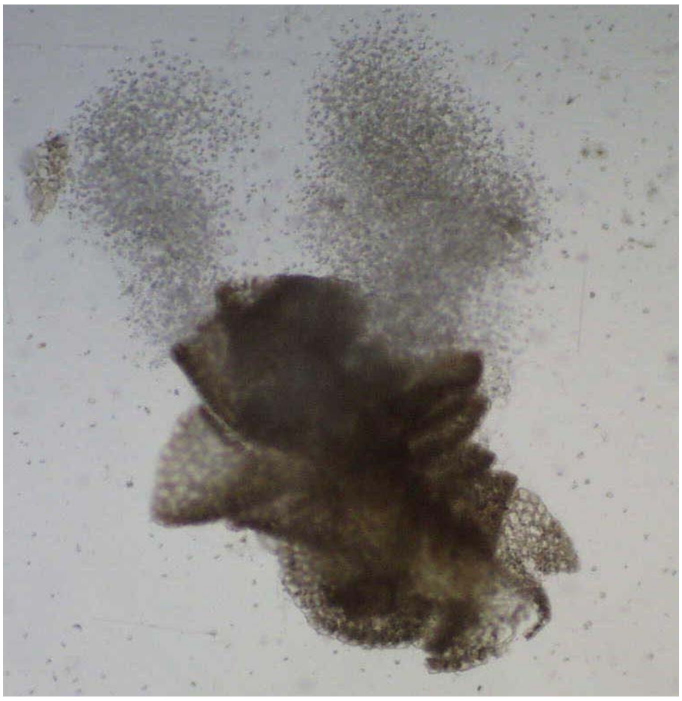
University of South Bohemia in České Budějovice
Biological Faculty

Master thesis

Population ecology of a leafy liverwort *Jungermannia caespiticia* Lindenb. in the Czech Republic



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ANNOTATION

I declare, that I worked this thesis out by myself, only with use of cited literature.

Four permanent manipulative experiments were realised in two mountain regions in the Czech Republic. The aim was to monitor population dynamics of the rare *Jungermannia caespiticia* with respect to competitive ability, growth form and regeneration. Revision of historical and current localities and targeted search for new localities was done. Main topics discussed in this thesis are: competitive ability, short-distance dispersal, the role of disturbance, habitat characteristics and distribution of *J. caespiticia*.

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CONTENTS

1. INTRODUCTION

Bryology has not benefited from a development of population biology in that extent as it has been for vascular plants (Wiklund & Rydin 2004, Økland 2000, Söderström *et al.* 1992), hence, for most bryophyte species the population data from monitoring in nature and sufficient amount of data from the past is not available or precise enough (Herben 1994). Precise knowledge of the habitat requirements, population dynamics, dispersal ecology and the distribution of species is importatnt for competent survey of species' state. The identification of the limiting factors for the species is substantial as well (Pohjamo & Laaka-Lindberg 2004, Hartley & Kunin 2003, Heinlen & Vitt 2003, Söderström *et al.* 2002, Herben 1994, During 1992). Our current knowledge of these parameters is insufficient with respect to bryophytes (Kimmerer 2005, Pohjamo & Laaka-Lindberg 2004, Ross-Davis & Frego 2004, Cleavitt 2002, Laaka-Lindberg & Heino 2001, Zechmeister & Moser 2001, Kimmerer & Driscolla 2000, Longton & Hedderson 2000). Most authors agree that further investigation in bryophyte ecology is needed (e.g. Ross-Davis & Frego 2004, Heinlen & Vitt 2003, Cleavitt 2002, Økland 1994, Söderström *et al.* 1992). Nevertheless, bryology made plausible progress in last decades, above all with respect to the knowledge of species' distribution (e.g. During 1992) and conservation efforts (e.g. Hallingbäck 2003, Zechmeister & Moser 2001, Longton & Hedderson 2000). Unfortunately, the research is restricted in few regions. Therefore, it is difficult to make any conclusions about the threat status of species.

Many species have disappeared from their original habitats (Pavoine *et al.* 2005, Hallingbäck 2003), so the importance of bryophyte conservation is increasing at present (Rydin & Barber 2001, During 1992, Söderström *et al.* 1992). The urgent task in current bryology is to collect data concerning rare and threatened species. Unfortunately, most of rare and threatened bryophytes belong to the ´data deficient´ category (Söderström *et al.* 1992), which includes species with too little relevant information available to enable a placement in any of the other categories of threat status (Hallingbäck 1998). With the aim of better understanding to a biology of the bryophytes and its conservation The European Commitee for Conservation of Bryophytes (ECCB) was found by IUCN in 1990 (Hallingbäck 2003, During 1992). Up to 1995 ECCB produced a Red Data Book of European bryophytes where belonged 35% of European bryoflora. 9% of total bryoflora was classified as endangered (Hallingbäck 2003). From many aspects the cause of bryophytes decline is in changing environment due to permanent human influence (Pohjamo & Laaka-Lindberg 2004, Hallingbäck 2003, Murray *et al.* 2002, Sibly & Hone 2002, Rydin & Barber 2001, Zechmeister & Moser 2000, During 1992). Compared to vascular plants, bryophytes do not possess roots and remain of low stature, what disable them to profit from buffering capacities of substrate. Assigning more temporary nature of their habitats, they are more susceptible to environmental changes (During 1986).

Species´ rarity is in general determined by combination of its reproductive and growth abilities, habitat specifity and habitat amount (Pavoine *et al.* 2005, Hallingbäck 1998). Due to insufficient survey, the threat status of many bryophytes is often overestimated (Söderström *et al.* 2002). For example, in several countries highly intensified searching has led to the discovery of many previously unrecorded species and rediscovery of several that thought to be extinct (e.g. Kučera *et al.* 2004, Zechmeister *et al.* 2002). On the other hand, as the result of overlooking the bryophytes, loss of diversity and an unknown amount of information may happen (Longton & Hedderson 2000, Söderström *et al.* 1992). If we want to make proper conclusions about the threat status and implementation of protective measures, it is neccessary to acquire more knowledge of ecology and distribution of species. Thereby more detailed research is needed (Hartley & Kunin 2003, Heinlen & Vitt 2003, Hallingbäck 2003, Økland 2000, During 1992, Herben & Söderström 1992).

Studies of the bryophyte ecology have concentrated mainly on mosses (Pohjamo & Laaka-Lindberg 2004, Laaka-Lindberg & Heino 2001, Shaw 2000). A few studies were performed in liverworts (Laaka-Lindberg 1999). Researchers were concentrated on growth patterns, reproduction, propagula dormancy, population demography or the overgrowth competition and sex-ratio. Despite of relatively broad spectrum of research intentions in Marchantiopsida, no general predictions can be made due to lack of similar studies. An appeal to the research in *Jungermannia caespiticia* was to contribute to our knowledge of this group of bryophytes.

Several methods can be used to study plant biology in general. No predictions can be made without parameter estimates based on real data (Herben & Söderström 1992). Population studies can clarify spatial characters of species, above all those, which form metapopulations (Kimmerer & Driscolla 2000), which is the case of most bryophytes (Herben & Söderström 1992), including *J. caespiticia*. Using experimental plots in natural habitats should give an objective information. Results from the long-term manipulative experiments will provide broader knowledge of ecology (Herben 1994). Demographical studies of populations may show critical stages in the life cycle (Herben 1994, Söderström *et al.* 1992) and regeneration experiments are powerful method especially for bryophyte dispersal to study (Ross-Davis & Frego 2004, Cleavitt 2002).

Observations based on permanent manipulative experimental plots were used in the first part of this study, which targets to reveal some facts from population ecology of the *J. caespiticia*. In the second part of this thesis I attempt to assess environmental requirements and current distribution and its change during the last century. In this case the procedure of revision and comparison with old data was used. Those parts together are aimed to afford a complex view on both population and metapopulation level of biology of the rare *J. caespiticia*. Subsequently, when incorporating acquired information, it will be possible to assess more precisely the threat status of *J. caespiticia* and if necessary, to propose some adequate conservation measures.

Studied Species

Jungermannia caespiticia (Marchantiopsida, Jungermanniaceae) is a small dioicous leafy liverwort growing in pale green tufts. It is an ephemeral pioneer species growing predominantly on temporary habitats on bare acidic soil. Most records are from anthropogenous sites in both lowlands and mountains. The species is remarkable, at least, because of its rarity regionally difficult to understand, as is the extreme disjunction in range (Schuster 1969), and endogenous gemmae, which are unique among Jungermanniales (Paton 1999). Except this species endogenous gemmae are known only in genus *Riccardia* and *Blasia* (Váňa 1974).

Outside Europe *J. caespiticia* is reported from few localities in Asia and North America. It is scattered throughout the Europe and classified as the rare species, red listed in many regional lists as well (see Söderström et al. 2002). In the Czech Republic it is classified as vulnerable (Kučera & Váňa 2003).

No detailed study on ecology of *J. caespiticia* was done in the past (Konstantinova pers. com., Kučera pers. com., Váňa pers. com.). Hence, only general information from floras and personal requests to field bryologists was available.

Nomenclature of bryophytes used in the text follows Kučera & Váňa (2003).

Objectives

- description of local population dynamic, competitive ability, short-distance dispersal abilities and the role of disturbance on the rare *J. caespiticia* by means of four simultaneous manipulative experiments in the Šumava and the Krkonoše Mts.

- revision of its historical and current localities and an attempt at finding new localities in the Czech Republic with the aim to assess current distribution and its changes
- to describe the characteristics of habitat of *J. caespiticia*

The data can be included and compared to a broader framework of other studies concerning liverworts.

Study sites

To extrapolate the results from the permanent manipulative experiment performed within my BSc. thesis in Nové Údolí, the next three experiments were started in two, southern and northern, mountain regions in the Czech Republic. They were started at the localities known before 2004, which contained suitable amount of the cover of *J. caespiticia* for the placement of experimental plots. The experiments were performed in Nové Údolí, Javoří Pila and Gsenget in the Šumava Mts. and in the valley of the Bílé Labe river in the Krkonoše Mts.

Paper contents

Paper 1: **Population ecology of a leafy liverwort *Jungermannia caespiticia* Lindenb.** – manuscript

Paper 2: **Distribution of the rare liverwort *Jungermannia caespiticia* Lindenb. in the Czech Republic (Central Europe)** – manuscript

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Population ecology of a leafy liverwort *Jungermannia caespiticia* Lindenb.

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Abstract: Four permanent manipulative experiments were used to monitor the populations of *Jungermannia caespiticia*. The treatments were realised to study an effect of competition intensity and disturbance in relation to population dynamic. Particular topics, treated and discussed in this thesis were: local population dynamic, competitive ability, the role of disturbance, short-distance dispersal and potential role of endogenous gemmae.

Key words: *Jungermannia caespiticia*, liverwort, population ecology, competition, endogenous gemmae, disturbance

Introduction

Studies of the bryophyte ecology, particulary the population ecological traits such as seasonality of growth and reproduction, effect of population density on reproductive effort, and population dynamics, including dispersal and colonization, have mainly concentrated on mosses (Pohjamo & Laaka-Lindberg 2004, Laaka-Lindberg & Heino 2001, Shaw 2000). Few studies were realized with liverworts (Laaka-Lindberg 1999), the exception being e.g. *Ptilidium pulcherimum* studied by Jonsson & Söderström (1988) and Söderström & Jonsson (1989), *Blasia pusilla* by Duckett & Renzaglia (1993), *Lophozia silvicola* by Laaka-Lindberg (1999) and Laaka-Lindberg & Heino (2001), *Sphaerocarpos texanus* by McLetchie (1999 and 2001) and *Anastrophyllum hellerianum* by Pohjamo & Laaka-Lindberg (2004). The overgrowth competition and sex-ratio dynamics were currently studied in *Marchantia polymorpha* by Crowley *et al.* (2005). Nevertheless, an increasing research effort has been devoted to the population dynamics and genetics of bryophyte populations in recent years, as the concern for species survival has increased with intensifying human interference in natural habitats of bryophytes (Laaka-Lindberg *et al.* 2003).

The urgent task in current bryology is to collect data concerning rare and threatened species (During 1992), which are of interest because of their high risk of extinction. A great deal of effort has been directed towards developing a scientific framework to understand the patterns and causes of rarity. Determining whether the cause of rarity is intrinsic (related to the biology of the species) or extrinsic to the species (related to environmental factors) can also aid in assessing population viability and in developing management plans to reduce the likelihood of extinction (Carlsen *et al.* 2002). A thorough understanding of how life-history and ecological traits vary among species in relation to rarity and commonness is central to providing a scientific basis for the development of strategies aimed at conserving species in the long-term (Hartley & Kunin 2003, Murray *et al.* 2002). Available evidence suggests that bryophyte conservation should primarily consider the importance of establishment and habitat requirements for rare species. Future understanding of causes of rarity in bryophytes will benefit most by exploring the ecological drivers that allow species to expand their ranges (Cleavitt 2005).

For competent survey of species´ situation is important to know its precise habitat requirements, population dynamics and dispersal ecology (Hartley & Kunin 2003, Heinlen & Vitt 2003, Söderström *et al.* 2002, Herben 1994). No predictions can be made without parameter estimates based on real data (Herben & Söderström 1992). Results from the long-term manipulative experiments will provide broader knowledge of ecology and population or habitat dynamic (Hartley & Kunin 2003, Herben 1994). An important parameter in the classification of the species´ status is the population growth rate (Hartley & Kunin 2003, Sibly & Hone 2002). Detailed studies of species-specific recruitment probabilities provide an important step in determining the life-history stages at which variation in performance among species can promote the maintenance of diversity (Dalling & Hubbell 2002). One of the often cited main factors controlling diversity is disturbance (e.g. Rydgren *et al.* 2004, Mackey & Currie 2000, Wootton 1998). Regarding its advantageous effects on an early invading species and poor competitors (Chase 2003), regeneration experiments can thus be useful to reveal dispersal abilities and establishment processes which are critical in community assembly (Cleavitt 2002, Kimmerer 2005, Ross-Davis & Frego 2004).

Jungermannia caespiticia has been classified as a rare species in Europe (Paton 1999, Schuster 1969) and vulnerable in the Czech Republic (Kučera & Váňa 2003), although it does not belong to well known species, and its real status is thus difficult to assess. It is nevertheless still an adept to be included into the new Red List of liverworts, prepared by the European Committee on Conservation of Bryophytes - ECCB (Váňa pers. com.). No detailed study on ecology of *J. caespiticia* was done in the past.

In this study of *J. caespiticia*, I used the means of four simultaneous manipulative experiments in the Šumava and the Krkonoše Mts. in the Czech Republic with the following aims: 1) to describe its local population dynamic and the role of disturbance, 2) to assess its competitive ability and 3) to explore its reproductive strategy with respect to short-distance dispersal and potential role of endogenous gemmae. The results from this study will provide broader knowledge of ecology and dynamics of the rare *J. caespiticia* at the population level. Incorporating the data acquired from the parallel study of its distribution in central Europe, the results can be used for application of conservation measures.

Studied Species

Jungermannia caespiticia (Marchantiophyta, Jungermanniaceae) is an early invading ephemeral species growing predominantly in pale green tufts on bare acidic soil and temporary habitats, frequently vegetatively propagating by means of endogenous gemmae (Schuster 1969, Velenovský 1901), which are unique among Jungermanniales (Paton 1999), whereas the production of sporophytes is not common. It is a species with low competitive ability (Paton 1999). Most records are from anthropogenous sites, e.g. road sides or forest paths, in both lowlands and mountains. It reaches to 2600 m.a.s.l. in Alps (Frey 1995). *J. caespiticia* is often associated with *Gymnocolea inflata, Lophozia bicrenata, Cephalozia bicuspidata* (Váňa 1974), *J. gracillima, Nardia geoscyphus, Atrichum tenellum* (van Melick 1983), *Blasia pussila, Scapania nemorea, Calypogeia muelleriana*, *Diplophyllum apiculatum* (Schuster 1969) and *Ditrichum heteromallum* (anonymus 2000).

Nomenclature of bryophytes used in the text follows Kučera & Váňa (2003).

Methods

Study sites

The experiments were realised in Nové Údolí (N48°49'29"; E013°48'00"), Javoří Pila (N49°02'40"; E013°26'15"), Gsenget (N49°04'50"; E013°20'50" and N49°04'24"; E013°21'24") and the valley of the Bílé Labe river (N50°44'45"; E015°38'20" - N50°44'30"; E015°38'45") in the Czech Republic. The locality Gsenget has two parts distant ca 750 meters. Mean temperatures at all studied localities are 12–14 °C in June and -6 - -7 °C in January, and mean precipitation in growing season is 600-700 mm (Quit 1971). Other characteristics are summarized in Table 1.

	N. Údolí	J. Pila	Gsenget	B. Labe
region	cental Šumava Mts.	cental Šumava Mts.	western Šumava Mts.	Krkonoše Mts.
locality	abandoned sand pit	forest path	footpath sides, ditches	road side, earth bank
altitude	850	1050	980, 1030	910-960
substrate	sand (acidic)	sandy-loamy (acidic)	sandy-loamy (acidic)	sandy-loamy (acidic)
surrounding vegetation	spruce forest, mesic meadow	spruce forest, wet meadow	wet meadow; beech forest	spruce forest

Table 1. The characteristics of the experimental localities

Experimental design

15 permanent plots 15x15 cm were established in each studied locality and fixed with wooden sticks. Plots were divided in three groups according to impact, each group with five replications. In the first group the vegetation surrounding the tufts of *J. caespiticia* was removed (*remsur*), the second group included plots with completely removed vegetation cover (*remcom*) and the third group was left without impact (control). The aim was to test the effects of different types of disturbance and different levels of competition on the dynamic and reproduction of *J. caespiticia*. *Remsur* plots represented the disturbance in the close neighbourhood of *J. caespiticia* and enabled to observe its reaction on both disturbance and loss of potential competitors. *Remcom* plots showed the process of colonization of free substrate and subsequent succession in places, where *J. caespiticia* co-occurs with other bryophytes. *Remcom* plots were established in microsites, where *J. caespiticia* was previously present. Vegetation cover and top soil surface, which could contain fragments or propagula, were removed using tweezers and a knife.

Relatively small population size of *J. caespiticia* at studied localities allowed me to cover whole local population range, and therefore I expected minimal effect of different environmental conditions (except Gsenget which contains two parts distant ca 750 meters). On the other hand, due to small population size, it was not possible to perform some recurrent experimental design, as I had to follow specific positions of *J. caespiticia* islets.

Data collection

The data were collected twice, in the beginning and in the end, in the growing season if possible, to catch the differences in cover, which have arisen during summer and winter periods. The experiment in Nové Údolí was established in May 2001 within the framework of my earlier preliminary study (Sova 2003). The dates of the collection are summarized in Table 2. Due to the destruction by human activity, only nine plots (three replications for each group) remained in Gsenget after May 2005 due to human-caused destruction.

	N. Údolí	J. Pila	Gsenget	B. Labe
2001	may, october			
2002	april, october			
2003	april, october			october
2004	may, october	june, october	july, november	july, october
2005	september	may, october	may, october	september

Table 2. The design of the data collection at the localities

Parameter measurements

Soil moisture was only roughly estimated, based on a scale from 1 to 5. The aim was to find out whether studied localities differ markedly in the water content. 1 - dry, 2 – moist, 3 - wet, 4 - saturated and 5 - submerged substrate.

The density of bryophyte cover is based on a proportional scale from 1 to 5. Appropriate relative densities to the scale degrees (in brackets), visually assessed in the field according my estimation, are: 0 (1); 0.25 (2); 0.5 (3); 0.75 (4) and 1 (5). Degree 1 corresponds to an empty substrate, 2 approximately to the density up to 30%, 3 to interval 30–60%, 4 to 60–90% and degree 5 corresponds to more than 90%, which means continuous bryophyte cover.

The cover of each species in the plots was measured according the following method. Real situation from particular plots was drawn on a milimeter-scaled graph paper. For more precise estimation the cardboard with 15×15 cm square aperture and 3 cm mesh size was used. Similar parts of the cover (p), which were suggested to be of similar species composition, were drawn with the same color. The cover of each part (Cp) was counted exactly, as particular cover of a milimeter-scaled graph paper was counted, and multiplied by the appropriate relative density of the cover (Dp). Samples of species were taken uniformly from all (*j*) different parts of the plots. With regard to the plot and bryophyte size, samples were taken with tweezers to avoid the adverse effect on the rest of the cover. The species composition and ratios were determined in the laboratory. The value of relative abundance of the species *i* in appropriate parts (A*i*p) was estimated visualy for each species. A*i*p corresponds to biomass proportion ratio of the species *i* from biomass of all species. The cover of the species *i* (C*i*) equals the sum of covers of *j* types of different parts, which included species *i* (Cp*ij*), multiplied by relative abundance of species *i* in those parts (A*i*p*j*). The covers were weighted by their densities (Dp*j*). Than $\mathbf{C}\boldsymbol{i}\mathbf{=Cp}\boldsymbol{ij}\mathbf{*A}\boldsymbol{i}\mathbf{p}\boldsymbol{j}\mathbf{*Dp}\boldsymbol{j}$. Mean covers of the species present in the plots were counted for each type of the plot. When the cover values were put on a time scale, the dynamics of a single species, respectively of whole assemblage, was acquired.

The growth rate was estimated by means of relative accessions, which were obtained from differences between consequent readings. Calculation of accessions was performed with mean cover values for each plot type and expressed in percents. Growth and competitive abilities of *J. caespiticia* were commented regarding its dynamic differences within the plot types, respectively within different kind of disturbance and competition intensity.

As an attempt to find out the mechanism or factors influencing the tuft establishment (e.g. the pressure of competitiors), the growth form of *J. caespiticia* was recognized as 1) tuft, 2) dispersed plants among other bryophytes, and 3) juvenile form. The growth forms were recognized ex-post in the laboratory from the cover samples. Juvenile plants were distinguished from dispersed adult plants as being smaller, with loosely arranged leaves and without propagula.

To find out the dependence of propagulum production on season, impact, soil moisture, growth form of *J. caespiticia* or competition intensity, the occurrence of dispersal propagula (sporophyte and gemmae) was recorded in all plots during the experiment in the field and in the samples determined in the laboratory.

Analyses

The relationship of tufts and dispersed *J. caespiticia* covers was tested with correlation test; the differences in gemmae occurrence between tufts and dispersed *J. caespiticia* were tested with t-test for independent variables; the dependence of juvenile *J. caespiticia* and gemmae occurrence on a plot type was tested with ANOVA (generalized linear/nonlinear models with binomial distribution); the differences in cover of *J. caespiticia* between plot types in particular localities and the differences in bryophyte cover density between experimental localities were tested with ANOVA (repeated measurements); soil moistures in the localities and in plot types in particular localities were compared with Kruskal-Wallis test; the changes in soil moisture in particular localities were tested with Friedmans test; the changes of bryophyte cover in particular localities were tested with simple regression, and the effect of soil moisture on the cover of *J. caespiticia* was tested with multiple regression. The tests were realized using Statistica 5.5 software (StatSoft Inc. 1984 – 1999). To show bryophyte species distribution in the experimental localities, redundancy analysis (RDA) and Monte-Carlo permutation test from CANOCO for Windows version 4.5 (ter Braak & Šmilauer) were used. Only the results significant at 5% p-level are presented.

Results

Species distribution

The results of Monte-Carlo permutation test showed significant differences in composition of bryophyte species in particular localities (number of permutations 499; first axe: eigenvalue=0.21, F=4.24, p=0.002; all axes: eigenvalue=0.4, F=3.55, p=0.002). The bryophytes common in all experimental localities were: *Jungermannia gracillima, Nardia scalaris, N. geoscyphus, Cephaloziella divaricata, Dicranella heteromalla* and *Pogonatum urnigerum*, which represent ca 18% of all species present in the localities. The species distribution was demonstrated by RDA (Fig. 1.), because maximal lenght of gradient in DCCA was 1.8 (Lepš & Šmilauer 2000). First two axes explained 34.4 % of total variability.

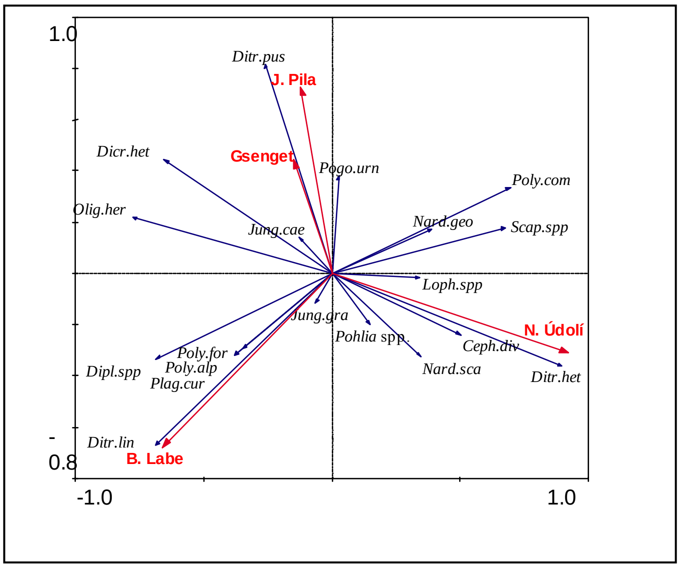

Figure 1. RDA diagram illustrating the distribution of the species in the experimental localities; *Ceph.div-Cephaliziella divaricata, Dicr.het-Dicranella heteromalla, Dipl.*spp.*-Diplophyllum obtusifolium* and *D. album, Ditr.het-Ditrichum heteromallum, Ditr.pus-Ditrichum pusillum, Jung.cae-Jungermannia caespiticia, Jung.gra-Jungermannia gracillima, Loph.spp-Lophozia* spp.,*Nard.geo-Nardia geoscyphus, Nard.sca-Nardia scalaris, Olig.her-Oligotrichum hercynicum, Pogo.urn-Pogonatum urnigerum, Plag.cur-Plagiothecium curvifolium, Poly.alp-Polytrichum alpinum, Poly.com-Polytrichum commune, Poly.for-Polytrichum formosum, Scap.*spp.*-Scapania curta* and *S. irrigua*

Soil moisture and cover density treatment

The results of Kruskal-Wallis test did not show significant differences in soil moisture between the experimental localities (the values from control plots measured from spring 2004 to summer 2005 were tested). The impacts did not influenced soil moisture. Kruskal-Wallis test did not show significant differences in soil moisture between the plot types in particular localities. The results of Friedmans test showed significant differences in soil moisture (in control plots) between particular measurements in N. Údolí: F(9; 36)=4.26, p=0.001. The test was nearly significant at 5% p-level in J. Pila: F(4; 16)=5.73, p=0.057 and Gsenget: F(3; 6)=4.25, p=0.062. Multiple regression did not show significant effect of soil moisture on the cover of *J. caespiticia* in those localities.

The experimental localities differed in bryophyte cover densities. The differences in bryophyte cover density between the localities were tested using the values from the control plots measured in the period from spring 2004 to summer 2005. The results of ANOVA (repeated measurements) show significant role of factor ´locality´: df=3, F=3.37, p=0.049. The lowest bryophyte cover density it was in B. Labe - 0.56±0.11 (±SD) and the highest in Gsenget - 0.82±0.01. In J. Pila it was 0.73±0.12 and in N. Údolí 0.77±0.17. The results of regression show that bryophyte cover density at the locality J. Pila changed significantly during the experiment (df=13, F=4.83, R^2=0.271, β=0.52, p=0.047), while no significant change was noted at other localities.

Dynamics of J. caespiticia

The dynamics of *J. caespiticia*, other dominant bryophyte and total cover in particular localities and plot types are illustrated in Fig. 2-5. The experiment in N.Údolí included nine measurements. The first four measurements (three in Gsenget) are used for comparison of the dynamics in studied localities. The cover of *J. caespiticia* and other bryophytes in the control plots was rather stable in all localities, except for the increase in the *Dicranella heteromalla* in Gsenget and *Ditrichum pusillum* at J. Pila. Most of the species had similar cover as *J. caespiticia*, except for the dominants (see Fig. 2-4). The other species with higher cover than *J. caespiticia* were *Dicranella heteromalla*, which reached about 20-30% in J. Pila and Gsenget, and *Cephaloziella divaricata* and *Scapania* spp., which reached about 10-15%. The control plots in B. Labe were an exception, because *J. caespiticia* was dominant species there. In *remsur* plots, *J. caespiticia* was the first species to disperse and kept subsequently the highest cover at least for 1.5 year at all experimental localities except J. Pila. The dominant species in J. Pila was *Ditrichum pusillum*. *J. caespiticia* overgrewed the other bryophytes in J. Pila, but started to increase not before the last measurement. In *remcom* plots, *J. caespiticia* mostly appeared as the first species, quickly expanded and stayed as a dominant species. J. Pila was an exception. The trend was similar to *remcom* plots in the other localities, but *Ditrichum pusillum* was the first species, which appeared and dominated there. In autumn 2005 it was already overgrown by *J. caespiticia*, which increased rapidly. Regarding longer data set from N. Údolí, *J. caespiticia* reached maximum cover after three years of experiment duration in all plot types. For three years it had been a dominant species in *remsur* and *remcom* plots. After third year it started to decrease, while the cover of the other bryophytes was increasing. In the control plots it almost disappeared in 2005 and in *remsur* and *remcom* plots its cover quickly decreased.

The dynamics of *J. caespiticia* in the control, *remsur* and *remcom* plots was compared. Each locality was tested individually. To obtain comparable results from N. Údolí, I tested only the first four measurements in order to have the adequate amount to the repeats as at other localities. The removal of surrounding cover significantly influenced the growth of *J. caespiticia* in N. Údolí and Gsenget. Removal of complete cover had significant effect only in N. Údolí. The latter locality was also the only one, where growth of *J. caespiticia* differed between *remsur* and *remcom* plots. All significant effects of the impacts on growth of *J. caespiticia* were positive.The results of ANOVA (repeated measurements) refer to time and impact interaction. Comparison of control and *remsur* plots in N. Údolí: df=4, F=3.32, p=0.022 and Gsenget: df=3, F=3.97, p=0.035, control and *remcom* plots in N. Údolí: df=4, F=6.87, p<0.001, and *remsur* and *remcom* plots in N. Údolí: df=4, F=3.69, p=0.014. The tests performed with all obtained measurements in N. Údolí showed significant results from comparison of control and *remcom* plots: df=9, F=3.43, p=0.002, and *remsur* and *remcom* plots: df=9, F=3.84, p=0.001.

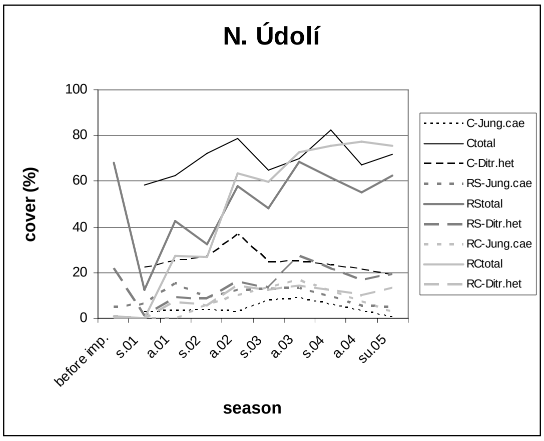

Figure 2. The dynamics of *J. caespiticia* (*Jung.cae*), *Ditrichum heteromallum* (*Ditr.het*) and total cover; s-spring, a-autumn, su-summer; C-control plots, RS-surrounding vegetation removal, RC-complete cover removal

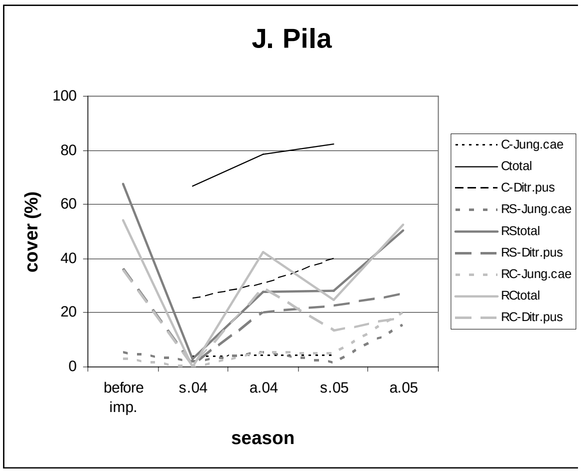

Figure 3. The dynamics of *J. caespiticia* (*Jung.cae*), *Ditrichum pusillum* (*Ditr.pus*) and total cover; s-spring, a-autumn; C-control plots, RS-surrounding vegetation removal, RC-complete cover removal

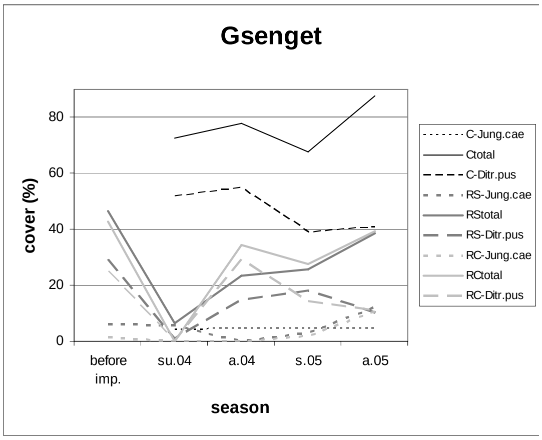

Figure 4. The dynamics of *J. caespiticia* (*Jung.cae*), *Ditrichum pusillum* (*Ditr.pus*) and total cover; s-spring, su-summer, a-autumn; C-control plots, RS-surrounding vegetation removal, RC-complete cover removal

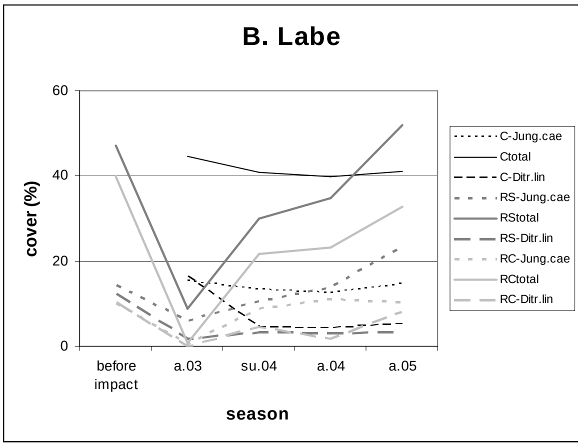

Figure 5. The dynamics of *J. caespiticia* (*Jung.cae*), *Ditrichum lineare* (*Ditr.lin*) and total cover; s-spring, su-summer, a-autumn; C-control plots, RS-surrounding vegetation removal, RC-complete cover removal

Between plot-types differences in the cover of the tufts and dispersed *J. caespiticia* were tested with ANOVA (repeated measurements). The results refer to cover and time interaction. Removal of the cover surrounding the tufts significantly influenced the dynamic between tufts and dispersed plants in N. Údolí: df=7, F=3.85, p=0.002, and J. Pila: df=3, F=19.53, p<0.001. Complete cover removal had significant effect on the dynamic between tufts and dispersed plants in N. Údolí: df=7, F=5.88, p<0.001, J. Pila: df=3, F=3.79, p=0.023, and B. Labe: df=3, F=4.36, p=0.014. The dynamic of dispersed plants differed significantly between control and *remsur* plots in N. Údolí: df=6, F=2.3, p=0.049. The effects on the rest combinations were not significant at 5% p-level.

Correlation (r) of cover proportions between dispersed *J. caespiticia* and the tufts in particular plot types was treated. The dynamics of particular growth forms is illustrated in Fig. 6. Only r > 0.5 / < -0.5 are shown. r values in the control plots were: r=-0.96 in J. Pila and r = -0.96 in Gsenget. They were negative for all treated localities. The situation for *remsur* plots was analogous, with r value in N. Údolí –0.64. The trends in *remcom* plots were different, positive in N. Údolí: r = 0.6, J. Pila: r = 0.76 and negative in Gsenget r = -0.94 (and B. Labe).

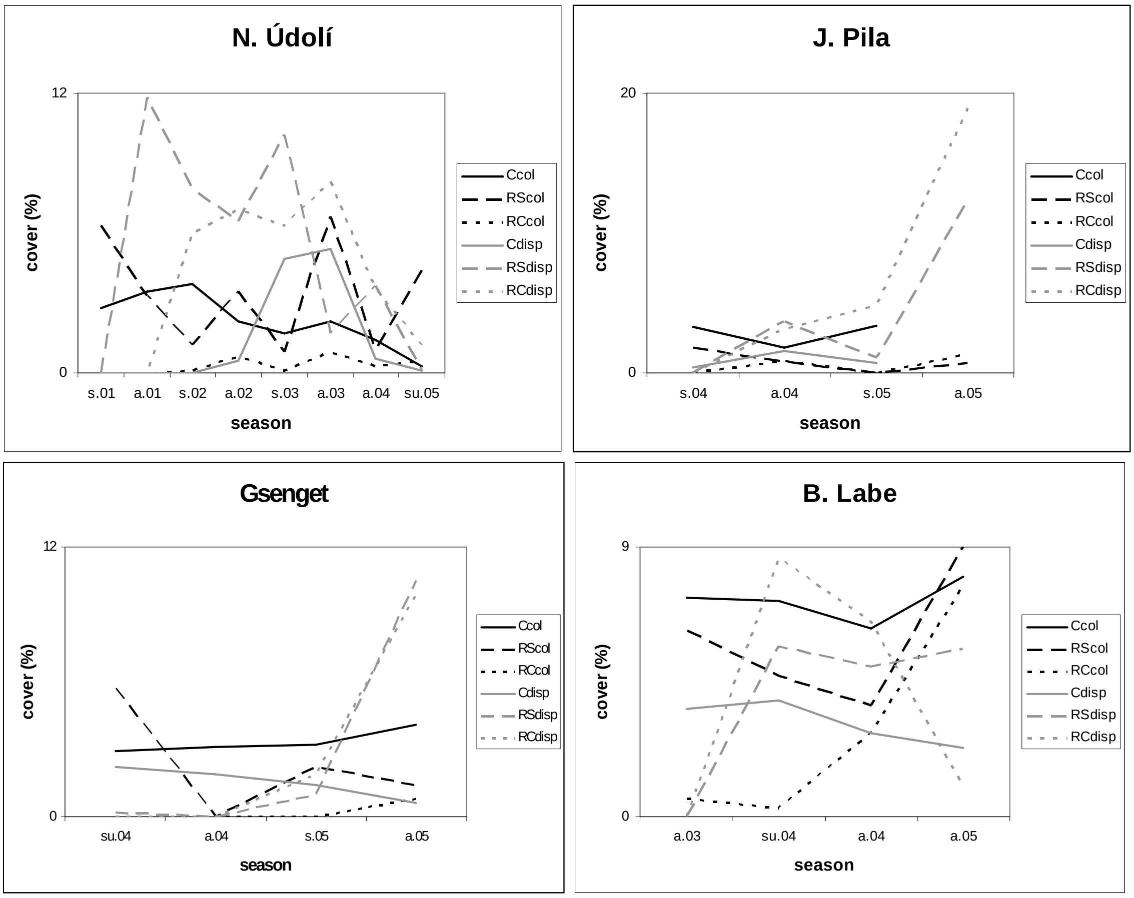

Figure 6. The dynamics of particular growth forms of *J. caespiticia* (col-tufts, disp-dispersed plants); C-control plots, RS-surrounding vegetation removal, RC-complete cover removal; s–spring, a–autumn, su–summer

I recorded the occurrence of juvenile form of *J. caespiticia* in particular plot types. Plot type had no significant effect on the occurrence of juvenile form of *J. caespiticia*. Average proportions of juvenile form occurrence from all experimental localities were: 13.8% of control plots, 43.3% of *remsur* plots and 28% of *remcom* plots.

Gemmae and sporophyte occurrence

Plot type had no significant effect on the occurrence of gemmae. Gemmae were present in 48.8% of control plots, in 45% of *remsur* plots and in 36.3% of *remcom* plots. Gemmae occurrence did not differ significantly between tufts and scattered plants of *J. caespiticia*. In average, it was present in 34.7% both of tufts and dispersed plants. The proportions of gemmae occurrence in particular plot types were recorded during the experiment and it was found that gemmae occurrence showed dependence on a season, as illustrated in Figure 7.

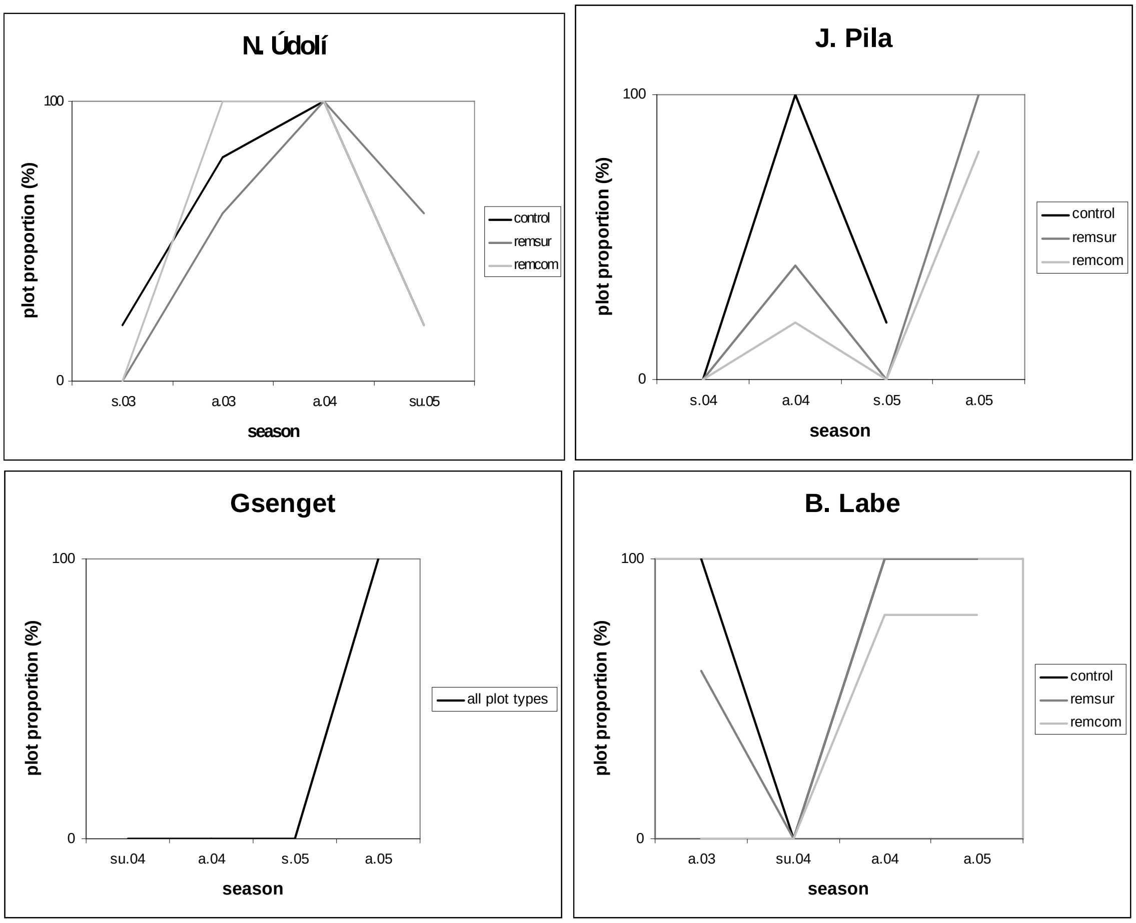

Figure 7. The proportions of gemmae occurrence in all plot types; C-control plots, RS-surrounding vegetation removal, RC-complete cover removal; s–spring, su–summer, a–autumn

Sporophytes were recorded - in N. Údolí (spring and autumn 2003) in *remcom* plot in dispersed cover of *J. caespiticia* within the cover with relative density 0.5 and 0.75, in J. Pila (spring 2005) in *remcom* plot in a tuft with relative density 0.9 and in Gsenget (spring 2005) in a control plot in tufts with relative densities 0.5 and 1.

Discussion

Environmental and species influences

Significant differences in bryophyte cover density between the localities led to an assumption that there is at least one factor, namely the density of potential competitors, which could influence the course of the experiments. It is therefore proper to discuss the dynamic of *J. caespiticia* individually at each locality and to include potential effect of the cover density. I suppose that the differences in bryophyte cover densities reflect the effect of another untested parameter, which is probably the frequency of habitat disturbance. B. Labe is the locality with the lowest average bryophyte cover and it is the only experimental locality, where *J. caespiticia* occured on a slope. The substrate dynamics of the slopes is more intensive, being difficult for species to keep there (Klausmeier 2001). Winter operated as a disturbance factor too, because the covers of the bryophyte species were decreasing after the winter periods (Fig. 2. and 4.). In contrast to other bryophytes in the plots, *J. caespiticia* was able to compensate the winter decreases with rapid increase of its cover in spring (Fig. 2. and 5.). No detailed observation of the recovery of *J. caespiticia* after the winter period is available. One of the possible explanations is the mass production of gemmae (discussed in the following text).

Soil moisture was found to be similar between the localities. Nevertheless, it was changing within three tested localities, but the results of regression showed that these changes did not influence the cover of *J. caespiticia*.

Bryophyte species composition differed between the experimental localities, as illustrated in RDA diagram (Fig. 1.), but it should be noted that similar morphological types are present in the localities, e.g. *Ditrichum* genus occurred in all studied sites, but particular species differed, or *Scapania* genus was not present in B. Labe, but it was substituted with *Diplophyllum* spp.. I suppose that the bryophyte assemblages in particular studied microlocalities were of similar character and represented thus similar influence on *J. caespiticia*.

The role of impacts

The impacts, performed in the beginning of each experiment, simulated disturbance and reduction of competition intensity. I supposed that the cover of *J. caespiticia* in *remsur* plots will be higher and the succession will be faster than in *remcom* plots. This assumption was based on a presumption that tufts can directly expand to free soil. The expected pattern was only apparent in B. Labe (Fig. 5). The cause was probably in destructive effect of removal on the tufts left in plots. Already established tufts in bryophyte cover may be facilitated by surrounding bryophytes. *J. caespiticia* could suffer after the removal of surrounding cover e.g. with more intensive dessication or with increased desintegration of the tuft islets, which might decrease its fitness and longevity. This is supported with the results from five year period in N. Údolí, where significant differences in the dynamics of *J. caespiticia* were between all plot types except control and *remsur*. Similar effect of removal of surrounding vegetation was described on clonal moss *Hylocomium splendens* by Økland (2000).

J. caespiticia started its expansion immediately after the impact in *remcom* plots. The exception was N. Údolí, where it started one season later. I suggest, it had occurred there earlier, because the young plants of *J. caespiticia* are likely to be confused with some plants of *Jungermannia gracillima* var. *gracillima* (e.g. Paton 1999, Duda & Váňa 1970 and Schuster 1969), which were present just in the season after the removal, where *J. caespiticia* was missing. Also its cover (5%) in the first season after the impact corresponds to belong rather to *J. caespiticia*. *J. gracillima* itself seemed to occur there later in the spring of 2002. Regrettably, it is not possible to find it out at present, so original data were not altered.

The results of statistical tests treating the differences in the dynamic of *J. caespiticia* between particular plot types were inconsistent for tested localities. During my previous work (Sova 2003) performed in N. Údolí, the significant effect within all plot types on the cover of *J. caespiticia* was found. With respect to the other localities the similar effect was found only in Gsenget between control and *remsur* plots. Relatively high cover of *J. caespiticia* in the control plots in B. Labe was probably the main cause of non-significant differences in its cover between plot types, because it eliminated the differences between them. In the case of J. Pila and Gsenget, *J. caespiticia* started to increase its cover in the last measurements. It is possible that the differences in the dynamics will appear later.

Competition ability

Relatively low increase of *J. caespiticia* in the impacted plots in J. Pila can be explained with rapid increase of *Ditrichum pusillum* in both *remsur* and *remcom* plots. Its rather high cover in early stage of succession might disable *J. caespiticia* from expansion. This can be interpreted as the negative effect of interference competition, which is also evident in *remcom* plots in N. Údolí (Fig. 2) and J. Pila (Fig. 3.). Similar effect was observed e.g. by Wiklund & Rydin 2004 on the colonies of a bark inhabiting moss *Neckera pennata*. Competitor density restricting remarkably growth of *J. caespiticia* was about 70% in the impacted plots in N. Údolí. More observations from the other experiments is necessary to make more precious conclusions about the limiting cover density.

With respect to relatively small size of *J. caespiticia*, there is coincidence with Økland (2000), who suggested that species persistence is dependent on its size, so that large-sized species can easily suppress small-sized species. Smaller species will then be in more danger of becoming localy extinct. The size of *J. caespiticia* is probably an important factor which disable it from long-term persistence in bryophyte associations. The effect of large-sized species suppressing small-sized species was also reported by Corradini & Clément (1999) on *Polytrichum commune*. Weak competitive ability of *J. caespiticia* probably restricts it to mostly ephemeral habitats with bare substrata. The dynamics of such temporaly habitats is often independent on presence of species. Occurrence of species occupying those habitats is therefore determined mainly by habitat dynamic (Johnson 2000).

Trends in increasing the cover and becoming one of the dominant species in the impacted plots were common in all experimental localities during the first two-three years after the disturbance. The following measurements from N. Údolí possibly predict what will happen in the other experimental localities. With regard to the habitat character, I suppose that analogous situation may happen in J. Pila and Gsenget. After several years *J. caespiticia* will reach its maximum cover and subsequently will decrease due to increased competition intensity. Different situation will potentially happen in B. Labe. It is the only locality, where *J. caespiticia* dominate in the control plots at relatively high and stable cover. I suppose it is due to more intensive substrate dynamics, creating continuous disturbances. *J. caespiticia*, as a week competitor, is advanced in such conditions, where other species are disabled to establish (Klausmeier 2001).

Short-distance dispersal

Stable and high cover in the control plots in B. Labe is probably sustained with high gemmae production. This agree with Zonneveld (1995), who claims that the mass effect and vicinism can operate in combination and in this way contribute to the stability of pioneer vegetation. Early expansion of *J. caespiticia* in *remcom* plots indicates that some abundant reproductive propagula gave arise to *J. caespiticia*. It is difficult, with acquired data, to assess whether it was spores or gemmae. I suppose, that most of *J. caespiticia* individuals origin from the gemmae, because I recorded them regulary in most of the plots in the experimental localities. Most of the authors affirm the abundance of gemmae on *J. caespiticia* too (e.g. Paton 1999, Váňa 1974, Schuster 1969 and Velenovský 1901).

The occurrence of gemmae did not depend on the plot type or growth form of *J. caespiticia*. It indicates that individual plants produce gemmae independently on the surrounding cover density. The production of gemmae seemed to alter in treated localities within the seasons (Fig. 7.). It was shown that gemmae occured with maximum frequency in autumn. I suggest, that *J. caespiticia* is directed to built the gemmae in the second half of growing season. In general, the timing of propagula production can be the result of selective pressure (Mathias *et al.* 2001). In the case of *J. caespiticia*, the timing may be set by trade-off between growth and reproductive effort and it could indicate some energetical cost of endogenous gemmae. In comparison, low-cost exogenous gemmae on *Lophozia silvicola* and *Anastrophyllum hellerianum* occured independently on season and shoot density (Pohjamo & Laaka-Lindberg 2004, Laaka-Lindberg 1999). Different results were obtained by Kimmerer (1991) on a moss *Tetraphis pelucida*. He observed significant relationship between shoot density and reproductive modes. Seasonal dependence of gemmae production lead to a presumption that endogenous gemmae in *J. caespiticia* are predetermined to be an overwintering means. They may replace spore function, ensuring further colonization of identical dynamical habitat. It corresponds to a statement of Laaka-Lindberg (1999), who claimed that asexual propagula, often large in size, germinate better and faster than spores. It is not known if they are released before or after winter season, but their role is probably to be ready to grow as soon as possible and establish dense tufts, which are relatively capable to resist the competition of other bryophyte species. Dormant gemmae can quickly colonize empty space created by shoot mortality during winter (Laaka-Lindberg & Heino 2001). This fact could explain continuous increase of *J. caespiticia* in N. Údolí and B. Labe, despite the reducing effect of winter. This way of pre-emptive competition has generally been considered as advantageous, especially in unpredictable habitats (Pohjamo & Laaka-Lindberg 2004), but compared to *J. caespiticia* it concern targeted expansion to particular habitat. Gemmae production on *J. caespiticia* is in coincidence with general pattern, presented e.g. by Travis & Dytham (1999), where the dispersal is expected to be favoured in temporal habitats, as species need to be able to track a moving resource. The dynamical habitats on slopes do not move in space, but still change themselves, and effective dispersal is thus sustaining *J. caespiticia* at one particular site. In general, specific conditions require specific adaptations (Poethke *et al.* 2003) and the various modes of reproduction play an important role in the life cycles, especially in stands with high disturbance, which is not only the case of bryophytes (Zechmeister & Moser 2001).

The production of sporophytes on *J. caespiticia* is reported to occur rarely in Britain and discoveries were made in the period from May to June (Paton 1999), whereas Velenovský (1901) recorded sporophytes in autumn. I have occasionally recorded fertile plants of *J. caespiticia* at periodically visited localities in N. Údolí, J. Pila and Gsenget both in spring and autumn.

Growth form

J. caespiticia is characteristic with the occurrence in the form of tufts. Few authors have mentioned of scattered plants of *J. caespiticia* among other bryophyte species (e.g. Smith 1990, Schuster 1969) and no literature, describing dispersed plants of *J. caespiticia* on bare soil, was found. I suppose that these dispersed juvenile or mature plants play an important role not only in the tuft establishment but in maintaining the tufts and populations. This statement is based on mostly negative values of the correlation coefficients of tufts and dispersed plants proportions. Fig. 6. refers to an interior population dynamics and shows very convincing course of the tufts and dispersed plants dynamics, particulary at the localities J. Pila and N. Údolí. It seems that the cover of tufts is mutually replaced with dispersed plants. It is neccessary to include the role of disturbance, which creates free space for potential expansion of the tufts, which can be subsequently established from the scattered plants already present in the cover. The results showed that the cover of scattered form of *J. caespiticia* increased after the removal of vegetation, as illustrated in Fig. 6..

Conclusions

It was shown that *J. caespiticia* is an ephemeral pioneer species, connected predominantly with disturbed habitats with low density of other bryophyte species. Low competitive ability is caused by small size of individual plants and its growth form. The populations of *J. caespiticia* are maintained by permanent disturbance, which reduces the density of bryophyte cover. It was found that the tufts are not the only form of occurrence of *J. caespiticia*. Dispersed plants were common in all plot types and possibly play a role in tuft establishment and sustaining the cover of *J. caespiticia*. Endogenous gemmae probably play a role in sustaining the local populations on frequently disturbed substrata.

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Distribution of the rare liverwort *Jungermannia caespiticia* Lindenb. in the Czech Republic (Central Europe)

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Abstract: Historical and current localities of *Jungermannia caespiticia* in the Czech Republic were revised and new localities were searched. The changes between recent and historical distribution and its relation to habitat availability were discussed.

Key words: *Jungermannia caespiticia*, rare liverwort, distribution, Czech Republic

Introduction

Many species have disappeared from their original habitats (Pavoine *et al.* 2005, Hallingbäck 2003) and there is a constant increase in the number of endangered bryophyte species at national and international scales (Zechmeister *et al.* 2002). Unfortunately, most of rare and threatened bryophytes belong to the ′data deficient′ category (Söderström *et al.* 1992). Due to insufficient survey the threat status of many bryophytes is often overestimated (Söderström *et al.* 2002). In several countries highly intensified searching has led to the discovery of many previously unrecorded species and rediscovery of several that thought to be extinct (e.g. Kučera *et al.* 2004, Zechmeister *et al.* 2002, During 1992). On the other hand, as the result of overlooking the bryophytes, loss of diversity and an unknown amount of information may happen (Longton & Hedderson 2000, Söderström *et al.* 1992).

Jungermannia caespiticia is probably one of the species, which is able to take advantage of certain types of disturbed sites, e.g. roads or sand pits (Paton 1999, Melick 1983, Konstantinova pers. comm.), which occure commonly at the landscape. Its rarity, regionally difficult to understand, as is the extreme disjunction in range (Schuster 1969), is somewhat confounding. To explain this phenomenon more knowledge of its distribution, habitat requirements and population ecology is needed. *J. caespiticia* is considered to belong to the data deficient category concerning its distribution and abundance in most of European countries (Váňa pers. comm.). The species is inconspicuous and easily overlooked by field bryologist. It is therefore necessary to do intent research to this particular species to acquire more precious information on its distribution. Afterwards we can deduce proper conclusions about the status assessment and implement some protective measures. Metapopulation structure (Armstrong 2005, Fahrig 1998) and disturbance intensity (Rydgren *et al.* 2004, Wootton 1998), which relate directly to a species persistence in landscape, are also useful to be studied. Changes in abundance, fertility and general vitality of species can be detected by comparison with old data and specimens. It is a useful way of obtaining reliable information on the past distribution of species (Herben 1994, During 1992).

The main objectives of this study of *J. caespiticia* are: 1) to assess its current distribution in the Czech Republic, 2) to assess changes in the distribution during last century, 3) to find out how the distribution is related to habitat quality and habitat amount. Additional target was to compare its actual and historical distribution in neighbouring countries to extent the results to Central European region. To obtain the historical data, I could use the treatment of Duda & Váňa (1970), who summarized the records from 23 localities in the Czech Republic from the 19th to the first half of the 20th century. The data can be used for conservation management or compared to other studies concerning distributions of a rare species.

Studied species

Jungermannia caespiticia (Marchantiopsida, Jungermanniaceae) is an ephemeral pioneer species growing predominantly in pale green tufts on bare acidic soil and temporary habitats like road edges, forest paths, abandoned sand pits etc. in both lowlands and mountains. Outside Europe, where it is scattered throuhout, *J. caespiticia* is reported as a rare from Asia (Transcaucasus area) and North America (Western Canada, North-western and North-central USA). In Europe it is classified as a rare species, red-listed in many, particulary Central European regional lists (e.g. Netherlands – susceptible, Denmark – potentially threatened, Belgium – rare, Austria – potentially threatened, Czech Republic – vulnerable, Hungary – vulnerable, Bulgaria – rare; Söderström et al. 2002), being more frequent in the north and north-east Europe (Konstantinova pers. com., Schuster 1969). It is an adept to be included into the new Red List of liverworts in preparation under ECCB (Váňa pers. comm.). The distribution of *J. caespiticia* is shown in Figure 3.

Nomenclature of bryophytes used in the text follows Kučera & Váňa (2003), that of vascular plants follows Kubát (2002).

Methods

Revision of the localities

The historical localities were revised following Duda & Váňa (1970), who summarized the records of *J. caespiticia* between the years 1836 and 1966. It is a matter of 23 localities (Tab. 1.). There was no exact localization in the article or on the specimens from local herbarias' collections. While searching in the field I had to use the information on habitat or associated species with *J. caespiticia* from literature and my own experience. According its habitat character, it was most useful to search along the road sides, ditches, banks, sand or stone pits and other habitats in the area of the historical localities, where bare or disturbed substrata were available. Such stands were easily detectable with use of a hiking maps (1:50 000). Based on literature (Anonymus 2000; Anonymus 2004) and personal communication (Kučera, Palice, Plášek) the list of seven recent localities, where *J. caespiticia* was recorded since 1996, was established (Tab. 1.). Potential suitable habitat was searched and measured also at the sites, where no previous records of *J. caespiticia* were done (Tab. 1.). Searching was also performed in the surrounding of recent localities.

When potentially suitable site was found, several parameters were recorded: presence of *J. caespiticia*, occurrence of sporophyte and gemmae, associated bryophyte species, dominant vascular vegetation, actual soil moisture, classification of soil type, soil pH, altitude, mean annual temperatures and mean precipitation in growing season. Such sites as road sides or ditches were observed and sampled in surrounding of particular localities. Mean number of sites measured at each locality was 3.8. Bryophyte species present right on bare substrate and dominant vascular species in close neighbourhood were recorded. Soil moisture was roughly estimated on the base of a scale from 1 to 5. The aim was to find out whether studied localities differ markedly in a water content. The values of soil moisture were not exactly measured, and therefore serve just for orientation. Particular degrees of a scale were assessed according my estimation: 1 – dry, 2 – moist, 3 - wet, 4 - saturated and 5 - submerged substrate. Soil type was classified as sand, loam, clay, organic or its combination. One to two soil samples for pH measurement (cca 50 ml) were collected at some sites from each locality and measured in the laboratory with *Hanna instruments HI 9024 microcomputer, pH meter* according to Zbíral (1995). Altitude was determined after Duda & Váňa (1970) and from hiking maps (1:50 000). Mean annual temperatures and precipitation in growing season follows Quitt (1971).

Analyses

t-test for independent variables was used to find out the differences between the historical and recent localities in altitude, mean annual temperatures and mean precipitation in growing season. Mann-Whitney U-test was used to find the differences in pH, soil moisture and soil type. Statistical tests were performed with the parameters measured in historical and recent localities of *J. caespiticia*. No characteristics except altitude were available for the historical localities. Other parameters were acquired at present and they were also tested. The aim was to find wheter those parameters differ between the historical and recent localities. More than one site was usually measured. In the case of altitude, I used average values for each locality. Regarding soil moisture, soil pH and soil type, all values acquired in the historical and current localities were compared. Due to closeness of 8 localities in Cvikov region, Javoří Pila and Modrava, and Gsenget and Polední mt., these localities were tested as one. Localities Černé lake (1996) and the valley of the strem Rohovec (1999) were included in recent localities. Statistica 5.5 software (StatSoft Inc. 1984 – 1999; Lepš, 1996) was used to perform the tests. Redundancy analysis (RDA) and Monte-Carlo permutation test from CANOCO for Windows version 4.5 (ter Braak & Šmilauer) was used to show the species distribution between tested localities and relation to environmental parameters. Only the results significant at 5% p-level are presented.

Results

The localities treated in this study are listed and described in Table 1. I was able to visit 17 of 23 historical localities, listed in Duda & Váňa (1970) between June 2004 and October 2005. *J. caespiticia* was rediscovered at four sites: Železná Ruda, Jelení hora (Pomezní Boudy), Bílé Labe and Cvikov – mt. Klíč. The habitat character is similar at all sites. It is bare or sporadically inhabited soil along the paths, roadsides and on earth banks in partially open habitats surrounded by spruce forest, except mt. Klíč (described below). Two subpopulations were discovered in the area of Železná Ruda. The first was ca 500m north from Debrník, which is distant 1 km south from Železná Ruda, on and along the footpath, just at the end of a ski lift, 800 m.a.s.l., with soil moisture 3 and pH 4.8. The second subpopulation was situated ca 1km north-east from the first one, in the direction to Kozak, 930 m.a.s.l., on the path with a subtle spring, soil moisture 3 and 4, and sandy-loamy substrate. The cover of *J. caespiticia* was not more than one square meter at each locality. Area directly at Pomezní Boudy was a cultural landscape and no discoveries of *J. caespiticia* were performed.

It occured 4 km south-west from Pomezní Boudy. Also two subpopulations were discovered. Both surrounded by spruce forest. One at the end of the valley of Jelení stream before the bridge, ca 1000 m.a.s.l.. Soil was sandy–loamy with organic admixture, moisture 2-3 and pH 4.6. Only few cm^2 among other bryophytes on stony ground was present. The second subpopulation was distant ca 2 km south-east from there on the east slope of the valley at ca 1050 m.a.s.l. on bare sandy–loamy soil along the road. There was quite abundant population scattered on ca 3 km long earth bank and ditch along the road from Jelení mt. to Žacléřské Boudy. The locality B. Labe is situated in the valley of the river Bílé Labe, from U Svozu to the bridge below Bílé Labe chalet, on a road side slope in the Krkonoše mts., 910–960 m.a.s.l.. The substrate was acid, sandy to loamy and soil moisture was 2-3. This locality was known before the revision. Historical locality in the valley of B. Labe, given in Duda & Váňa (1970), was 2 km distant to the east, at 1250 m.a.s.l.. Currently *J. caespiticia* have not occured there.

Locality	Locality type (occurrence of *J. caespiticia*)	altitude	Mean annual temperature (°C)	mean precipitation in growin season (mm)	soil pH
Rabštejnská Lhota (Chrudim)	H	320	7	400-450	4.2
Domovina (Chomutov)	H	525	7.5	350-400	4.5
Železná Ruda	H, R	880	6	500-600	4.1
Smědava (Jizerské mts.)	H	920	5	600-700	4.6
Proseč n. Nisou	H	530	7	350-450	4.2
Mohelnice (Beskydy)	H	690	6	500-600	4.7
Vysoký Kámen (Bruntál)	H	675	6	500-600	4.5
Pomezní boudy (Krkonoše mts.)	H	990	3	600-700	4.5
Bílé Labe (Krkonoše mts.)	H, C, R	1250	3	600-700	4.6
Libčice n. Vltavou	H	225	8	350-400	4.7
Jevany (Český Brod)	H	455	7	400-450	4.3
Litice n. Orlicí	H	435	7	400-450	4.6
Cvikov (incl. 8 localities)	H, R	585	6.5	450-500	5.1
Jetřichovice (Č. Kamenice)	H*	330	6.5	450-500	
Bílý stream valley (Vever. Bitýška)	H*	400	7.5	350-400	
Kolín	H*	200	7	400-450	
N. Údolí (Šumava mts.)	C, R	850	6	500-600	5.2
Modrava (Šumava mts.)	C, R	1025	3	600-700	5.7
Javoří Pila (Šumava mts.)	R	1040	3	600-700	
Poledni mt. (Šumava mts.)	R	1250	3	600-700	
Gsenget (Šumava mts.)	C, R	1130	3	600-700	
Černé lake (Šumava mts.)	C	1175	6	500-600	
Špindlerův Mlýn	R	755	3	600-700	5
Michlův mill (Vrchlabí)	R	800	5	600-700	4.4
Jelení boudy (Krkonoše mts.)	R	1025	3	600-700	4.5
Vidnava	C, R	280	7	400-450	5
stream Rohovec (Beskydy)	C	490	6	500-600	4.3
Tok (Brdy)	X	865	6	500-600	4.5
Dobřív (Rokycany)	X	460	7	400-450	4.7
Mokré (Č. Budějovice)	X	450	7.5	350-400	
Zbraslav	X	350	8	350-400	
Mníšek p. Brdy	X	450	7.5	350-400	

Table 1. The list of the localities treated in this study. Altitudes and soil pH are mean values from treated areas. Occurrence of *J. caespiticia*: R-recent (confirmed during this study), C-current (from the end of the 20th century), H-historical (according Duda & Váňa 1970), X-without recent and historical records of *J. caespiticia*, H*-not revised yet

The fourth locality was discovered in the upper part of the hill Klíč, at 700-760 m.a.s.l., 4 km north-west-west from Cvikov. It was present in a small (to 1cm^2) tufts among other bryophytes. Soil was sandy-loamy, moisture 2-3 and pH 5.1. The population is not large. I registered the presence of *J. caespiticia* when determining the collected samples. The surrounding vegetation is predominantly grassland with *Nardus stricta* and *Molinia caeruela* with spare occurrence of *Sorbus aucuparia*, *Picea abies* and *Fagus sylvatica*.

I visited also current localities. After the revision of those localities the presence of *J. caespiticia* was confirmed in all of them except Černé jezero (avalanche slope) and the valley of the stream Rohovec in Beskydy. B. Labe, Modrava and Gsenget belong to the localities with the most vital populations of *J. caespiticia*. It was scarely spread in more extensive areas, similarily to the population on Jelení mt., mainly along road sides, ditches and forest paths. Populations in N. Údolí and in Vidnava are restricted at one site. In N. Údolí, in sand pit, the total cover of the liverwort does not reach more than 1m^2. In Vidnava, only individual plants dispersed among other bryophytes were found in the cover sample from the shore of flooded kaolin pit.

Several potentially suitable habitats were observed (Tab. 1.) to find, whether *J. caespiticia* was present. The species was discovered at three sites in the frame of two different areas. The first was in Šumava mts. in Javoří Pila. It is a forest path in central Šumava mts., 1050 m.a.s.l., with acidic sandy-loamy soil and moisture 1-2. The path is surrounded by a spruce forest and a wet meadow. The second area was in Krkonoše mts., where two sites with *J. caespiticia* were found – 1) near Michlův mill, 3 km south from Špindlerův Mlýn, over the crossing of tourist paths, where it covers densely and continuously few square meters on the human-made slope surrounded with a spruce forest; 2) south from Špindlerův Mlýn, where only small amount of *J. caespiticia* was found on the edges of a ski slopes and along the road, on bare soil or among other bryophytes. All of these discoveries neighboured to the areas, where population of *J. caespiticia* recently occur.

Gemmae were found at all localities with *J. caespiticia* except Vidnava. Sporophyte was recorded only in N. Údolí and J. Pila (during permanent plot experiments in paralel study). The distribution of the bryophyte species from all treated localities, according Tab. 1., and the relation to selected environmental parameters, is illustrated in Fig. 1.

The results of t-test comparing historical and recent localities of *J. caespiticia* were significant for altitude: df=26; t=2,36; p=0,026; mean annual temperatures: df=26; t=-2,48; p=0,02 and mean precipitation in growing season: df=26; t=2,77; p=0,01. The results of

Mann-Whitney U-test were significant only for pH: U=60; Z=2,55; p=0,011. The ranges of the values for altitude and pH in historical and recent localities are illustrated in Fig. 2.

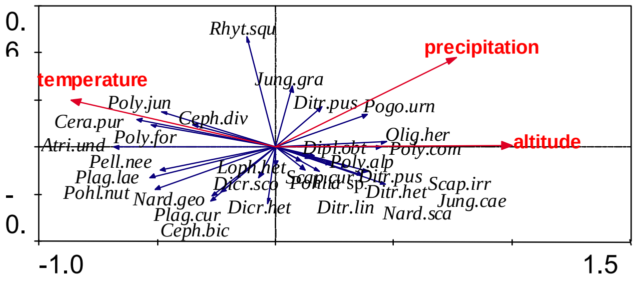

Figure 1. RDA diagram illustrates the distribution of the bryophyte species from all treated localities. The relation to altitude, mean annual temperatures and mean precipitation in growing season is shown. Only the species present at least at 10% of the localities are shown.

Add Figure 1: Atri.und-Atrichum undulatum, Ceph.bic-Cephalozia bicuspidata, Ceph.div-Cephaloziella divaricata, Cera.pur-Ceratodon purpureus, Dicr.het- Dicranella heteromalla, Dicr.sco-Dicranum scoparium, Dipl.obt-Diplophyllum obtusifolium, Ditr.het-Ditrichum heteromallum, Ditr.lin-Ditrichum lineare, Ditr.pus-Ditrichum pusilum, Jung.cae-Jungermannia caespiticia, Jung.gra-Jungermannia gracillima, Loph.het-Lophocolea heterophylla, Nard.geo-Nardia geoscyphus, Nard.sca-Nardia scalaris, Olig.her-Oligotrichum hercynicum, Pell.nee-Pellia neesiana, Plag.cur-Plagiothecium curvifolium, Plag.lae-Plagiothecium laethum, Pogo.urn-Pogonatum urnigerum, Pohl.nut-Pohlia nutans, Poly.alp-Polytrichum alpinum, Poly.com-Polytrichum commune, Poly.for-Polytrichum formosum, Poly.jun-Polytrichum juniperinum, Rhyt.squ-Rhytidiadelphus squarrossus, Scap.irr-Scapania irrigua

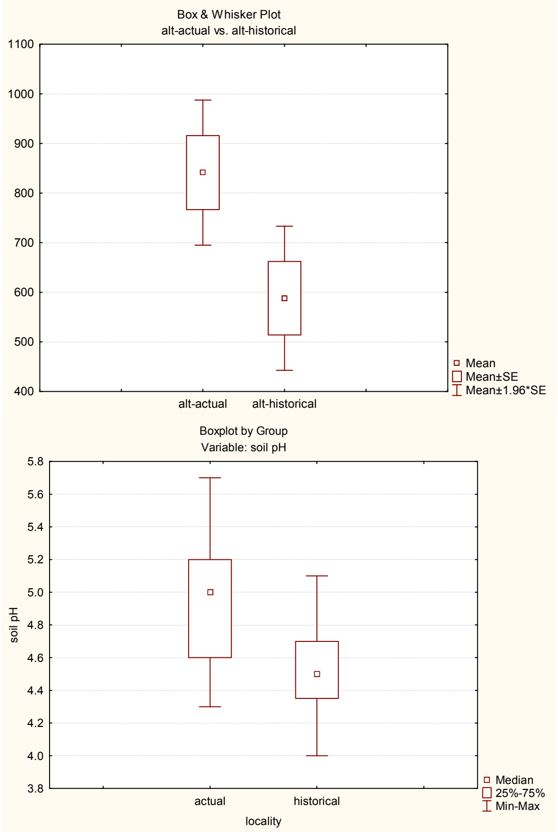

Figure 2. The differences in altitude (alt) and soil pH between historical and recent localities of *J. caespiticia*.

Discussion

Recent distribution

I attempted at searching as many localities of *J. caespiticia* as possible. Despite of that, I tried to search broad spectrum of environment, all recent localities were discovered only in mountains. I made a list of 12 recent localities (Tab. 1.). Except Vidnava, they were all situated in mountane or submontane regions. Recent distribution of *J. caespiticia* in the Czech Republic is shown in Figure 3. The population in Vidnava was the less viable one and the most vital populatins were found in the Krkonoše mts.. The pattern of distribution of *J. caespiticia* in the Czech Republic can be described as regionaly rare and locally more frequent. Usually more subpopulations occured nearby, which was the case of e.g. localities Jelení mt., Modrava and Gsenget. Individual populations were mostly very small in total cover, but few of them, e.g. Polední and Jelení mt., is scattered on a long stripe, usually following line disturbance, e.g. road ditch or forest path. Only one part of the population in the valley of the river Bílé Labe occured in naturaly disturbed habitat on a slope along small spring. All the other populations of *J. caespiticia* were in man-made habitats.

Including neighbouring countries, relatively abundant is the species in Austria. Within a few years it had disappeared. As a lot of new forest roads has appeared in Austria, it is certainly nowadays more frequent than in former times. It prefers higher regions and sometimes it reaches the subalpine belt (up to about 1700 m.a.s.l.). In Styria it is not rare in siliceous regions, in other parts of Austria more rare. (Köckinger pers. comm.). It is very sparsely distributed species in Germany, more frequently distributed in Fichtelberg Mts. *J. caespiticia* is red-listed there (Müller 2004). The distribution of *J. caespiticia* an extremly rare species in Poland with one locality in Western Carpatians (Stebel pers.comm.). *J. caespiticia* had two localies in Hungary, both in North Hungarian Mountain range. The last record was from 1956. Since then it was not found again. It should be put to the criticaly endangered category. According to the old Hungarian redlist (Rajczy 1990) it was placed into the endangered category (Papp pers comm.).

Changes in the distribution

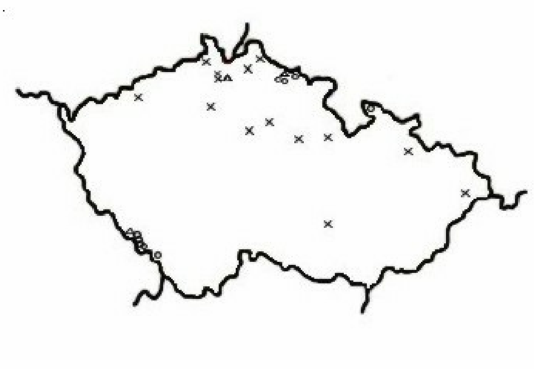

Figure 3. The distribution of *J. caespiticia* in the Czech Republic; crosses-historical localities according Duda & Váňa)1970), circles-recent localities, triangles-both historical and recent occurrence

Revision of the localities, both historical and recent, was done to find out whether the distribution range of *J. caespiticia* changed in the Czech Republic. I supposed that *J. caespiticia* will not be present at most of those localities, because of the changes in landscape during the decades, especially regarding an ephemeral character of habitat of *J. caespiticia* (Anonymus 2000, Paton 1999, Frey *et al.* 1995, van Melick 1983, etc.). Nevertheless it is possible that the populations of the liverwort migrate in the landscape, mainly as the result of substrate dynamics in neighbourhood of the historical localities. From the historical localities, only Bílé Labe, Železná Ruda and Klíč mt. (Cvikov region) are also listed among the recent localities. The distribution of *J. caespiticia* from the second half of 19th century till present is illustrated in Figure 3. It seems that *J. caespiticia* ceased to appear in lowlands and occure more frequently, respectively it persists, in mountains. The shift of the localities is supported with the results of t-test. In my previous work (Sova 2003) I ascribed this to potential change in climatic, namely precipitation, and soil moisture conditions in the landscape. These parameters relate directly to water availability, which is limiting for many bryophyte species, and their change could negatively influence the distribution of *J. caespiticia* in lowlands. Another explanation is that the change in the distribution during the decades relates rather to amount of suitable habitat. *J. caespiticia* recquires habitats with disturbed substrata and low competition intensity (Sova MS I). Such conditions are more likely to appear on dynamical substrata (Rydgren *et al.* 2004, Klausmeier 2001, Wooton 1998) or at intensively managed landscape. Large amount of dynamical substrata can occur on steep slopes in the mountains. Disturbance in lowlands has several causes, but main factor is possibly human activity. With regard to *J. caespiticia*, most suitable kind of disturbance is creation of paths, roads or sand pits. Landscape management have changed in last decades and amount of disturbances, like creation of sand pits, in natural and semi-natural lowland habitats decreased (Duda 1996). My experience from field confirm this statement, because most of sand and stone pits, which I visited during revisions, were abandoned and overgrowing with vegetation. It is possible that the amount of the populations of *J. caespiticia* in lowlands oscilate dependently on the intensity of management, mainly the forestry. Outlast of.*J. caespiticia* in mountain areas can be explained by natural substrate dynamics on the slopes, which creates suitable habitats for a week competitor *J. caespiticia*. Also the results from t-test showed, that the historical localities, where *J. caespiticia* occured in the past and those, where it is still present, differed in altitude. The hypothesis concerning habitat dynamics would be more acceptible with knowledge of changes in mean temperatures and precipitation from the second half of 19th century. If they have not changed, they have not affected the distribution of *J. caespiticia* and its prevalent occurrence in mountains would be probably because of suitable habitat availability. If mean temperatures rised, it could indirectly influenced the range of *J. caespiticia* and shifted it to higher altitudes. This pattern is in general described e.g. by Kienast *et al.* 1998 and it supports the hypothesis of distribution influenced by environmental factors. Comparing the situation in the Czech Republic to that in neighbouring countries, it seems that it is similar in general. *J. caespiticia* occures more frequently in mountain range rather than in lowlands and it appears dependently on disturbances in the landscape, as it have been in Austria. More frequent occurrence of *J. caespiticia* in north and north-east Europe, where mountains are not present, seems to correlate with colder climate conditions, similar to those in mountains. This lead again to the theory of changes in landscape conditions. On the other hand, more severe winter can have stronger negative effect on bryophyte cover density, which provide more space for a week competitors like *J. caespiticia*. Together with the fact that it occupies mostly antropogenous sites in north-east Europe (Konstantinova pers. comm.), it relates to the theory of habitat availability. The changes in the distribution refer both to the shift in environmental conditions and to the lack of suitable habitat. With current knowledge, it is immpossible to assess, how given parameters affects the distribution of *J. caespiticia*. In fact, the relationships between the distribution and other factors, like climatic and habitat parameters, may be more complicated and further study is needed.

Conclusions

J. ceaspiticia is recently known at 13 localities in the Czech Republic. The shift in the occurrence probably happened. It seems that *J. caespiticia* decreased in lowlands and persit in mountains. Its decline in lowlands was ascribed to the changes in the landscape management. It is supposed that similar situation in occurrence is in whole region of central Europe. Its distribution is sparse but on a wide range.

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4. CONCLUSIONS

This study showed that *J. caespiticia* is an ephemeral pioneer species, predominantly connected with disturbed habitats with low density of other bryophyte species. It was able to persist as a dominant species ca 2,5 year after the disturbance. Then its cover was rapidly decreasing.

It was concluded that its low competitive ability is due to a small size of individual plants and its growth form. After the fourth year of succession, it was quickly suppressed by the other bryophyte species, and therefore reducing the bryophyte cover by permanent disturbance is necessary to maintain the populations of *J. caespiticia*.

The tufts are not the only form of occurrence of *J. caespiticia*. Dispersed plants were common in all plot types and possibly play a role in tuft establishment and sustaining the populations.

Endogennous gemmae are probably dominant propagule type responsible for sustaining the local population. The type of propagules responsible for colonizing bare substrata in neighbourhood of the populations.

J. caespiticia is recently known at 13 localities in the Czech Republic. The shift in the parameters of occupied habitats was recorded. It seems that *J. caespiticia* is missing in lowlands and persit in mountains. Its absence in lowlands was ascribed to the changes in the landscape management and current absence of creation of new suitable habitats. It is suggested that similar situation in occurrence is in whole region of central Europe.

It was assessed that *J. caespiticia* is not actually in the threat of extinction in central Europe. Its distribution is sparse, but on a wide range. The most important parameter regarding rarity is small population size. An appropriate measure proposed to maintain the populations were to create regular disturbances in the areas of recent populations.

The role of several factors influencing species occurrence remains unexplored. Further research, primarily of sexual reproduction and population genetics, is needed.