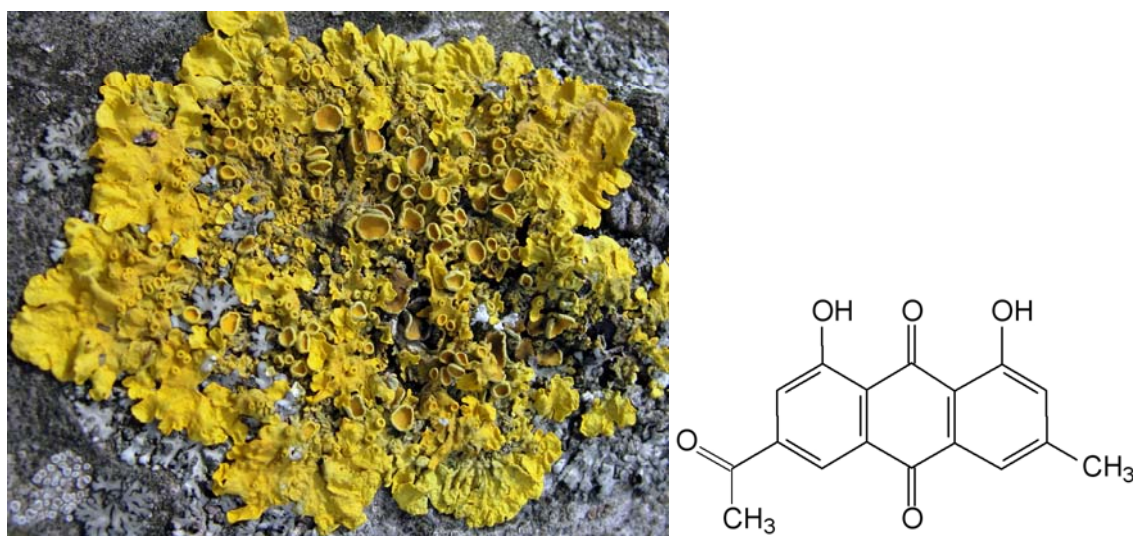
## Effect on metal homeostasis and pollution tolerance

Lichen secondary metabolites are sensitive to heavy metal accumulation and might play a general role in metal homeostasis and pollution tolerance. According to BIALONSKA and DAYAN (2005) the levels of atranorin, physodic acid and hydroxyphysodic acid significantly decreased in thalli of *Hypogymnia physodes* transplanted to the vicinity of a chemical plant producing chromium, phosphorous and sulfur compounds. In contrast, the level of physodalic acid increased significantly, suggesting that this compound might be effective against pollution stress.

Usnic acid and divaricatic acid were both found to significantly increase the intracellular uptake of  $\text{Cu}^{2+}$  in *Evernia mesomorpha* and in *Ramalina menziesii* (usnic acid only) (HAUCK et al. 2009), but intracellular uptake of  $\text{Mn}^{2+}$  was reduced. The influence of the compounds facilitate the survival of the two lichen species.

## Photoprotection

Lichens use a number of strategies to protect the light-sensitive algal symbionts against high levels of light and the damaging effects of UV radiation, *e.g.*, light screening and UV-B protection by lichen compounds. The light-screening theory was formulated by ERTL (1951), who found that cortical lichen compounds increase the opacity of the upper cortex, and thus decrease high incident irradiance reaching the algal layer. Light screening cortical pigments (such as parietin, usnic acid, vulpinic acid) regulate solar irradiance reaching the algal layer (GALLOWAY 1993, SOLHAUG and GAUSLAA 1996, see also FARKAS 2007) by absorbing much of the incident light and thus protecting the photosynthetic partner against intense radiation (RAO and LEBLANC 1965) (**Figure 4**). UV-B inhibits photosynthesis and damages DNA. Several lichen secondary metabolites (including atranorin, calycin, pinastric acid, rhizocarpic acid, usnic acid, vulpinic acid) have strong UV absorption abilities and might function as filters for excessive UV-B irradiation (RUNDEL 1978, SOLHAUG and GAUSLAA 1996).



**Figure 4.** The anthraquinone parietin is an orange cortical pigment and widespread in Teloschistaceae, thus also occurs in *Xanthoria parietina*. Parietin protects the photosynthetic apparatus of the photobiont against intense radiation.

## Allelopathy

Lichen secondary metabolites can function as allelopathic agents, *i.e.*, they may affect the development and growth of neighboring lichens, fungi, mosses and vascular plants, as well as microorganisms (LAWREY 1995, MACÍAS et al. 2007, ROMAGNI et al. 2004, RUNDEL 1978). Competition occurs between lichen thalli for space and light on a variety of substrates, and plays important roles in determining the structure of lichen communities and the distribution of individual species (ARMSTRONG and WELCH 2007). Lichen secondary chemistry might play a role in this competition (ARMSTRONG and WELCH 2007).

## Antimicrobial activity

Atranorin, fumarprotocetraric acid, gyrophoric acid, lecanoric acid, physodic acid, protocetraric acid, stictic acid and usnic acid showed relatively strong antimicrobial effects against six bacteria and ten fungi, among which were human, animal and plant pathogens, mycotoxin-producers and food-spoilage organisms (RANKOVIĆ and MIŠIĆ 2008). Since

microorganisms have developed resistance to many antibiotics, pharmacologists need to pursue new sources for antimicrobial agents. All these results suggest that lichens and their metabolites yield significant new bioactive substances for the treatment of various diseases caused by microorganisms.

### **Antiherbivore activity**

Lichens are grazed by herbivores, *e.g.*, insects, mites, snails, slugs. However, herbivory on lichens seems to be rare, presumably due to their low nutritional quality, specific structural features and the production of defense compounds (NIMIS and SKERT 2006, PÖYKKÖ *et al.* 2005). It is known that natural plant-derived products have a less detrimental impact on the environment than synthetic chemicals, and thus lichen substances could be good candidates for new pesticides (DAYAN and ROMAGNI 2001).

### **Cytotoxic, antitumor, and antiviral activity**

Many lichen secondary metabolites exhibit cytotoxic and antiviral properties and could be potential sources of pharmaceutically useful chemicals.

Human Papilloma Virus can cause cervical cancer. Due to clinical experiments, the adjuvant treatment with usnic acid and zinc sulphate after radiosurgery promotes reepithelization and reduces recurrence (SCIRPA *et al.* 1999). Usnic acid decreases proliferation of human breast cancer cells and human lung cancer cells without any DNA damage (MAYER *et al.* 2005), accordingly, it may represent a novel source for a natural non-genotoxic anticancer drug (chemotherapeutic agent).

### **Allergy to lichen substances**

Lichen substances can be contact allergens (*e.g.*, atranorin, lobaric acid, stictic acid). They can cause occupational allergic contact dermatitis in forestry and horticultural workers (“woodcutter’s eczema”), as well as cause non-occupational allergic dermatitis during all kinds of outdoor activities, such as cutting firewood, hunting, and using cosmetics (perfumes, after-shave lotions, sunscreen products) that contain lichen metabolites (AALTO-KORTE *et al.* 2005). Various skin and respiratory symptoms have been observed, such as erythema, itching, scaling, contact urticaria, rhinitis, and asthma (AALTO-KORTE *et al.* 2005, MITCHELL and CHAMPION 1965).

### **Candidates for antipyretic and analgesic drugs**

Some lichen substances have been shown to relieve pain effectively or reduce fever and inflammation in various mammals, and it is reasonable to assume that these compounds also could be effective in humans. VIJAYAKUMAR *et al.* (2000) reported that usnic acid, isolated from *Roccella montagnei*, showed significant anti-inflammatory activity in rats. Diffractaic and usnic acids have an analgesic effect in mice *in vitro* (OKUYAMA *et al.* 1995), and usnic acid also is an antipyretic.

### **Conclusions**

More than 1000 secondary products have been identified to date in lichens, and new compounds will certainly be found from poorly studied or newly discovered lichens, especially from the under-collected tropics. Furthermore, development in analytical

techniques will result in the more complete knowledge of the biological activities of lichen secondary substances, as well as their role in lichen symbiosis.

## Acknowledgements

The preparation of this paper was supported by the Hungarian Scientific Research Fund (OTKA T047160 and K81232).

## References

References not listed here can be found in MOLNÁR and FARKAS (2010).

- AMO de PAZ G., RAGGIO J., GÓMEZ-SERRANILLOS M. P., PALOMINO O. M., GONZÁLEZ-BURGOS E., CARRETERO M. E., CRESPO A. 2010: HPLC isolation of antioxidant constituents from *Xanthoparmelia* spp. *Journal of Pharmaceutical and Biomedical Analysis* 53: 165–171.
- CULBERSON W. L. 1969: The use of chemistry in the systematics of the lichens. *Taxon* 18: 152–166.
- CULBERSON C. F., ELIX J. A. 1989: Lichen substances. In: DEY P. M., HARBORNE J. B. (eds.): *Methods in plant biochemistry, Vol. 1. Plant phenolics*. Academic Press, London, pp. 509–535.
- ELIX J. A. 1996: Biochemistry and secondary metabolites. In: NASH T. H. III (eds.): *Lichen biology*, 1st ed.. Cambridge University Press, pp. 155–180.
- ELIX J. A., STOCKER-WÖRGÖTTER E. 2008: Biochemistry and secondary metabolites. In: NASH T. H. III (eds.): *Lichen biology*, 2nd ed.. Cambridge University Press, pp. 104–133.
- FARKAS E. 2007: *Lichenológia – a zuzmók tudománya*. MTA Ökológiai és Botanikai Kutatóintézete, Vácrátót, 193 pp.
- FEIGE G. B., LUMBSCH H. T. 1995: Some types of chemical variation in lichens. *Crypt. Bot.* 5: 31–35.
- HAWKSWORTH D. L. 1976: Lichen chemotaxonomy. In: BROWN D. H., HAWKSWORTH D. L., BAILEY R. H. (eds.): *Lichenology: progress and problems*. The Systematics Association Special Volume, No. 8, Academic Press, London and New York, pp. 139–184.
- MOLNÁR K., FARKAS E. 2010: Current results on biological activities of lichen secondary metabolites: a review. *Zeitschrift für Naturforschung* 65C: 157–173.
- NYBAKKEN L., GAUSLAA Y. 2007: Difference in secondary compounds and chlorophylls between fibrils and main stems in the lichen *Usnea longissima* suggests different functional roles. *Lichenologist* 39: 491–494.
- NYLANDER W. 1866: Circa novum in studio Lichenum critericum chemicum. *Flora* 49: 198–201.
- SCIRPA P., SCAMBIA G., MASCIULLO V., BATTAGLIA F., FOTI E., LOPEZ R., VILLA P., MALECORE M., MANCUSO S. 1999: Terapia adiuvante con un preparato a base di zinco solfato e acido usnico delle lesioni genitali da Human Papilloma Virus (HPV) dopo trattamento chirurgico distruttivo. *Minerva Ginecologica* 51: 255–260.
- STOCKER-WÖRGÖTTER E. 2008: Metabolic diversity of lichen-forming ascomycetous fungi: culturing, polyketide and shikimate metabolite production, and PKS genes. *Natural Product Reports* 25: 188–200.
- STOCKER-WÖRGÖTTER E., ELIX J. A. 2002: Secondary chemistry of cultured mycobionts: formation of a complete chemosyndrome by the lichen fungus of *Lobaria spathulata*. *Lichenologist* 34: 351–359.

# Global ecosystems in a post-fossil world

BÁLINT CZÚCZ<sup>1</sup>

## Abstract

In the last few decades oil has been consumed at a much faster pace than new reserves have been discovered. We are approaching the point where about the half of the ultimately recoverable reserves has been consumed up. When this point is reached, global oil production will attain a peak (“peak oil”) and arrive in a period of unavoidable decline. This will definitely result in considerable ecological impacts, changing both conscious (land use) and external (pollution) environmental impacts of human activities. Peak oil will challenge modern western conservationism, promoting a shift from a global towards a local perspective, and from conservation towards sustainability in the focus. Given the vital importance of ecosystems and ecosystem services in a post-oil era, it is crucially important how we manage to lead through our ecosystems during the transition period. Integrated impact assessments are urgently needed to facilitate a smooth transition into a post-peak-oil era, without disrupting world’s still plentiful biotic resources during the transition.

## Introduction

Ecologists have been long warning society that the concept of continual growth on a finite planet is flawed and may result in some form of a decline driven by natural constraints sooner or later (MEADOWS et al. 1972, EHRENFELD, 2005). Current trends of industrialization and globalization raise a series of issues (i.a. climate change, ozone depletion, erosion of biodiversity), which have the potential to exert detrimental impact on our civilization in the near future. A less recognized, but potentially imminent threat for the status quo of our society is known as ‘peak oil’, which is set to bring the age of cheap oil to an end in the near future (CAMPBELL and LAHERRERE, 1998). This term refers to the point when global oil production reaches a peak followed by inevitable decline, approximately when half of the oil reserves have been used up. This event would mean for global economies that extensive growth in terms of oil consumption is no longer possible, and supply constraints will drive up prices even for unchanged demand. The resulting imbalance in oil production and demand can be seen as the first hard symptom of reaching the limits for our growth-centred society, which will have tremendous consequences for modern Western civilization. Since at present the functioning of our society is based on the cheap availability of fossil fuels, the forthcoming oil shortage will pose a great challenge for all human activities, with potentially dramatic influence on ecosystems and nature conservation.

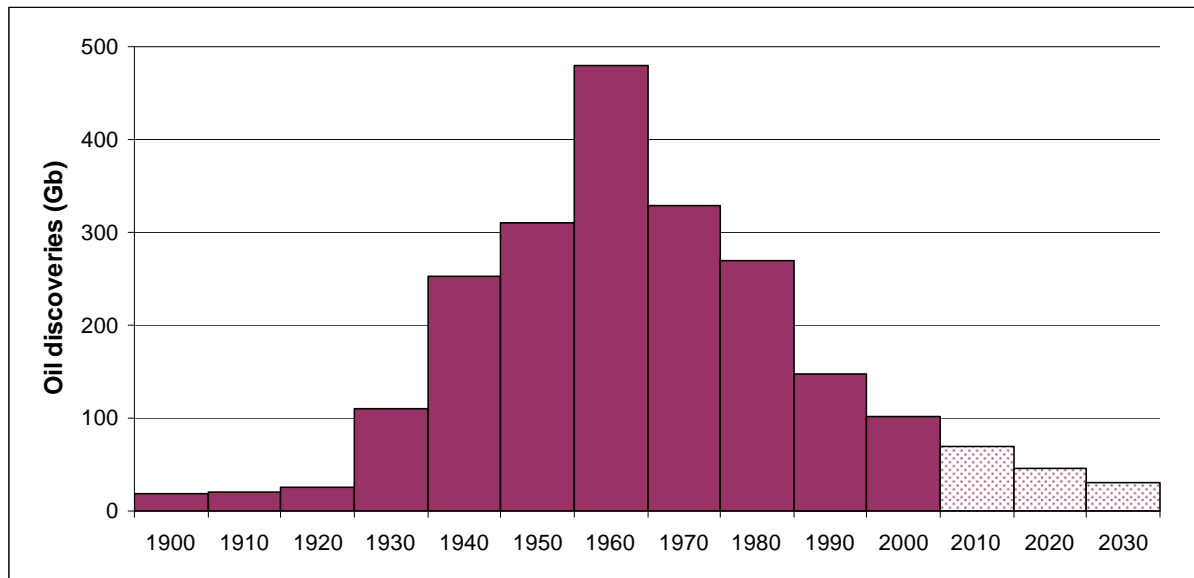
## Peak oil

According to geological considerations, the production of an oil field follows a bell shape curve, where the production starts to decline well before all resources are depleted. The first oil fields drilled contained good quality oil under high pressure relatively close to the surface. During the last 150 years the “low hanging fruits” of the most easily accessible oil sources have been used up, and despite enormous efforts, new discoveries are in steady decline since

---

<sup>1</sup> czucz@botanika.hu

the early 1960s (CAMPBELL and LAHERRERE 1998, Fig 1). In 1956 analyzing the trends in new discoveries and the production curves of individual oil fields Shell geologist M. King Hubbert formulated a model to predict the timing of the peak production of larger areas. With his model Hubbert successfully predicted the peaking of oil production in the conterminous US by 1970 (HUBBERT, 1956). Since then a wide series of oil producing nations, including all industrialized countries, have reportedly reached their peak production (WWI, 2005), indicating that global oil production might not be far from peaking either.



**Figure 1.** Historical oil discoveries and an extrapolation for the future (Source: ASPO)

Abundance, high energy concentration, and the ease of extraction, storage and transportation have made petroleum a fuel of choice for present-day human societies. There are no easy alternatives for oil (HIRSCH et al. 2005). Apparently, natural gas could be a salient substitute, but unfortunately it also faces a similar peak-and-decline future (ALEKLETT and CAMPBELL, 2003). Other fossil alternatives, such as tar sands, oil shales and extra heavy oils (sometimes termed as “non-conventional” oils) and coal all have some significant drawbacks, being both technically (no mature technology to produce effective substitutes in adequate quantity) and environmentally (demand large-scale strip mining and energy-intensive pre-processing) unfeasible (SALAMEH, 2003). Nuclear power and renewables are also limited as a substitute, since they are unlikely to be able to meet the energy needs of modern western societies in the foreseeable future due to scaling problems (SALAMEH, 2003, EWG 2006). Declining availability of oil constrains use of the entire human energy infrastructure because petroleum products are used to extract, deliver, and process all fuels and raw materials (and to manufacture “alternative” energy technologies) (HIRSCH et al. 2005).

The consequences of shortfalls in oil production can be illustrated by the aftermath of the US oil peak in 1970, creating the conditions for the energy crises of the ‘70s, where ~5% of decline in production resulted in nearly quadrupling prices and a 3% drop in the US GDP (HIRSCH, 2008). However, at that time it was possible to return to business as usual based on foreign oil – an option that will not be available in the present case. World’s oil dependency has only increased since then. For example, for every one joule of food consumed in the United States, around 10 joules of fossil energy have been used to produce it (PFEIFFER, 2006). Hydrocarbons are feedstock for plastics, pharmaceuticals, fertilizers, electronic components, but most importantly oil is the most convenient and versatile fossil fuel,

currently accounting for about 43% of the world's total fuel consumption and 95% of global energy used for transportation (IEA, 2007).

Peak oil, similarly to climate change, constitutes a typical post-normal problem (FUNTOWICZ and RAVETZ, 1993), where facts are uncertain, values are diverse and stakes are high. No wonder that the both the timing and the potential consequences of peak oil are still under intensive debate among scientific, industrial and governmental communities. While governmental agencies and multinational oil companies tend to draw an optimistic picture on future oil availability, other more critical calculations place global production peak in the very near future, or even in the recent past (BENTLEY and BOYLE, 2008). In fact, oil production has not increased significantly since 2005 despite the heavy increase in fuel prices and the habitual pledges of the major producers to increase production. The current economic crisis and the increased price volatility of oil may actually be regarded as symptoms of having approached or reached peak oil (HAMILTON 2009). Accordingly, we may have arrived or will arrive soon at a major turning point of human history with several severe social, economic and environmental implications, which demand careful consideration and proactive preparation (HIRSCH et al. 2005).

### **Facets of peak oil for biodiversity**

Limited availability of fossil fuels will impose a huge impact on humanity, no matter when the actual peak arrives. As human activities are by far the most important drivers of global ecological changes, social regime shifts will definitely induce ecological changes. On the other hand, these changes can impose detrimental feedback on the human society, gradually deprived of its energetic self-sufficiency based on the continuous flux of appropriated fossil fuels.

But what kind of impacts peak oil will have on ecosystems and ecosystem services? Naively one could assume that fuel scarcity and the accompanying breakdown of energy intensive solutions could bring instant relief on nature, but the reality will definitely be more detailed, partly depending on the policy choices to be formulated in face of the challenges. Raising energy concerns, for example, might defeat environmental considerations; resulting in environmentally detrimental solutions on any scales from local to global, e.g. oil production from tar sands already in process demands vast strip mines, large amounts of water, and produces large quantities of different wastes and CO<sub>2</sub> due to its relatively poor energy efficiency. Other potential policy responses, such as extended biofuel plantations hold the same controversies. Cutting down on fuel usage will definitely bring significant changes to the current energy-intensive forest management and agricultural practice. The pattern of change, however, will deeply depend on the local socio-economical driving forces and can result in either abandonment or over-exploitation. As a general trend, human activity will be more localized, which can also have serious implications on ecosystems. In Table 1 we summarize the most evident mechanisms, by which fuel scarcity and the resulting social transitions may affect biodiversity.

	<b>Advantages</b>	<b>Disadvantages</b>
<b>Agriculture</b>	decrease in cultivation intensity	potential increase in agricultural (+biofuel) area
<b>Forests</b>	return to traditional forest management schemes	potential overexploitation of forests for firewood
<b>Tourism and transportation</b>	decrease in pressure of new alien introductions due to limited mobility and commerce, landscape diversity should increase since all basic human needs should be met more locally	decrease in tourism revenues, including ecotourism
<b>Climate policy</b>	decrease in CO <sub>2</sub> emissions (from oil and natural gas)	potential increase in CO <sub>2</sub> emissions (non-conventional oil and coal)
<b>Conservation policy</b>	increasing focus on local sustainability	declining interest in large scale issues, weakening of international programs and institutions

**Table 1.** The most important impacts of peak oil on ecosystems grouped by sectors (CZÚCZ et al. 2010)

From the perspective of the human perception of ecosystems and their services a further layer of thought can be added. Modern western society found ways to increase the supply of provisioning services (or ecosystem goods, such as food or fibre production) at the expense of other services (such as pollination, water regulation or aesthetic beauty) – by means of intensive management techniques powered by fossil energy (MEA, 2005). The problem is deeply rooted in the fundamentals of market economy, which absorbed ecosystem goods relatively easily, whereas all other, non-provisioning services were barred outside as commons. Observing the decline in these commons, their protection became the main focus of modern conservationism. The descent towards a low-carbon society will presumably change this situation. Modern, coordinated, large-scale conservation activities are likely to give way to a local, sustainability-centred attitude, which currently can be detected in poor countries (ROE and ELLIOTT, 2005).

## Conclusions

The descent towards a low-carbon society will probably be accompanied by economic turmoil and a high level of social tensions, which will definitely cause major impact on ecosystems as well. It is important to enumerate these potential impacts and assess the uncertainties, so that when things happen to arrive, society would not be taken by surprise. Surprise and panic can initiate the worst solutions. Even though the potential challenges caused by peak oil are of a similar magnitude to those caused by climate change, there has been very little scientific and policy attention devoted to this complex issue. Similarly to climate change, integrated impact, adaptation and vulnerability assessments are urgently needed to facilitate a smooth transition into a post-peak-oil era, without disrupting world's still plentiful biotic resources during the transition.

## References

ALEKLETT K., CAMPBELL C. J. 2003. The peak and decline of world oil and gas production. *Minerals and Energy – Raw Materials Report*, 18(1): 5-20.

- BENTLEY R., BOYLE G. 2008: Global oil production: forecasts and methodologies. *Environment and Planning B: Planning and Design* 35: 609–626.
- CAMPBELL C. J., LAHERRERE J. H. 1998: The end of cheap oil. *Scientific American* 278: 60-65.
- CZÚCZ B., GATHMAN J. P., MCPHERSON G. R. 2010: The impending peak and decline of petroleum production: an underestimated challenge for conservation of ecological integrity. *Conservation Biology* 24: 948-956.
- EHRENFELD D. 2005: The environmental limits to globalization. *Conservation Biology* 19: 318-326.
- EWG (Energy Watch Group) 2006: Uranium resources and nuclear energy. EWG-Series No. 1/2006. EWG, Berlin, 48 pp.
- FUNTOWICZ S. O., RAVETZ J. R. 1993: Science for the post-normal age. *Futures* 25: 739-755.
- HAMILTON J. D. 2009: Causes and consequences of the oil shock of 2007–08. *Brookings Papers on Economic Activity*, Spring 2009: 215–261.
- HIRSCH R. L. 2008: Mitigation of maximum world oil production: Shortage scenarios. *Energy Policy* 36: 881-889.
- HIRSCH R. L., BEZDEK R., WENDLING R. 2005: Peaking of world oil production: impacts, mitigation and risk management. Report to U.S. Dept. of Energy – Natl. Energy Technol. Lab. Science Applications International Corporation, San Diego, CA, 91 pp.
- HUBBERT M. K. 1956: *Nuclear Energy and the Fossil Fuels*. Publication No. 95. Shell Development Company, Exploration and Production Research Division, Houston, TX. 57 pp.
- IEA (International Energy Agency) 2007: *Key world energy statistics 2007*. IEA, Paris, 82 pp.
- MEA (Millennium Ecosystem Assessment) 2005: *Ecosystems and Human Well-Being: Synthesis*, Island Press, Washington, DC, 160 pp.
- MEADOWS D. H., MEADOWS D. L., RANDERS J., BEHRENS W. W. 1972: *The Limits to Growth* Potomac Associates, Washington, DC, 205 pp.
- PFEIFFER D. A. 2006: *Eating Fossil Fuels: Oil, Food and the Coming Crisis in Agriculture*. New Society Publishers, Gabriola Island, BC, 144 pp.
- ROE D., ELLIOTT J. 2005: *Poverty-conservation linkages: A conceptual framework*. Poverty and Conservation Learning Group, International Institute for Environment and Development, London, UK. 12 pp.
- SALAMEH M. G. 2003: Can renewable and unconventional energy sources bridge the global energy gap in the 21st century? *Applied Energy* 75: 33-42.
- WWI (World Watch Institute) 2005: *State of the World 2005: Redefining Global Security*. Norton, NY, 107 pp.