Occurrence of heliophilous species on isolated rocky outcrops in a forested landscape: relict species or recent arrivals?

Výskyt heliofilních druhů na izolovaných skalních výchozech v lesnaté krajině: relikty nebo penetranty?

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Nineteen isolated rocky outcrops of different sizes, tops of which were covered with natural grassland vegetation, were studied in the forested submontane belt (630–1020 m a.s.l.) of the Šumava Mts in the southern part of the Czech Republic, Central Europe. The species of vascular plants present in the treeless sites at each locality were identified. Those species with an Ellenberg indicator value for light equal 6 or higher were considered to be heliophilous. The distance to the nearest secondary treeless area was measured. There were 43 heliophilous species (23%) recorded among the 184 species identified. The number of species and the number of heliophilous species varied independently of the altitude and extent of the treeless area on the rocky outcrops, but were significantly correlated only with the distance to man-made treeless areas. The highest number of heliophilous species was recorded within approximately 400 m from the nearest man-made treeless area. Although the relict nature of some of the heliophilous species on the rocky outcrops cannot be completely excluded, obviously most of the species colonized these localities from nearby secondary treeless areas since their creation in the Middle Ages.

K e y w o r d s : Czech Republic, ordination, relicts, species number, vascular plants

Introduction

In the temperate forest zone of inland Europe, heliophilous plant species did not have many opportunities to survive the expansion of closed woodland during the Holocene period (Berglund 1986). As well as for the alpine belt, patches of dry grassland in the lowlands and scattered wetlands, and various rocky habitats are assumed to have played a prominent role in the survival of heliophilous species in the Central European landscape (Ellenberg 1988, Lang 1994). Rocky sites were probably important refugia for heliophilous species adapted to mesic and dry site conditions (Küster 1996).

The importance of dry grasslands as relict sites for heliophilous species in the forest zone of Central Europe has been emphasized many times (Jeník 1969, Vera 2000), as that of wetlands (Brown 1997). Of the rocky sites, a similar role was stressed for canyon valley slopes along streams (Chytrý & Vicherek 1996), isolated rocky hills (Sádlo 1996) and screes (Sádlo & Kolbek 1994, Brabec & Cílek 1998, Rejmánek et al. 2004). However, rather small rocky outcrops have not yet been considered to be important role in the survival of heliophilous species in the forested landscape of Central Europe.

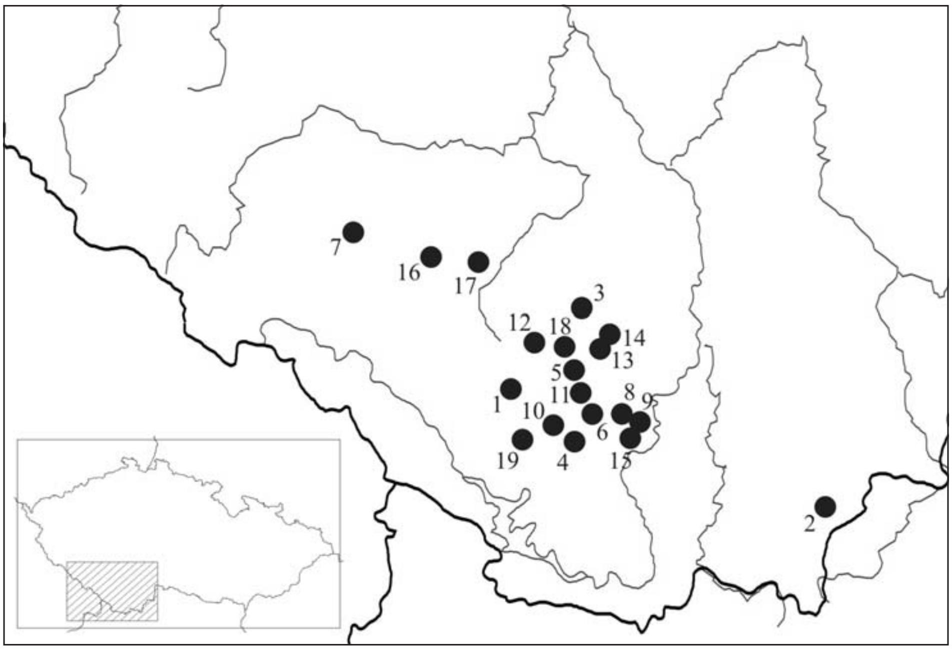

Fig. 1. – Location of the study sites. The numbers correspond to those in Table 1.

Table 1. – Site characteristics of the cryogenic rocky outcrops studied.

No.	Locality	Altitude(m)	Bedrock	Extent of the treeless area on localities (m^2)	Distance to the nearest treeless area (m)	Number of species	Number of heliophilous species
1	Černá stěna	1020	granite	100	1300	27	0
2	Hojná Voda	860	gneiss	200	200	16	4
3	Kozí kámen	660	gneiss	180	150	41	8
4	Kraví hora	860	gneiss	620	400	63	7
5	Kuklov	720	granulite	540	100	78	21
6	Mlýnské vrchy	810	granulite	630	600	19	1
7	Na hradě	870	gneiss	1600	200	60	15
8	Ohrada	855	granulite	560	1200	17	1
9	Ohrada2	800	granulite	100	950	19	2
10	Pražačka	890	gneiss	350	20	52	14
11	Ptačí stěna	790	granulite	210	700	29	2
12	Rohanovský vrch	950	gneiss	520	1100	14	2
13	Stržíšek	630	granulite	300	350	18	2
14	Štěnice	640	granulite	470	200	32	11
15	U Martínka	790	granulite	280	500	19	1
16	Věnec	760	gneiss	700	300	32	6
17	Vlachovo Březí	670	gneiss	100	50	26	6
18	Vrato	810	gneiss	220	100	64	18
19	Zelenka	970	granite	310	0	56	19

In the southern part of the Czech Republic there are isolated rocky outcrops of cryogenic origin (Chábera & Novák 1976), of which the tops are covered with small patches of natural grassland. Most of them are still surrounded by forest. They were studied with the object of determining: (a) How many heliophilous species occur on these rocky outcrops? and (b) Are they relict species?

Methods

Study sites

The 19 isolated rocky outcrops topped with treeless vegetation studied are located in the submontane belt of the Šumava Mts in the southwestern part of the Czech Republic (Fig. 1, Table 1). The rocks were not completely shaded by the adjacent forest. The altitude varied between 630 and 1020 m a.s.l. All sites were formed of acidic bedrock, namely gneiss, granite and granulite (Chábera & Novák 1976). The region was intensively colonized by man during the Middle Ages, which resulted in man-made (secondary) treeless areas, mainly around settlements (Beneš 1996).

Field sampling and data elaboration

On each rocky outcrop (Table 1), the size of the natural treeless area was measured. The vertical projection of the tree canopy was estimated. Steep slopes and walls, with typical rocky vegetation, were not included. A list of all the species of vascular plants present on the treeless sites was compiled for each locality. Those species with an Ellenberg indicator value for light of 6 or higher (Ellenberg et al. 1991) were considered as heliophilous (Appendix 1). Altitude of the top of each rocky outcrop and the distance to the nearest secondary treeless area were derived from detailed maps (1: 10 000).

Relationships between the number of species and the site variables were evaluated using the regression analysis in program Statistica 6 (StatSoft Inc. 2001). The unconstrained ordination method of Detrended Correspondence Analysis (DCA) (ter Braak & Šmilauer 1998) was used to determine vegetation pattern. The input data consisted of presence or absence of species. Nomenclature follows Kubát et al. (2002).

Results

The total number of species and the number of heliophilous species were significantly afffected by neither altitude ($F = 0.000$, $P = 0.990$ for all species; $F = 0.634$, $p = 0.440$ for heliophilous species) nor the extent of the treeless area on the rocky outcrop ($F = 1.921$, $P = 0.185$ for all species; $F = 0.921$, $P = 0.351$ for heliophilous species). Both were, however, significantly correlated with the distance of the rocky outcrop from a man-made treeless area (Fig. 2). For the heliophilous species, the total variance explained was 69.1% ($F = 38.560$, $P < 0.001$) and for all species 35.4% ($F = 10.400$, $P = 0.005$).

In the DCA ordination (Fig. 3), the localities were arranged approximately along the first axis (eigenvalue 0.390), according to the number of heliophilous species present, reflecting the distance to the nearest man-made treeless area. The second axis (eigenvalue 0.297) is difficult to interpret.

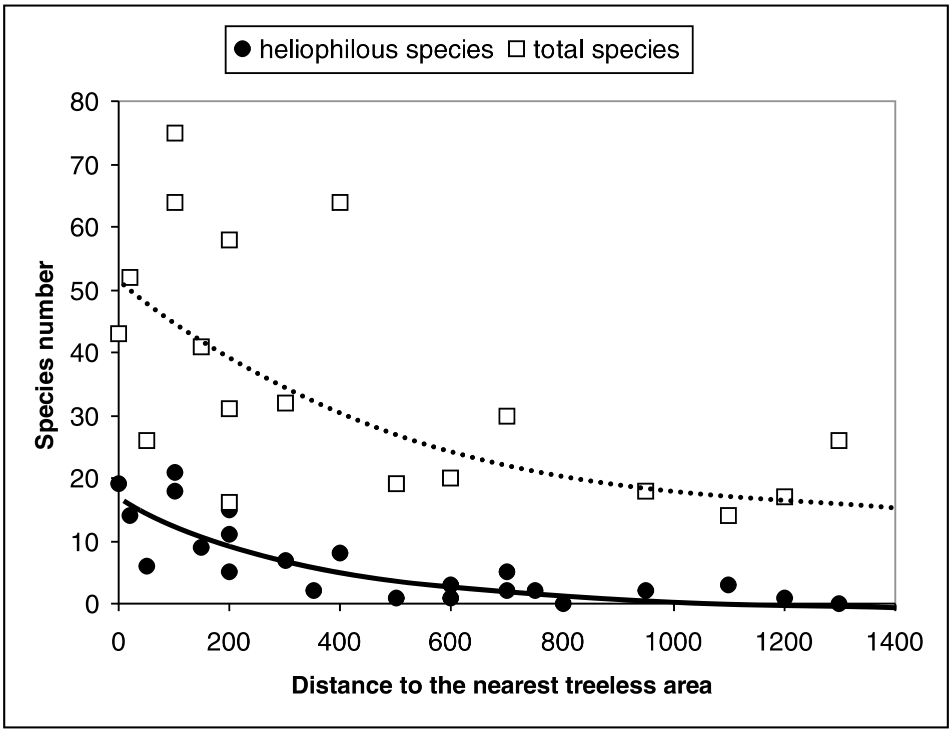

Fig. 2. – The relationships between the total number of species, the number of heliophilous species and the distance between a rocky outcrop and the nearest man-made treeless area. Quadratic regression was used because it provided a better fit than linear regression.

Discussion

These rocky outcrops can be seen as habitat islands and the theory of island biogeography (MacArthur & Wilson 1967) can be tentatively applied to interpret the species occurrence on them. Of the two main parameters of this theory, the area of the 'islands' appeared to be insignificant, whereas the distance from the 'mainland' was significant. It appeared that the distance of a rocky outcrop to the nearest man-made treeless area is the most important environmental variable determining the number of heliophilous species. It implies that the present occurrence of many species is of secondary origin and that they have probably colonized the rocks since the creation of the treeless areas by man, which happened in the Medieval Period, largely in the 13th century (Beneš 1996). However, the relict nature of the occurrence of at least some species cannot be completely excluded for some rocky sites in this country (Sádlo 1996). Especially those species, occurring on isolated rocky outcrops that do not possess light anemochorous seeds, such as, e.g. *Hypericum perforatum* and *Nardus stricta*. But the number of heliophilous species on the most isolated rocky outcrops was very low or even zero. A higher number of heliophilous species was present on rocky outcrops located up to approximately 400 m from a man-made treeless patch (Fig. 2). Probably not only heliophilous species colonized the rocky outcrops from the nearby man-made treeless areas. Such treeless areas are more species rich than the rather monoto-

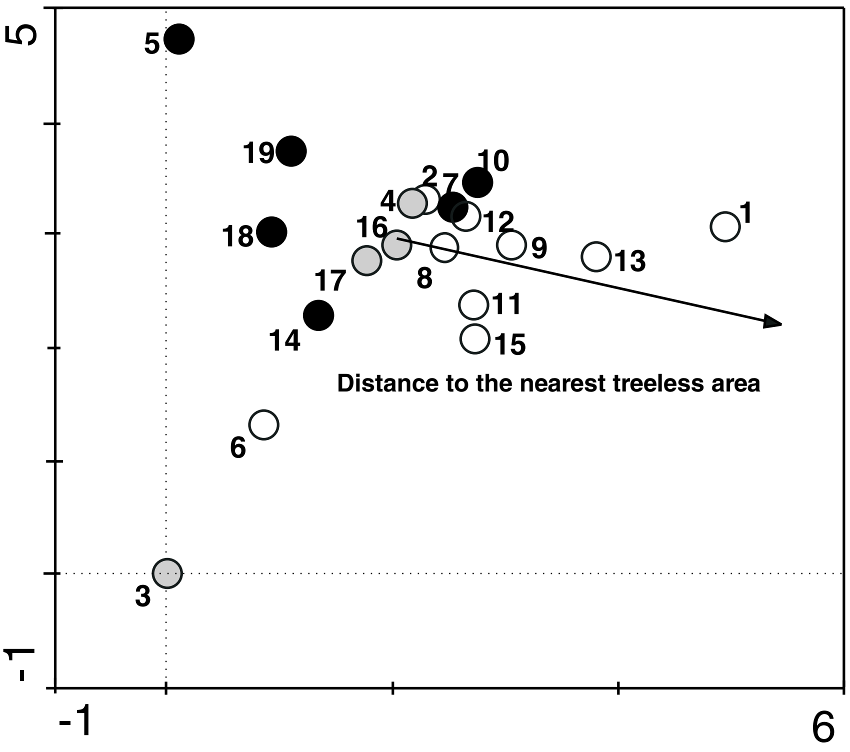

Fig. 3. – DCA ordination of localities. The rocky outcrops with 0–5 heliophilous species are indicated by open circles, those with 6–10 species by shaded circles, and those with more than 10 species by black dots. The numbers correspond to to the localities listed in Table 1.

nous forests. About two thirds of the regional flora occurs in man-made grasslands in the region (Prach et al. 1997). This may explain the fact that increase in the total number of species with decrease in the distance to treeless patches cannot be attributed to an increase in heliophilous species only (Fig. 2).

Although the relict origin of the heliophilous species was not confirmed, the relict nature of the treeless vegetation is expected (Mucina et al. 1993, Sádlo 1996), especially in grassland vegetation dominated by *Calamagrostis arundinacea*, in which most of the heliophilous species considered in this study occurred.

The relationship between the number of species and the extent of the treeless area on the top of a rocky outcrop appeared to be insignificant. Kubešová & Chytrý (2005) concluded the same for bryophytes occurring on talus slopes. But in the case of some other habitats or real islands, which have been studied in Central Europe, significant relationships between the number of species and area were found, e.g. in small woodlands in an agricultural landscape (Dzwonko & Loster 1989) and small artificial islands in fishponds (Rejmánková & Rejmánek 2002).

The insignificant influence of altitude on the number of species is probably due to the narrow range of altitudes and the rather uniform character of the landscape, which the thermophilous species from the lowlands and mountain species from higher elevations have not colonized. Some of the heliophilous species, such as *Origanum vulgare, Koeleria* *pyramidata, Hypericum perforatum* and *Digitalis grandiflora*, are slightly thermophilous, and their occurrence on sunny spots of the rocky outcrops studied is close to their altitudinal limits (Procházka 2005).

It must be stressed, that a rather specific habitat was studied. It is not surprising that the small rocky outcrops do not play important role as relic sites for heliophilous species, as do, for example, alpine grasslands (Rybníček & Rybníčková 2004), glacial cirques (Jeník et al. 1983), and rocky valley slopes along streams (Chytrý & Vicherek 1996). Because of the great distance of our study sites from these habitats, colonization by heliophilous species from these habitats is unlikely.

Finally, the questions put in the introduction can be answered: (a) The rocky outcrops studied appeared to be important habitats for heliophilous species. There were 43 of such species among the 184 species occurring on the outcrops (23%). (b) However, most of these species came from nearby secondary treeless areas since their creation by man in the Medieval Period.

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Souhrn

Studováno bylo celkem 19 kryogenních, izolovaných skalních útvarů s vyvinutým primárním bezlesím na jejich temeni. Všechny lokality se nacházely v podhůří české části Šumavy včetně Novohradských hor, v nadmořských výškách od 630 do 1020 m n.m. (obr. 1, tab. 1). Na každém skalním útvaru byl pořízen seznam druhů vyskytujících se na bezlesí, které bylo vymezeno jako plocha mimo zápoj korun dřevin při kolmé projekci. Dále byla změřena vzdálenost studované lokality od nejbližšího druhotného bezlesí. Druhy s Ellenbergovým indikačním číslem pro světlo rovným 6 nebo vyšším (Ellenberg et al. 1991) byly považovány za heliofilní (Appendix 1).

Z celkového počtu druhů 184, zaznamenaných na všech lokalitách, bylo 43 (tj. 23 %) považováno za heliofilní. Počet heliofilních druhů a celkový počet druhů na lokalitě byly průkazně korelovány jen se vzdáleností k druhotnému bezlesí (obr. 2 a 3), zatímco vliv rozlohy primárního bezlesí na lokalitě a vliv nadmořské výšky se ukázaly jako neprůkazné.

I když nelze úplně vyloučit reliktnost výskytu některých heliofilních druhů alespoň na některých studovaných lokalitách, zdá se, že většina z nich pronikla na skalní útvary až druhotně z blízkého sekundárního bezlesí, jehož vznik lze klást ve studované krajině do středověku, převážně do 13. století. Výrazně vyšší počet heliofilních druhů se nacházel na skalách do vzdálenosti cca 400 m od sekundárního bezlesí. Přesto lze považovat výskyt heliofilních druhů na studovaných kryogenních skalních útvarech za významný, obohacující lokální i regionální flóru a vegetaci.

References

Beneš J. (1996): The synantropic landscape history of the Šumava Mountains (Czech side). – Silva Gabreta 1: 237–241.

Berglund B. E. (ed.) (1986): Handbook of Holocene palaeoecology and palaeohydrology. – Blackwell, New York, etc.

Brabec E. & Cílek V. (1998): Ekologie sutí Českého středohoří. Kritická recenze a přehled výsledků. – In: Cílek V. & Kopecký J. (eds.), Pískovcový fenomén: klima, život a reliéf, p. 49–59, Česká speleologická společnost, Praha.

Brown A. G. (1997): Alluvial geoarchaeology. – Cambridge University Press, Cambridge.

Chábera S. & Novák V. (1976): Kryogenní mezoformy v navrhované chráněné krajinné oblasti Blanský les. – Sborník Jihočes. Muz. v Českých Budějovicích, Ser. Přírodní vědy, 16: 41–66.

Chytrý M. & Vicherek J. (1996): Přirozená a polopřirozená vegetace údolí řek Oslavy, Jihlavy a Rokytné. – Přírodověd. Sborn. Západomorav. Muz. Třebíč, 22: 1–125.
Dzvonko Z. & Loster S. (1989): Distribution of vascular plant species in small woodlands on the Western Carpathian foothills. – Oikos 56: 77–86.
Ellenberg H. (1988): Vegetation ecology of Central Europe. – Cambridge Univ. Press, Cambridge.
Ellenberg H., Weber H. E., Düll R., Wirth V., Werner W. & Paulissen D. (1991): Zeigerwerte von Pflanzen in Mitteleuropa. – Scr. Geobot. 18: 1–248.
Jeník J. (1969): Otázka stepní v Čechách a ve světě. – Zpr. Čs. Bot. Společ. 4: 128–131.
Jeník J., Bureš L. & Burešová Z. (1983): Revised flora of Velká Kotlina cirque, the Sudeten Mountains, I. – Preslia 55: 25–61.
Kubát K., Hrouda L., Chrtek J. jun., Kaplan Z., Kirschner J. & Štěpánek J. (eds.) (2002): Klíč ke květeně České republiky. – Academia, Praha.
Kubešová S. & Chytrý M. (2005): Diversity of bryophytes on treeless cliffs and talus slopes in a forested central European landscape. – J. Bryol. 27 (in press).
Küster H.-J. (1996): Geschichte der Landschaft in Mitteleuropa. Von der Eiszeit zur Gegenwart. – C. H. Beck, München.
Lang G. (1994): Quartäre Vegetationsgeschichte Europas. Methoden und Ergebnisse. – Gustav Fischer Verlag, Stuttgart.
MacArthur R. H. & Wilson E. O. (1967): The theory of island biogeography. – Princeton Univ. Press, Princeton, N.J.
Mucina L., Grabherr G. & Wallnöfer S. (1993): Die Pflanzengesellschaften Österreichs, III. – Gustav Fischer Verlag, Stuttgart.
Prach K., Štech M. & Beneš J. (1997): Druhotné bezlesí – opomíjená složka biodiversity Šumavy. – Silva Gabreta 1: 243–247.
Procházka F. (2005): Květena Šumavy. – Ms. [Depon in Kat. Bot., Biol. Fak. Jihočes. Univ., České Budějovice]
Rejmánek M. & Rejmánková E. (2004): Species diversity of plant communities on calcareous screes: the role of intermediate disturbance. – Preslia 76: 207–222.
Rejmánková E. & Rejmánek M. (2002): Biogeography of artificial islands: effects of age, area elevation, and isolation on plant species richness. – Preslia 74: 307–314.
Rybníček K. & Rybníčková E. (2004): Pollen analyses of sediments from the summit of the Praděd range in the Hrubý Jeseník Mts (Eastern Sudetes). – Preslia 76: 331–347.
Sádlo J. (1996): Reliktní vegetace Bořeně u Bíliny a možnosti její historické interpretace. – Severočes. přírodou, Litoměřice, 29: 1–16.
Sádlo J. & Kolbek J. (1994): Náčrt nelesní vegetace sutí kolinního až montánního stupně České republiky. – Preslia 66: 217–236.
StatSoft Inc. (2001): STATISTICA for Windows (data analysis software system), version 6. – StatSoft, Tulsa.
ter Braak, C. J. F. & Šmilauer, P (1998): CANOCO Release 4. Reference manual and user's guide to Canoco for Windows: Software for Canonical Community Ordination. – Microcomputer Power, Ithaca, New York.
Vera F. W. M. (2000): Grazing ecology and forest history. – CABI Publ., Wallingford.

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Appendix 1. – List of heliophilous species, i.e. those with an Ellenberg indicator value for light of 6 or higher (Ellenberg et al. 1991), which were recorded on the rocky outcrops.

Achillea millefolium, Acinos arvensis, Agrostis capillaris, Anthoxanthum odoratum, Arenaria serpyllifolia, Arrhenatherum elatius, Avenula pubescens, Brachypodium pinnatum, Carex pallescens, C. pairae, Carlina acaulis, Clinopodium vulgare, Dactylis glomerata, Danthonia decumbens, Digitalis grandiflora, Festuca ovina, F. rubra agg.*, Galium album, G. pumilum, Helianthemum nummularium, Hieracium pilosella, H. sabaudum, Hypericum perforatum, Jasione montana, Knautia arvensis, Koeleria pyramidata, Lathyrus pratensis, Linaria vulgaris, Lotus corniculatus, Luzula campestris, Lychnis viscaria, Nardus stricta, Origanum vulgare, Phleum pratense, Pimpinella saxifraga, Poa angustifolia, P. compressa, Potentilla tabernaemontani, Securigera varia, Taraxacum* sp.*, Thymus pulegioides, Trifolium medium, Verbascum lychnitis*