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Bc. Thesis

Comparative study of coexisting ruderal species

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Anotace:

Comparative study concerned 18 species coexisting within ruderal site in Zliv. The selected traits related to species population dynamics were studied.

Prohlašuji, že jsem tuto bakalářskou diplomovou práci vypracovala sama pouze s použitím citované literatury.



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1. INTRODUCTION

1.1. Metapopulation dynamics

Due to human pressure, many terrestrial habitats are being rapidly changed, destroyed and fragmented, species are becoming extinct and gene pools are reduced - and all this at an increasing and historically unprecedented rate (Zschokke et al. 2000). As many species live in fragmented landscapes where populations are patchily distributed, the theory of metapopulation dynamics has received much attention (Eriksson and Kiviniemi 1999).

Recently there are an increasing number of studies focusing on plant metapopulations (van der Meijden et al. 1992; Ouborg 1993; Eriksson 1996; Husband and Barrett 1996; Tilman 1997; Boeken and Shachak 1998; Eriksson and Jacobsson 1998; Eriksson and Kiviniemi 1999; Hanski 1998). At the same time, a growing number of studies try to formulate mathematical models in order to study the interaction of different mechanisms, which effect plant communities, to make predictions and to formulate testable hypothesis enquiring influence of species traits on vegetation composition (Winkler and Klotz 1997; de Jong et al. 2000; Keymer et al. 2000; Hanski 2001; Vandermeer and Carvajal 2001). Several studies summarised and tested models' predictions on real communities or data from previous studies (Glenn and Collins 1990; Collins and Glenn 1991; Tilman 1994; Leishman and Murray 2001; Leishman 2001).

While conventional metapopulation theory involves species with frequent population turnover, limited migration and random extinction, it is likely that metapopulation dynamics and dispersal, is a feature of most species (Husband and Barrett 1996). In addition metapopulation dynamics play an important role in affecting vegetation pattern and distribution of species. Species traits concerned in this study are closely correlated with metapopulation dynamics of the studied species.

1.2. Rural sites

Species inhabiting rural sites often spread along roads and railways and as a result of this spatial structure, the demography and genetics of populations is a product not only of local environmental conditions but also processes operating on a regional scale (Husband and Barrett 1996). As rural sites are under strong human influence, communities inhabiting rural habitats must be adapted to frequent disturbances (Grime et al. 1988).

Where frequent and severe disturbances becomes the dominant influence upon vegetation, natural selection is likely to favour those genotypes in which rapid growth and early reproduction increase the probability that sufficient offspring will be produced to allow the survival and reestablishment of the population (Grime et al. 1988, Tilman et al. 1994).

Therefore winter annual and biennial species with large production of seeds and perennial species with intensive vegetation growth are of great importance in such habitats (Květena ČR 1). Persistent seed bank is another strategy that frequently occurs among plants inhabiting especially sites subjected to temporally unpredictable disturbance (Grime et al. 1988). Due to the long-scale migration along roads and railways, areas of these communities expand recently (Květena ČR 1).

1.3. Invasibility

The important impact of this long-scale migration is penetration of invasive species to such communities and their further propagation in region. Many ecologists have proposed qualitative descriptions of invading species (Robinson et al. 1995, Lodge 1993). Such species are said to be characterised by the following: related to genetics and reproduction (high genetic variability, phenotypic plasticity, vegetative reproduction, single plant reproduction); related to population dynamics (r-selected traits, high dispersal rate); related to physiology and autecology (eurytopy, polyphagy, large native range, human commensalism). Similarly, general descriptions of invulnerable habitat have been offered: early successional, disturbed, low diversity of native species (Lodge 1993).

From a number of studies several hypothesis have emerged concerning the central role that community structure (i.e., species richness, diversity, dominance) may have on invasibility (Smith and Knapp 1999). However recent studies have described both positive (Robinson et al. 1995) and negative (Tilman 1997, 1999) relationship between community diversity and invasibility. Observational studies (such as Lonsdale 1999) have suggested that diversity and abundance of invaders are positively correlated with native plant diversity. Smith and Knapp (1999) also supported this hypothesis.

Dukes (2001) found out that loss of species alone does not effect community invasibility but that communities with fewer species may be more likely to decline as a consequence of invasion. Other factors such as disturbance may also be important. Disturbances may directly enhance the success of invasive species by altering resource availability and productivity (Burke and Grime 1996). As disturbance affect community structure in several ways, it is difficult to separate direct from indirect effect on invasibility (Smith and Knapp 1999).

1.4. Rural vegetation

Studied vegetation in the site in Zliv can be generally described as alliance *Dauco-Melilotion*. This alliance includes mostly subthermophilic, moderately nitrophilic communities of mainly biennial and perennial species inhabiting sunny, predominantly anthropogenic

habitats (Hejný et al. 1979). Such communities colonise mainly stony and gravelly, gravelly and sandy or cinder substrates. They occur in river alluviums, in quarries, along railways, near railway stations and on road verges (Hejný et al. 1979). These communities stabilise surface of road and railways embankments and thus prevent development of water erosion. Some occurring species have generous root system, which can penetrate solid substrates. This function is important mainly on bare road and rail embankments and on new made-up grounds (Hejný et al. 1979).

Communities of alliance *Dauco-Melilotion* tend to spread out and frequently penetrate to untended urban habitats (Květena ČR 1). According to the C-S-R theory most of studied species belong to intermediate strategies competitive-ruderals, stress-tolerant ruderals or competitive stress-tolerant ruderals (Grime et al. 1988).

Species that occurred in the study locality have different life forms and life cycles. Eight out of eighteen studied species can be described as biennials. Biennial plants are typical examples of organisms that survive as metapopulations, i.e. as interacting groups of local populations. The group of species that we call biennials in fact shows a range of life-history strategies. Some species are strictly biennial; most species, however, may delay flowering for one or several years (van der Meijden et al. 1992). Flowering is usually delayed if rosette size is below a certain threshold (de Jong et al. 1989).

For biennials, the primarily factor limiting survival, growth or seed production seems to be a small- to large-scale disturbance of environment, providing an area of bare soil (Hart 1977, Werner 1977, Silvertown 1984). Therefore most habitats are only temporarily suitable for biennials, still these populations survive on the landscape level (van der Meijden et al. 1992). Compared with perennials and annuals biennials usually yield four to five times the number of seeds (Hart 1977). Biennials have an appropriate growth strategy for exploiting resources in sites available intermittently. In these sites annuals sell out too early, having to undergo the high risk of seedling establishment each season. Perennials play safe by keeping stores in vegetative organs; their rate of increase is greater only if the site remains favorable for many seasons. Biennials store just enough to survive to the second season, giving themselves twice as much time for assimilation, and then put all resources into seed production (Hart 1977).

Studied species also differed in ability to create seed bank. Among native species there were also four invasive species. Consequently it was interesting to compare species germination ability, recruitment and other traits.

The main aim of this study was to compare selected traits of species coexisting in the real community.

1.5. Aims and questions:

1. To compare germination ability of studied species.
2. To compare performance of native and invasive species in respect of studied traits.
3. To compare seed production per plant.
4. To compare seedling recruitment of studied species.
5. To determine key factors influencing vegetation pattern.
6. To compare neighbour vegetation composition of studied species.
7. Can species frequency in the locality be explained by any of studied traits?

2. METHODS

2.1. Study site

The field part of the study was performed on a rural site, near a local railway station in Zliv (385 m a.s.l.), with a mean annual temperature of about 7°C, a mean annual precipitation of about 600 mm (Chábera et al. 1985). This was a strait strip of ground (about 1m wide) just beside a rail embankment with sandy and gravelly soil and many stones.

Vegetation composition changed with increasing distance from the rail embankment. Soil became more loamy and vegetation cover was perceptibly higher. Vegetation can be generally described as phytosociological alliance *Dauco-Melilotion*. 64 vascular plant species were found at the studied area. *Centaurea stoebe*, *Artemisia vulgaris*, *Poa compressa*, *Echium vulgare*, *Trifolium arvense* were common species. The main vegetation forming factors were frequent disturbances. The impact of disturbances was apparent mainly near the rails.

2.2. Studied plant species

The study concerns 18 species that occur in the locality. Species were selected to suitably characterise the studied site in Zliv. The goal of this selection was to involve dominant species as well as less frequent ones that do not have an ecological optimum in the locality. Dominant species (regarding species frequency in relevés) were *Artemisia vulgaris*, *Centaurea stoebe*, *Echium vulgare*, *Poa compressa* and *Trifolium arvense* (see Tab. 1 for frequency values). *Solidago canadensis*, *Berteroa incana*, *Oenothera biennis*, *Oenothera issleri*, *Verbascum lychnitis* and *Verbascum thapsus* figured among the rather rare species. In addition we wanted to include species with different life cycles, life forms, types of clonality and different ability to create seed banks (tabs. 2, 3).

2.3. Germination

Seeds for two germination experiments were collected during autumn 1999 in Zliv. Seeds were germinated after 10-day cold storage (refrigerator 5°C).

Long-term experiment

Experiment was performed in a greenhouse (10 x 20 m). Germination was monitored for 61 days (8.3-7.5.2001) and proceeded in light. 50 seeds were sown per species in three replicates on Petri dishes with moistened filter papers. Seeds were counted every 3-4 days.

Tab. 1. List of species appeared in relevés. Nomenclature according Dostál (1989). Bold lettering is used for studied species. N - number of species occurrence out of 7785 total observations of individuals. % of ind. - frequencies of species occurrence.

SPECIES	N	% of ind.	SPECIES	N	% of ind.
<i>Acetosella vulgaris</i>	56	0.719	<i>Matricaria maritima</i>	36	0.462
<i>Achillea millefolium</i>	13	0.166	<i>Medicago lupulina</i>	43	0.552
<i>Agropyron repens</i>	8	0.102	<i>Mellilotus sp.</i>	148	1.901
<i>Artemisia vulgaris</i>	294	3.776	<i>Oenothera biennis</i>	19	0.244
<i>Brassica napus</i>	10	0.128	<i>Oenothera issleri</i>	315	4.046
<i>Berteroa incana</i>	21	0.269	<i>Papaver rhoeas</i>	3	0.038
<i>Bromus tectorum</i>	9	0.115	<i>Plantago lanceolata</i>	120	1.541
<i>Calamagrostis epigeios</i>	52	0.667	<i>Plantago major</i>	16	0.205
<i>Capsella bursa-pastoris</i>	1	0.012	<i>Plantago media</i>	27	0.346
<i>Carex hirta</i>	61	0.783	<i>Poa compressa</i>	1042	13.38
<i>Centaurea stoebe</i>	1493	19.17	<i>Polygonum aviculare</i>	10	0.128
<i>Cerastium arvense</i>	25	0.321	<i>Potentilla reptans</i>	72	0.924
<i>Cirsium arvense</i>	4	0.051	<i>Rumex crispus</i>	1	0.012
<i>Conyza canadensis</i>	91	1.168	<i>Senecio sp.</i>	2	0.025
<i>Dactylis glomerata</i>	35	0.449	<i>Setaria glauca</i>	2	0.025
<i>Daucus carota</i>	124	1.592	<i>Solidago canadensis</i>	5	0.064
<i>Deschampsia cespitosa</i>	1	0.012	<i>Sonchus oleraceus</i>	79	1.014
<i>Echium vulgare</i>	466	5.985	<i>Spergularia rubra</i>	100	1.284
<i>Erodium cicutarium</i>	1	0.013	<i>Stenactis annua</i>	437	5.613
<i>Erysimum durum</i>	187	2.402	<i>Tanacetum vulgare</i>	89	1.143
<i>Fragaria vesca</i>	30	0.385	<i>Taraxacum sp.</i>	218	2.800
<i>Geranium robertianum</i>	17	0.218	<i>Trifolium arvense</i>	751	9.646
<i>Geranium pusillum</i>	9	0.115	<i>Trifolium hybridum</i>	63	0.809
<i>Hieracium sp.</i>	535	6.872	<i>Trifolium pratense</i>	4	0.051
<i>Holcus lanatus</i>	123	1.579	<i>Trifolium repens</i>	144	1.849
<i>Hypericum perforatum</i>	109	1.400	<i>Verbascum lychnitis</i>	56	0.719
<i>Lactuca serriola</i>	8	0.102	<i>Verbascum thapsus</i>	77	0.989
<i>Lamium sp.</i>	9	0.115	<i>Veronica persica</i>	5	0.064
<i>Lathyrus pratensis</i>	1	0.013	<i>Vicia cracca</i>	10	0.128
<i>Lathyrus sylvestris</i>	5	0.064	<i>Vicia sepium</i>	1	0.012
<i>Linaria vulgaris</i>	59	0.757	<i>Viola arvensis</i>	1	0.012
<i>Lolium perenne</i>	2	0.025	<i>Viola tricolor</i>	30	0.385

Germinated seeds were removed to avoid inhibiting the germination of other seeds. Subsequent additions of water were made as necessary to prevent drying out.

Short-term experiment

Germination took place in a greenhouse and in a room. For both treatments half of the seeds was germinated in light and half in the dark. 50 seeds of each species were sown on filter paper in three replicates on Petri dishes with moisturised filter papers. Petri dishes in the room treatment were placed randomly. Germination lasted for two weeks (21.6-4.7.2001). Temperature in the room treatment for both light and dark treatment was about 17.5°C at night and during colder days and about 24°C during sunny days. Temperature in

the greenhouse treatment was about 33°C in light and about 30°C in a paper box. Temperature was about 20°C during nights.

Tab. 2. List of traits from the Biological Traits database. This table shows common classification according to the traits. Fuzzy coding used for the final analysis is not shown. *H. citreus*
 long-term seed bank - seeds persisting for at least 5 years, and often much longer
 short-term seed bank - seeds persisting more than 1 year, usually less than 5 years
 transient seed bank - seeds rarely persisting more than one year.

Plant species	Life form (sensu Raunkiaer)	Life cycle	Diaspore bank longevity
<i>Artemisia vulgaris</i>	hemicryptophyte	polycarpic perennial	long-term
<i>Berteroa incana</i>	hemicryptophyte	polycarpic perennial	long-term
<i>Centaurea stoebe</i>	hemicryptophyte	biennial	long-term
<i>Conyza canadensis</i>	therophyte	summer annual	transient
<i>Daucus carota</i>	hemicryptophyte	monocarpic perennial	long-term
<i>Echium vulgare</i>	hemicryptophyte	biennial	short-term
<i>Erysimum durum</i>	hemicryptophyte	biennial	long-term
<i>Hypericum perforatum</i>	hemicryptophyte	polycarpic perennial	long-term
<i>Linaria vulgaris</i>	geophyte	polycarpic perennial	long-term
<i>Melilotus officinalis</i>	hemicryptophyte	biennial	long-term
<i>Oenothera biennis</i>	hemicryptophyte	biennial	long-term
<i>Oenothera issleri</i>	hemicryptophyte	biennial	long-term
<i>Poa compressa</i>	hemicryptophyte	polycarpic perennial	short-term
<i>Solidago canadensis</i>	hemicryptophyte	polycarpic perennial	transient
<i>Tanacetum vulgare</i>	hemicryptophyte	polycarpic perennial	transient
<i>Trifolium arvense</i>	therophyte	winter annual	short-term
<i>Verbascum lychnitis</i>	hemicryptophyte	biennial	long-term
<i>Verbascum thapsus</i>	hemicryptophyte	biennial	long-term

Tab. 3. Types of clonality from CLO-PLA2 database. *f. citreus*

Species	Type of clonality
<i>Artemisia vulgaris</i>	<i>Dactylis glomerata</i> , <i>Rumex acetosella</i>
<i>Berteroa incana</i>	non clonal
<i>Centaurea stoebe</i>	non clonal
<i>Conyza canadensis</i>	non clonal
<i>Daucus carota</i>	non clonal
<i>Echium vulgare</i>	non clonal
<i>Erysimum durum</i>	non clonal
<i>Hypericum perforatum</i>	<i>Rumex acetosella</i> , <i>Fragaria vesca</i>
<i>Linaria vulgaris</i>	<i>Rumex acetosella</i>
<i>Melilotus officinalis</i>	non clonal
<i>Oenothera biennis</i>	non clonal
<i>Oenothera issleri</i>	non clonal
<i>Poa compressa</i>	<i>Dactylis glomerata</i>
<i>Solidago canadensis</i>	<i>Aegopodium podagraria</i>
<i>Tanacetum vulgare</i>	<i>Aegopodium podagraria</i>
<i>Trifolium arvense</i>	<i>Trifolium pratense</i>
<i>Verbascum lychnitis</i>	non clonal
<i>Verbascum thapsus</i>	non clonal

2.4. Seed weight

Weighed seeds were collected in autumn 1999. 100 seeds of each species were weighed in ten replications except for *Conyza canadensis* and *Solidago canadensis*. The fluffy seeds of these species were very small and light. 500 seeds were weighed for *Conyza canadensis* and 1500 for *Solidago canadensis*.

2.5. Seedling recruitment

Seeds for this experiment were collected in autumn 1999 in Zliv. Experimental plots were placed in the BF JCU experimental garden, near the greenhouse. The upper layers of soil with plants and most of their roots were removed. To imitate special habitat conditions (trophy and soil moisture regime) as much as possible, a gravely substratum from the source habitat was taken to the experimental garden. Plots (20 x 20 cm) were filled with the substratum to a depth about 10 cm. 100 seeds of each species were sown in early May in six replications in a completely randomised design. Seeds were placed just beneath the soil surface (0,5-1 cm deep). Plots were watered every one or two days due to an unusual drought.

2.6. Species distribution

Data on abundance and distribution were obtained during two years of monitoring (1999 and 2000). 225 relevés were performed and placed randomly around the studied habitat to describe the heterogeneity of the site. They were taken after vegetation peak in July-September when most species finished flowering and start to mature. Four environmental variables ("vegetation cover", "stones", "moss" and "soil") were estimated for each relevé. Their values represented the estimated cover of each substratum in individual relevé (percentages from 0 to 100).

2.7. Seed production

Five randomly chosen individuals of each studied species were collected to estimate the production of seed per plant. Ten to twenty fruits of each individual plant were randomly chosen with an effort to select mature but not open fruits. A lower number of seeds in open fruits could cause underestimation of total seed production. The production of seeds per fruit was counted. The production of fruits per plant for each species was counted as an average from ten values counted for individuals. The total production of seeds per plant was estimated as average for ten individuals of each species.

2.8. Distances

Six individuals of each studied species were randomly selected. For each individual five distances to the nearest other individual of the same species were measured with an effort to not include one certain individual more than once.

2.9. Neighbouring composition

To detect species composition of neighbours, six individuals were randomly selected for each species. For each individual the five nearest plants were identified. In the case of clonal plants I tried to distinguish species composition for tufts.

2.10. Final analysis

We tried to reveal which species traits significantly affect species distribution. Inputs for this analysis were final outputs from my own experiments (germination, seed weight, seedling recruitment, species distribution from relevés, production of seeds per plant, measuring average distances between species, neighbouring composition).

The additional source of primary data was, next to my own observations, the Biological Traits of Vascular Plants database (Kleyer 1995) and CLO-PLA2 the database of clonality (Klimeš and Klimešová 1999). The Biological Traits of Vascular Plants database contains data on 25 ecological characteristics for 491 higher plants. The missing ecological traits, which were not cited in the database, were completed from various floras and other publications (Slavík 1990-1997, Dostál 1989, Grime et al. 1988).

Four traits were selected for final analyses from the both databases: type of clonality, life form, longevity of seed bank and life cycle. Many of the species traits had several states. In these cases fuzzy coding was used.

3. STATISTICAL ANALYSIS

3.1. Germination

Analyses of the germination experiment were performed using the STATISTICA package. Data from the short-term experiment were subjected to two- and three-way ANOVA with fixed factors "species", "light" and "temperature" to test the differences in final germination values between species and to detect the effect of treatments. A Tukey Honest Significant Difference (HSD) test was used to find out pairs of significantly different species.

Yule's Q coefficient (Yule 1912) was used to express the preference for germination in the light or dark. The value of this coefficient ranges between -1 to 1, with preferences for a given factor increasing towards the extremes. Q coefficients were computed using final germination rates light vs. dark for two temperatures (room and greenhouse treatment).

The S-PLUS package (Anonymous 1995) was used to test the effect of species, family and invasibility on final germination values. The dependent variable in this analysis was the final value of germinated seeds from the long-term experiment set as a binomial variable. Independent variables were nominal variables family and invasibility.

3.2. Seed weight

The S-PLUS package was also used to test the effect of species, family and invasibility on seed weight. The dependent variable was seed weight. Independent variables were nominal variables invasibility and family.

3.3. Seedling recruitment

The average final rate of recruited individuals and the average final rate of fertile individuals were counted. Their values for each species were inputs for the final analysis.

3.4. Species distribution

Multivariate statistical methods (Canonical Correspondence Analysis-CCA) in the CANOCO package (ter Braak and Šmilauer 1998) were used for evaluation of the composition of vegetation at the studied site in Zliv. The species cover values were log-transformed.

3.5. Distances

The S-PLUS statistical package was used to compare species distances and to test the effect of family and invasibility on its value. The dependent variable was distance and independent variables were family and invasibility. Model was create with a nested design (individuals were nested in species).

3.6. Neighbouring composition

Multivariate statistical method (CCA) was also used to find out if there are any differences in the generic composition of the neighbour vegetation of studied species. The frequencies of species occurrence were weighted by species abundance. To demonstrate the tendencies of studied plants to grow with certain species, the set of data was regarded as

phytosociological research, where studied species entered CCA analysis as "samples" and species, which occurred around them as "species".

3.7. Final analysis

Principal Component Analysis (PCA) was performed on sets of data that included both species traits from databases and final outputs from my own experiments. All data were log-transformed.

List of traits from experiments:

- average final germination rates for light
- average final germination rates for dark
- average final germination rates for long-term experiment
(all rates were angular transformed before entering PCA)
- average seed mass
- average final rate of recruited individuals from experimental garden
- average rate of fertile individuals from garden experiment
- species frequencies from relevés
- average distance
- average number of seeds per plant

List of traits from both databases:

- clonality
- three types of life form (hemicryptophytes, therophytes, geophytes)
- five types of life cycle (summer annual, winter annual, biennial, monocarpic perennial, polycarpic perennial)
- three types of seed bank (transient, short-term persistent, long-term persistent)

CANODRAW and CANOPOST were used for graphic outputs for all the analyses performed in CANOCO.

Table of abbreviations of species names.

ArteVulg	<i>Artemisia vulgaris</i>	Melilo.sp.	<i>Melilotus sp.</i>
BertInca	<i>Berteroa incana</i>	OenoBien	<i>Oenothera biennis</i>
CentStoe	<i>Centaurea stoebe</i>	OenoIssl	<i>Oenothera issleri</i>
ConyCana	<i>Conyza canadensis</i>	PoaComp	<i>Poa compressa</i>
DaucCaro	<i>Daucus carota</i>	SoliCana	<i>Solidago canadensis</i>
EchiVulg	<i>Echium vulgare</i>	TanaVulg	<i>Tanacetum vulgare</i>
ErysDuru	<i>Erysimum durum</i>	TrifArve	<i>Trifolium arvense</i>
HypePerf	<i>Hypericum perforatum</i>	VerbLych	<i>Verbascum lychnitis</i>
LinaVulg	<i>Linaria vulgaris</i>	VerbThap	<i>Verbascum thapsus</i>

4. RESULTS

4.1. Germination

Short-term

The final germination percentages were significantly affected by species as well as temperature and light regimes (for species and light $p < 10^{-6}$, for temperature $p = 0.000022$).

The final germination percentages varied among species and light/temperature treatments as well (Figs. 1, 2).

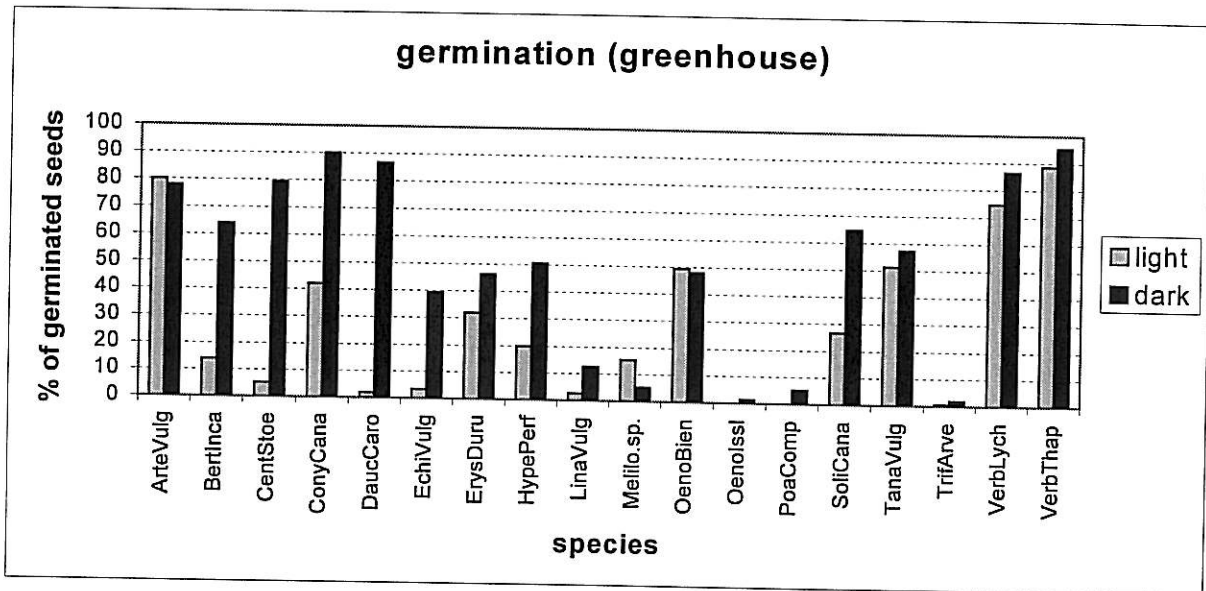


Fig. 1. Final germination percentages in the light and dark treatment for the greenhouse treatment. Grey bars represent final germination percentages in light, black bars in the dark.

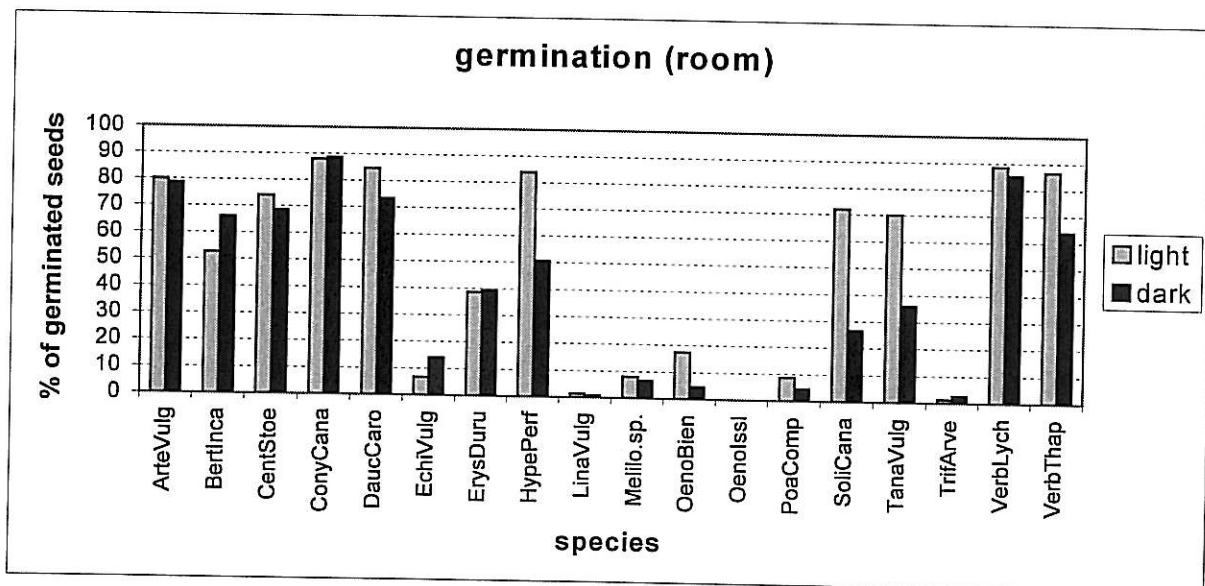


Fig. 2. Final germination percentages in the light and dark treatment for the room treatment. Grey bars represent final germination percentages in light, black bars in the dark.

Comparison between the final percentages for the room and greenhouse treatment showed that three species (*Artemisia vulgaris*, *Verbascum thapsus*, *Verbascum lychnitis*) germinate in the high rates both in the greenhouse and room treatment (percentages for light and dark were similar) (Figs. 1, 2).

In the greenhouse treatment all species except of *Oenothera biennis*, *Melilotus sp.* and *Artemisia vulgaris* prefer dark for germination (Fig. 3). Species *Oenothera issleri* and *Poa compressa* germinated in light only, but their germination percentages were very low (0.67% for *O. issleri*, 2.67% for *P. compressa*) (Fig. 1).

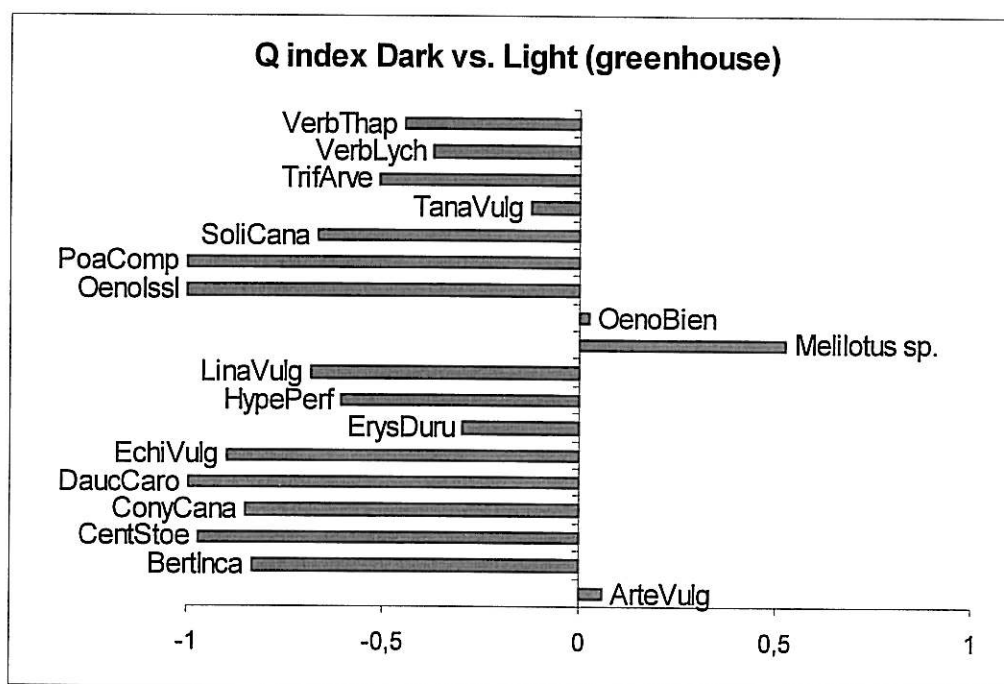


Fig. 3. Preferences of studied species for germination in light vs. dark (expressed as the value of Q index) in the greenhouse treatment. Negative values indicate preference for dark, positive for light.

Trifolium arvense, *Linaria vulgaris* and *Melilotus sp.* germinate in the dark and light as well but their final germination percentages were quite low. Species *Oenothera biennis* seemed to prefer higher temperatures (in the greenhouse treatment) regardless of light regime (Figs. 1,2).

Preferences for light and dark were not so distinct in the room treatment. In contrast to the greenhouse treatment most species prefer light. The differences between the light and dark values were greatest for *Hypericum perforatum*, *Solidago canadensis* and *Tanacetum vulgare* (all of them prefer light) (Fig. 4). Five species *Trifolium arvense*, *Erysimum durum*, *Echium vulgare*, *Conyza canadensis*, *Berteroa incana* prefer germination in the dark. *Oenothera issleri* did not germinate at all.

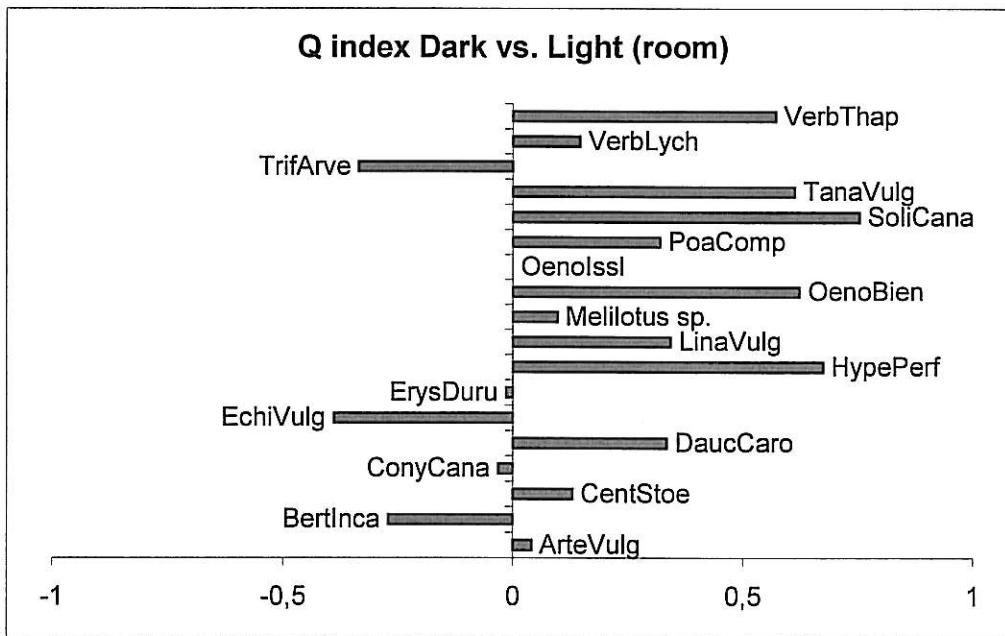


Fig. 4. Preferences of studied species for germination in light vs. dark (expressed as the value of Q index) in the room treatment. Negative values indicate preference for dark, positive for light.

Comparing the average values for light and dark (Fig. 5) confirmed *Artemisia vulgaris*, *Verbascum thapsus* and *Verbascum lychnitis* as species germinating very well both in the dark and light. On the other hand *Linaria vulgaris*, *Melilotus sp.*, *Oenothera issleri*, *Poa compressa* and *Trifolium arvense* hardly achieved 10% of germinated seeds. Species *Berteroa incana*, *Centaurea stoebe*, *Daucus carota*, *Conyza canadensis* distinctive preferred dark.

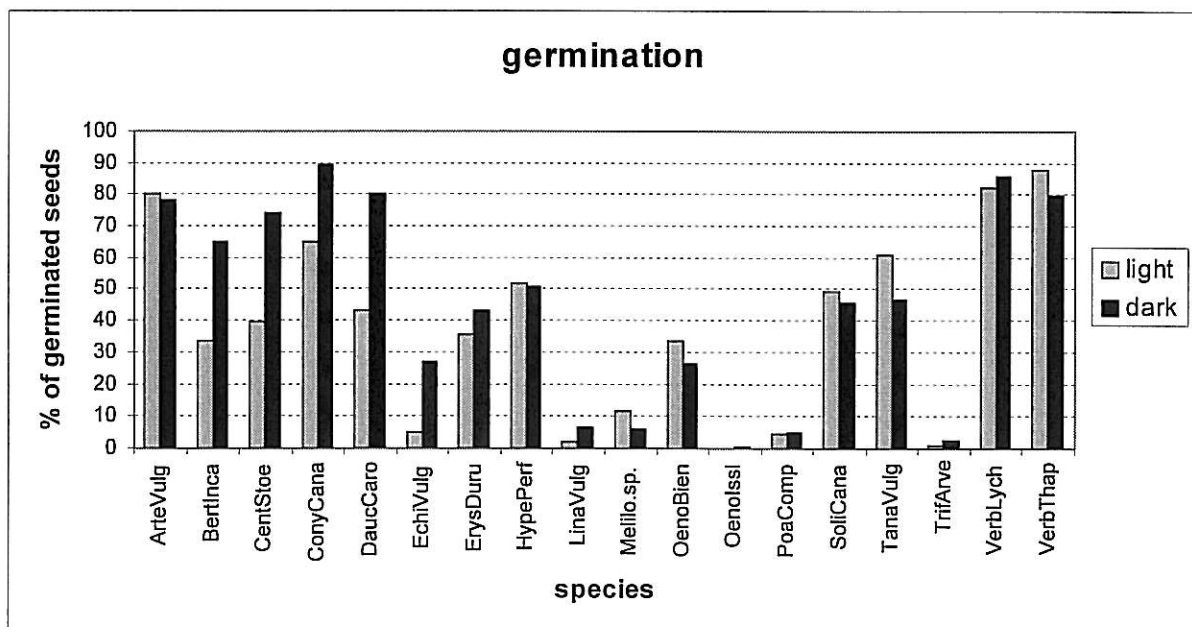


Fig. 5. Final average germination percentages for species in the light and dark treatment.

A Tukey (HSD) test showed significant differences between selected species. *Verbascum thapsus* x *Verbascum lychnitis* did not differ significantly (both germinated very well), whereas difference between *Oenothera biennis* x *Oenothera issleri* was significant ($p=0.000036$). The differences among invasive species (*Conyza canadensis*, *Oenothera biennis*, *Oenothera issleri*, *Solidago canadensis*) were all significant ($p=0.000036$).

Table 5 resumes p values for species from family *Asteraceae*. The large-seeded (see Tab. 4) *Centaurea stoebe* differed significantly from the small-seeded *Artemisia vulgaris* and *Conyza canadensis* but not from the small-seeded *Solidago canadensis* and *Tanacetum vulgare*. The invasive species *Conyza canadensis* differed significantly from all species except of *Artemisia vulgaris*. *Solidago canadensis* differed next to *Conyza canadensis* from *Artemisia vulgaris* either.

Tab. 4. Seed sizes, standard deviations and number of weighed seeds. Seeds were weighed in 10 replicates.

Plant species	Seed size (mg)	SD	Number of seeds
1. <i>Artemisia vulgaris</i>	0.122	0.011	100
2. <i>Berteroa incana</i>	0.562	0.051	100
3. <i>Centaurea stoebe</i>	1.411	0.049	100
4. <i>Conyza canadensis</i>	0.045	0.0005	500
5. <i>Daucus carota</i>	0.635	0.022	100
6. <i>Echium vulgare</i>	2.743	0.077	100
7. <i>Erysimum durum</i>	0.188	0.006	100
8. <i>Hypericum perforatum</i>	0.105	0.005	100
9. <i>Linaria vulgaris</i>	0.135	0.006	100
10. <i>Melilotus sp.</i>	2.757	0.102	100
11. <i>Oenothera biennis</i>	0.474	0.015	100
12. <i>Oenothera issleri</i>	0.629	0.026	100
13. <i>Poa compressa</i>	0.164	0.009	100
14. <i>Solidago canadensis</i>	0.040	0.003	1500
15. <i>Tanacetum vulgare</i>	0.121	0.003	100
16. <i>Trifolium arvense</i>	0.417	0.030	100
17. <i>Verbascum lychnitis</i>	0.095	0.003	100
18. <i>Verbascum thapsus</i>	0.118	0.009	100

Tab. 5. Comparison of p values for species from family *Asteraceae*. Significant values and invasive species are shown in bold lettering.

Species	<i>ArteVulg</i>	<i>CentStoe</i>	<i>ConyCana</i>	<i>SoliCana</i>	<i>TanaVulg</i>
<i>ArteVulg</i>	x	0.000036	0.9999	0.000036	0.000036
<i>CentStoe</i>	0.000036	x	0.000036	0.276511	0.99948
<i>ConyCana</i>	0.9999	0.000036	x	0.000036	0.000036
<i>SoliCana</i>	0.000036	0.276511	0.000036	x	0.970901
<i>TanaVulg</i>	0.000036	0.999948	0.000036	0.970901	x

Long-term

Comparisons of final percentages from the short- and long-term germination experiment show table 6.

Tab.6. Final average percentages for the short-term (light and dark) and long-term experiment (light).

Plant species	Short-term germ. (aver. rate for light)	Long-term germ. (aver. rate for light)	Short-term germ. (aver. rate for dark)
1. <i>Artemisia vulgaris</i>	80.00	66.66	78.33
2. <i>Berteroa incana</i>	33.33	84.66	65.00
3. <i>Centaurea stoebe</i>	39.67	57.34	74.00
4. <i>Conyza canadensis</i>	65.00	87.34	89.33
5. <i>Daucus carota</i>	43.33	72.72	80.00
6. <i>Echium vulgare</i>	5.00	20.00	26.67
7. <i>Erysimum durum</i>	35.33	63.34	43.00
8. <i>Hypericum perforatum</i>	52.00	63.34	50.66
9. <i>Linaria vulgaris</i>	2.00	51.34	6.66
10. <i>Melilotus sp.</i>	11.67	35.34	6.00
11. <i>Oenothera biennis</i>	33.34	65.34	26.33
12. <i>Oenothera issleri</i>	0.00	15.34	0.67
13. <i>Poa compressa</i>	4.33	76.00	5.00
14. <i>Solidago virgaurea</i>	49.33	70.66	45.66
15. <i>Tanacetum vulgare</i>	60.67	84.00	46.67
16. <i>Trifolium arvense</i>	1.00	20.00	2.33
17. <i>Verbascum lychnitis</i>	82.00	93.34	86.00
18. <i>Verbascum thapsus</i>	87.66	84.66	79.67

The effects of species, family and invasibility on final values from the long-term germination experiment were tested. The effect of species (Fig. 6) and family (Fig. 7) were both significant: $F(17)=43.686$, $p<10^{-6}$ and $F(8)=8.506$, $p<10^{-6}$, respectively. Family *Scrophulariaceae* achieved the highest final germination values (see Fig. 7). It was due to *V. thapsus*, *V. lychnitis*. However the range of values is quite wide (due to low values of *Linaria vulgaris*). Similar situation is in family *Onagraceae*. (*O. biennis* with high and *O. isleri* with low final values). In the case of one-species families range of values is not so wide (*Apiaceae*, *Hypericaceae*, *Poaceae*). The impact of invasibility was not significant.

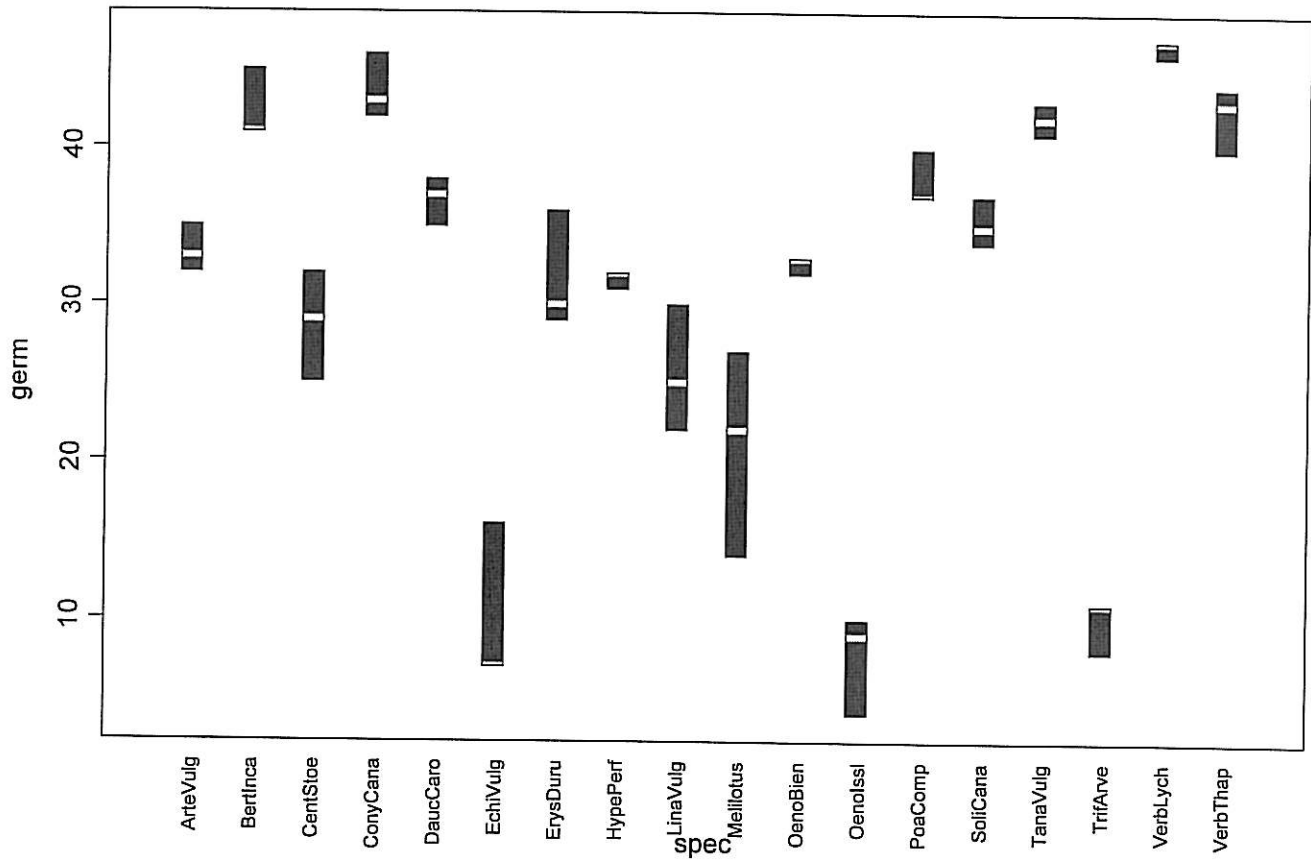


Fig. 6. The overview of species final numbers of seeds from long-term germination experiment.

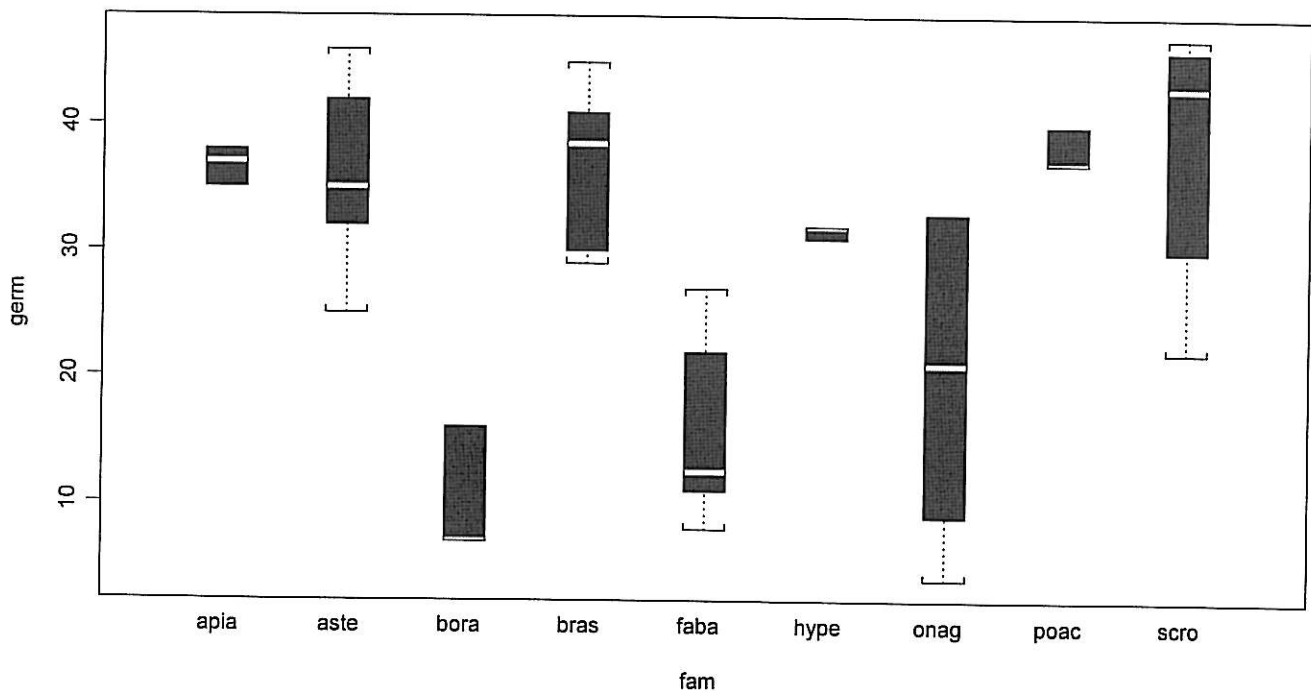


Fig. 7. The overview of final numbers of seeds from long-term germination experiment for particular families.

4.2. Seed weight

The effect of three traits was tested using S-PLUS package. The effect of all of them was significant.

Species (Fig. 8): $F(17)=2933.834, p<10^{-6}$

Family (Fig. 9): $F(8)=39.567, p<10^{-6}$

Invasibility (Fig. 10): $F(1)=4.244, p=0.0409$

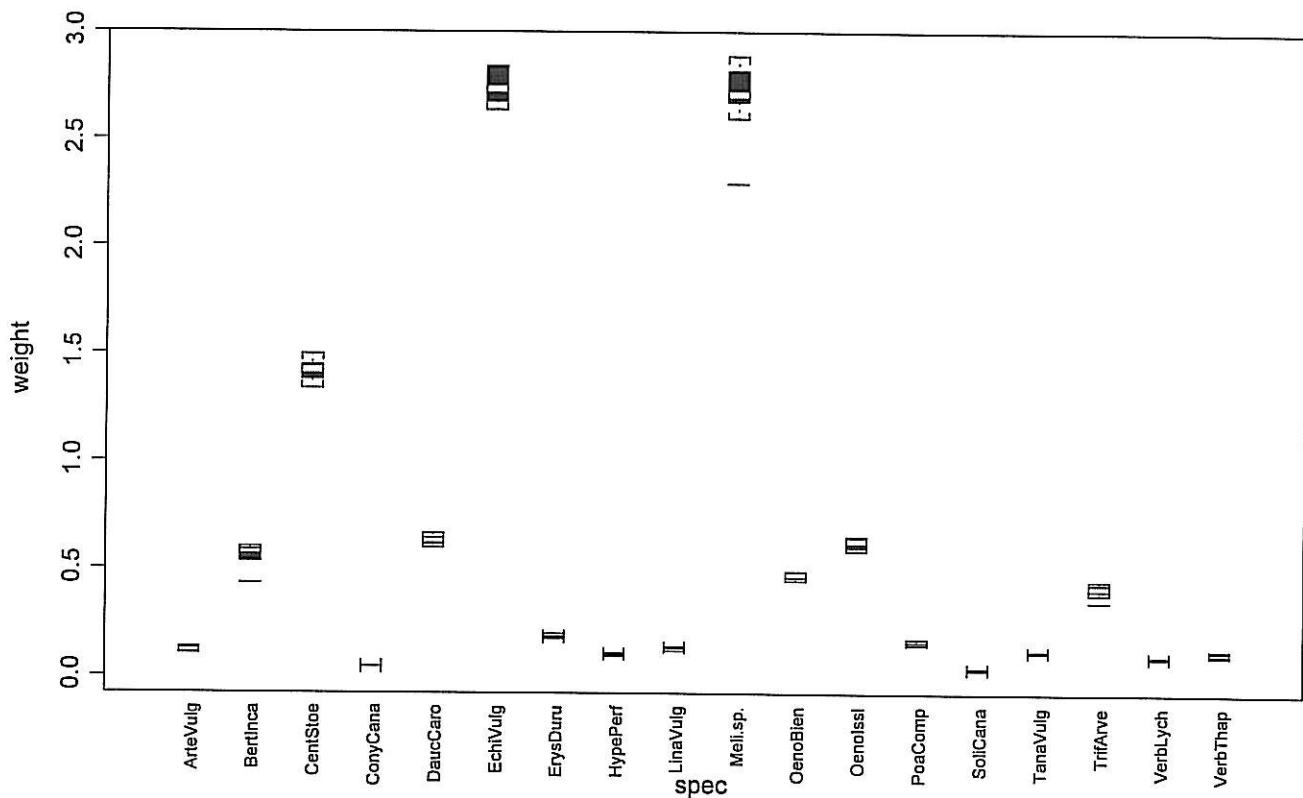


Fig. 8. The overview of species seed weight.

The effect of family

The range of weight values is small for one-species families (*Apiaceae*, *Hypericaceae*, *Poaceae*, *Boraginaceae*) (Fig. 9). In the case of *Asteraceae* the outer weight value belongs to *Centaurea stoebe* (abscissas represent ten replicated measures). The widest range has family *Fabaceae* that included small-seeded *Trifolium arvense* and *Melilotus.sp.* (species with the heaviest seeds).

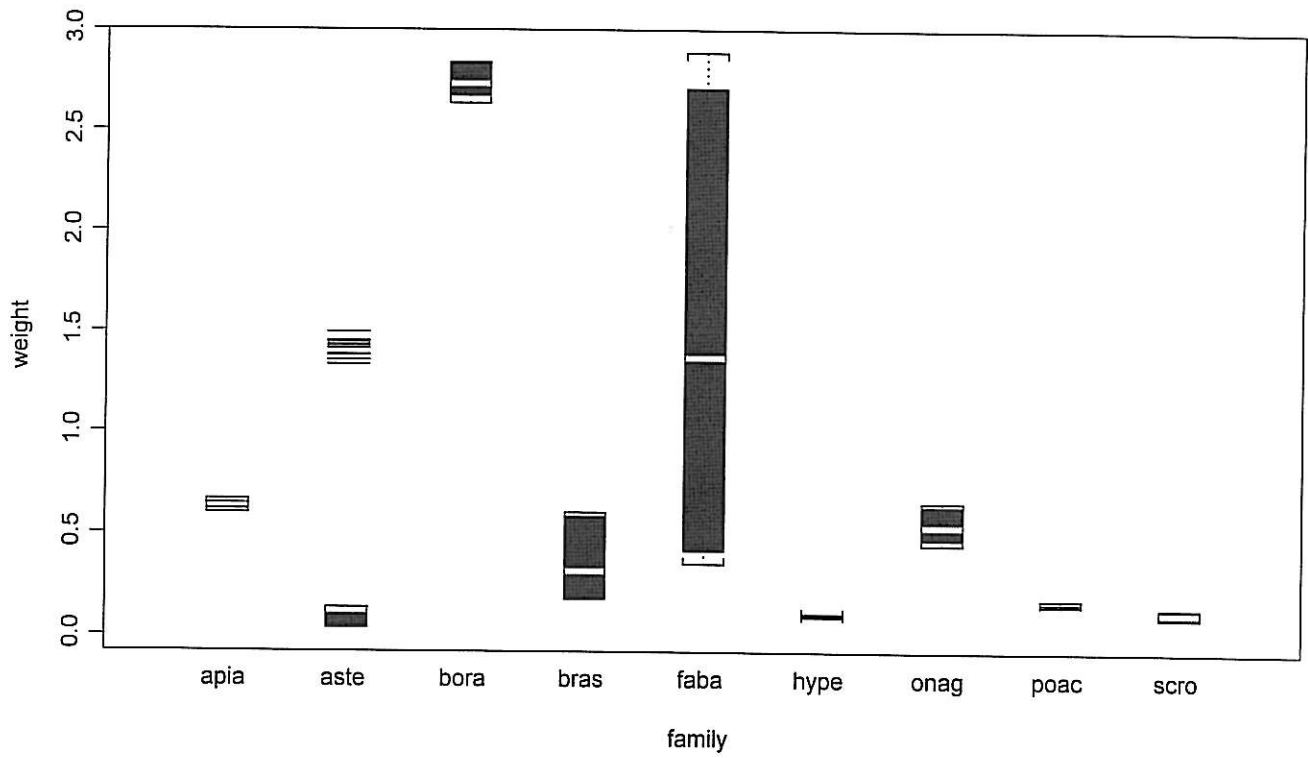


Fig. 9. The overview of on seed weight for particular families.

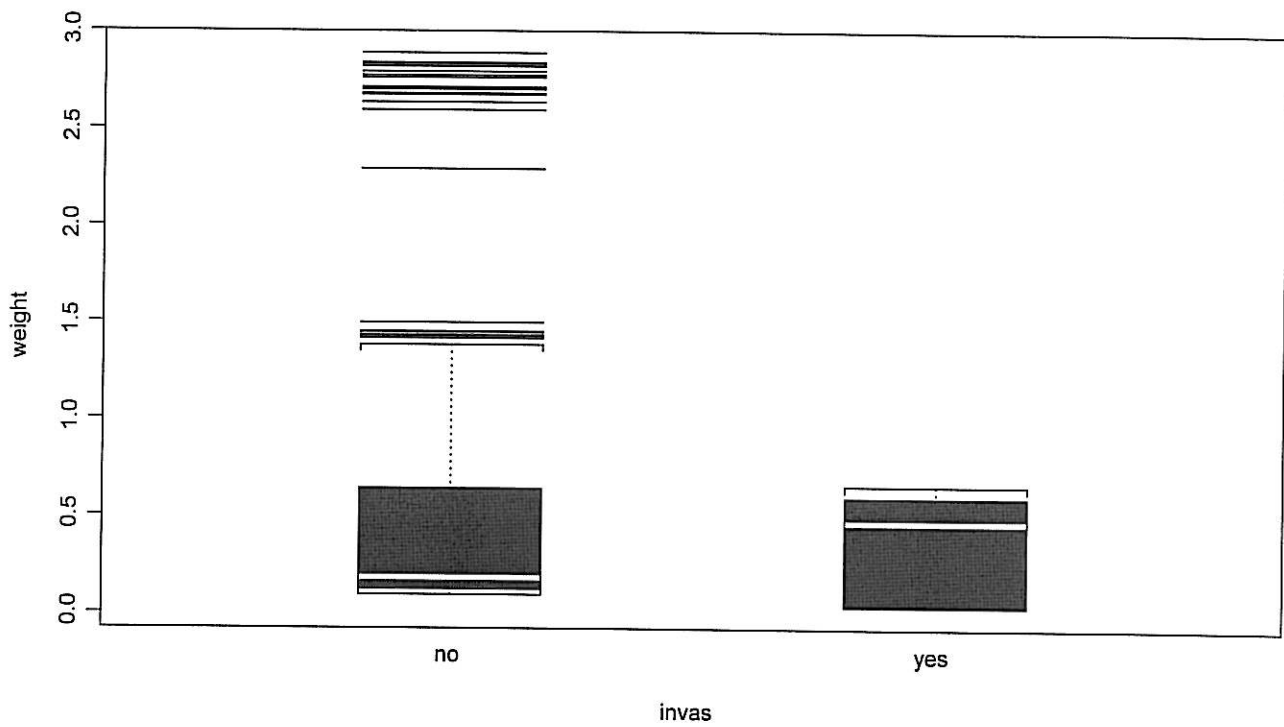


Fig. 10. The overview of seed weight for invasive and native species.

The effect of invasibility

The invasive species *Solidago canadensis* and *Conyza canadensis* represented two species with very light seeds (Tab. 4). Another two invasive species *Oenothera biennis* and *Oenothera issleri* belonged to species with average weight of seed. Native species showed the wide range of weight values (Fig. 10).

4.3. Seedling recruitment

The final germination rates for each species were quite low (Fig. 11). None individual survived till the end of the experiment in the case of *Melilotus sp.* and *Solidago canadensis*. Species *Centaurea stoebe*, *Artemisia vulgaris* and *Echium vulgare* achieved the highest rates (6%, 3.3%, 2.8%, respectively).

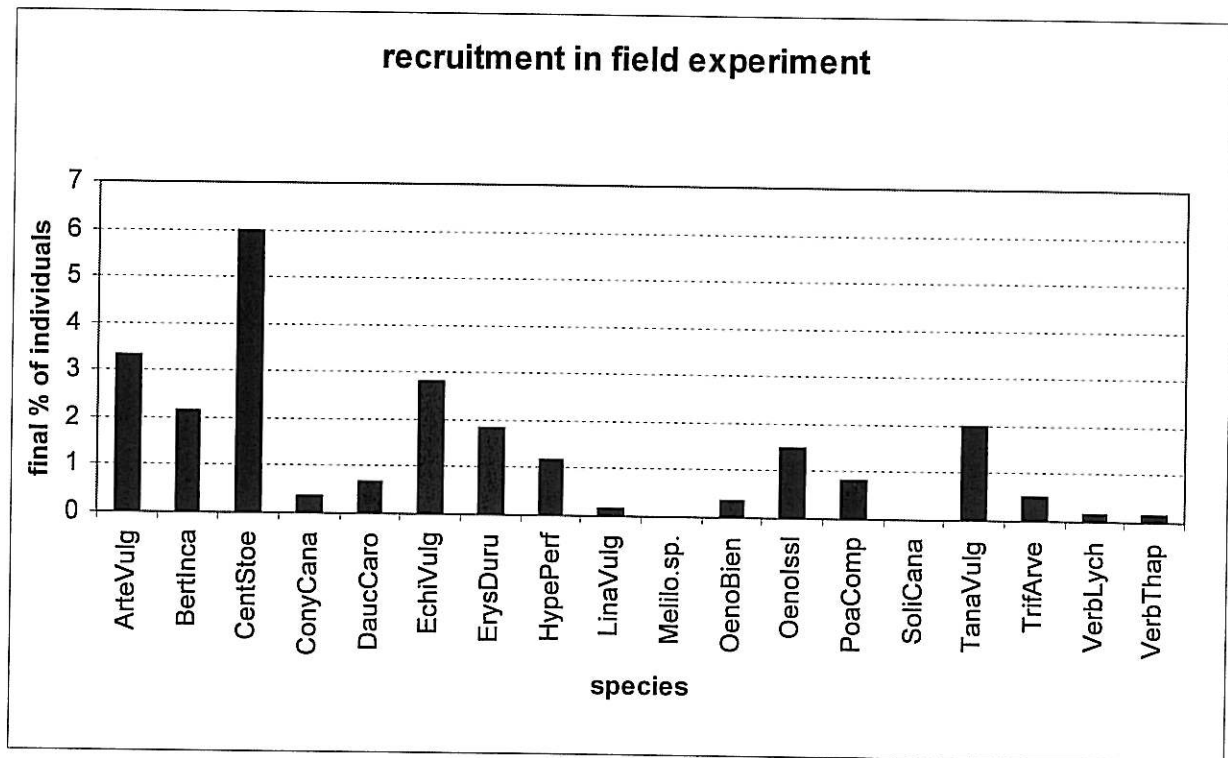


Fig. 11. Final percentages of individuals successfully recruited from seeds for particular species in the field experiment.

4.4. Species distribution

Demography data from phytosociological sampling were analysed by CANOCO for Windows. DCA analysis confirmed previous assumption that CCA is appropriate for data processing (length of gradient 3.84 on 1st axis and 4.17 on 2nd canonical axis). Table 7 summarised results of Monte Carlo permutation test.

Tab. 7. Results of Monte Carlo permutation test.

	Eigenvalue	explained variability	F-ratio	p-value
1 st axis	0.174	17.4%	4.378	0.002
all axis	0.338	33.8%	2.173	0.001

To demonstrate species occurrence at the locality and relation between environmental variables CCA biplot is shown (Fig. 12).

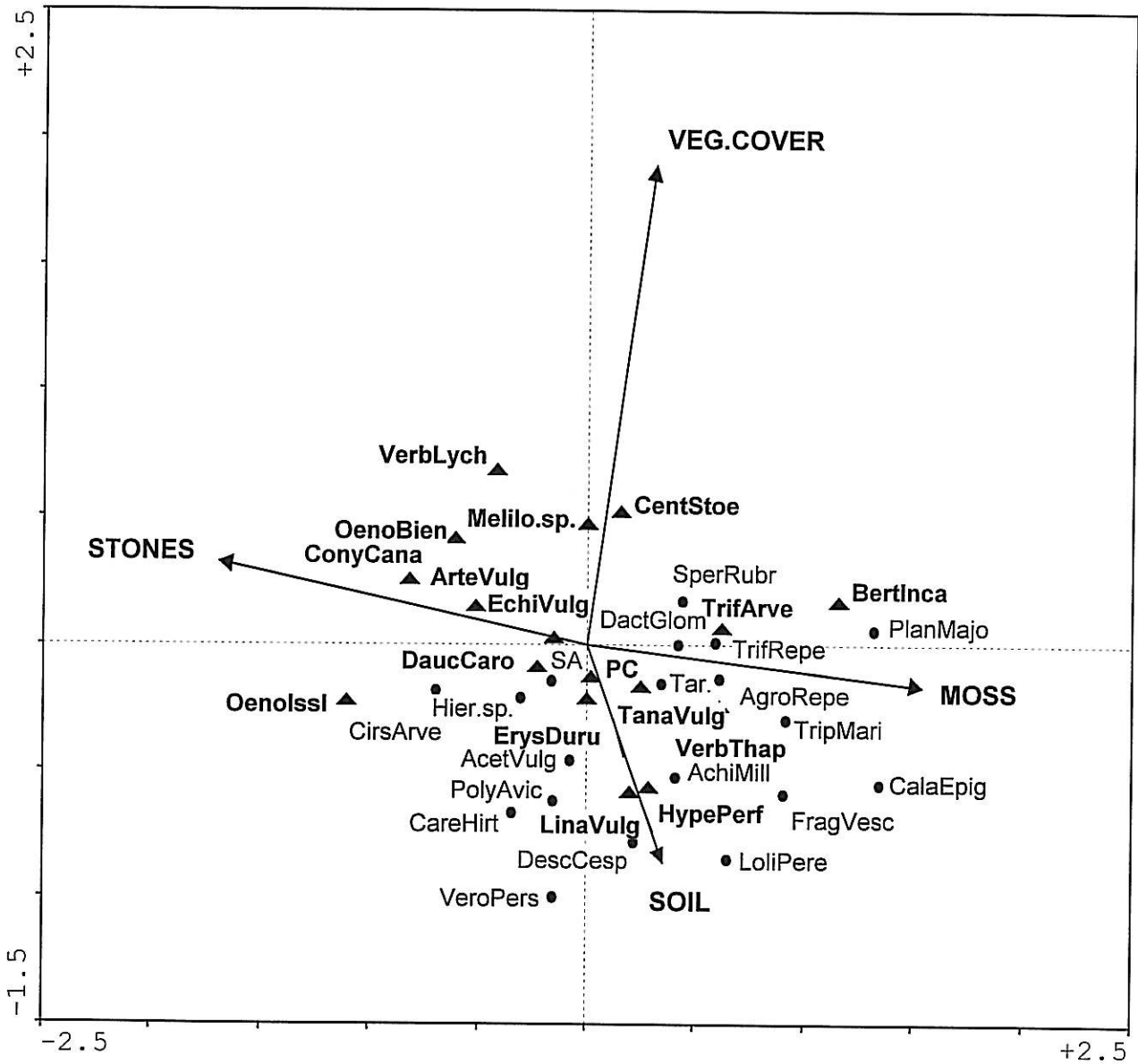


Fig. 12. CCA ordination diagram (1st and 2nd axis are shown) displaying relation of species from relevés and explanatory variables vegetation cover, moss, stones and soil. Abbreviations of species names represent first four letters from either names of species. Exceptions are: Tar-Taraxacum, PC-Poa compressa, SA-Stenactis annua. Triangles represent studied species, circles other species.

- there is no correlation neither between environmental variables “veg.cover” x “stones” nor between “veg.cover” and “moss”
- on the contrary “stones” is strongly negatively correlated with “moss” as well as “veg.cover” with “soil”
- species *Conyza canadensis*, *Oenothera biennis*, *Verbascum lychnitis*, *Oenothera issleri*, *Artemisia vulgaris* occur more frequently at gravely soil with higher amount of stones
- species *Centaurea stoebe* is positively correlated with the higher vegetation cover. It is quite common to find almost pure stands of *Centaurea* rosettes at different ages.
- species *Trifolium arvense*, *Verbascum thapsus* and *Berteroa incana* seemed to prefer places with the higher moss cover
- completely different correlation with respect to all environmental variables for *Verbascum thapsus* and *Verbascum lychnitis* is quite unexpected
- *Linaria vulgaris* and *Hypericum perforatum* are positively correlated with bare soil
- species with centroids projected close to the intercept point of canonical axis (*Poa compressa*, *Echium vulgare*) have almost no reference to the observed environmental variables

4.5. Seed production

Seeds were counted manually. Table 8 shows average number of fruits per plant, average number of seeds per fruit and average total seed production per plant.

4.6. Distance

Data from intraspecific measuring of distance were evaluated by S-PLUS program with nested design. The interspecific differences were significant: $F(17, 19)=16.148$, $p<10^{-6}$ (Fig. 13). The effect of family was examined and was also significant: $F(8, 99)=3.507$, $p=0.00131$. The effect of invasibility was not significant.

4.7. Neighbouring composition

The aim of this analysis (CCA) was to evaluate if some pattern in species composition can be revealed. The first two ordination axis explain 80.1% of variation in the data ($F=1.630$, $p=0.001$).

Tab. 8. Table shows average number of fruits per plant, number of seeds per fruit and total average number of seeds per plant. Species *Daucus carota*, *Echium vulgare*, *Melilotus officinalis* and *Poa compressa* have low-seeded fruits and therefore number of seeds per plant and number of fruits per plant is not stated.

Species	Number of fruits per plant \pm SD	Number of seeds per fruit \pm SD	Number of seeds per plant \pm SD
<i>Artemisia vulgaris</i>	1409.2 \pm 884.07	9.7 \pm 2.43	13266.4 \pm 7716.98
<i>Berteroa incana</i>	253.2 \pm 138.52	8.9 \pm 1.97	2404.0 \pm 1570.80
<i>Centaurea stoebe</i>	192.4 \pm 118.93	14.0 \pm 8.06	2536.2 \pm 1388.84
<i>Conyza canadensis</i>	441.0 \pm 107.21	27.4 \pm 4.93	11998.6 \pm 3083.36
<i>Daucus carota</i>	x	x	2154.0 \pm 235.61
<i>Echium vulgare</i>	x	x	2306.6 \pm 584.72
<i>Erysimum durum</i>	243.6 \pm 98.05	29.7 \pm 9.71	8487.5 \pm 5379.84
<i>Hypericum perforatum</i>	122.6 \pm 31.84	63.5 \pm 9.04	7688.6 \pm 2064.14
<i>Linaria vulgaris</i>	43.6 \pm 18.67	114.7 \pm 22.67	5057.1 \pm 2486.43
<i>Melilotus officinalis</i>	x	x	848.8 \pm 381.27
<i>Oenothera biennis</i>	89.3 \pm 57.98	158.8 \pm 58.76	15000.8 \pm 13601.7
<i>Oenothera issleri</i>	139.0 \pm 87.84	107.6 \pm 28.45	14956.4 \pm 9452.00
<i>Poa compressa</i>	x	x	1130.6 \pm 229.31
<i>Solidago canadensis</i>	563.0 \pm 241.80	15.0 \pm 2.72	8471.2 \pm 3570.11
<i>Tanacetum vulgare</i>	68.8 \pm 17.76	153.9 \pm 47.36	10397.5 \pm 2828.73
<i>Trifolium arvense</i>	168.2 \pm 26.06	64.8 \pm 13.62	10841.9 \pm 1858.45
<i>Verbascum lychnitis</i>	2797.2 \pm 556.10	25.5 \pm 6.87	72115.4 \pm 19089.5
<i>Verbascum thapsus</i>	334.0 \pm 265.71	353.2 \pm 90.37	119997.0 \pm 119120.00

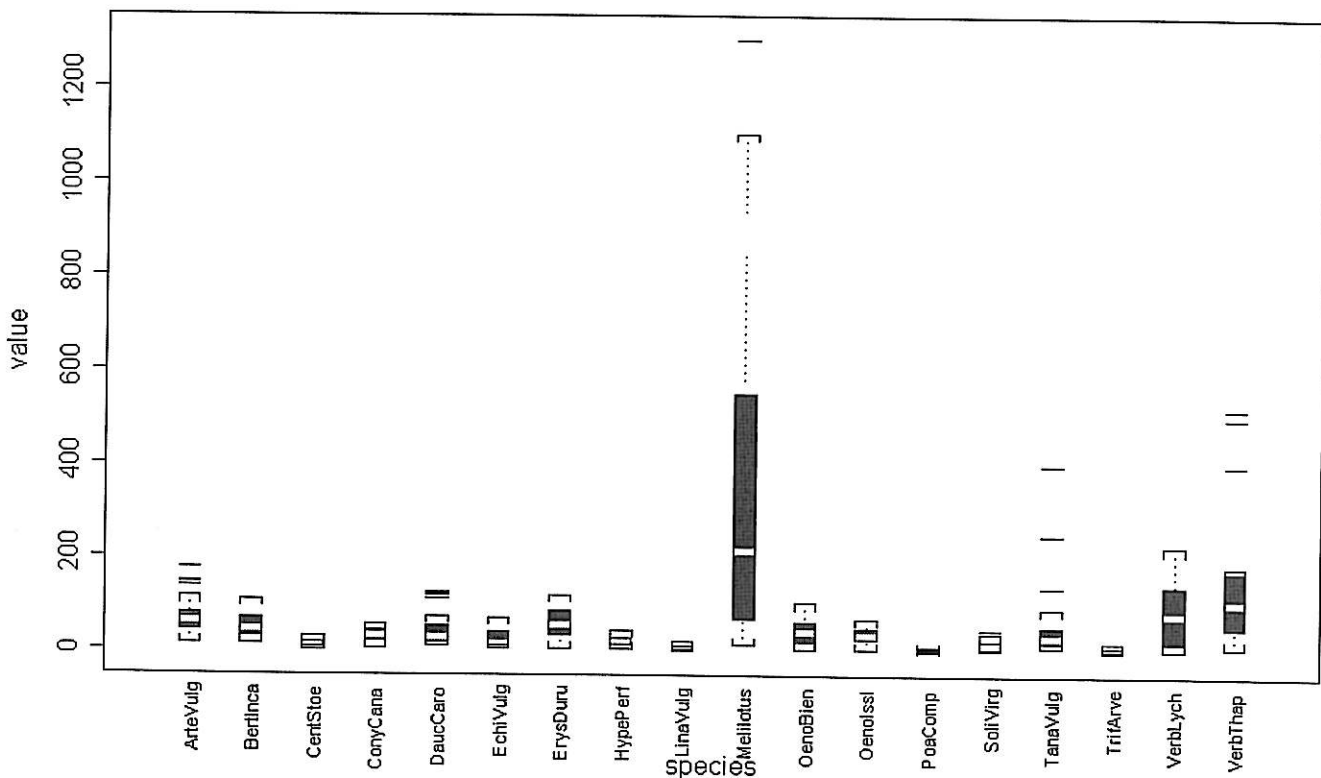


Fig. 13. The overview of species distances (cm), measured between the nearest individuals.

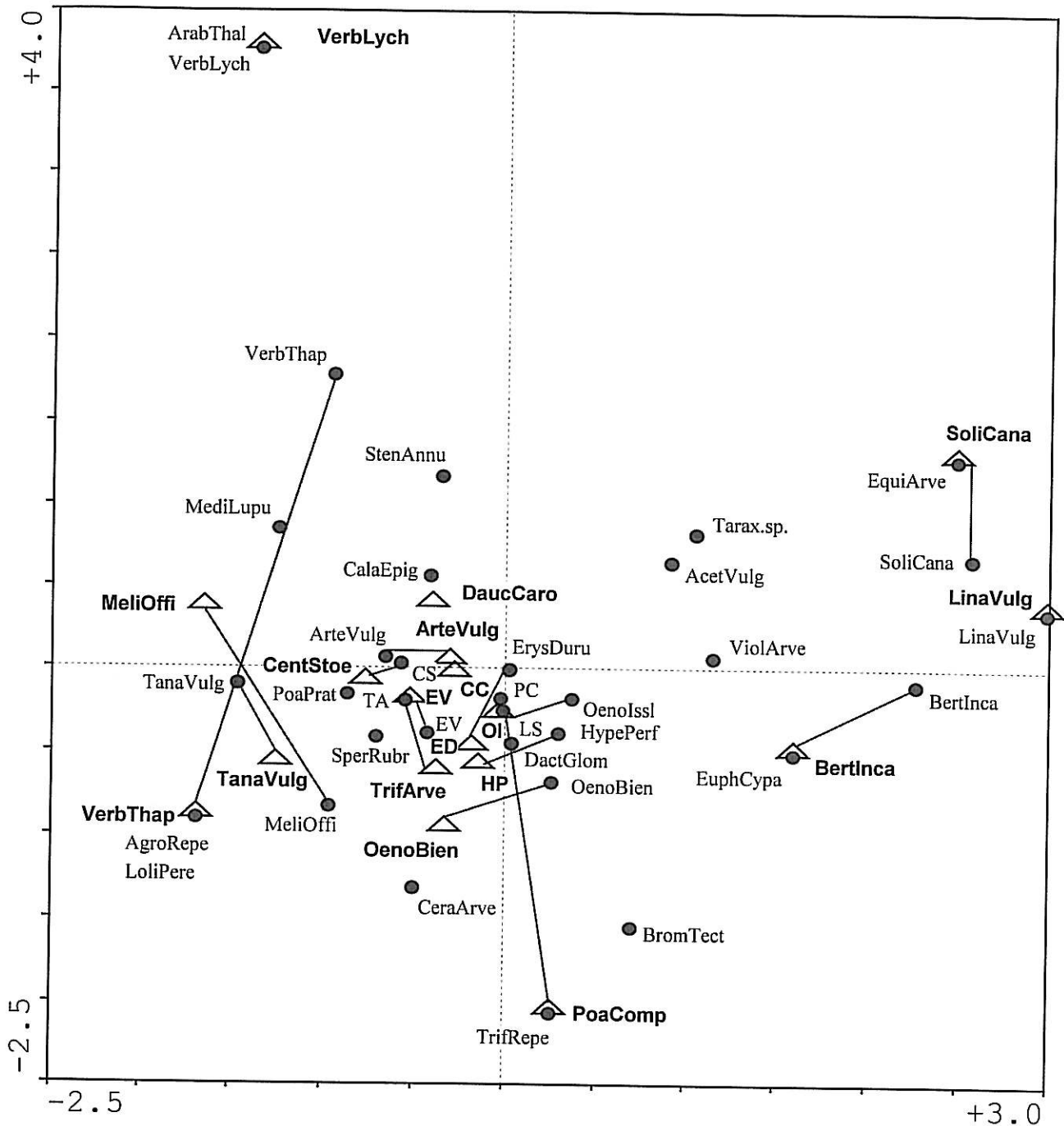


Fig. 14. CCA ordination diagram from analysis of species neighbour composition. Triangles represent studied species, circles species occurred around them. Abbreviations of species names represent first four letters from either names of species. Exceptions: CC-*Conyza canadensis*, CS-*Centaurea stoebe*, ED-*Erysimum durum*, EV- *Echium vulgare*, HP-*Hypericum perforatum*, LC-*Lactuca serriola*, OI-*Oenothera issleri*, PC-*Poa compressa*, TA-*Trifolium arvense*.

Some species were very frequent whereas some appeared only couple of times. Species which occurred less than five times: *Agropyron repens*, *Arabidopsis thaliana*, *Bromus tectorum*, *Cerastium arvense*, *Equisetum arvense*, *Euphorbia cyparissias*, *Lolium perenne*, *Melilotus officinalis*, *Poa pratensis*, *Tanacetum vulgare*, *Taraxacum sp.*, *Verbascum thapsus*, *Verbascum lychnitis*. The clonal species *Poa compressa* and *Trifolium arvense* were recorded 152 and 94 times, respectively (out of 540 observations in total).

Because the differences among species were such great the frequencies of species occurrence were weighted by their abundance. Fig. 14 shows results of CCA analysis. Points representing "sample" and "species" are linked to show the tendencies of species to grow in clumps. Species with small distance between these two points tended to grow together. Species with long abscissas linking "sample" and "species" points usually grew with the most common species.

4.8. Final analysis

The values of "species" (traits observed and gained from the database and my own outputs) were divided by their standard deviations. The lengths of arrows therefore indicate quality of approximation for traits by the ordination diagram (Fig. 15). According to "seed mass" (quite long arrow) species are divided into two big groups. Species below the 1st axis are big in size with the average (*Daucus carota*, *Oenothera biennis*, *Oenothera issleri*, *Erysimum*) to the highest seed weight (*Echium vulgare*, *Centaurea stoebe*, *Melilotus sp.*). Species above the 1st axis are negatively correlated with seed mass (*Solidago canadensis* has the lowest seed weight) (see tab. 4).

- The main trait "species frequency" is strongly negatively correlated with the germination rates and with the number of seeds per plant and positively correlated with the number of individuals, the frequency of fertile individuals and the seed mass. There is no correlation between the species frequency and the average distance.
- All the clonal species (except of *Artemisia vulgaris*) are negatively correlated with the average distance. The seed mass is negatively correlated with the final germination percentages.
- "Life form terophyte" is related with the short-term seed bank and with the annual life cycle (all three traits characterise *Trifolium arvense*).
- "Life cycle polycarpic perennial" is positively correlated with clonality (all clonal species except of *Trifolium arvense* are polycarpic perennials). Clonality is also positively correlated with the transient seed bank.
- "Life cycle geophyte" is positively correlated with clonality (the only two geophytes *Solidago canadensis* and *Linaria vulgaris* are clonal species).
- "Life form hemicryptophyte" is related with the long-term seed bank. All species projected in the 3rd quadrant have the long persisting seed bank and are hemicryptophytes as well. This life form is also positively correlated with the biennial life cycle.

The germination traits are closely associated and positively correlated with the number of seeds per plant.

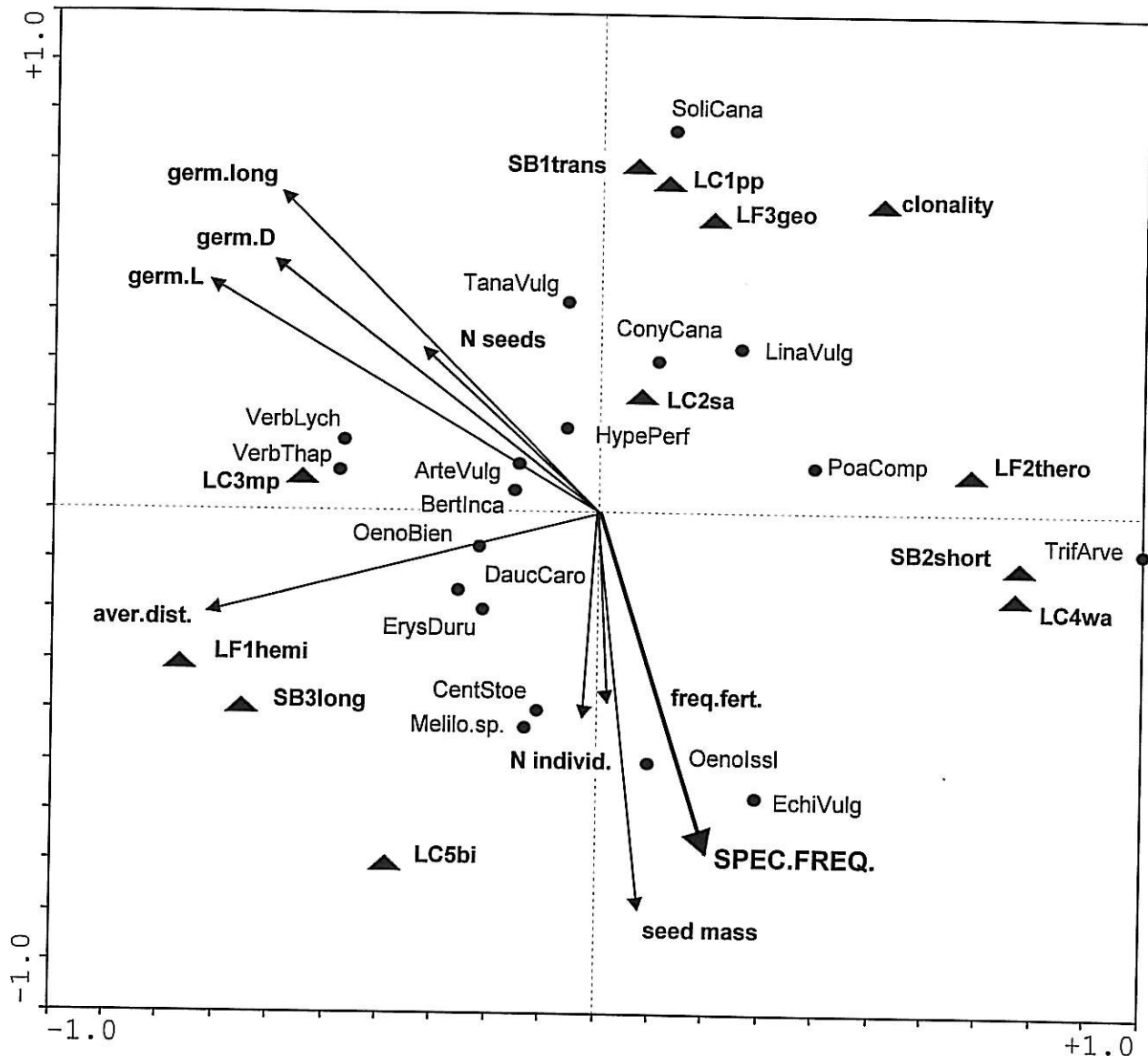


Fig. 15. Final PCA ordination diagram. Measured traits are for better orientation displayed as arrows and traits obtained from databases as triangles (placed in the ends of arrows). Abbreviations of species names represent first four letters from either names of species. Abbreviations of species traits: **germ.long**-final germination rates from the long-term experiment, **germ.D**-final germination percentages from short-term experiment (dark), **germ.L**-final germination rates from short-term experiment (light), **aver.dist.**-average distance between individuals from the study site, **N individ.**-final percentages of recruited individuals from the field experiment, **seed mass**-seed mass (mg), **spec.freq.**-frequency of species from relevés, **freq.fert.**-final frequency of fertile individuals from the field experiment, **N seeds**-total average seed production per plant, **SB1trans**-transient seed bank, **SB2short**-short-term seed bank, **SB3long**-long-term seed bank, **clonality**-presence of clonality, **LF1hemi**-life form hemicryptophyte, **LF2thero**-life form therophyte, **LF3geo**-life form geophyte, **LC1pp**-life cycle polycarpic perennial, **LC2sa**-life cycle summer annual, **LC3mp**-life cycle monocarpic perennial, **LC4wa**-life cycle winter annual, **LC5bi**-life cycle biennial.

Multiply regression for species traits used in final PCA was counted, using software STATISTICA for Windows. Significance was tested with Bonferroni correction at level 0.0025. None of 21 species traits passed this level but two traits the short-term seed bank and the final number of individuals from recruitment field experiment were close to the level of significance ($p=0.0039$, 0.0499 , respectively).

5. DISCUSSION

This study compared species growing at the rural site near the railway station in Zliv. As human population and its influence upon vegetation growth escalates such vegetation types are more frequent. The similar vegetation types can be found not only near railways but also on road verges, sunny wasteland, etc. The study concerned 18 species. Most species are common in Zliv and also in other sites of this sort. Nevertheless, some of the species occur more often in other habitats. *Hypericum perforatum* can be more frequently found on calcareous wasteland, sunny hillsides, wood and road verges (alliances *Cynosurion*, *Arrhenatherion*) (Grime et al. 1988, Květena ČR 2), *Verbascum lychnitis* on sunny hillsides, wood verges, road slopes etc. (alliances *Festucion valesiaceae*, *Bromion erecti*) (Květena ČR 4).

5.1. Germination

Comparison of the final germination rates from the short- and long-term germination experiment revealed differences among species (see Tab. 1). Species, which germinated soon, acquired comparable greater final rates (according to my experience when counting). On the contrary, species that germinated at close of the end of the experiment differed strongly in the final rates (such as *Linaria vulgaris*, *Oenothera biennis*, *Oenothera issleri*, *Poa compressa*, *Trifolium arvense*).

As expected from other studies (Grime et al. 1988) species in our set of data with the long-term seed bank tended to prefer light for germination (see Fig. 4). The inhibiting effect of darkness was observed for most species known to form reserves of buried seeds. The exceptions were *Erysimum durum* (but its preference for dark treatment was very low) and *Berteroa incana*. This inhibiting effect of darkness can also occur in certain species with more transient seed bank e.g. *Tanacetum vulgare*, *Solidago canadensis* (see also Grime et al. 1988). Negative relationship between dark treatment and preferences for germination in light of species with the long-term seed bank were apparent especially for the room treatment (Fig. 4). In the case of the greenhouse treatment most species preferred the dark treatment (Fig. 3). As the temperatures were quite high in the greenhouse I guess that most species preferred the dark treatment because of lower temperature. Q index for greenhouse therefore showed rather preferences for different temperatures than for the dark or light treatment.

Rapid germination should be characteristic of the species of greatest abundance in the area (Grime et al. 1988). Species *Artemisia vulgaris*, *Berteroa incana*, *Centaurea stoebe* were conformable with this assumption. On the contrary frequent species *Poa compressa*

and *Trifolium arvense* achieved slow and low germination rates. van Kleunen et al. (2001) revealed for species with spreading growth form that with increasing vegetation density, allocation to sexual reproduction increases more than allocation to vegetative reproduction. Vegetation cover was not very high in the study locality in Zliv thus preference of *P. compressa* and *T. arvense* to reproduce mainly vegetatively was consistent with Kleunen's observations.

Species *Verbascum thapsus* and *Verbascum lychnitis* had the highest final germination rates (Fig. 5) though were quite rare in the study locality. *V. thapsus* requires bare ground for successful seedling establishment and have ability to colonise early in the successional sequence (Gross 1980). But when later-arriving species reduces the amount of open ground the local population of this species is not able to maintain high abundance (Gross and Werner 1982). No large disturbance occurred in the locality during the two-year study. Populations of both *V. thapsus* and *V. lychnitis* were usually restricted closely to the railways where the frequency of small-scale disturbances was high.

5.2. Seed weight and seed production

Studied species differed strongly according to the seed weight. The lightest seed had *Solidago canadensis* (0.040 mg) and the heaviest *Melilotus sp.* (2.757 mg) (Tab. 4). The effect of invasibility on the seed weight was significant ($p=0.0409$, Fig.10) and native species showed wide range of weight values. But it can be caused by unequal species representation in both groups (4 invasive and 14 native species).

Seed size and number of seeds are traits that are often assumed to be traded off. Venable and Brown (1988) suggested that seed size, seed dispersal ability and seed dormancy should be treated as coadapted traits that reduce risk in variable environment. Leishman (2001) experimentally showed that larger seeds have a greater probability of winning in competition against smaller seeds and presented evidence from literature for trade off between the number of seeds and the size of seeds produced. This was (for some species) consistent with my observations. The most frequent species (see Tab. 1) *Centaurea stoebe* belonged among species with the heaviest seeds (Tab. 4).

Colonisation vs. competition trade offs such as between seed size and number had been suggested as important mechanisms for determining plant community composition (Gross 1980, Eriksson and Jakobsson 1998, Jakobsson and Eriksson 2000). Two species from my set of data, *Verbascum thapsus* and *Verbascum lychnitis*, seemed to fit this trade off. Both had small-sized seeds and the largest amount of seeds per plant from the studied species (see Tabs. 1, 4). On the other hand no negative correlation between seed sizes and probability of establishment was also reported (Tilman 1997, Leishman and Murray 2001).

Recent studies (Leishman and Murray 2001) suggested that the observed significant positive seed size and abundance correlation might be driven by the association between large seeds and large growth forms, as large growth forms tend to be dominant. The high frequencies of occurrence of species *Artemisia vulgaris*, *Centaurea stoebe*, *Echium vulgare* and *Oenothera issleri* (Tab. 1) corresponded this theory because all these species have large grow forms.

It seems likely that patterns of seed size and abundance in communities are determined by a complex set of factors related to other features of a species strategy (dispersal, growth forms, longevity) and to biotic and abiotic factors, rather than by a simple colonisation vs. competition trade off (Leishman and Murray 2001). Frequent species *Poa compressa* and *Trifolium arvense* have small-sized seeds (Tab. 4) and their frequency is caused by vegetative reproduction.

5.3. Seedling recruitment

Final rates of recruited seedlings were low (Fig. 11). In the case of *Melilotus sp.* and *Solidago canadensis* only one single individual emerged for both species. Species with the highest rates were those that achieved high final rates in germination experiments (Tab. 5) (*Artemisia vulgaris*, *Centaurea stoebe*) or achieved average germination rates but were frequent in the study habitat (*Echium vulgare*, *Erysimum durum*, see Tab. 5).

Although this experiment was established to compare recruitment ability, some competition abilities could be observed as well. Robust and fast growing species *Artemisia vulgaris*, *Centaurea stoebe*, *Berteroa incana* tended to overgrow smaller species and thus contributed to their exclusion (*Melilotus sp.*, *Solidago canadensis*) or caused their small size (*Daucus carota*).

Individuals of species in the experimental garden were bigger then individuals in the study habitat (average height in the experimental garden was 153.3 cm for *Artemisia vulgaris*, 110 cm for *Berteroa incana*, 158 cm for *Centaurea stoebe*, 131 cm for *Echium vulgare*). It was probably due to better soil and trophy conditions and water regime. The greater height did not matter because the goal of this experiment was relative comparison of recruitment abilities of the studied species.

Most of successfully survived individuals of all species also matured. Exceptions were *Linaria vulgaris* with only one survived individual that was small and sterile and *Verbascum lychnitis* (one small rosette that did not mature). Despite the fact that this experiment lasted for 1 year most biennial species successfully matured. One individual of *Oenothera issleri* matured even 5 months after seeding. These observations are consistent with previous studies revealing that there is a threshold for rosette size below which "biennial" species do

not mature (de Jong et al. 1989). Additionally it seems that if "biennial" species grow in good conditions, which allow them to develop rosette big enough to mature, they can do so even during first year.

Kiviniemi (2001) supported previous hypothesized (Eriksson and Jacobsson 1998) positive effect of seed size on establishment ability. The heaviest seeds in my data set (Tab. 4) belonged to species with the highest final recruitment rates (*Berteroa incana*, *Centaurea stoebe* and *Echium vulgare*, for recruitment rates see Fig. 11). On the other hand other species with high recruitment rates (*Artemisia vulgaris*, *Erysimum durum*, *Tanacetum vulgare*) were species with average-sized seeds. This is in agreement with conclusions of many studies (Eriksson and Jacobsson 1998, Kiviniemi 2001) that colonization ability is not a simple function of one particular trait value, e.g. seed size.

5.4. Species distribution

Final output from this analysis (Fig. 12) confirmed observations from the study site. Species *Oenothera issleri*, *Oenothera biennis* and *Verbascum lychnitis* preferred stony soil near the railways with high rate of disturbances. Previous studies (Gross 1980, Gross and Werner 1982) revealed that *Oenothera biennis* and *Verbascum thapsus* require bare ground for successful seedling establishment.

V.thapsus and *V.lychnitis* interestingly showed different correlation to all environmental variables. This was probably caused by intermittent disturbances that opened ground farther from the railways, where cover of "soil" and "moss" was higher. Rosettes of *V. thapsus* occupied such places more frequently and thus environmental traits for *V.thapsus* differed from those for *V. lychnitis*.

Species *Linaria vulgaris* and *Hypericum perforatum* preferred places with high soil cover, where amount of stones was low (Fig. 12).

Solidago canadensis did not occur in this graph. It is partly because this species was not so frequent at the locality (additionally it mainly grew at sites that were not included in the study and as a clonal species forming individual-rich stands which are however quite rare). On the other hand some dead fertile individuals were observed still they did not affect this analysis. It can be concluded that the habitat of *Solidago canadensis* growing on urban wasteland may only be seriously narrowed by species with vegetative growth or considerable height (Cornelius and Faensen-Thiebes 1990). Both types of species are frequent at the study site. In addition *Solidago canadensis* is not adapted to frequent annual disturbances. Sexual propagation is delayed until its second year of development. Thus frequent disturbances, which are common in the inner cities or railway stations, may prevent this species from completing its life cycle (Cornelius 1990).

5.5. Distances

Statistical analysis confirmed expected assumption that species differ in average distances measured among the same species ($p < 10^{-6}$). The biggest measured distances had *Melilotus officinalis*, *Verbascum lychnitis*, *Verbascum thapsus* and *Tanacetum vulgare*. These species were not among the frequent species (see Tab. 1) and therefore the distances between the nearest individuals of these species were quite long (for *Melilotus officinalis*, which is quite rare, the longest distance was about 12 m). On the contrary clonal species with vegetative reproduction such as *Poa compressa*, *Trifolium arvense* and *Linaria vulgaris* had small range of measured values that were quite low (see Fig. 13).

5.6. Neighbouring composition

The aim of this analysis was to reveal some pattern of species composition. Studied species entered this analysis as "samples" and species, which occurred around them as "species". In the case of *Verbascum lychnitis* and *Linaria vulgaris* points representing "sample" and "species" were projected at the same position (Fig. 14). It corresponds with situation observed in reality. *V. lychnitis* was in fact limited on one place, where its rosettes composed almost pure stand. Adult individuals were confined to the neighbour of the rail embankment. Situation was similar in the case of the clonal *L. vulgaris*.

Centaurea stoebe and *Echium vulgare* were frequent at the locality and thus distances between "species" and "sample" centroids for these species were short, indicating that these species tended to create stands with high cover. Abscissa linking together points for "species" and "sample" was longest for *Verbascum thapsus* and *Melilotus officinalis* (Fig. 14). Both species were rare and their neighbours were mainly the most frequent species.

Abscissa was also quite long for *Poa compressa* (although one would expected this clonal grass species rather to create pure stands). This was due to effort to differ single individuals (genets). Compact well distinctive clump was regarded as one individual. Another nearest tuft could be quite away. On the other hand if a single culm was found, different species (not *P. compressa* itself) were neighbours (including various seedlings).

In the case of *P. compressa* there is a discrepancy between results of this experiment and the previous one (measuring distance). When measuring distances to the nearest individual of the same species, *P. compressa* tended to have small distances to other individuals. But graphic output from this analysis (Fig. 14) showed that *P. compressa* tended to grow rather with other species than to create pure stands. Low number of measuring (5 observations for 6 individuals per species) probably caused this discrepancy. The rest of species did not differ so much from each other.

5.7. Final analysis

The aim of this analysis was to determine if measured traits or species characteristics from databases could evaluate some patterns in vegetation composition. The frequencies of species obtained from relevés "species frequency" seemed to be strongly positively correlated with seed size (Fig. 15). This was consistent with recent studies (Leishman 2001).

Results of this analysis also revealed pronounced negative correlation between seed size and number of seeds, which confirmed (at least for this data set) importance of seed size vs. number trade off (Eriksson and Jacobsson 1998, Jacobsson and Eriksson 2000). Number of successfully recruited individuals from the field experiment "number of individuals" and "frequency of fertile individuals" was strongly correlated with each other as well as with "seed mass". Final germination rates were strongly negatively correlated with seed mass.

Recent studies revealed positive (Jacobsson and Eriksson 2000, Leishman 2001) and none (Tilman 1997, Leishman and Murray 2001) correlation between recruitment ability and seed size. Recruitment ability represented as number of successfully recruited individuals ("N individ.") was strongly positively correlated with seed mass in my sets of data. The average distance between individuals of the same species was not correlated with "species frequency". This was presumably because except of three species with long average distances (*Melilotus officinalis*, *Verbascum thapsus*, *Verbascum lychnitis*) the rest of species had similar distances.

All clonal species (except of *Artemisia vulgaris*) were negatively correlated with average distance. Average distance for *Artemisia vulgaris* was 71.13 cm. This species, although is clonal, does not form extensive stands (Grime et al. 1988). Non-clonal species achieved similar values as *A.vulgaris* whereas clonal species had much lower values. Common problem, when studying clonal plants, is that one stem do not correspond one individual (genet) but correspond one ramet.

"Life cycle polycarpic perennial" was positively correlated with "clonality" and "transient seed bank" and "biennial life cycle" with "long-term seed bank" (Fig. 15). In the North-West European flora shorter-lived species generally tend to have longer-lived seeds and vice versa (Thomson et al. 1998). This correlation is important mainly for species of highly disturbed habitats such as ruderal sites (Stöcklin and Fisher 1999).

Germination traits were closely associated and positively correlated with number of seeds per plant. Species *Verbascum thapsus* and *Verbascum lychnitis* were positively correlated with these traits; both were the best germinating species (see Fig. 5) and their seed production was the biggest among studied species (Tab. 8).

"Life form hemicryptophyte" was related with "long-term seed bank" and with "biennial life cycle". 8 out of 18 studied species were "biennials" (or monocarpic perennials, semelparous

perennials, Silvertown 1984). Often different biennials can be found growing together at the same sites (*Echium vulgare*, *Cirsium vulgare*, *Verbascum thapsus*) indicating that biennial behavior is an adaptation to a special set of circumstances (van der Meijden et al. 1992). These must be related to disturbances of the environment. Explosive population development usually follows large-scale natural or man-made disturbances in several communities (van der Meijden et al. 1992). Without disturbances biennials are losers compared to perennials. It is only during the first years following disturbance that biennials are successful. Biennials start from a larger seed bank and have higher reproductive allocation (Hart 1977), enabling them to build up a new seed bank or to reach new sites at a faster rate than perennials (van der Meijden et al. 1992).

But what allows existence of biennials even in the older succession series? Boeken and Shachak (1998) showed that even areas with an undisturbed soil surface are capable of receiving new colonizers after a period of high extinction rates or low colonization rates due to limited arrival of propagules. Vegetation cover was not very high at the studied site and there were patches of bare soil between vegetation islets. These patches may accepted new colonizers and allow presence of biennials even in the older succession series.

Long-term seed bank was strongly negatively correlated with clonality. Clonal plant species, which reproduce primarily by vegetative growth and therefore move gradually across the landscape (Robinson et al. 1992), were more likely to persist in large fragments than in small fragments, where colonization was limited by habitat disruption. Clonal species tended to have transient or short-term seed bank. 4 clonal species from my sets of data have short-term seed bank (*Poa compressa*, *Solidago canadensis*, *Tanacetum vulgare*, *Trifolium arvense*). The rest of clonal species *Artemisia vulgaris*, *Hypericum perforatum* and *Linaria vulgaris* have long-term seed bank. Tilman (1997) found out that longer-lived seeds constitute better buffer against risks of local extinction caused by stochastic processes than shorter-lived seeds.

Ecologists have long been fascinated with what allows coexistence of different species with diverse traits in one habitat. The diversity-productivity hypothesis (Naeem 1994, Tilman et al. 1996) is based on the assumption that interspecific differences in the use of resources by plants allow more diverse plant communities to utilise more fully limiting resources and thus attain greater productivity. Other observational and field experiments support the hypothesis that biodiversity influences ecosystem productivity (Naeem 1994) and stability (McNaughton 1977, Tilman and Downing 1994). Whereas classical competition theory predicts competitive exclusion of species with similar requirements, recent ideas (Bengtsson et al. 1994) stress that species diversity may be explain by a multitude of processes acting at different scales, and that similarities in competitive abilities may facilitate coexistence.

It seems that both these theories can be used to explain coexistence of many species in my study site. Quite high total number of species (64) may contribute to quality utilisation of resources. On the other hand there are groups of species with similar traits (life form, bank longevity, life cycle etc.) and this fact could explain coexistence due to Bengtsson. Zobel (1992) pointed out that if the competitive abilities of species are made more similar, e.g. by herbivory, or disturbance, a higher number of vascular plant species can coexist. It seems to me that this theory is suitable for the study site, which is under intensive human influence.

Some studies (Tilman et al. 1994) suggested that there is a trade off between dispersal and local competitive ability that may cause threshold effect when habitat are fragmented, causing a decline in species that were competitively superior (hence most abundant) in the landscape. On the contrary Eriksson and Jacobsson (1998) showed that abundance at some intermediate spatial scale reflects colonization properties. A possibility is that the present landscape is so fragmented that the abundance of many species is determined by dispersal rather than by competitive ability (Eriksson and Jacobsson 1998).

Spatial structure is an unavoidable result of the discrete nature of individual organisms (Tilman 1994). It may allow a number of competing species to stably coexist in a physically homogenous habitat even though a single species is the superior competitor (Tilman 1994). The study site was consistent with this pattern. Dominant competitively forcible species (such as *Centaurea stoebe*) did not cause exclusion of rare and small species (see Tab. 1 for list of species).

Species that act as metapopulations live with a threshold requirement for habitat (Kareiva and Wennergren 1995), below which they face inevitable extinction (long before all of the habitat has been removed). Studies of occupancy, recruitment and extinction thresholds provide a useful framework for estimating potentially endangered species (Eriksson and Kiviniemi 1999).

6. CONCLUSIONS

1.

Species differed strongly in their germination ability. Clonal species *Linaria vulgaris*, *Poa compressa*, *Trifolium arvense* and invasive species *Oenothera issleri* achieved the lowest final germination rates.

Species also differed in timing of germination. Species with low final germination rates generally started to germinate at close of the end of the experiment.

This study confirmed assumption that germination of species with long-term seed bank is inhibited by dark. 11 out of 13 species with long-term seed bank preferred light for germination.

✓ for long-term
germination reported!

2.

Invasive species differed significantly in their germination ability. *Conyza canadensis* belonged to the best-germinated species. The final rates of *Solidago canadensis* and *Oenothera biennis* were average among all studied species. *Oenothera issleri* was the worst germinated species at all.

Solidago canadensis preferred light for germination. So did *Oenothera biennis*, which seemed to prefer higher temperatures. *Oenothera issleri* successfully germinated only in greenhouse dark treatment. *Conyza canadensis* preferred dark treatment.

3.

Species *Verbascum thapsus* and *Verbascum lychnitis* have the biggest seed production per plant. Species *Poa compressa* and *Melilotus sp.* produce the lowest number of seeds. Other species do not differ much.

4.

The best recruiting species were *Centaurea stoebe*, *Artemisia vulgaris* and *Echium vulgare*. The worst were *Melilotus sp.* and *Solidago canadensis*. No invasive species was among the best recruited species.

5.

The main factors determining distribution pattern in the studied habitat seemed to be type of substrate and frequency of disturbances.

6.

Species differed significantly in their distances to the nearest same species. *Linaria vulgaris* and *Verbascum lychnitis* tended to create pure stands where the distances were low. On the contrary *Verbascum thapsus* and *Melilotus sp.* seemed to grow with the most common species (high distances).

7.

Species frequencies in the locality can be explained mainly by seed weight. My set of data is consistent with seed size vs. number trade off.

7. PERSPECTIVES

Rural sites similar to the study locality are under intensive human influence. Fate of communities inhabiting these localities is thus uncertain. During autumn 2001 a large-scale, dramatic disturbance happened to my studied site. Vegetation cover disappeared under new made-up ground (see Appendix). It would be interesting to monitor further development in the locality. There is a set of basic characteristics (such as type of new substrate, its trophy

and soil moisture regime, species representation in its seed bank etc.) that can influence species composition. However, it is likely that next scenario will be following (I directed my attention to studied species) ...

Species *Verbascum thapsus*, *Verbascum lychnitis*, *Oenothera biennis* and *Oenothera issleri* produce large numbers of very small seeds that are capable of remaining viable in the soil for 80-100 years (Baskin and Baskin 1998, Gross 1982) and require bare soil for successful establishment (Gross 1980, 1982). These life history characteristics allow them to colonize rapidly a newly created disturbed area (Gross 1980) and it is likely that rosettes of these biennial plants will be among first species newly occurred in the locality.

Annual plants will probably play an important role in inhabiting the site. However, only two annual species were involved in my study. Their seeds are not always available and they were not as frequent and important for vegetation pattern as biennials or perennials. In the case of *Trifolium arvense* its clonality will be more important than its annual life cycle. *Conyza canadensis* was not among frequent species (so was not other annual plants) and because annual species tend to have short-term seed bank their arrival to the site is rather stochastic.

Clonal species (such as *Poa compressa*, *Trifolium arvense*, *Linaria vulgaris*) that can regenerate by vegetative growth can inhabit disturbed areas also quite soon.

Invasive species, which spread along railways, may also be among sooner-arrive species. Especially *Oenothera biennis* and *Oenothera issleri*, which are able to inhabit bare soil (Gross 1980, 1982) and have long-term seed banks (Baskin and Baskin 1998). *Conyza canadensis* is also likely to appear in the locality soon. On the contrary *Solidago canadensis*, which can withstand competitive pressure by means of its clonal growth (Cornelius 1990) is likely to be among the later-arriving species.

Artemisia vulgaris (Grime et al. 1988) may also be an early colonist (high level of seed production, persistent seed bank) which is later replaced by taller species with greater potential for dominance (such as *Centaurea stoebe*). Species with shorter-lived seeds (e.g. *Daucus carota*) are less likely to be among the initial colonists on a newly created sites, simply because their seeds are not likely to be present in the seed pool (Gross 1982). The first appearance of this later-arriving species is thus dependent upon the dispersal of propagules from source population outside the disturbed site (Gross 1982). On the other hand *Daucus carota* do not require bare ground for establishment (comparing with *Oenothera* and *Verbascum* species).

However, large component of community structure is determined by stochastic variation in patterns of immigration and extinction. Both these factors depend on the species ability to compete with neighbours or withstand periodic disturbance (Collins and Glenn 1991). Return flow of species from disturbed sites can in addition augment diversity of adjacent undisturbed

areas (Boeken and Shachak 1998). The further species composition also depends on frequency of disturbances. Since too many disturbances may be disadvantageous for all species, diversity tends to peak at intermediate levels of disturbance (Bengtsson et al. 1994).

Tab. 9. Pattern of traits related to species population dynamics. Used characteristics were estimated on the base of studied traits. Invasive species are shown in bold lettering.

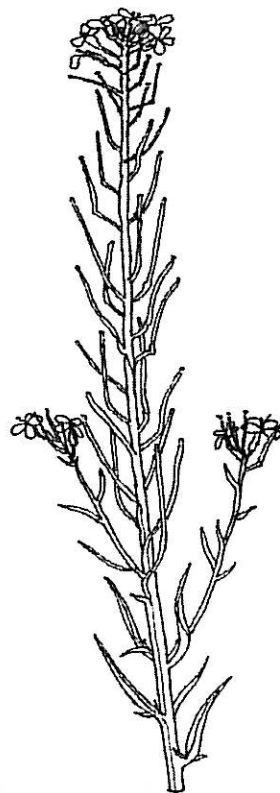
Species	Family	Invasibility	Final germination rate in light	Final germination rate in the dark	Seed pool	Average number of recruited individuals	Frequency from relevés	Final rate of fertile individuals from recruitment experiment
ArteVulg	Asterace.	no	very high	very high	high	high	high	very high
BertInca	Brassicac.	no	medium	high	medium	medium	low	very high
CentStoe	Asterace.	no	medium	very high	medium	very high	very high	high
ConyCana	Asterace.	yes	high	very high	high	low	medium	low
DaucCaro	Apiaceae	no	medium	very high	medium	low	medium	medium
EchiVulg	Boraginac.	no	low	medium	medium	high	high	very high
ErysDuru	Brassicac.	no	medium	medium	high	medium	medium	medium
HypePerf	Hypericac.	no	high	high	high	medium	medium	very high
LinaVulg	Scrophula.	no	low	low	medium	low	low	very low
Melilo.sp.	Fabaceae	no	medium	low	low	very low	medium	very low
OenoBien	Onagrace.	yes	medium	medium	high	low	low	low
OenoIssl	Onagrace.	yes	very low	very low	high	medium	high	medium
PoaComp	Poaceae	no	low	low	low	medium	very high	very low
SoliCana	Asterace.	yes	high	high	high	very low	very low	very low
TanaVulg	Asterace.	no	high	high	high	medium	medium	medium
TrifArve	Fabaceae	no	very low	low	high	low	high	medium
VerbLych	Scrophula.	no	very high	very high	very high	low	low	very low
VerbThap	Scrophula.	no	very high	very high	very high	low	low	low

Table 9 shows synoptic overview of studied species traits that might be related with species ability to inhabit newly created habitats. Species *Artemisia vulgaris*, *Berteroa inacana*, *Centaurea stoebe* have mainly high or medium levels of all studied traits and all were frequent in the study habitat. On the contrary *Poa compressa* and *Trifolium arvense* belonged to species with very low, low or medium levels of all studied traits except of the frequency from relevés. This is because of their intensive vegetative growth, which is not comprehend in any studied traits. Species *Linaria vulgaris* and *Melilotus sp.* had very low to medium levels of the traits. These species were not very frequent and *Melilotus sp.* seemed to be declining in the site.

Soon-arriving species seemed to have very high to high germination rates and seed pool and very low to low frequencies of recruited and fertile individuals from the field experiment and frequencies of species from the study site. Next to *Verbascum thapsus* and *Verbascum lychnitis* such species are likely to be *Conyza canadensis* and *Solidago canadensis* either. All these species are small-seeded. On the contrary large-seeded *Echium vulgare* had low to medium germination rates and seed pool and high to very high frequencies of recruited and fertile individuals from the field experiment and frequency of occurrences in relevés.

Frequent species *Oenothera issleri* had high level only for the seed pool. *Oenothera biennis* have also large seed pool, however, its frequency in relevés was low. This is probably because populations of *Oenothera biennis* were in fact restricted to two or three smaller places and therefore its occurrence in relevés was lower.

In virtue of these facts together with availability of diaspores from neighbour vegetation I suppose that community, which will arise in the studied site, will be similar to the old one. At least in the case of dominant species. They will probably be *Artemisia vulgaris*, *Berteroa incana*, *Centaurea stoebe*, *Echium vulgare*, *Poa compressa*, *Trifolium arvense*. They will likely be *Oenothera issleri* and *Oenothera biennis* either. *Conyza canadensis* and *Solidago canadensis* had both transient seed bank. Their arrival and successful recruitment is consequently largely stochastic. Further presence of less dominant species and annuals is mainly stochastic and therefore not easy to predict.



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APPENDIX



The study site in Zliv (3.7. 2001)



The same site after disturbance (28.11. 2001)



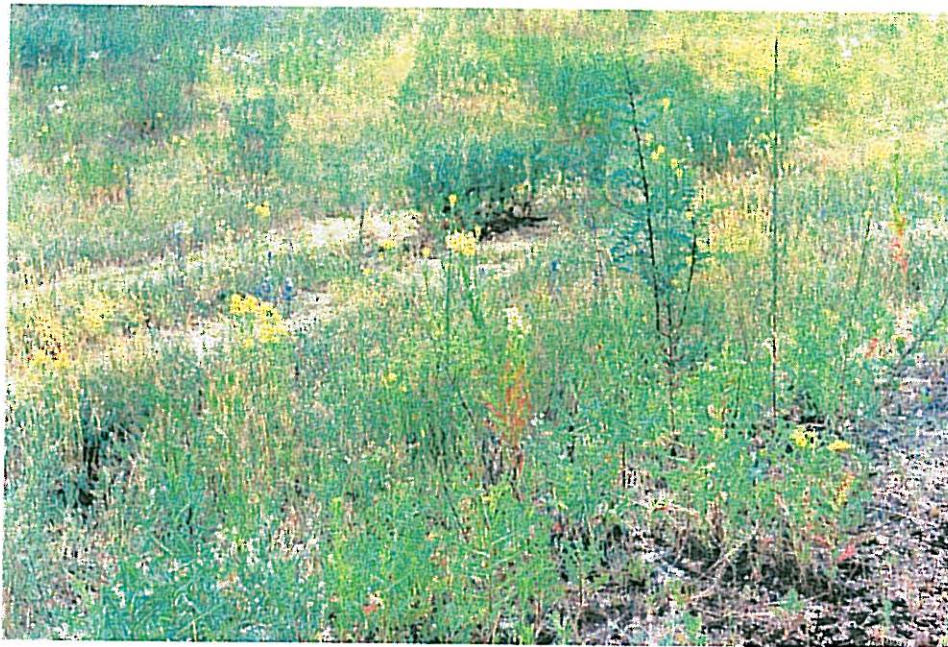
Populations of *Oenothera biennis*, *Oenothera issleri* (Zliv 3.7. 2001)



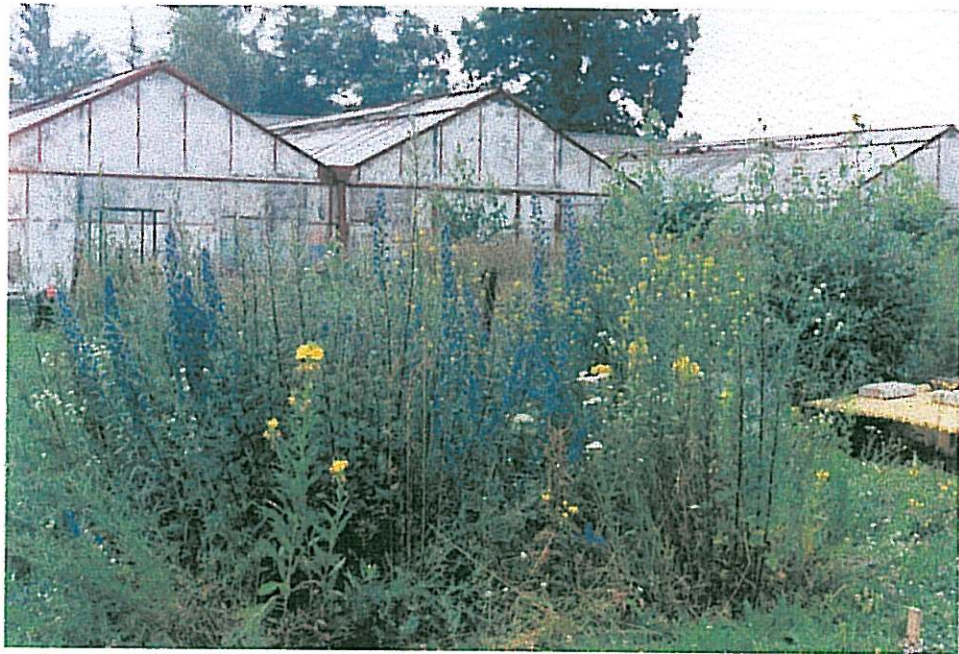
Show must go on ... new life on the embankment after disturbance.



The population of *Echium vulgare* (Zliv 3.7.2001)



The population of *Lactuca serriola* (Zliv 3.7.2001)



The experimental garden (Sádka 4.7.2001)



Harvesting of the experimental garden (25.11.2001)