

University of South Bohemia, Faculty of Biological Sciences
Department of Botany
2004



Master Thesis

A comparative study of germination abilities of ruderal species

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Annotation

Desetová L. (2004): A comparative study of germination abilities of ruderal species. Master Thesis, Faculty of Biological Sciences, University of South Bohemia, České Budějovice

The present study concerned germination abilities of 18 plant species coexisting in ruderal localities near 9 local railway stations within South Bohemia. Four germination attributes; time to the beginning of germination (germination lag), time taken to achieve 50% of final germination (germination speed), germination percentages in diurnal light - dark cycle and germination percentages in the dark; were calculated for each species. The ecological implications of the observed germination biology are discussed together with the ecological characteristics of the studied species.

Acknowledgements:

I am grateful mainly to my supervisor, Standa Mihulka, for valuable methodical suggestions and comments to the manuscript. I would like to thank Petr Šmilauer and Jan Lepš for help with statistics. I am thankful to my family and friends for broad support, and Onyx for encouraging me in all ways.

Dedicated to the memory of my father.

I hereby state that I worked this study out myself using only the cited literature.

České Budějovice
25th April 2004



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1. INTRODUCTION

1.1. Rural sites and vegetation

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). Rural communities must be, due to a strong human influence, adapted to frequent disturbances (Grime et al. 1988).

Vegetation often inhabiting railways' banks in a mesic climate can be generally described as an association *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. Communities of the association *Dauco - Melilotion* tend to spread out and frequently penetrate to untended urban habitats (Slavík 1990 - 1997). According to the C - S - R theory most species have the intermediate strategies competitive - ruderals, stress - tolerant ruderals or competitive stress - tolerant ruderals (Grime et al. 1988).

Species that occurred on such places have different life forms and life cycles. 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 and become a short - lived monocarpic perennials (van der Meijden et al. 1992, van Breemen 1984, Silvertown 1984). Flowering is usually delayed if rosette size is below a certain threshold (de Jong et al. 1989). For biennials, the primary factor limiting survival, growth or seed production seems to be a small - to large - scale disturbance of environment, providing an area of bare soil. Therefore most habitats are only temporarily suitable for biennials, still these populations survive on the landscape level (van der Meijden et al. 1992). 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). Thus, they are well - adapted to colonization of open, disturbed habitats which are intermittently available (van Breemen 1984).

However, 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 species with large production of seeds and perennial species with intensive vegetation growth are of great importance in such habitats (Slavík 1990 - 1997). Persistent seed bank is another strategy that frequently occurs among plants inhabiting especially sites subjected to temporally unpredictable disturbance (Grime et al. 1988, Baskin and Baskin 1998).

1.2. Germination

It has been found in many plant species that the fate of the next generation, as far as the germination of seeds is concerned, can be modified by various factors e.g. daylength, temperature, light quality, altitude and even maturation conditions of the seeds when they are still on the mother plant (Gutterman 1992, Benech - Arnold et al. 2000). The phenotypic influences ensure that, even under the most suitable conditions for germination, only a portion of the total seed bank population of a certain plant species will be ready to germinate (Gutterman 1992). The genotypic influences of a plant species ensure that the adaptation of the plant to its habitat conditions is such that germination occurs in the right season and in the right place (Gutterman 1992). Interactions between

environmental factors have a great impact on the germination of some species. These differential responses to main environmental factors and their interaction could account for differences across species of seed germination and seedling emergence timing, which represent differences in adaptation and survival strategies (Leon and Owen 2003).

The enormous seed production of most plants, coupled with the general paucity of seedlings, is a vivid testimony to the intensity of seed mortality (Crawley 1992). Much of the loss of seeds from the soil seems to be attributable to germination, and therefore rates of loss are greatest under conditions which favour germination i.e. shallow burial in warm, well - aerated, moist soil. For the same reason, rates of loss are higher in disturbed rather undisturbed soil (Thompson 1992, Roberts and Boddrell 1984). Spatial and temporal variation in seed death rates can have important consequence for plant coexistence (Crawley 1992).

In a general sense the role of seed banks in vegetation dynamics is well - understand, and is clearly intimately connected with disturbance (Thompson 1992). Soil disturbance generally coincides with destruction of established vegetation and hence, is a good predictor of reduced competition by established plants (Pons 1992). Some seeds are very long - lived and many reports highlight the remarkable longevity of such seeds, the record breakers in the survival game (*Verbascum thapsus* 100 and *Oenothera biennis* 80 years). It is likely that the same periods of survival in soil seed banks can be achieved by different strategies (Murdoch and Ellis 1992).

Seeds largely rely on dark - dormancy for avoidance of germination in the soil and hence, for the formation of a persistent seed bank (Pons 1991, 1992). Benech - Arnold et al. (2000) defined two kinds of factors that affect dormancy: those that govern changes in the degree of dormancy (i.e. temperature and moist conditions) and those that remove the ultimate constraints for seed germination once the degree of dormancy is low (i.e. light, fluctuating temperatures and nitrate concentrations). Plants commonly delay their reproduction by allocating a part of their offspring into an innate dormant state, thus forming a seed bank (Baskin and Baskin 1998). Innate dormancy helps prevent precocious germination on the mother plant and ensure temporal dispersal of seeds. Innate dormancy not only varies with genotype but also with maturation environment. E.g. seeds produced in warm, dry summers are likely to have less dormancy than those produced in cool moist ones (Murdoch and Ellis 1992).

Chilling, temperature fluctuations and light in various combinations showed additive effects or positive interactions, concerning germination rates, in a number of species. Simultaneous operation of several environmental factors together is more the rule than the exception under field conditions. The various interactions complicate ecological interpretations, but can be viewed as tools which the seed can use for the fine tuning of its germination (Pons 1992, Benech - Arnold et al. 2000).

Some ecological factors are related to competition (nutrient tolerance, light requirement, height) and others relate more to the process of establishment e.g. germination and seed bank (Blomqvist et al. 2003). Traits of the studied species involved in this study are connected mainly with the processes of establishment (germination abilities and requirements, seed bank).

1.3. Species coexistence

It is known that plants with contrasting strategies can live together in a community (Hill et al. 2002). Communities of the association *Dauco - Mellilotion* are not exceptions to this rule. Different biennials can be often found to grow together in such communities indicating that biennial behaviour can be an adaptation to a special set of circumstances (van der Meijden et al. 1992). These are probably related to disturbances of the environment. Without disturbances biennials are losers compared to perennials (van der Meijden et al. 1992). It is only during the first years following disturbance that biennials are successful. They 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).

Ecologists have been always fascinated with what allows coexistence of different species with diverse traits in one habitat. There are a lot of studies concerning plant species coexistence, richness and competition (Goldberg 1987, Zobel 1992, Bengtsson et al. 1994, Gaudet and Keddy 1995, Zobel 1997, Aikio et al. 2002, Chesson and Neuhauser 2002, Aarssen et al. 2003, Cornwell and Grubb 2003, Blomqvist et al. 2003, Rajaniemi 2003). The diversity - productivity hypothesis (Naeem et al. 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 utilize more fully limiting resources and thus attain greater productivity. Some observational and field experiments support the assumption that biodiversity influences ecosystem productivity (Naeem et al. 1994) and stability (McNaughton 1977, Tilman and Downing 1994). Oksanen (1996) pointed out that the most common unimodal productivity - diversity curve can be an artefact of limited plot size. From low to intermediate productivity, individuals become less sparse and the number of individuals, and therefore the potential number of species in a plot increase. As productivity increases, individual plants become larger, the plots become full, and fewer larger plants and consequently fewer species fit in the plot.

Whereas classical competition theory predicts competitive exclusion of species with similar requirements, recent ideas (Bengtsson et al. 1994) stress that species diversity may be explained by a multitude of processes acting at different scales, and that similarities in competitive abilities may facilitate coexistence. 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. Spatial structure which is an unavoidable result of the discrete nature of individual organisms, may allow a number of competing species to stably coexist in a habitat even though a single species is a superior competitor (Tilman 1994). Dominant competitively forcible species thus may not cause entirely exclusion of small species even though these show high extinction values, as observed by Blomqvist et al. (2003).

Recent experiments (Mouquet et al. 2004) illustrates that both immigration and local competition contribute to explaining species diversity in herbaceous plant communities. Lately, there has been an increasingly provided evidence for the importance of community processes at both local and regional spatial scales (Kneitel and Chase 2004).

1.4. Invasibility

The association *Dauco - Melilotion* belongs among vegetation types that harbour both archeophytes and neophytes with a comparable frequency (Pyšek et al. 2002). Due to a long - scale migration along roads and railways, areas of these communities has expanded recently (Slavík 1990 - 1997). 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, and human commensalism). Similarly, general descriptions of invulnerable habitat have been offered: early successional, disturbed, low diversity of native species or lack of species that are ecologically similar to the invader (Lodge 1993).

From a number of studies several hypotheses 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) relationship between species diversity and invasibility. Some 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. Symstad (2000) revealed in his experimental study, that overall invasion success was negatively related to plant functional group richness, but there was only weak evidence that resident species repelled functionally similar invaders. Other factors, particularly the different responses of resident functional groups to the initial disturbance (removing one of the functional groups) seem to have been more important to community invasibility. Dukes (2001) found out that loss of species alone does not affect community invasibility but that communities with fewer species may be more likely to decline as a consequence of invasion. Foster et al. (2002) suggested that the positive correlation between invasibility and plant diversity could be due to the influences of factors that contribute to spatial variation in diversity (soil disturbance, light availability).

Disturbance is often cited as an important precursor for invasion of an ecosystem (Robinson et al. 1995, Burke and Grime 1996, Lake and Leishman 2003). 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). Indirect effect can occur through changes in community composition and through differences among species in the time course of their resistance and resilience to the disturbance (Symstad 2000, Lake and Leishman 2003).

Stampe and Daehler (2003) pointed out that even composition of the mycorrhizal fungi community belowground can influence the structure of the plant community aboveground, and may play a role in facilitating or repelling invasion.

1.5. Metapopulations

Due to human pressure, many terrestrial habitats are being rapidly changed, destroyed and fragmented (Zschokke et al. 2000). Consequently, 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 has been 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). At the same time, a growing number of studies try to formulate mathematical models in order to study the interaction of different mechanisms, which affect 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, Vandermeer and Carvajal 2001, Hanski 2001, Higgins et al. 2003, Aarsen et al. 2003). Findings from such studies provide useful information that can be applied when preparing manipulation experiments and also reveal challenging trends in modern ecology. Still, further evidence from experiments is needed (Aarssen et al. 2003) and field tests doing so are of great importance (e.g. Silvertown and Bullock 2003). Several studies also summarised and tested models' predictions on the 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. Baguette and Stevens (2003) stressed that demographic rates (birth, death, emigration, immigration) cannot be considered independently from the environmental conditions in which the local population or the metapopulation is

immersed, and that this is precisely the merit of the concept of metapopulation - environmental systems. Additionally, in the real, natural world some species are distributed in metapopulations where regional processes (immigration and emigration) are more important than local dynamics (birth and death) (Baguette and Stevens 2003). Blomqvist et al. (2003) found out, during 25 - year long period, that colonisation rather than extinction had been a more important determinant of plant species trends around grassland ditch banks. Thus, the real pattern of diversity depends to a great extent on the metapopulation dynamics of a particular species (Ouborg 1993).

1.6. Aims and questions

- Compare germination ability of the studied species between the studied habitats and light treatments.
- Compare species abundance and distribution between the studied habitats and attempt to determine key factors influencing vegetation pattern.
- Can the species frequencies within the studied habitats be explained by any of the studied traits?

2. METHODS

2.1. Studied sites

The field part of the study was performed on nine rural sites, near the railway stations in Dívčice, Zliv, Hluboká nad Vltavou - Zámostí, Kamenný Újezd, Velešín, České Velenice, Kaplice, Omlenice and Rybník (Fig. 1). The basic characteristics of the studied habitats summarises Table 1. The plant community in Zliv was studied in detail in the bachelor work (Desetová 2002) and acted as a reference habitat according to which the new habitats were selected. The aim of this selection was to involve habitats with similar environmental conditions. All studied communities are situated near the railway stations and thus can be potentially connected through a seed flow with each other. The frequency of disturbances affects these communities as well, the aim concerning this factor was to involve communities similar according to succession stages (i. e. very early succession stages, with less developed communities without generative plants were avoided). The soil in the studied habitats is usually sandy and gravelly, with many stones; the soil was stony mainly at Dívčice and Hluboká nad Vltavou - Zámostí. Vegetation can be generally described as a phytosociological alliance *Dauco - Melilotion*. 110 plant species were found at all studied sites, but only 40 were "common" (i. e. appeared at least in five percent of all phytocenological relevés from all studied sites).

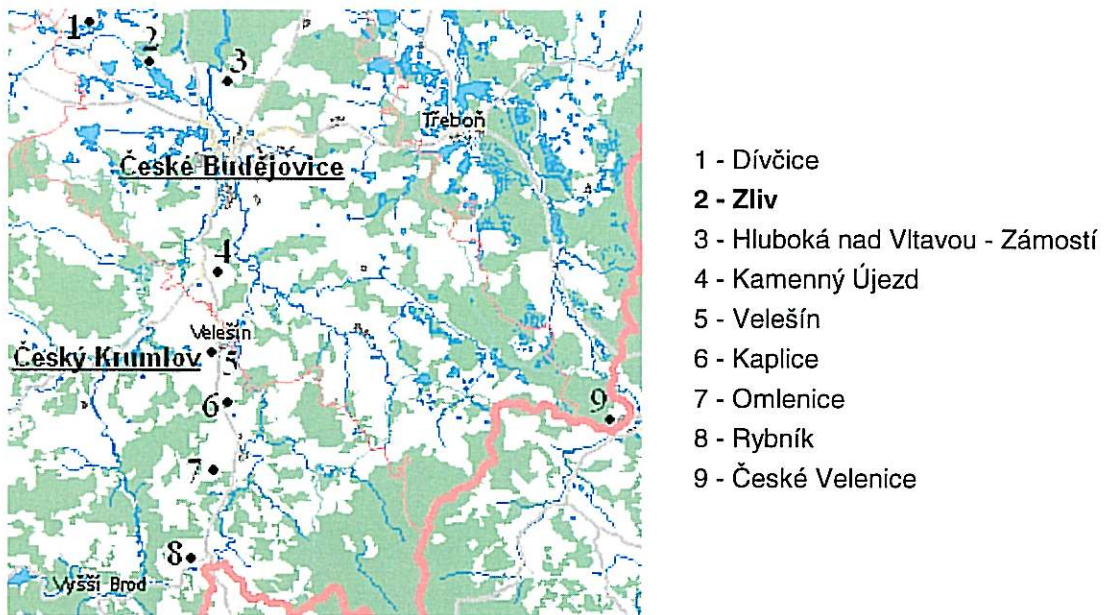


Fig. 1. Displays geographical position of all studied habitats. The habitat in Zliv (bold lettering in the legend) acted as a reference habitat according to which the new habitats were selected. The longest distance between habitats is 72 kilometres (Dívčice - Rybník and Dívčice - České Velenice).

2.2. Studied plant species

The bachelor work (Desetová 2002) concerned 18 plant species that occurred in Zliv. Three of them were not included in the new experiments because it was not possible to gain enough seeds from most habitats (*Berteroa incana*, *Centaurea stoebe* and *Oenothera issleri*). The goal of the selection was to involve dominant species as well as less frequent ones that might not have an ecological optimum in the studied habitats. The dominant species (regarding species frequencies in

relaves) were *Poa compressa*, *Artemisia vulgaris* and *Daucus carota*. *Verbascum lychnitis*, *Linaria vulgaris* and *Solidago canadensis* figured among the rather rare species. The studied species differed strongly in their seed weight and have different life cycles, life forms, types of clonality and ability to create a seed bank (Tables 2, 3, 4).

Table 1. Basic characteristics of the studied habitats. Data on the elevation (metres above sea level), latitude (N) and longitude (E) of the studied habitats were obtained at: <http://www.heavens-above.com/countries.asp#S>.

HABITAT	elevation	latitude	longitude
České Velenice	498	48°46'	14°58'
Dívčice	395	49°07'	14°22'
Hluboká - Zámostí	365	49°03'	14°26'
Kamenný Újezd	471	48°54'	14°27'
Kaplice	544	48°44'	14°29'
Omlenice	636	48°44'	14°27''
Rybník	635	48°39'	14°26'
Velešín	525	48°50'	14°28'
Zlív	375	49°04'	14°22'

2.3. Germination

Seeds for two germination experiments were collected from all studied habitats during autumn 2002. Seeds were collected directly from plants before seed shattering occurred. As both genotypic and phenotypic differences can affect germination (Bazzaz and Ackerly 1992), seeds from at least two populations of the studied species were tested. Only two species were found in all eight habitats: *Hypericum perforatum* and *Verbascum thapsus*. Seeds were dried at $22 \pm 2^\circ\text{C}$ for 10 days and stored under dry and dark laboratory conditions at $20 - 25^\circ\text{C}$ in glass bottles until initial tests commenced. During dry storage, seeds undergo physiological changes which are often reflected in a decline of innate dormancy (Murdoch et Ellis 1992, Probert 1992). This so called after - ripening is a function of environment as well as time. The longer and warmer is the storage environment, the greater is the loss of dormancy (Murdoch and Ellis 1992).

Germination abilities of the studied species were investigated under greenhouse (large - scale temperature fluctuations) and laboratory conditions (almost constant temperature). Four germination attributes were calculated for each species and habitat. Time to the beginning of germination (germination lag), time taken to achieve 50% of the final germination percentages (germination speed - $t(50)$), the final germination percentages in diurnal light and dark cycle (greenhouse) and the final germination percentages in the continuous darkness (laboratory). Germination lag and speed correspond with the first occurrence of germination or achievement of 50% germination among three Petri dishes of each species. Final germination percentages represent the average value of three Petri dishes of each species.

Greenhouse experiment

Seeds were germinated after 9 - day cold - wet stratification ($4 - 5^\circ\text{C}$). Wet chilling at temperatures close to 5°C is optimal for the dormancy breaking (Probert 1992, Benech - Arnold et al. 2000). While short periods of chilling are associated with relief of innate dormancy, longer periods could lead to induced dormancy (Murdoch and Ellis 1992). Dormancy level and the light requirements of seeds may change dramatically over relatively short - time periods during stratification (Noronha et al. 1997); additionally during previous experiments some seeds showed the ability to germinate even

during 10 - day chilling, that is why the stratification was not longer. The depth of dormancy also varies between species, between populations within a species and between individual seeds within a single seed population (Probert 1992).

Germination was performed in a greenhouse (10 x 20 m). Germination was monitored for 55 days (10.4. - 3.6.2003) and proceeded in diurnal light and dark cycle. Temperature at night was 5 - 15°C and fluctuated between 15 - 27°C during day. 50 seeds in 3 replicates of each species were sown in Petri dishes (9 cm diameter) with moisturised filter papers. Once in every three or four days germination was checked, germinated seeds were counted and removed to avoid inhibiting germination of the rest of the seeds. The emergence of radicle was used as the criterion of germination. Subsequent additions of water were made as necessary to prevent drying out.

Laboratory experiment

Seeds were germinated without stratification and germination experiment was carried out in a laboratory. Germination was monitored for 24 days (17.2. - 12.3.2004) and proceeded in the dark. Temperature was about 22 - 25°C both for day and night. 50 seeds were sown per species in 3 replicates in Petri dishes (9 cm diameter) with moisturised filter paper. Seeds were regularly counted (every 3 days) and removed. Additions of water were not necessary. Experiment was terminated when 6 days had passed without any further germination.

During this experiment also germination of 18 species from the reference habitat in Zliv was examined. Seeds were five years old (seeds were lab - stored in the dark, at temperature 20 - 25°C, in small glass bottles) and their germination abilities were last checked three years ago. 50 seeds in 3 replicates of each species were sown in Petri dishes with moisturised filter paper.

In addition, the effect of seed scarification on germination abilities of species *Echium vulgare* was examined. Seeds of this species from all habitats were scarified with sand paper and 50 seeds were sown in 3 replicates in Petri dishes (9 cm diameter) with moisturised filter paper. Both scarified and untreated seeds were kept under identical conditions.

2.4. Seed weight

Seed mass was measured only for the reference habitat in Zliv (Table 2). Weighted seeds were collected during autumn 1999. 100 seeds of all species were weighted in ten replicates. Exceptions were *Conyza canadensis* and *Solidago canadensis*. The fluffy seeds of these species are very small and light. 500 and 1500 seeds of these species were weighted, respectively.

2.5. Species distribution

Data on abundance and distribution of the studied species were obtained from all studied sites during spring 2003. 25 releves (50 x 50 cm) were performed and placed randomly around each of the studied sites. The smaller size of releves was chosen as it is more operative in habitats with high level of disturbance and thus considerably heterogeneous. Four environmental variables ("vegetation cover", "stones", "moss" and "soil") were estimated for each releve. Their values represented the estimated cover of each substratum in an individual releve (percentages from 0 to 100). Due to a high level of extensive anthropogenic disturbances it was not possible to repeat phytocenological survey in the reference habitat in Zliv.

2.6. Seed production

Data on the seed production of the studied species were measured only for the reference habitat in Zliv (Table 5). Five randomly chosen individuals of each studied species were collected to estimate the production of seeds 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 an open fruit could have caused an 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 of the values counted for individuals. The total production of seeds per plant was estimated as an average of five individuals of each species.

2.7. Final analyses

The aim of these analyses was to reveal which species traits significantly affect species distribution. Inputs for these analyses were final outputs from the experiments and observations (final germination percentages from both treatments, seed weight, seed production, species frequencies from relevés). The additional sources of the primary data were The Biological Traits of Vascular Plants database (Kleyer 1995), CLO - PLA2 the database of clonality (Klimeš and Klimešová 1999) and The Ecological Database of the British Isles (Peat and Fitter 1994). The Biological Traits of Vascular Plants database contains data on 25 ecological characteristics of 491 higher plants. The Ecological Database of the British Isles consists of data on 130 ecological and morphological characteristics of 1770 species of higher plants. The missing ecological traits, which were not cited in the databases, were completed from various floras and other publications (Slavík 1990 - 1997, Dostál 1989, Grime et al. 1988). Four traits were selected for the final analyses: clonality (Table 3), life form, life cycle and longevity of a seed bank (Table 4).

Table 2. Seed masses and standard deviations (values for one seed) of the studied species. Seeds were weighted in ten replicates per 100, exceptions were *Conyza canadensis* and *Solidago canadensis* (weighted per 500 and 1500, respectively). Seed masses were measured only for the reference habitat in Zliv (Desetová 2002).

SPECIES	SEED MASS (mg)	SD
<i>Artemisia vulgaris</i>	0.122	0.011
<i>Berteroa incana</i>	0.562	0.051
<i>Centaurea stoebe</i>	1.411	0.049
<i>Conyza canadensis</i>	0.045	0.006
<i>Daucus carota</i>	0.635	0.022
<i>Echium vulgare</i>	2.743	0.077
<i>Erysimum durum</i>	0.188	0.006
<i>Hypericum perforatum</i>	0.105	0.005
<i>Linaria vulgaris</i>	0.135	0.006
<i>Melilotus officinalis</i>	2.757	0.102
<i>Oenothera biennis</i>	0.474	0.015
<i>Oenothera issleri</i>	0.629	0.026
<i>Poa compressa</i>	0.164	0.009
<i>Solidago canadensis</i>	0.040	0.173
<i>Tanacetum vulgare</i>	0.121	0.003
<i>Trifolium arvense</i>	0.417	0.030
<i>Verbascum lychnitis</i>	0.095	0.003
<i>Verbascum thapsus</i>	0.118	0.009

Table 3. Types of clonality from the CLO - PLA2 database (Klimeš and Klimešová 1999). Table shows also clonality type, still for the final analyses species were divided into clonal or non-clonal. Nomenclature according Kubát et. al (2002).

SPECIES	CLONALITY TYPE
<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>	non clonal
<i>Verbascum lychnitis</i>	non clonal
<i>Verbascum thapsus</i>	non clonal

Table 4. List of the species traits from the databases. The table shows common classification according to the traits (Peat and Fitter 1994, Kleyer 1995). Fuzzy coding used for the multivariate analyses is not shown. Invasive status according to Pyšek et al. (2002). The species not mentioned in this study were regarded as native. Three categories of alien plants are distinguished: casual, invasive and naturalised. Life cycle types: PP - polycarpic perennial, Bi - biennial, SA - summer annual, MP - monocarpic perennial, WA - winter annual.

SPECIES	INVASIVE STATUS	LIFE CYCLE	LIFE FORM	SEED BANK
<i>Artemisia vulgaris</i>	native	PP	hemigr.	short
<i>Berteroa incana</i>	naturalised	PP	hemigr.	long
<i>Centaurea stoebe</i>	native	Bi	hemigr.	long
<i>Conyza canadensis</i>	invasive	SA	thero.	trans.
<i>Daucus carota</i>	native	MP	hemigr.	long
<i>Echium vulgare</i>	naturalised	Bi	hemigr.	short
<i>Erysimum durum</i>	native	Bi	hemigr.	long
<i>Hypericum perforatum</i>	native	PP	hemigr.	long
<i>Linaria vulgaris</i>	naturalised	PP	geo.	long
<i>Melilotus officinalis</i>	invasive	Bi	hemigr.	long
<i>Oenothera biennis</i>	invasive	Bi	hemigr.	long
<i>Oenothera issleri</i>	casual	Bi	hemigr.	long
<i>Poa compressa</i>	native	PP	hemigr.	short
<i>Solidago canadensis</i>	invasive	PP	hemigr.	trans.
<i>Tanacetum vulgare</i>	invasive	PP	hemigr.	trans.
<i>Trifolium arvense</i>	native	WA	thero.	short
<i>Verbascum lychnitis</i>	native	Bi	hemigr.	long
<i>Verbascum thapsus</i>	native	Bi	hemigr.	long

Table 5. The table shows the average number of fruits per plant, the number of seeds per plant and the total average number of seeds per plant. The overall seed production was measured for the reference habitat in Zliv of five randomly chosen individuals of each studied species (Desetová 2002). Number of seeds per fruit was counted of 10 - 20 fruits of each species. Species *Melilotus officinalis*, *Poa compressa*, *Daucus carota* and *Echium vulgare* have low - seeded fruits and therefore the number of fruits per plant and number of seeds per fruit is not stated.

SPECIES	N of fruits p.plant ± SD	N of seeds p.fruit ± SD	N of seed p.plant ± SD
<i>Artemisia vulgaris</i>	1409.2 ± 884.07	9.7 ± 2.43	13 266.4 ± 7 716.98
<i>Berteroa incana</i>	253.2 ± 138.52	8.9 ± 1.97	2 404.0 ± 1 570.80
<i>Centaurea stoebe</i>	192.4 ± 118.93	14.0 ± 8.06	2 536.2 ± 1 388.84
<i>Conyza canadensis</i>	441.0 ± 107.21	27.4 ± 4.93	11 998.6 ± 3 083.36
<i>Daucus carota</i>	x	x	2 154.0 ± 235.61
<i>Echium vulgare</i>	x	x	2 306.6 ± 584.72
<i>Erysimum durum</i>	243.6 ± 98.05	29.7 ± 9.71	8 487.5 ± 5 379.84
<i>Hypericum perforatum</i>	122.6 ± 31.84	63.5 ± 9.04	7 688.6 ± 2 064.14
<i>Linaria vulgaris</i>	43.6 ± 18.67	114.7 ± 22.67	5 057.1 ± 2 486.43
<i>Melilotus officinalis</i>	x	x	848.8 ± 381.27
<i>Oenothera biennis</i>	89.3 ± 57.98	158.8 ± 58.76	15 000.8 ± 13 601.70
<i>Oenothera issleri</i>	139.0 ± 87.84	107.6 ± 28.45	14 956.4 ± 9 452
<i>Poa compressa</i>	x	x	1 130.6 ± 229.31
<i>Solidago canadensis</i>	563.0 ± 241.80	15.0 ± 2.72	8 471.2 ± 3 570.11
<i>Tanacetum vulgare</i>	68.8 ± 17.76	153.9 ± 47.36	10 397.5 ± 2 828.73
<i>Trifolium arvense</i>	168.2 ± 26.06	64.8 ± 13.62	10 841.9 ± 1 858.45
<i>Verbascum lychnitis</i>	2797.2 ± 556.10	25.5 ± 6.87	72 115.4 ± 19 089.50
<i>Verbascum thapsus</i>	334.0 ± 265.71	353.2 ± 90.37	119 997.0 ± 119 120

3. STATISTICS

Analyses of germination experiments were performed using the STATISTICA package. Data from both experiments were subjected to two - way ANOVA with fixed factors "treatment" and "habitat" to test the differences in the final germination percentages between species and to detect the effect of treatment (diurnal light - dark cycle or continuous darkness) and habitat (eight studied habitats). Data were analysed for each species separately and a model with a random factor "habitat" was tested for each species. A Tukey Honest Significant Difference (HSD) test was used to find out significantly different pairs (5 % level of significance for all statistical analyses). The final germination percentages were arcsin - transformed prior the analyses to achieve better distribution properties.

Two - way ANOVA with fixed factors "species" and "experiment" was used to test the differences in the final germination percentages between species from the old and new experiment performed on seeds from the reference habitat in Zliv. A Tukey Honest Significant Difference (HSD) test was used to find out significantly different pairs. The final germination percentages were arcsin - transformed.

Pearson chi - square statistic in ANOVA package was used to find out if the studied species differed in their germination abilities and to detect if the scarification of *Echium vulgare* seeds significantly influenced the final germination percentages.

One - way ANOVA with fixed factors was used to test the differences in the final germination rates, germination lag and germination speed ($t(50)$) between the species. Data were analysed for each attribute and treatment separately. The final germination percentages were arcsin - transformed. A Tukey Honest Significant Difference (HSD) test for unequal N was used to find out significantly different pairs.

Multiply Regression in the STATISTICA package was used to evaluate which species traits significantly affect the final germination percentages (arcsin - transformed). Data were analysed for two light treatments separately using a forward stepwise method. There were 11 explanatory variables for both analyses: germination lag, germination speed ($t(50)$), seed mass, number of seeds per plant and dummy variables clonality, three life forms (hemicryptophyte, therophyte, geophyte), three types of seed bank (transient, short - and long - term).

Multiply Regression was performed on the set of data that included all species traits both from experiments and from databases to evaluate which of 16 traits significantly affects species frequencies from releves. A stepwise forward selection was used. Explanatory variables were: the final germination percentages (light and dark cycle, continuous darkness), seed mass, number of seeds per plant and dummy variables: clonality, three types of life form (hemicryptophyte, therophyte, geophyte), three types of seed bank (transient, short - and long - term), five types of life cycle (summer annual, winter annual, biennial, monocarpic perennial, polycarpic perennial).

Principal Component Analysis (PCA) in the CANOCO package (ter Braak and Šmilauer 1998) was performed on the above mentioned traits to find out which of these traits are positively or negatively correlated with the species frequency from releves. All data were log - transformed, centered and standardized before running the analysis.

Residual Direct Analyses (RDA) in the CANOCO (ter Braak and Šmilauer 1998) package was performed on the same sets of data as PCA. Explanatory variable was frequency of species from releves and the rest 16 traits figured as "species". All data were log - transformed, centered and standardized before running the analysis.

Multivariate statistical methods (Detrended Correspondence Analysis - DCA and Canonical Correspondence Analysis - CCA) in the CANOCO package (ter Braak and Šmilauer 1998) were used for evaluation of the composition of vegetation in the studied habitats. The species values were log - transformed. CANODRAW was used for graphic outputs of the analyses performed in the CANOCO.

4. RESULTS

4.1. Species distribution

Demography data from phytosociological sampling from eight habitats were analysed by CANOCO for Windows. Detrended Correspondence Analysis, DCA confirmed previous assumption that CCA is an appropriate method for data processing (the longest gradient 4.7). Table 6, 7 summarise results of Monte Carlo permutation tests.

Table 6. Results of Monte Carlo permutation test. Habitat was used as a supplementary variable.

	Eigenvalue	explained variability	F-ratio	p-value
1 st axis	0.140	14.0%	2.152	0.011
all axes	0.318	31.8%	1.652	0.001

Table 7. Results of Monte Carlo permutation test. Habitat was used as a covariable.

	Eigenvalue	explained variability	F-ratio	p-value
1 st axis	0.097	9.7%	1.588	0.005
all axes	0.252	25.2%	1.393	0.001

To demonstrate species occurrence in the studied localities and relation between the environmental variables a CCA biplot is shown (Fig. 2).

- The most frequent species among all studied localities were *Poa compressa* (appeared in 67.6% of all releves), *Artemisia vulgaris* (44.9%), *Daucus carota* (21.3%), *Hypericum perforatum* (20%), *Tanacetum vulgare* (19.6%), *Trifolium arvense* (18.7%) and *Oenothera biennis* (15.1%).
- Species *Echium vulgare* (14.7%), *Conyza canadensis* (13.8%), *Melilotus officinalis* (12.4%), *Erysimum durum* (10.7%) and *Verbascum thapsus* (10.7%) were less numerous.
- The less frequent species were *Solidago canadensis* (8.9%), *Linaria vulgaris* (8%) and *Verbascum lychnitis* (4.9%).
- Species *Berteroa incana*, *Linaria vulgaris*, *Conyza canadensis*, *Oenothera biennis*, *Oenothera issleri*, *Verbascum thapsus* and *Echium vulgare* occur more frequently at gravely soils with higher amount of stones.
- Species *Daucus carota*, *Trifolium arvense* and *Solidago canadensis* seemed to prefer places with higher cover of moss or bare soil.
- Species with centroids projected close to the intercept of canonical axes (*Melilotus officinalis* and *Poa compressa*) have almost no reference to the observed environmental variables (mainly species *Poa compressa* appeared in nearly all releves independently on the substrate).

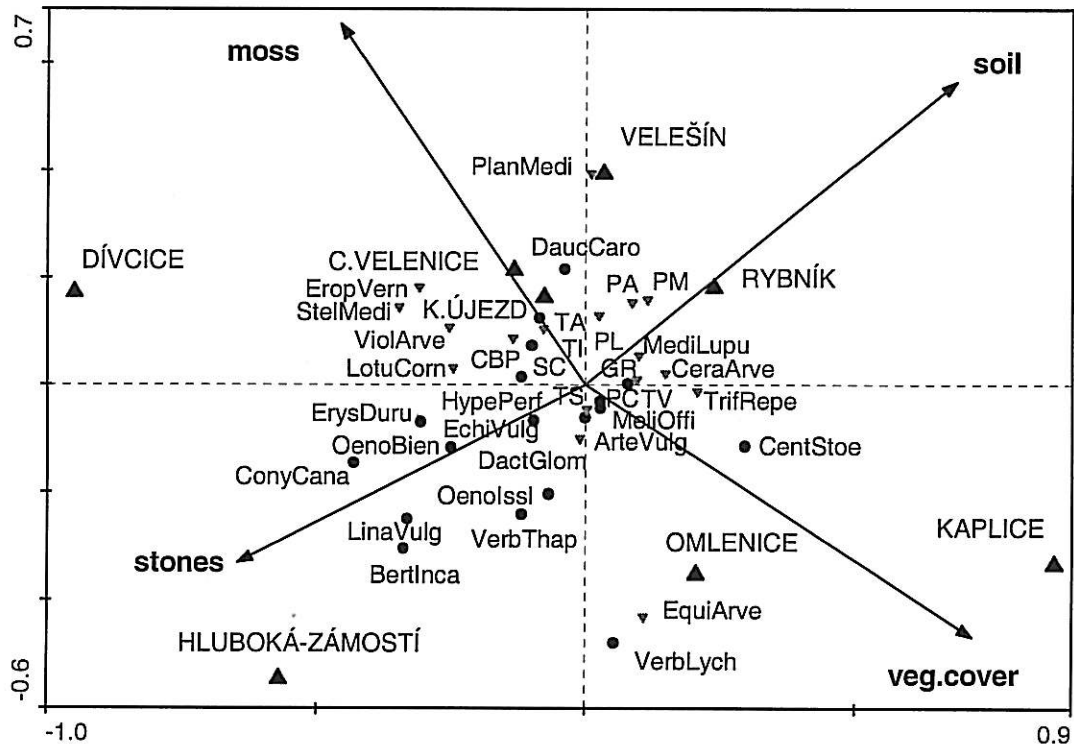


Fig. 2. CCA ordination diagram (1st and 2nd axes are shown) displaying relation of species from eight studied habitats and explanatory variables from relevés. Explanatory variables represent the estimated cover of four substrates (moss, soil, stones and cover of vegetation) in an individual releve. Studied species are displayed as circles, others as down - triangles. Abbreviations of species names represent first four letters from either name of species. Exceptions are: **GR** - *Geranium robertianum*, **TS** - *Taraxacum sp.*, **TV** - *Tanacetum vulgare*, **PM** - *Plantago major*, **PA** - *Poa annua*, **CBP** - *Capsella bursa - pastoris*, **TI** - *Tripleurospermum inodorum*, **PL** - *Plantago lanceolata*, **TA** - *Trifolium arvense*, **SC** - *Solidago canadensis*, **PC** - *Poa compressa*. Nomenclature according Kubát et al. (2002).

4.2. Germination - greenhouse experiment

Seeds were germinated after 9 - day cold - wet chilling. Germination was monitored for 55 days and proceeded in diurnal light - dark cycle. Three used germination attributes (germination lag, germination speed and germination percentages) were significantly different among the studied species. Table 8 summarises values of all used traits of each species (the average values of all habitats of a species).

Table 9 shows separation of the studied species due to the median value of a particular attribute. The following threshold values were determined ad hoc in order to involve species with similar values of a particular attribute in one group.

germination lag: $F(14) = 8.9, p < 10^{-6}$

- 11 species (73%) had germination lag ≤ 15 days (*Artemisia vulgaris*, *Conyza canadensis*, *Erysimum durum*, *Hypericum perforatum*, *Melilotus officinalis*, *Poa compressa*, *Solidago canadensis*, *Tanacetum vulgare*, *Trifolium arvense*, *Verbascum lychnitis*, *Verbascum thapsus*).
- 4 species (27%) had lag > 15 days (*Daucus carota*, *Echium vulgare*, *Linaria vulgaris*, *Oenothera biennis*).

- The shortest lag had *Melilotus officinalis* (9 days).
- Species *Linaria vulgaris* started to germinate after 20.5 days (the average of 4 habitats).

germination speed $t(50)$: $F(14)= 25.3$, $p < 10^{-6}$

- 14 out of 15 species were half germinated within 25 days, except of *Linaria vulgaris*.
- Species *Trifolium arvense* was half - germinated within 9 days and had the shortest $t(50)$.
- Species *Linaria vulgaris* needed 55 days (the whole length of the experiment) to achieve 50% of the final germination percentages.

germination percentages: $F(14)= 34.8$, $p < 10^{-6}$

- 8 species (53%) had final germination percentages more than 75% (*Artemisia vulgaris*, *Conyza canadensis*, *Hypericum perforatum*, *Oenothera biennis*, *Solidago canadensis*, *Tanacetum vulgare*, *Verbascum lychnitis*, *Verbascum thapsus*).
- 7 species (47%) achieved less than 40% (*Daucus carota*, *Echium vulgare*, *Erysimum durum*, *Linaria vulgaris*, *Melilotus officinalis*, *Poa compressa*, *Trifolium arvense*).
- Maximum germination percentages had species *Verbascum lychnitis* (96%, the average value of 2 habitats).
- Minimum germination percentages achieved *Trifolium arvense* (6.7%, the average value of 2 habitats).

Table 8. Overview of the germination traits (germination lag, germination speed $t(50)$) and the final germination percentages) for both treatments (L/D - diurnal light - dark cycle, D - continuous darkness). Numbers in brackets represent the number of habitats of each species. The average values of all habitats and standard deviations are shown for each species. Abbreviations of species names represent first four letters from either name of species.

SPECIES	germination lag		germination speed		germination %	
	L/D	D	L/D	D	L/D	D
ArteVulg (7)	12 ± 0	3 ± 0	12.4 ± 1.1	3.4 ± 1.1	85.4 ± 13.9	77.3 ± 11
ConyCana (5)	10.8 ± 1.6	3 ± 0	12.6 ± 1.3	3 ± 0	80.3 ± 12.1	80.8 ± 14.5
DaucCaro (6)	17.8 ± 3.6	3 ± 0	24.3 ± 5.5	5.5 ± 1.2	11.1 ± 8.6	34.6 ± 21.8
EchiVulg (3)	16.3 ± 6.1	3 ± 0	22.3 ± 2.3	3 ± 0	19.8 ± 22.9	80.7 ± 14.5
ErysDuru (5)	11.4 ± 1.3	3 ± 0	12 ± 0	3 ± 0	21.2 ± 14.3	18.8 ± 10.7
HypePerf (8)	14.8 ± 2.2	6.8 ± 1.4	21.8 ± 2.1	9.8 ± 1.4	81.3 ± 15.2	48.2 ± 22
LinaVulg (4)	20.5 ± 1	6 ± 3	55 ± 0	6 ± 3	17 ± 9	0.3 ± 0.7
MeliOffi (6)	9 ± 0	4.2 ± 2.9	24.2 ± 12.2	7.8 ± 4	8.1 ± 5.7	1.7 ± 1
OenoBien (7)	15.4 ± 2.7	3.9 ± 1.5	21.1 ± 3.2	4.3 ± 1.6	82.1 ± 17.9	4.3 ± 4.4
PoaComp (7)	14.3 ± 3.9	3 ± 0	22.4 ± 5.2	3.4 ± 1.1	38.3 ± 19.1	48.2 ± 19.4
SoliCana (3)	12 ± 0	3 ± 0	14 ± 1.7	6 ± 3	85.3 ± 2.7	63.1 ± 23.1
TanaVulg (7)	12 ± 0	3.4 ± 1.1	13.4 ± 2.7	3.9 ± 1.5	83.8 ± 7.5	54.5 ± 6.4
TrifArve (2)	9 ± 0	4.5 ± 2.1	9 ± 0	7.5 ± 2.1	6.7 ± 2.8	10.3 ± 3.3
VerbLych (2)	15 ± 0	3 ± 0	17 ± 2.8	4.5 ± 2.1	96 ± 0	33.7 ± 0.5
VerbThap (8)	15 ± 0	5.6 ± 1.1	18.3 ± 2.1	7.5 ± 1.6	95.3 ± 4	41 ± 21.3

4.3. Germination - laboratory experiment

Seeds were germinated without stratification and germination experiment was carried out in a laboratory. Germination was monitored for 24 days and proceeded in the continuous darkness.

Germination attributes - all species

Three used germination attributes (germination lag, germination speed and final germination percentages) were significantly different among the studied species.

germination lag: $F(14)= 5.7, p < 10^{-6}$

- 8 species (53%) started to germinate after 3 days (*Artemisia vulgaris*, *Conyza canadensis*, *Daucus carota*, *Echium vulgare*, *Erysimum durum*, *Poa compressa*, *Solidago canadensis*, *Verbascum lychnitis*).
- 7 species (47%) had lag longer than 3 days (*Hypericum perforatum*, *Linaria vulgaris*, *Melilotus officinalis*, *Oenothera biennis*, *Tanacetum vulgare*, *Trifolium arvense*, *Verbascum thapsus*).
- The longest lag had species *Hypericum perforatum* (6.75 days).

germination speed $t(50)$: $F(14)= 8.8, p < 10^{-6}$

- All species were half - germinated within ten days.
- Species *Conyza canadensis*, *Echium vulgare* and *Erysimum durum* achieved 50% germination during the 1st observation (in 3 days).
- The longest $t(50)$ had *Hypericum perforatum* (9.75 days, the average value of 8 habitats).

germination percentages: $F(14)= 16.8, p < 10^{-6}$

- 5 species (33%) achieved more than 50% (*Artemisia vulgaris*, *Conyza canadensis*, *Echium vulgare*, *Solidago canadensis*, *Tanacetum vulgare*).
- 10 species (67%) had final germination percentages lower than 50% (*Daucus carota*, *Erysimum durum*, *Hypericum perforatum*, *Linaria vulgaris*, *Melilotus officinalis*, *Oenothera biennis*, *Poa compressa*, *Trifolium arvense*, *Verbascum lychnitis*, *Verbascum thapsus*).
- Maximum germination had *Conyza canadensis* (80.8, the average of 5 habitats).
- Minimum germination showed *Linaria vulgaris* (0.3%, the average of 4 habitats).

Table 9. Summary of the germination traits (germination lag, germination speed $t(50)$ and final germination percentages) for both treatments (**L/D** - diurnal light - dark cycle, **D** - continuous darkness). Numbers in brackets represent number of habitats of each species. Threshold values represent medians of each trait within the treatment.

SPECIES TRAITS	light/dark cycle						dark					
	germ.lag		t(50)		germ.%		germ.lag		t(50)		germ.%	
	≤14,3	>14,3	≤18,3	>18,3	≤80,3	>80,3	≤3	>3	≤4,5	>4,5	≤41	>41
ArteVulg (7)	*		+			0	*		+			0
ConyCana (5)	*		+		0		*		+			0
DaucCaro (6)		*		+	0		*			+	0	
EchiVulg (3)		*		+	0		*		+			0
ErysDuru (5)	*		+		0		*		+		0	
HypePerf (8)		*		+		0		*		+		0
LinaVulg (4)		*		+	0			*		+	0	
MeliOffi (6)	*			+	0			*		+	0	
OenoBien (7)		*		+		0		*	+		0	
PoaComp (7)	*			+	0		*		+			0
SoliCana (3)	*		+			0	*			+		0
TanaVulg (7)	*		+			0		*	+			0
TrifArve (2)	*		+		0			*		+	0	
VerbLych (2)		*	+			0	*		+		0	
VerbThap (8)		*	+			0		*		+	0	

Scarification of seeds of *Echium vulgare*

The effect of seed scarification on germination abilities of species *Echium vulgare* was examined. Seeds of this species from all habitats were scarified with sand paper and both scarified and untreated seeds were kept under identical conditions (continuous darkness, low temperature fluctuations).

Next to the seeds from three new habitats of this species (Hluboká - Zámostí, K. Újezd, Velešín) seeds from the reference habitat in Zliv were also examined. Seeds from Zliv were 5 years old and their germination abilities were last checked 3 years ago. Scarification significantly negatively affected germination of *Echium vulgare* (Table 10).

Table 10. Final germination percentages of scarified and untreated seeds of *Echium vulgare* (dark treatment).

HABITAT	treatment (%)		Pearson chi - square= 8.316 df= 1 p= 0.00393
	scarified	non-scarified	
Hluboká - Zámostí	84.0	88.0	
K. Újezd	41.3	90.0	
Velešín	64.7	64.0	
Zliv	29.3	17.3	

Zliv - old and new germination experiment

Germination of 18 species from the reference habitat in Zliv was examined. Seeds were 5 - year old and their germination abilities were last checked 3 years ago (germination proceeded under the same conditions: continuous darkness, low temperature fluctuations; still the seeds in the old experiment were stratified, the new experiment ran without stratification). As the values of germination lag and germination speed differs between the experiments (because of 10 - day stratification), only the differences between final germination percentages were tested. The effect of both species and experiment was significant, so was the effect of experiment on species germination.

species (1): $F(17)= 82.79$ experiment (2): $F(1)= 420.59$ 1 x 2: $F(17)= 35.32$
 $p < 10^{-6}$ $p < 10^{-6}$ $p < 10^{-6}$

- 10 species (55.6%) significantly differed in germination percentages among the old and new experiment (*Artemisia vulgaris*, *Berteroa incana*, *Centaurea stoebe*, *Conyza canadensis*, *Linaria vulgaris*, *Hypericum perforatum*, *Poa compressa*, *Solidago canadensis*, *Verbascum lychnitis*, *Verbascum thapsus*).
- The rest 8 species (44.4%) did not differ (*Daucus carota*, *Echium vulgare*, *Erysimum durum*, *Melilotus officinalis*, *Oenothera biennis*, *Oenothera issleri*, *Tanacetum vulgare*, *Trifolium arvense*).
- 4 from the above mentioned species achieved less than 5% in both experiments (*Melilotus officinalis*, *Oenothera biennis*, *Oenothera issleri*, *Trifolium arvense*).
- In the old experiment 8 species (44.4%) exceeded 50% germination (*Artemisia vulgaris*, *Berteroa incana*, *Centaurea stoebe*, *Conyza canadensis*, *Daucus carota*, *Linaria vulgaris*, *Verbascum lychnitis*, *Verbascum thapsus*).
- In the new experiment all species had germination lower than 50% except of *Daucus carota* (60%).

- In the new experiment 6 species (33.3%) did not germinate at all (*Berteroa incana*, *Conyza canadensis*, *Linaria vulgaris*, *Melilotus officinalis*, *Oenothera issleri*, *Solidago canadensis*).
- *Poa compressa* was the only species that germinated significantly better in the new experiment (36%) than in the old (4.7%).

Figure 3 a,b summarises the three germination attributes (germination lag, germination speed $t(50)$ and final germination percentages) of the studied species of both experiments.

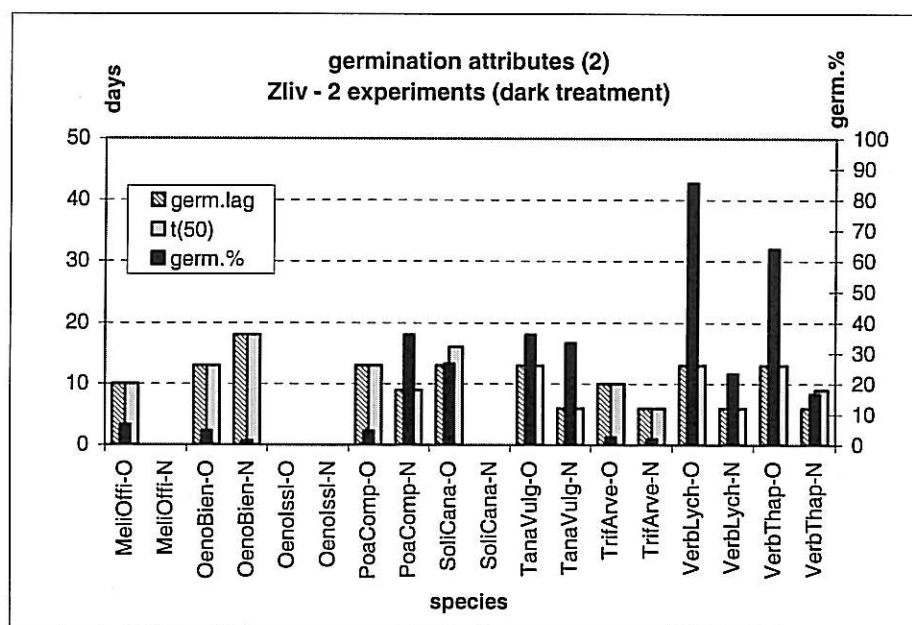
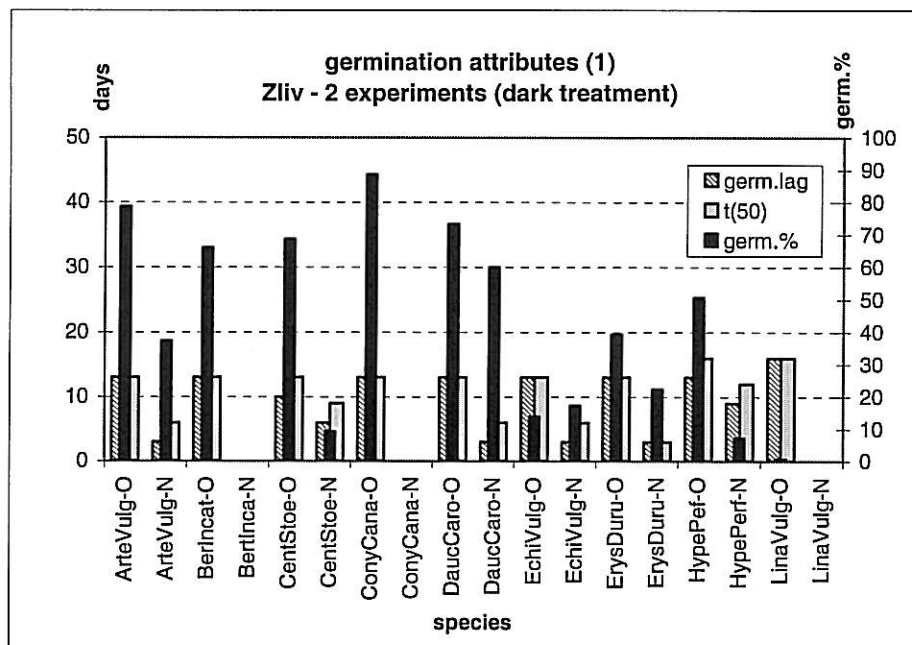


Fig. 3a,b. Three germination attributes. Germination lag - striped bars and germination speed $t(50)$ - grey bars respond to the left axis (days). Final germination percentages - black bars respond to the right axis (%). Germination proceeded in the dark, under laboratory conditions with low temperature fluctuations. O - the old experiment conducted 3 years ago, N - the new experiment on the same seed set (5 - year old seeds). Abbreviations of species names represent first four letters from either name of species.

4.4. Germination - effect of treatment and habitat

To test the differences in the final germination percentages between species and to detect the effect of light treatment and habitat two - way ANOVA was performed. Two models, with fixed and random factor "habitat", were tested for each species. Table 11 (pages 20, 21) summarizes the final germination percentages in both light treatments and achieved levels of significance of factors "treatment" and "habitat" for each species and habitat.

4.5. Time course of germination

Fig. 4 (pages 22 - 26) summarises the course of germination of all studied species in both light - dark and dark treatments. Fig. 4 displaying the time course of germination involves also the final germination percentages of all species from the reference habitat in Zliv. In the case of light - dark treatment (Fig. 4.1-15a) the values from previous experiment in the greenhouse were used to compare the germination percentages among the reference habitat in Zliv and the new ones.

In the case of dark treatment (Fig. 4.1-15b) the 5 - year old seeds from Zliv were germinated together with seeds from the other habitats. Experimental conditions were the same (dark, no chilling and temperature fluctuations). No statistical test was used to compare the final germination rates between the reference habitat in Zliv and other habitats because any estimates and interpretation would be rather tricky.

- The course of germination in the light - dark treatment was for most species similar among the different habitats.
- On the other hand, the course of germination in the dark treatment was more diverse among the different habitats of one species.
- In the dark treatment germination was noticeably rapid, vast majority of seeds germinated within 10 days, species *Echium vulgare* and *Erysimum durum* achieved the final germination percentages within three days.
- The allogamic species (*Daucus carota*, *Echium vulgare*, *Linaria vulgaris*, *Melilotus officinalis*, *Solidago canadensis*, *Verbascum lychnitis*, *Verbascum thapsus*) generally had the similar trend of time course among the different habitats (considering only light - dark treatment, in the dark the course was different even in the case of the allogamic species).
- In the case of apomictic species *Poa compressa* the differences among habitats were remarkably higher compared with the allogamic species.
- In the light - dark treatment species can be divided into two groups, considering the length of germination lag (time to the beginning of germination):

In the case of species that started to germinate during the first observation (*Artemisia vulgaris*, *Conyza canadensis*, *Erysimum durum*, *Solidago canadensis*, *Tanacetum vulgare*) the time course of germination generally resembled the logarithmic curve (Fig. 5a).

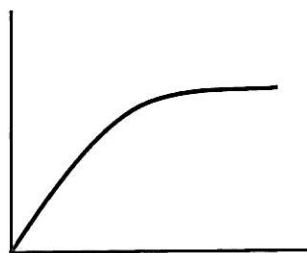


Fig. 5a. The time course of germination of fast germinating species generally resembles the logarithmic curve. For Fig. 4 see pages 22-26.

The time course of germination of species with longer lag, that usually did not germinate during the first observations (*Daucus carota*, *Echium vulgare*, *Hypericum perforatum*, *Oenothera biennis*, *Verbascum lychnitis*, *Verbascum thapsus*) generally resembled the sigmoid curve (Fig. 5b).

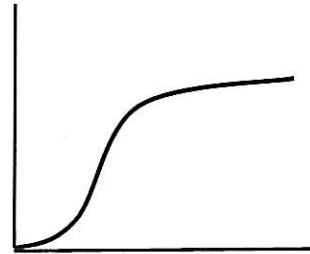


Fig. 5b. The time course of germination of slower germinating species generally resembles the sigmoid curve.

Species *Linaria vulgaris*, *Melilotus officinalis* and *Trifolium arvense* achieved very low final germination percentages and it was not possible to classify them reasonably according to the time course of germination.

4.6. Germination - multiply regression

In order to evaluate which species traits significantly affect germination of the studied species, data were subjected to multiply regression. Data were analysed for two light treatments separately.

Diurnal light - dark treatment

Three out of eleven explanatory variables had significant positive effect on germination: production of seeds per plant ($p= 0.0064$), transient seed bank ($p= 0.04$) and clonality ($p= 0.035$). Though, the effect was significant only without Bonferroni correction and the whole test was very weak.

Dark treatment

None out of the eleven explanatory variables had significant effect on germination, even without Bonferroni correction. Nevertheless, the model indicated negative effect of the long - term seed bank on germination in the dark (in the light - dark treatment the effect of the long seed bank was positive, but not significant).

Table 11. Germination percentages in diurnal light - dark cycle and continuous darkness. Life history type (**Bi** - biennial, **PP** - polycarpic perennial, **SA** - summer annual, **WA** - winter annual) and seed mass is shown for each species (brackets following the species names). Statistical differences in final germination percentages were tested for each species with fixed factors and with random factor "habitat". * P < 0.05; ** P < 0.01; *** P < 0.001; NS - not significant value

HABITAT	LIGHT -	DARK	Treatment	Fix: Habitat	1 x 2
	DARK		(1)	(2)	
			Treatment	Ran: Habitat	1 x 2
			(1)	(2)	
			***	***	***
<i>Artemisia vulgaris</i> (PP; 0.12 mg)			NS	***	***
Dívčice	66.7	81.3			
Hlu. Zámostí	96.7	79.3			
K. Újezd	64.7	60.7			
Kaplice	90.0	85.3			
Omlenice	94.7	91.3			
Rybník	88.7	78.7			
Velešín	96.7	64.7			
			NS	***	NS
<i>Coryza canadensis</i> (SA; 0.05 mg)			NS	***	NS
Č. Velenice	66.0	62.7			
Kaplice	70.7	68.7			
Omlenice	82.7	87.3			
Rybník	96.0	97.3			
Velešín	86.0	88.0			
			***	***	**
<i>Daucus carota</i> (MP; 0.64 mg)			*	***	**
Č. Velenice	21.3	33.3			
Dívčice	21.3	50.0			
Hlu. Zámostí	2.7	10.7			
K. Újezd	10.7	69.3			
Kaplice	2.0	26.0			
Velešín	8.7	18.0			
			***	***	***
<i>Echium vulgare</i> (Bi; 2.74 mg)			NS	***	***
Hlu. Zámostí	46.0	88.0			
K. Újezd	4.0	90.0			
Velešín	9.3	64.0			
			NS	***	**
<i>Erysimum durum</i> (Bi; 0.19 mg)			NS	***	**
Dívčice	40.7	28.7			
Hlu. Zámostí	28.7	27.3			
Omlenice	8.7	3.3			
Rybník	6.0	12.7			
Velešín	22.0	22.0			
			***	***	**
<i>Hypericum perforatum</i> (PP; 0.11 mg)			***	***	**
Č. Velenice	87.3	24.7			
Dívčice	88.7	58.7			
Hlu. Zámostí	77.3	53.3			
K. Újezd	82.7	50.0			
Kaplice	93.3	74.7			
Omlenice	83.3	64.0			
Rybník	46.0	6.7			
Velešín	92.0	53.3			
			***	NS	NS
<i>Linaria vulgaris</i> (PP; 0.14 mg)			**	NS	NS
Kaplice	13.3	0			
Omlenice	15.3	0			
Rybník	30.0	1.3			
Velešín	9.3	0			

HABITAT	LIGHT - DARK	DARK	Treatment (1) Treatment (1)	Fix: Habitat (2) Ran: Habitat (2)	1 x 2 1 x 2
<i>Melilotus officinalis</i> (Bi; 2.76 mg)			***	*	NS
Č. Velenice	2.7	0	**	*	NS
K. Újezd	17.3	2.7			
Kaplice	11.3	1.3			
Omlenice	9.3	2.7			
Rybník	4.0	2.0			
Velešín	4.0	1.3			
<i>Oenothera biennis</i> (Bi; 0.47 mg)			***	***	***
Č. Velenice	88.6	1.3	***	***	***
Dívčice	90.0	4.0			
Hlu. Záměstí	92.0	1.3			
K. Újezd	92.0	2.0			
Kaplice	94.0	4.0			
Rybník	44.7	14.0			
Velešín	73.3	3.3			
<i>Poa compressa</i> (PP; 0.16 mg)			*	***	*
Č. Velenice	42.0	19.3	NS	***	*
Hlu. Záměstí	59.3	58.7			
K. Újezd	32.7	48.7			
Kaplice	34.0	36.7			
Omlenice	28.0	42.7			
Rybník	8.0	49.3			
Velešín	64.0	82.0			
<i>Solidago canadensis</i> (PP; 0.04 mg)			***	**	**
Č. Velenice	82.7	66.0	NS	**	**
Omlenice	85.3	84.7			
Velešín	88.0	38.7			
<i>Tanacetum vulgare</i> (PP; 0.12 mg)			***	*	NS
Č. Velenice	78.7	58.0	***	*	NS
Dívčice	73.3	49.3			
K. Újezd	80.0	50.7			
Kaplice	90.0	60.0			
Omlenice	94.7	51.3			
Rybník	88.7	64.7			
Velešín	81.3	47.3			
<i>Trifolium arvense</i> (WA; 0.42 mg)			NS	*	NS
Č. Velenice	4.7	8.0	*	*	NS
Hlu. Záměstí	8.7	12.7			
<i>Verbascum lychnitis</i> (Bi; 0.095 mg)			***	NS	NS
Omlenice	96.0	33.3	*	NS	NS
Velešín	96.0	34.0			
<i>Verbascum thapsus</i> (Bi; 0.12 mg)			***	***	***
Č. Velenice	94.7	46.7	***	***	***
Dívčice	94.7	11.3			
Hlu. Záměstí	86.7	16.0			
K. Újezd	98.0	26.0			
Kaplice	99.3	64.0			
Omlenice	94.0	58.7			
Rybník	98.7	40.7			
Velešín	96.0	64.7			

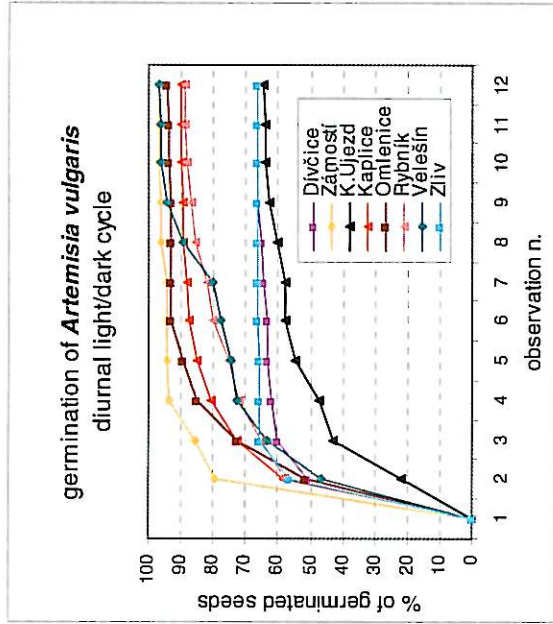


Fig. 4.1a, b

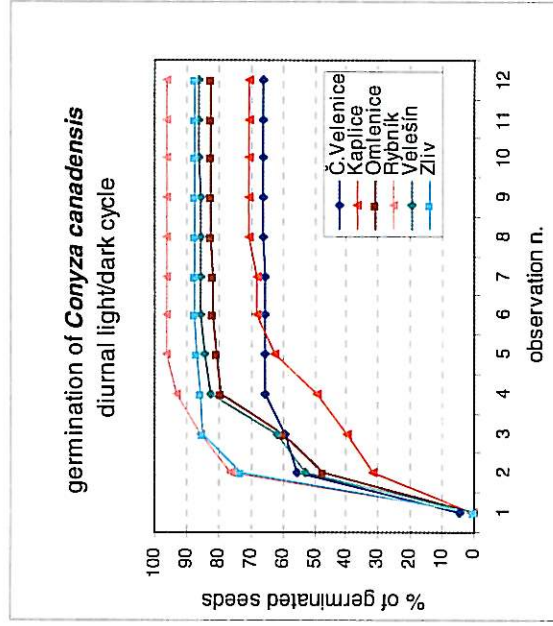


Fig. 4.2a, b

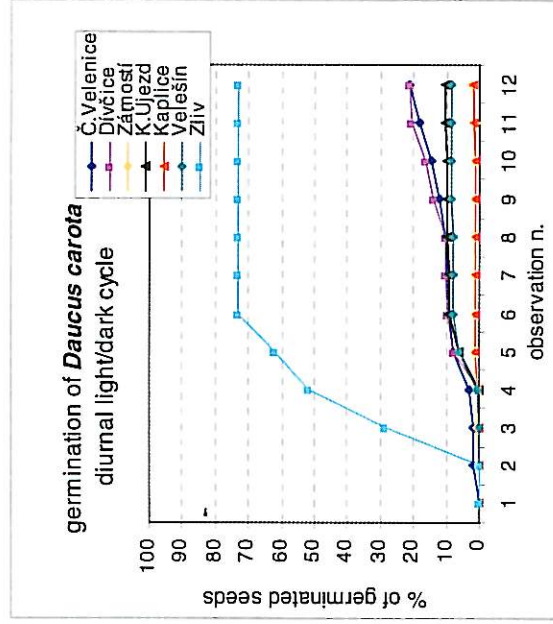
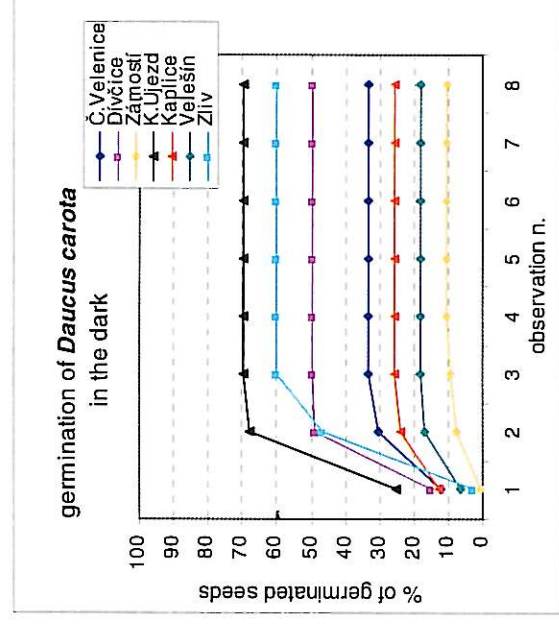
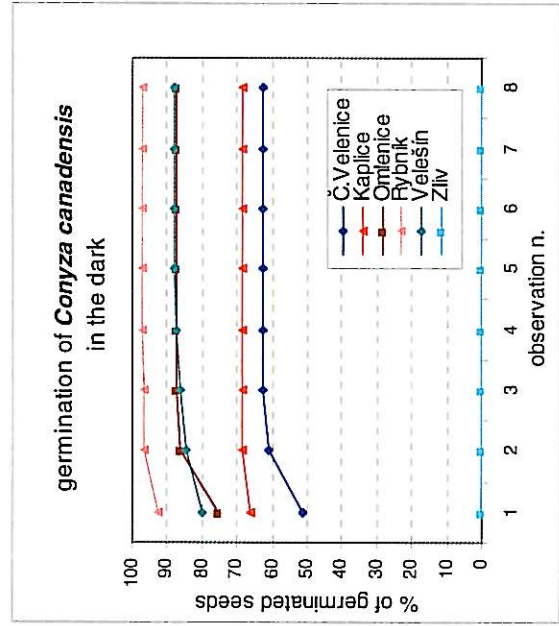
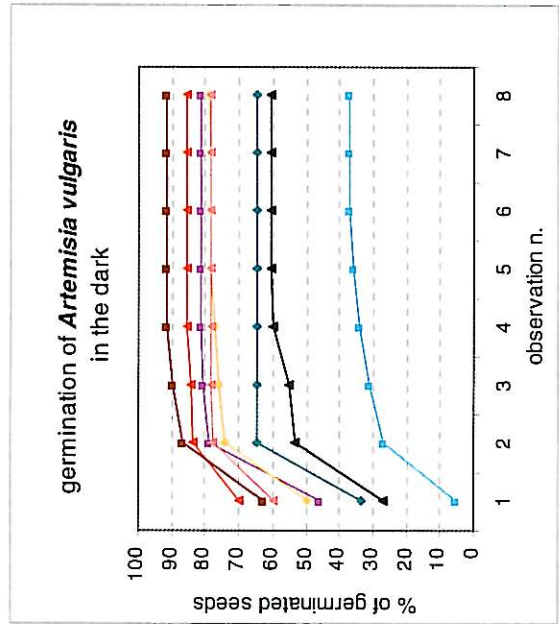


Fig. 4.3a, b



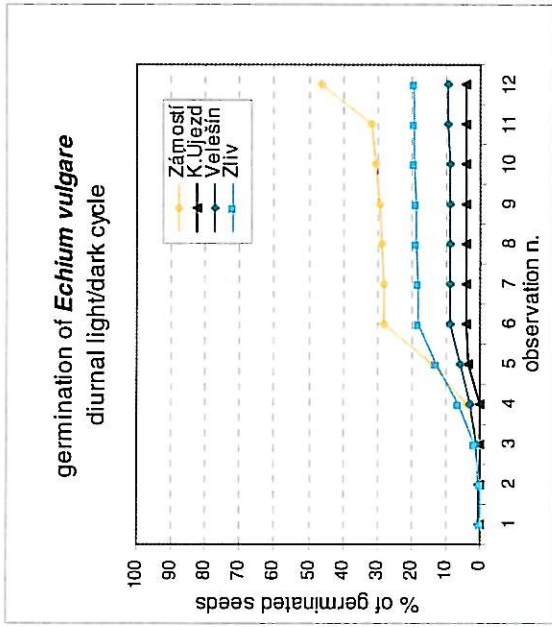


Fig. 4.4a, b

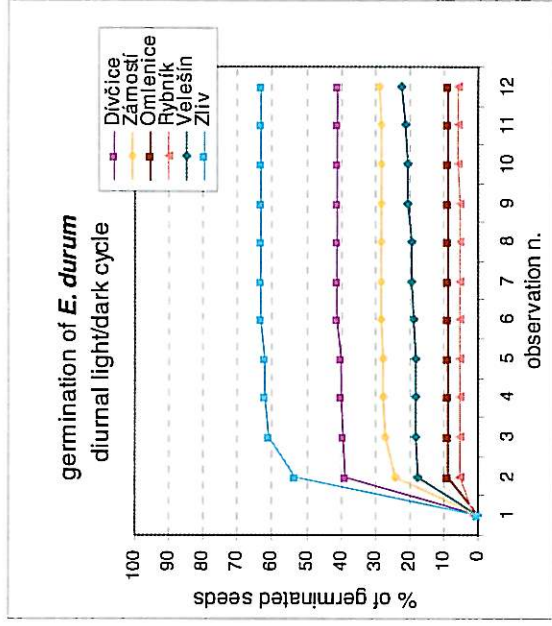
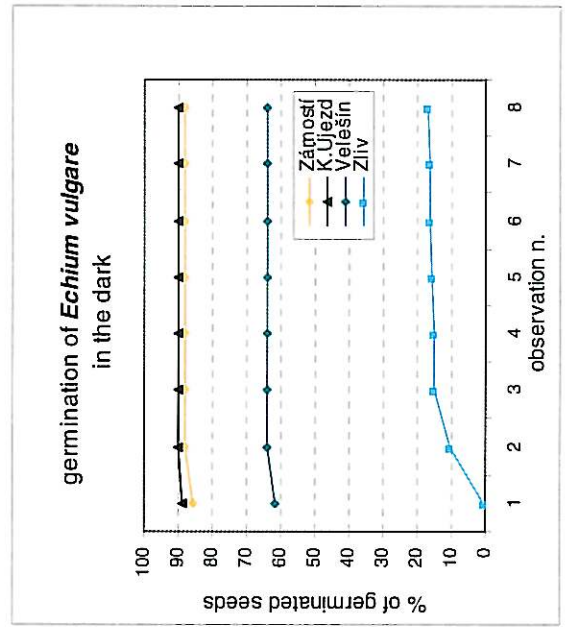


Fig. 4.5a, b

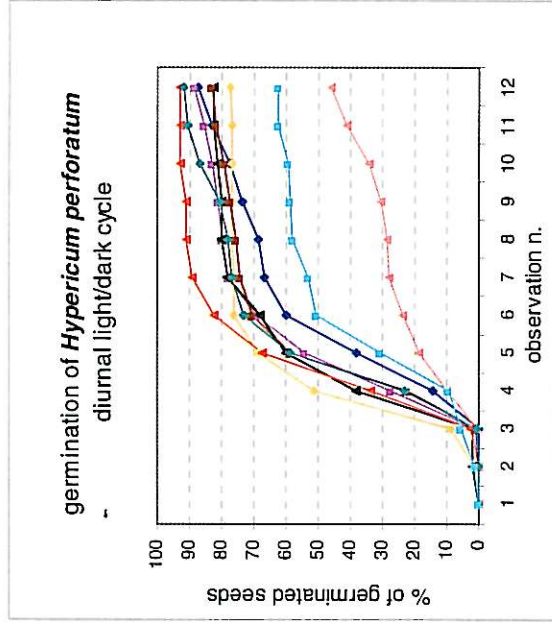
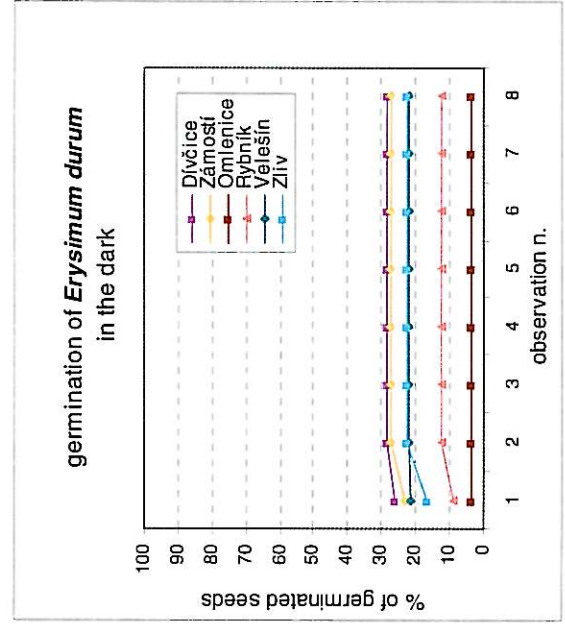
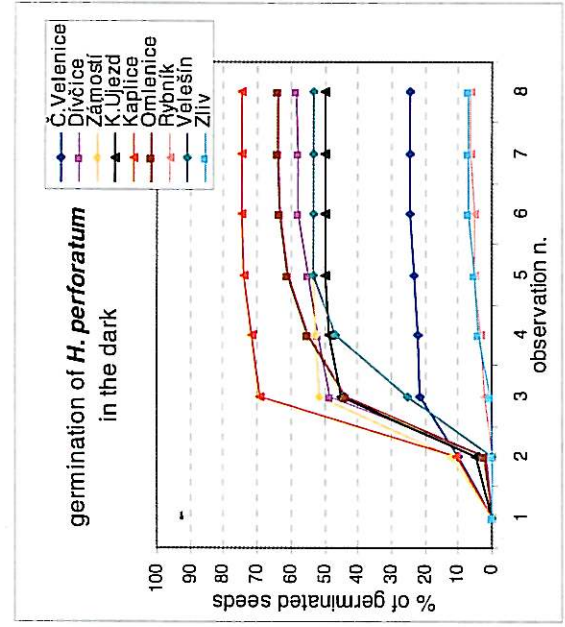


Fig. 4.6a, b



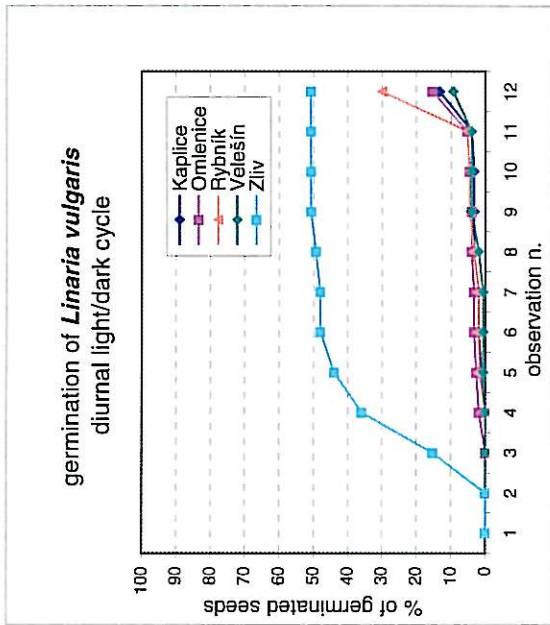


Fig. 4.7a, b

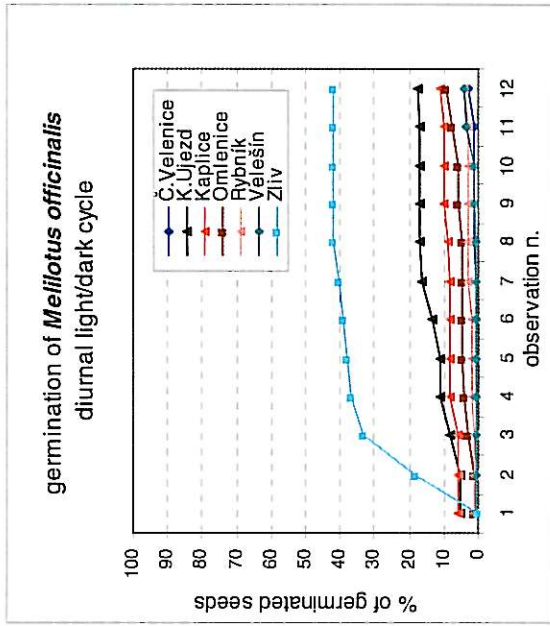
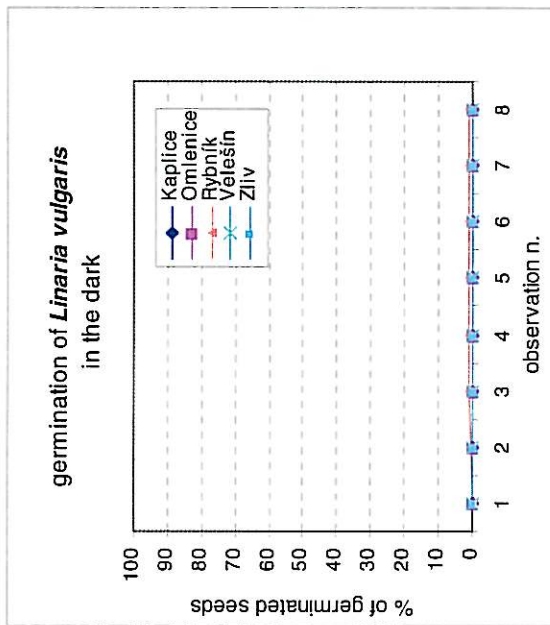


Fig. 4.8a, b

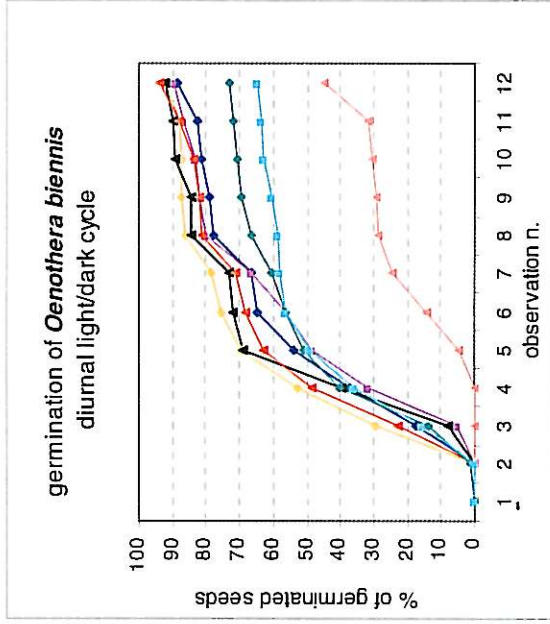
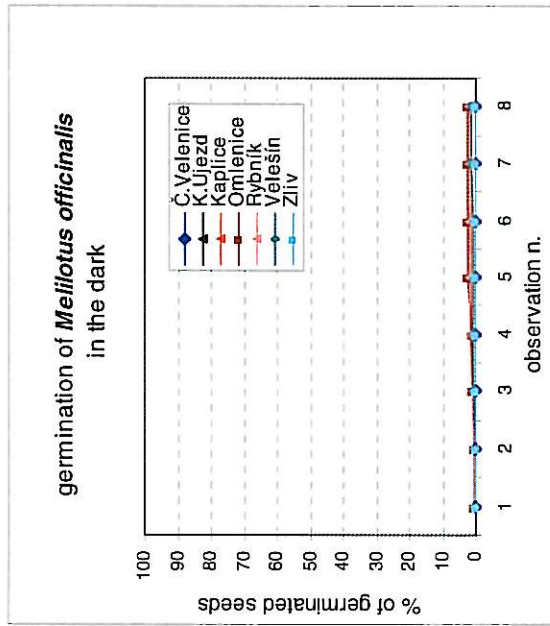
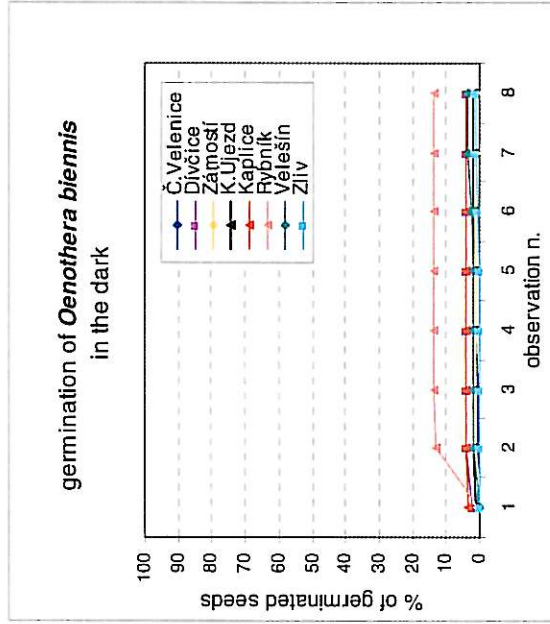


Fig. 4.9a, b



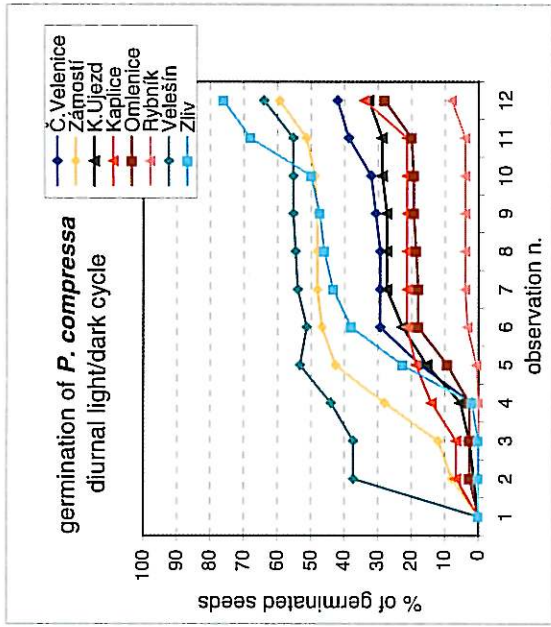


Fig. 4.10a, b

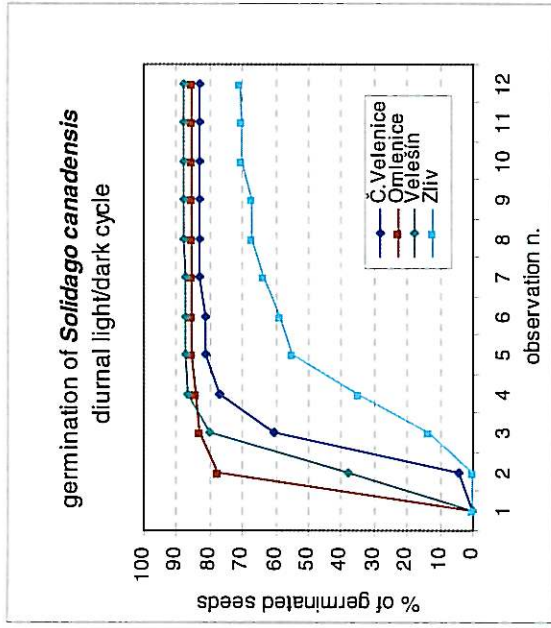
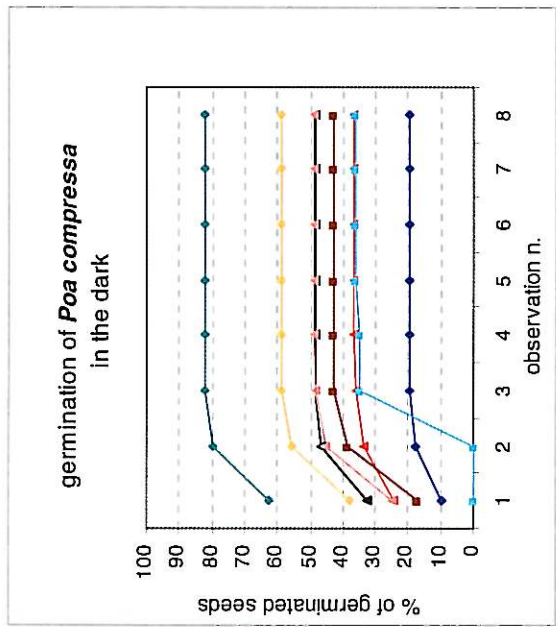


Fig. 4.11a, b

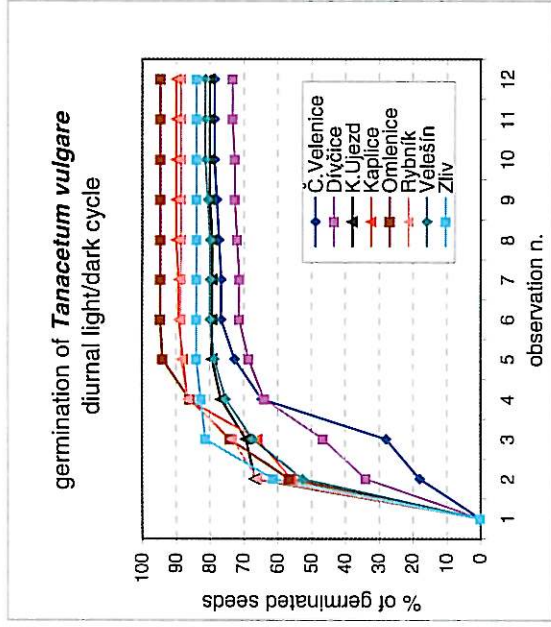
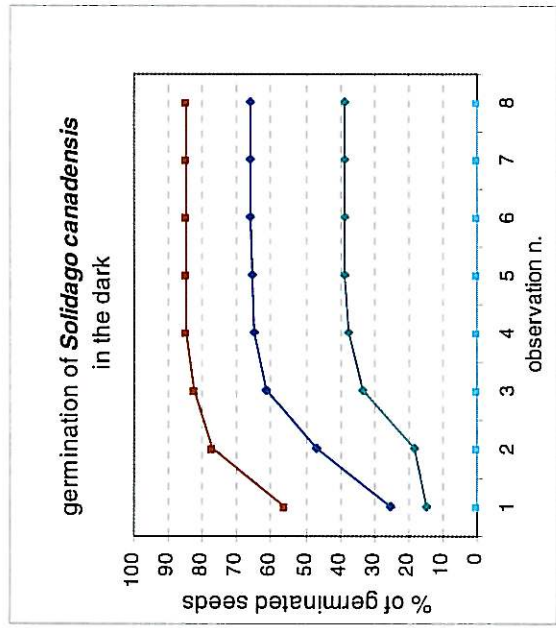
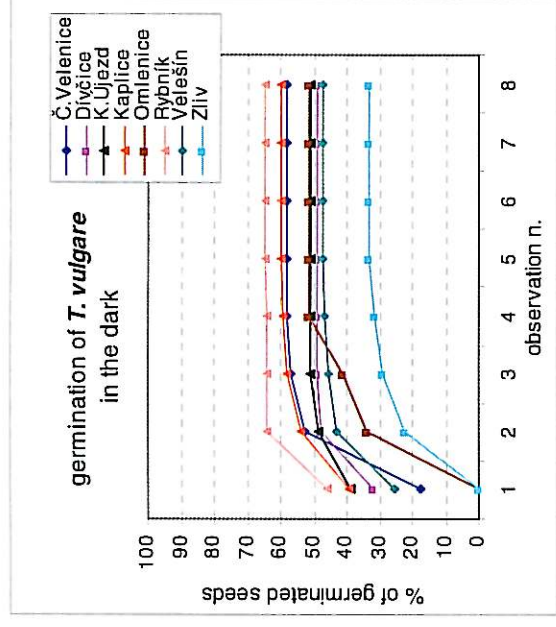


Fig. 4.12a, b



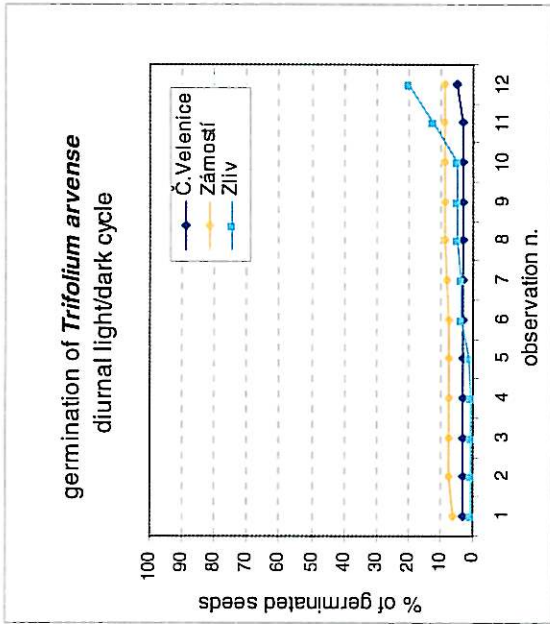


Fig. 4.13a, b

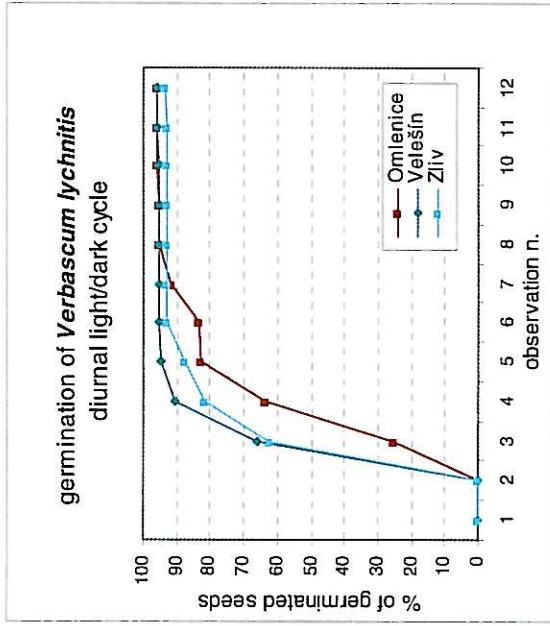
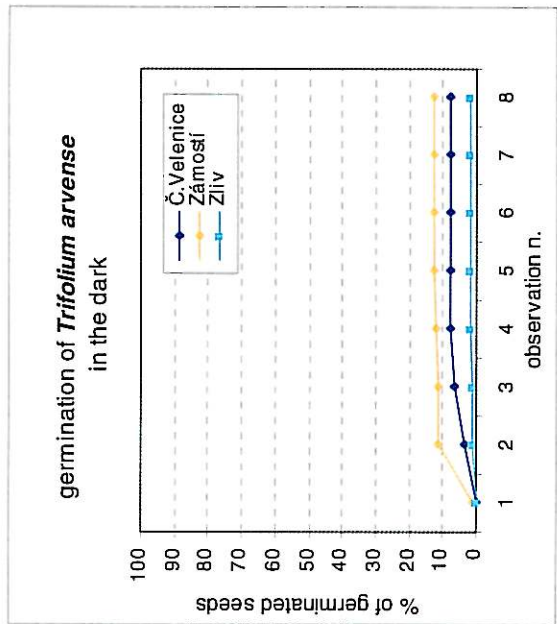


Fig. 4.14a, b

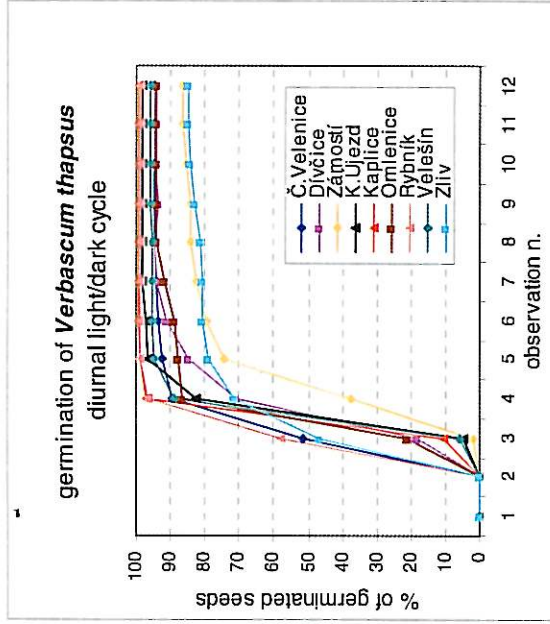
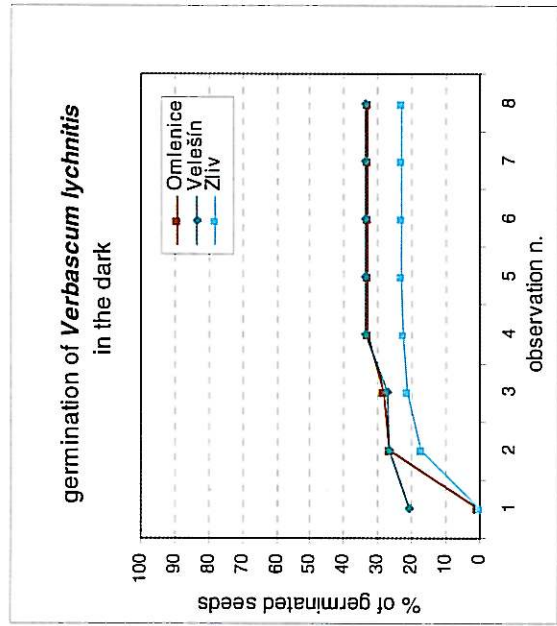
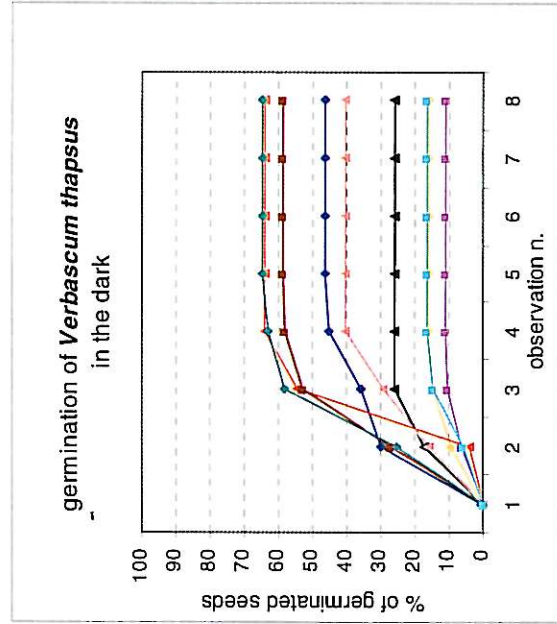


Fig. 4.15a, b



4.7. Final analyses

Analyses in the CANOCO package

The values of "species" (traits gained from the databases and outputs from the experiments and observations) were divided by their standard deviations. The lengths of arrows therefore indicated quality of approximation of traits by the ordination diagram (Fig. 4, 5).

PCA ordination diagram:

- Species in the right half of the ordination diagram (according to the second axis) are all biennials with long - term seed bank (*Daucus carota*, *Echium vulgare*, *Erysimum durum*, *Melilotus officinalis*, *Oenothera biennis*, *Verbascum lychnitis* and *Verbascum thapsus*).
- All species projected in the 4th quadrant are clonal (*Artemisia vulgaris*, *Hypericum perforatum*, *Linaria vulgaris*, *Poa compressa*, *Solidago canadensis*, *Tanacetum vulgare*).
- Germination in both treatments is negatively correlated with seed mass.
- There is no correlation between seed mass and the average seed production per plant.
- The trait species frequency from releves is positively correlated with transient and short - term seed bank, germination in the dark and clonality.

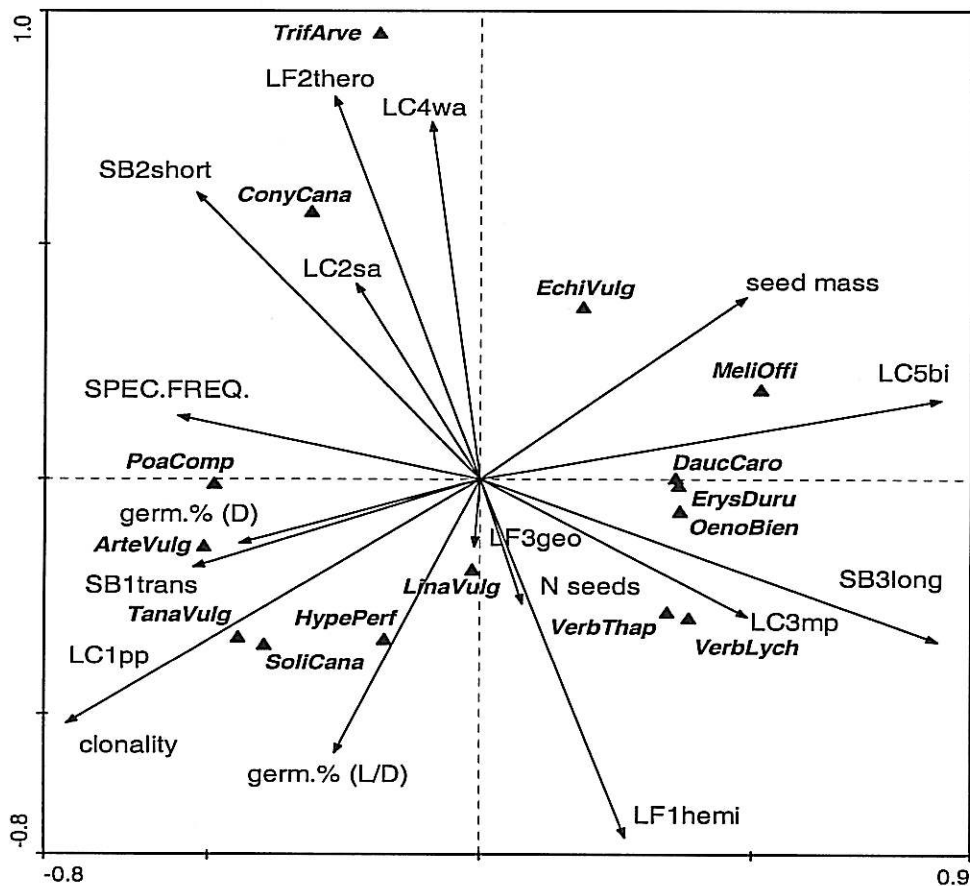


Fig. 6. Final PCA ordination diagram. Traits are displayed as arrows, species as up - triangles. Abbreviations of species names represent first four letters of either name of species. Abbreviations of species traits: **seed mass** - seed mass (mg), **germ.% (L/D)** - final germination percentages from diurnal light - dark treatment, **germ.% (D)** - final germination percentages from dark treatment, **spec.freq.** - frequencies of species from releves, **N seeds** - 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, **LC3** - life cycle monocarpic perennial, **LC4wa** - life cycle winter annual, **LC5bi** - life cycle biennial.

RDA ordination diagram:

When the trait species frequency from relevés was used as an explanatory variable the model was not significant. Summary of Monte Carlo permutation test: $F = 1.474$, $p = 0.188$.

- The explanatory variable species frequency from relevés was positively correlated with short - term seed bank, germination in the dark, clonality (and life cycle polycarpic perennial).
- Short - term seed bank seemed to be the best candidate to explain the species frequencies in the studied habitats (acute angle with the arrow of species frequency and quite long arrow).
- Long - term seed bank and life cycle biennial were both negatively correlated with the explanatory variable (comp. PCA diagram).
- Germination in diurnal light - dark cycle and life cycle winter annual were not correlated with the explanatory variable species frequency from relevés.

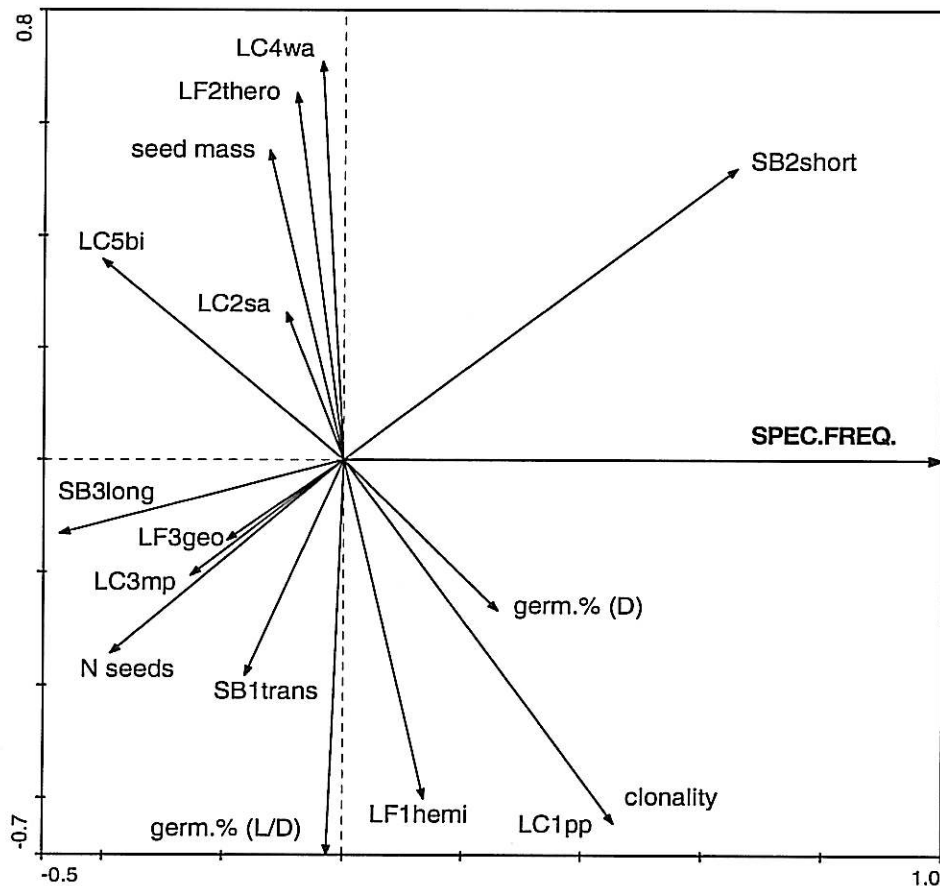


Fig. 7. Final RDA ordination diagram. Abbreviations of species traits: **seed mass** - seed mass (mg), **germ.% (L/D)** - final germination percentages from diurnal light - dark treatment, **germ.% (D)** - final germination percentages from dark treatment, **spec.freq.** - frequencies of species from relevés, **N seeds** - 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, **LC3** - life cycle monocarpic perennial, **LC4wa** - life cycle winter annual, **LC5bi** - life cycle biennial.

Multiply regression

All species traits used in the above mentioned ordination analyses were subjected to multiply regression. Two traits had significantly positive effect on species frequency from relevés: clonality ($p = 0.0091$) and short - term seed bank ($p = 0.021$), but the effect was significant only without Bonferroni correction.

5. DISCUSSION

5.1. Species distribution

Final output from CCA analysis (Fig. 2) confirmed previous observations from the studied sites. Species *Oenothera biennis*, *Verbascum thapsus*, *Conyza canadensis* and *Echium vulgare* preferred stony soils, which can be found mainly near the railways and have high rate of anthropogenic disturbances. During the detail examination of the reference habitat in Zliv (Desetová 2002) most of these species were found to prefer stony substrates as well. Previous studies (Gross 1980, Gross and Werner 1982) revealed that species *O. biennis* and *V. thapsus* require bare ground for successful seedling establishment. Species *Daucus carota* and *Trifolium arvense* seemed to prefer substrates with lower amount of stones and places with lower vegetation cover. Such preference may be in order to avoid competition with higher plant species which are better competitors.

5.2. Germination - greenhouse experiment

Germination of the studied species under diurnal light - dark cycle with natural temperature fluctuations varied widely (Table 8), from 6.7% (*Trifolium arvense*) to 96% (*Verbascum lychnitis*). Germination of seeds may be modified by a wide range of various factors (Gutterman 1992, Benech - Arnold 2000) and different species can have different responses to the main environmental factors (Leon and Owen 2003). Morgan (1998) confirmed that no single set of temperature or light conditions is likely to result in optimal germination of all species. However, some patterns in the germination abilities can be found. Some species germinated quickly (started to germinate after 12 days, including 9 - day chilling) and once emergence had begun, the time taken to achieve 50% of the final germination percentages was quite short (*Artemisia vulgaris*, *Tanacetum vulgare* and *Conyza canadensis* were half - germinated during 12 days).

Species that were rather slower in germination (more than 15 days) - *Daucus carota*, *Echium vulgare* and *Linaria vulgaris* had lower final percentages (less than 20%) than those that start to germinate quickly (*Artemisia vulgaris*, *Conyza canadensis*, *Solidago canadensis*, *Tanacetum vulgare*; all had more than 80% germination, Table 8). This, however, may simply reflect the fact that slow germinators did not have enough time to achieve maximum germination (Morgan 1998). Mainly species *Linaria vulgaris* showed the increase of germination close to the end of the experiment (during 43rd day of the experiment) (Fig. 4.7a). Another possible explanation is that species either have complex dormancy mechanisms (Pons 1992) or specific germination requirements that are not provided in simple germination experiments (Morgan 1998).

Species *Verbascum thapsus* and *V. lychnitis* achieved the highest germination percentages (both more than 95%) (Table 8). These species figured among the less frequent ones. *V. thapsus* requires bare ground for successful establishment and have an ability to colonize 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). But with its large and extremely long - term seed bank (Peat and Fitter 1994, Murdoch and Ellis 1992) the species can wait until the next disturbance prepares a suitable site for settlement.

All species were half - germinated within 25 days except of *Linaria vulgaris*; t(50) for this species was 55 days, the whole length of the experiment (Table 8).

5.3. Germination - laboratory experiment

Germination attributes - all species

Final germination percentages in the dark treatment without bigger temperature fluctuations varied from 0.3% (*Linaria vulgaris*) to 80.8% (*Conyza canadensis*) (Table 8). Generally, the time course of germination that ran without stratification in the dark was very fast. All species were half - germinated within 10 days. The highest final percentages had species that started to germinate quickly and were half - germinated during first 4 days of the experiment (*Artemisia vulgaris*, *Conyza canadensis* and *Echium vulgare*, Table 8).

In the case of the worst germinating species *Linaria vulgaris* only the population from Rybník germinated, populations from other three habitats failed to germinate at all. This species requires temperature fluctuations for successful germination (Peat and Fitter 1994). Thompson and Grime (1983) found out that germination of *L. vulgaris* significantly increased at temperature amplitude of 6°C. As this experiment ran under almost constant room temperature, the lack of higher temperature fluctuation is probably the reason of germination failure of this species. Sensitivity to temperature fluctuations in darkness was observed, among others, also in species of disturbed habitats, and was conspicuous in species forming persistent seed bank. This may be related to the possibility to detect depth of burial as well as canopy gaps (Thompson and Grime 1983, Pons 1992). Mainly the latter seem to be the crucial factor for *L. vulgaris* which is due to its tiny growth poor competitor.

Species *Trifolium arvense* achieved in both light treatments very low germination percentages (approx. 10%). It is known that seed coat of some species may be impermeable to water. This so called hard - seededness has been demonstrated for several species of *Fabaceae* and appears to be common to most if not all *Fabaceae* legumes (Murdoch and Ellis 1992, Probert 1992, Grime et al. 1981, Morgan 1998). Hard - seededness is reversible, a gradual increase in humidity leaves the hilar fissure of dried seed open. But a sudden increase in humidity causes the fissure to close (Murdoch and Ellis 1992). During sowing dried seeds were placed directly on moisturised filter paper and this could have enhanced the innate quiescence of *Trifolium arvense* and contributed to its low germination percentages. Very high temperature fluctuations or mechanical abrasion are known to break this type of innate quiescence (Murdoch and Ellis 1992). Still, the seeds of this species are small and scarification would not be easy. During mechanical scarification seeds are often smashed and the seed set of the species was not large enough to risk this.

Scarification of seeds of *Echium vulgare*

Previous germination experiments (Desetová 2002) and new greenhouse experiment showed quite low germination rates (10 to 20%) of this species. As the species have hard coat the effect of scarification of *E. vulgare* seeds was tested during the laboratory experiment. The effect of scarification was in total significantly negative (Table 10). Though, the considerably higher germination of scarified compared to non - scarified seeds was found for seeds from the reference habitat in Zliv, 29.3 to 17.3% (Table 10). These seeds were five years old and the final germination percentages of scarified seeds from this experiment (29.3%) were even higher than those obtained 3 years ago when germination of non - scarified seeds was last checked (14%). This confirms that *E. vulgare* is able to create short - to long - term seed bank as had been stated before (van Breemen 1984, Peat and Fitter 1994).

In all my experiments with different light regimes that yet have been conducted this species always achieved higher germination rates in the dark. Generally, the species germinated under wide variety of temperature and light conditions and seeds from different populations have demonstrated different germination characteristics. These conclusions coincide with those revealed by van Breemen (1984) for this species.

Zliv - old and new germination experiment

Germination of all studied species from the reference habitat in Zliv was examined under dark conditions with low temperature fluctuations. Seeds in the old experiment conducted three years ago were germinated with 10 - day stratification, the new experiment ran without stratification. Seeds were dry - stored for five years (20 - 25°C). The longer and warmer is the storage environment, the greater is the loss of dormancy (Murdoch and Ellis 1992). Thus, the long storage could have compensated for chilling and seeds should have been released from eventual innate dormancy.

In the old experiment germination was generally higher (44.4% of species had final percentages higher than 50%, Fig. 3a, b). In the new experiment none of the species exceeded 50% germination and six species (33.3%) did not germinate at all. Three of them (*Linaria vulgaris*, *Melilotus officinalis* and *Oenothera issleri*,) showed low germination in both experiments. All of them usually germinated badly in both treatments during all my experiments that yet have been done. Another three species (*Berteroa incana*, *Conyza canadensis* and *Solidago canadensis*) showed good germination during the old experiment. The difference was apparent mainly for *C. canadensis* (decrease from 88.66 to 0%).

Most species from my set of data known to form short - or long - term seed bank (Table 4) showed ability to germinate after 5 - year long storage. Even though germination ran in the dark and one would expect species with long - term seed bank to be inhibited in germination, it is presumed that survival in seed banks is achieved by different strategies (Murdoch and Ellis 1992). Other factors that strongly interfere with light are temperature fluctuations and water potential (Pons 1992). Additionally, due to after - ripening physiological changes in seeds germination requirements usually become less specific (Probert 1992). Consequently, I guess that species whose seeds remain viable during five years showed the basic requirement necessary to create a seed bank. Contrary, species with transient seed bank *Conyza canadensis* and *Solidago canadensis* fail to germinate at all. *T. vulgare* is also cited to have a transient seed bank (Kleyer 1995, Peat and Fitter 1994). The experiment with 5 - year old seeds from the reference habitat in Zliv showed that the differences between percentages achieved in the old and new experiment were not significantly different (Fig. 3b). In the light of these facts, it is likely that *T. vulgare* could be able to create short - term seed bank, still the viability in the natural conditions during burial may be different.

5.4. Germination - effect of treatment and habitat

Due to the significance of light treatment and habitat on final germination percentages species can be divided into three groups (Table 11). Germination of most species was significantly affected by both light treatment and habitat (*Artemisia vulgaris*, *Daucus carota*, *Echium vulgare*, *Hypericum perforatum*, *Oenothera biennis*, *Poa compressa*, *Solidago canadensis*, *Tanacetum vulgare* and *Verbascum thapsus*). Second group consist of species with germination significantly different among habitats but not among the two light treatments (*Conyza canadensis*, *Erysimum durum*, *Trifolium arvense*).

The third group involved species with germination significantly different among treatments but not among habitats (*Linaria vulgaris* and *Verbascum lychnitis*). For another three species (*Melilotus officinalis*, *Tanacetum vulgare* and *Trifolium arvense*) the effect of habitat was very low (Table 11). Generally, species with not or very low significant effect of habitat tend to be obligatory cross - pollinating (*M. officinalis*, *L. vulgaris*) or usually cross - pollinating (*V. lychnitis*, *T. arvense*, *T. vulgare*) (Peat and Fitter 1994). It is likely that metapopulation dynamics could play a significant role in affecting vegetation pattern and distribution of these species. Additionally, as Baguette (2003) stressed, some species are distributed in metapopulations where regional processes (immigration and emigration) are more important than local dynamics (birth and death). As all studied sites are located by the railway

and thus potentially connected by seed flow, regional processes can be of great importance here. Still, these effects are not likely to be found out during one - year study. Blomqvist et al. (2002) revealed during 25 - year study period that colonisation rather than extinction was a more important determinant of plant increase and decrease around grassland ditch banks.

The tests with random factor "habitat" usually caused lower level of significance, still for two species both studied factors and their interactions were highly significant (*Oenothera biennis* and *Verbascum thapsus*) (Table 11). It means that findings concerning these two species can be generalized because they showed consistent pattern of germination abilities which were tested among seven (*O. biennis*) and eight (*V. thapsus*) populations. Both species germinated better in the light; mainly germination of *O. biennis* was strongly inhibited by darkness (found also by Mihulka et al. 2003). Peat and Fitter (1994) cited partial germination requirements for light in the case of *V. thapsus* and absolute for *O. biennis*.

Most species germinated better under diurnal light - dark cycle. All populations of the following species achieved higher germination percentages in the light (Table 11): *Hypericum perforatum*, *Linaria vulgaris*, *Melilotus officinalis*, *Oenothera biennis*, *Solidago canadensis*, *Tanacetum vulgare*, *Verbascum lychnitis* and *Verbascum thapsus*. Peat and Fitter (1994) cited *H. perforatum* to have absolute germination requirements for light. Thomson and Grime (1983) found it insensitive to temperature fluctuations and wholly or partly inhibited by the dark and my observations are consistent with the latter.

On the other hand, all populations of three following species achieved higher germination percentages in the dark (*Daucus carota*, *Echium vulgare* and *Trifolium arvense*). *D. carota* have partial germination requirements for light, *E. vulgare* have none (Peat and Fitter 1994). van Breemen (1984) found out that *E. vulgare* germinated quickly under a wide variety of temperatures and in darkness just as well as in light. He revealed that even at 15 cm depth in the soil about 25% seeds of this species germinated. Most studies suggest that germination is the primary cause of depletion of buried seeds (Murdoch and Ellis 1992, van Breemen 1984, Thompson 1992, Roberts and Boddrell 1984), indicating that even seeds of species with the ability to create a seed bank could germinate in the dark.

It is believed that species with big seeds lacked light - requirement whereas many small seeded species had a light requirement at least for some of their seeds (Pons 1992). All species from my set of data that germinated better in the dark have high or very high seed mass (Table 2, 12). van Breemen (1984) argued that seedlings of *E. vulgare* are able to bridge a 2 - cm layer of soil. Tamet et al. (1996) revealed that seeds of *Daucus carota* can successfully emerged from 5 cm sowing depth. He also revealed that heavier seeds of this species had longer hypocotyl lengths and greater growth forces, which explained their better emergence from deep sowing. Heavy seeds also have better chance to cope with surface obstacles, e.g. dry soil crust (Tamet et al. 1996, for *D. carota* var. *sativus*). For big seeded species with bigger reserves this risk to germinate in the soil may be favourable because they can penetrate several centimetres of soil and emerge successfully (found also by Thomson and Grime 1983). This ability may be essential when disturbance occurs infrequently, e.g. only once in the lifetime of a seed. It is a better strategy to germinate because the seed may not encounter a second opportunity to establish (Pons 1992). Nevertheless, it can lead to large losses of seeds from a seed bank as observed by van Breemen (1984).

The third group involved species whose populations showed different preferences for light treatment (*Artemisia vulgaris*, *Conyza canadensis*, *Erysimum durum* and *Poa compressa*). Thomson and Grime (1983) found species *A. vulgaris* and *C. canadensis* insensitive to temperature fluctuations and partly inhibited by darkness. Most populations of these species in my observations germinated better in light - dark cycle, but the differences between both treatments were quite low (Table 11). Populations of the apomictic species *P. compressa* showed marked differences (Table 11, Fig. 4.10a).

On the other hand all allogamic species showed rather similar pattern with respect to light preference (*Daucus carota* Fig. 4.3a, *Echium vulgare* Fig. 4.4a, *Linaria vulgaris* Fig. 4.7a, *Melilotus officinalis* Fig. 4.8a, *Solidago canadensis* Fig. 4.11a, *Verbascum lychnitis* Fig. 4.14a, *V. thapsus* Fig. 4.15a).

5.5. Time course of germination

Light - dark treatment

Graphical output displaying the time course of germination (Fig. 4) involves also the final germination percentages of all species from the reference habitat in Zliv. In the case of light - dark treatment the values from the previous experiment in the greenhouse (Desetová 2002) were used to compare the germination percentages among the reference habitat in Zliv and the new ones. The germination ran under the identical conditions (diurnal light - dark treatment, natural temperature fluctuations, in the spring), still with seeds from different years. This had probably influenced the results as germination of seeds can be strongly influenced by the environmental factors (Gutterman 1992, Benech - Arnold 2000). In different plant species sometimes even small differences in temperature during plant development or seed maturation can have an influence on the germinability of the seeds. In general, higher temperatures and desiccation result in seeds with higher germinability and similar effect has been found for altering temperatures (Gutterman 1992).

On the whole, germination in this treatment was, among the studied habitats, more consistent and some trends could have been found out. On the contrary, germination in the dark was rather diverse among the habitats of a single species. Species *Daucus carota*, *Linaria vulgaris* and *Melilotus officinalis* usually achieved low germination percentages in light - dark treatment. When comparing the time course of germination of these species, the reference habitat in Zliv showed rather higher percentages (Fig. 4.3a, 4.7a, 4.8a, respectively). This indicates that environmental conditions can considerably influence germination of these species. On the other hand, another poorly germinating species, *Trifolium arvense* achieved practically the same final germination values within all studied habitats. This reflects that rather genotypic influences (innate quiescence caused by hard - seededness of seeds) play a crucial role in germination abilities of *T. arvense*.

Most allogamic species showed very similar time course of germination among all studied habitats (*Echium vulgare*, *Solidago canadensis*, *Verbascum lychnitis* and *Verbascum thapsus*) (Fig. 4.4a, 4.11a, 4.14a, 4.15a, respectively). The rest three allogamic species (*Daucus carota*, *Linaria vulgaris* and *Melilotus officinalis*) showed differences between the reference habitat and the new ones as discussed above. In the case of the apomictic species *Poa compressa* differences among the studied habitats were remarkably higher compared with the allogamic species (Fig. 4.10a). van Kleunen et al. (2001) revealed for species with spreading growth form that allocation to sexual reproduction increases more than allocation to vegetative reproduction only with increasing vegetation density. Vegetation cover is generally low among the studied habitats and it is likely that *P. compressa* reproduce mainly asexually and gene exchange between localities is probably low. My own experience is that in order to get enough seeds for germination experiments one has to mow almost whole population of this species, because the production of viable seeds is very low.

The time course of germination of species that started to germinate during the first observation generally resembled logarithmic curve (Fig. 5a). All of these species (*Artemisia vulgaris*, *Conyza canadensis*, *Solidago canadensis*, *Tanacetum vulgare*; except of *Erysimum durum*) achieved in both treatments more than 50% germination (Table 8). Fast germinating species with the ability to germinate under a wide variety of conditions are not likely to form a persistent seed bank (Morgan 1998). All above mentioned species (except of *E. durum*) have transient or short - term seed bank (Table 4).

Species that started to germinate later and the time course of their germination resembled sigmoid curve, had long - term seed bank (Fig. 5b). If seeds are to survive in the soil and form a seed bank, viability must be maintained for as long as germination is avoided by dormancy or quiescence (Murdoch and Ellis 1992). Therefore, species with slow germination (longer germination lag, Fig. 8) may be more likely to form a persistent seed bank (Morgan 1998).

Dark treatment

In the case of dark treatment the 5 - year old seeds from Zliv were germinated together with seeds from other habitats. Experimental conditions were the same (dark, no chilling and temperature fluctuations) nevertheless, some differences caused by the age of the seeds from Zliv could have been observed and therefore it was interesting to compare at least graphically the time course of germination. No statistical test was used to compare the final germination rates between the reference habitat in Zliv and other habitats because any estimates and interpretation would be rather tricky.

The comparison of the time course of germination of species *Conyza canadensis* and *Solidago canadensis* (Fig. 4.2b, 4.11b) revealed that while 1 - year old seeds from new habitats germinated in the dark, 5 - year old seeds failed to germinate at all. Both species are said to have only transient seed bank (Table 4) (Peat and Fitter 1994, Kleyer 1995). The germination biology of some species is not conducive to the formation of a persistent seed bank (Morgan 1998). In particular, a seed bank is unlikely to form mainly if seeds germinate readily in the dark and hence do not become dormant upon burial in the soil (Grime et al. 1981, Thompson and Grime 1983). The less strict germination requirements of these species and the inability to germinate after 5 - year storage are consistent with this statement.

When comparing the course of germination in the case of *Erysimum durum* between the two light treatments, a constant pattern appeared (Fig. 4.5a, b). In both treatments, habitats with the highest altitude (Rybník and Omlenice) achieved the lowest final germination percentages. Contrary, habitats with the lowest altitude (Dívčice, Hluboká nad Vltavou - Záměstí and Zliv) achieved the highest germination percentages. The species can be found mainly in planar and colline altitudinal vegetation zones, only rarely steps up to a supracolline zone, maximum mentioned altitude is about 600 m (Slavík 1990- 1997). The altitude of habitats Rybník and Omlenice is 635 and 636 m a.s.l., respectively (Table 1). It is likely that in such high altitudes the species do not grow in optimal climatic conditions and as has been cited before (Gutterman 1992, Benech - Arnold et al. 2000) the maturation conditions of mother plants influence the germination of seeds. No more obvious patterns could be found concerning the altitude and climate (temperature and precipitation) among the studied habitats (Appendix 1).

5.6. Germination - multiply regression

Although the tests for both light treatments were very weak and the effects were significant only without Bonferroni correction, they revealed some interesting facts.

Diurnal light - dark treatment

Three species traits had a positive effect on the final germination percentages: seed production per plant, transient seed bank and clonality. Two species with the highest germination percentages (*Verbascum lychnitis* and *V. thapsus*) had at the same time the highest seed production (Tables 5, 8). Four out of six clonal species (*Artemisia vulgaris*, *Hypericum perforatum*, *Solidago canadensis* and *Tanacetum vulgare*) figured among the species that achieved more than 80% germination. That is why clonality had a positive effect on germination in light - dark treatment. Species with transient seed bank (*Conyza canadensis* and *Solidago canadensis*) had rapid and high

germination in both treatments, but the positive effect on germination was revealed only in the light - dark treatment. These species also had the lowest seed mass (Table 2). Germination in darkness is usually almost inhibited in the species with the smallest seeds (Pons 1992, Schütz et al. 2002). But some species may be extremely sensitive to short and low light fluxes (Pons 1992). These could have occurred for example during seeding. A light - flash mechanism for breaking dormancy has been suggested long time ago (Sauer and Struik 1964). Milberg et al. (1996) revealed that germination of *Conyza canadensis* after short - duration light exposure was considerably higher than without it. He stressed that selection has favoured the ability to detect very low photon fluxes, which can occur during daytime at a few millimetres depth in soil. Still, when they compared groups of species classified according to seed mass, they did not find any significant differences in the frequency of extremely light sensitivity.

On the other hand germination of *Verbascum thapsus* after short light exposure was not much higher (Milberg et al. 1996). This species is known to form extremely long - term seed bank (Murdoch and Ellis 1992, Peat and Fitter 1994) and it is likely that it possess more strict germination requirements.

Dark treatment

In the dark treatment none of the traits was significantly correlated with germination. But the model indicated negative effect of long - term seed bank with germinability in the dark. This confirms that light is one of the principal factors controlling dormancy of seeds (Pons 1992). In both treatments seed weight was not correlated with the final germination percentages (found also by Morgan 1998).

5.7. Final analyses

The aim of these analyses was to reveal if any of the studied species traits could evaluate some patterns in vegetation composition among the studied habitats.

Life cycle polycarpic perennial was strongly positively correlated with clonality and transient seed bank; biennial life cycle with long - term seed bank (Fig. 6). In the North - West European flora shorter - lived species tend to have longer - lived seeds and vice versa (Thomson et al. 1998). This correlation is important mainly for species of highly disturbed habitats (Stöcklin and Fisher 1999). Different biennials can be often found growing together at the same sites (van der Meijden et al. 1992). Biennial life cycle is an ideal adaptation to the environment with high level of disturbances. Biennials start from a larger seed bank and have higher reproductive allocation (Hart 1977). Without disturbances biennials are looser compared to perennials (Hart 1977). It is only during the first years after large - scale disturbance that biennials are successful (Hart 1977). Fig. 6 shows that biennial life cycle is strongly negatively correlated with species frequencies from relevés, which is in line with the previous statement.

Long - term seed bank was negatively correlated with clonality (Fig. 6). Only two out of six clonal species in this data set had long - term seed bank (*Hypericum perforatum*, *Linaria vulgaris*). Clonal plant species, which reproduce primarily by vegetative growth and therefore move gradually across the landscape (Robinson et al. 1992), are more likely to persist in large than in small fragments, where colonization is limited by habitat disruption. Tilman (1997) found out that species with longer - lived seeds constitute better buffer against risks of local extinction caused by stochastic processes than shorter - lived seeds. On the other hand, a very short - lived seed bank may be a mechanism to reduce the risks of predation or loss of viability (van Breemen 1984).

Long - term seed bank and seed mass was negatively correlated with species frequency whereas short - term bank was correlated positively (Fig. 6). Self - thinning during succession reduces the densities of later stage, large seeded species (Guo 2003). This may also help explain, why, over

time, small seeded - species can have greater ranges of densities while large - seeded species are always low in densities (Guo 2003). Low seed mass or wind - dispersal can also be advantageous in open vegetations (Lake and Leishman 2003). Low seed mass connected with ease of burial and relative freedom from predation can be important contributor to seed bank longevity (Thomson 1992). Venable and Brown (1988) suggested that seed dormancy, seed size and seed dispersal ability should be treated as coadapted traits that reduce risk in variable environment. Still, when Murray (2003) surveyed literature for studies relating seed mass to plant abundance within local communities, the strongest pattern emerging is that there is no significant relationship between seed mass and abundance. When species frequency was used as an explanatory variable, there was no relationship with seed mass in the present study (Fig. 7).

Germination in both treatments was negatively correlated with seed mass. Species with very high or high seed mass (Table 12) usually had very low or low germination percentages in both treatments. Germination in the dark was strongly negatively correlated with biennial life cycle (Fig. 6). Most biennial species had long - term seed bank (exception is *Echium vulgare* with short - term seed bank, Table 4) and their germination was considerably lower in the dark. Light is known as one of the crucial factors controlling dormancy in seeds and their survival in a seed bank (Pons 1991, Pons 1992). The inhibiting effect of the dark was apparent mainly for *Hypericum perforatum*, *Oenothera biennis*, *Verbascum lychnitis* and *V. thapsus* (Table 8).

Rapid germination should be characteristic of the species of greatest abundance in the area (Grime et al. 1988). Though, only species *Artemisia vulgaris* and *Tanacetum vulgare* from the studied species were conformable with this assumption. Four out of five most frequent species were clonal (*Poa compressa*, *Artemisia vulgaris*, *Hypericum perforatum*, *Tanacetum vulgare*). The positive correlation between species frequency and clonality was revealed also by final PCA and RDA diagrams (Fig. 6, 7) and results of multiply regression indicated the same fact. If disturbances are not large - scaled small gaps in the vegetation tend to be filled by clonal growth of surrounding vegetation. Vegetative propagation allows allocation to growth rather to reproduction, which may be an advantage where disturbance increases resource availability and thus favours fast - growing species (Lake and Leishman 2003). Additionally, clonal species are likely to be persistent at some sites even if reproduction and recruitment are hindered (Eriksson and Kiviniemi 1999). Still buried seeds seem to be crucial to the recolonization of large gaps (Thompson 1992). Clonal species *Artemisia vulgaris*, *Hypericum perforatum* and *Tanacetum vulgare* figured among the best germinated species, the first two species have in addition ability to create a long - term seed bank. Presumably all these traits together play a role in enabling them to become frequent among the studied habitats. Another studies also suggested that colonization ability is not a simple function of one particular trait value (Eriksson and Jacobsson 1998, Kiviniemi 2001).

Four less frequent species (*Verbascum thapsus*, *Solidago canadensis*, *Linaria vulgaris* and *V. lychnitis*) are all cross - pollinating species; two latter even have an incompatibility system (Peat and Fitter 1994). Steffan - Dewenter and Tschardtke (1999) found out that habitat isolation may affect plant - pollinator interactions negatively by limiting the number of available pollinators and reducing the number of seeds per plant and, thereby, the potential success of plants. Seed set may also depend on the distance to the nearest plant population of the same species (Steffan - Dewenter and Tschardtke 1999). Blomqvist et al. (2002) found out that cross - pollinating species have a higher chance of decreasing than self - fertile species. At some early stages of the life history sibs may even profit, from the proximity of genetic relatives. In some species, self - fertilized seeds disperse less well than out - crossed seeds, which is the opposite of what would have been expected if dispersal were an adaptation to reduce sib competition (Willson 1992). In my set of data it appeared that self - sterile species were losers compared with self - fertile ones.

In the case of perennial species *Solidago canadensis*, sexual propagation is delayed until its second year of development (Cornelius 1990). Thus disturbances, which are common in the inner cities or near railway stations, may prevent this species from completing its life cycle (Cornelius 1990) and may have contributed to generally low frequency of this species among the studied habitats.

When RDA was used, i.e. the ordination constrained by the explanatory variable (species frequency from relevés), the same results were obtained as in the case of unconstrained ordination, PCA (Fig. 6, 7). Generally, the species frequency was positively correlated with short - term seed bank, clonality and germination in the dark (Fig. 6, 7). The possible positive effect of clonality and short - term seed bank was revealed also by the multiply regression, though the test was very weak.

5.8. Summary

Table 12 shows a synoptic overview all species traits and germination attributes of both light treatments. Species were grouped as having very high, high, low or very low levels of the studied traits. The threshold values were determined ad hoc in order to involve species with similar levels of a particular trait in one group.

- Species *A. vulgaris*, *T. vulgare*, *C. canadensis*, *S. canadensis* germinated fast and achieved high final percentages in both light treatments. They all have low or very low seed mass and transient or short - term seed bank.
- Germination of species known to form a long - term seed bank was usually lower in the dark treatment.
- Differential responses to the main germination conditions (light, temperature fluctuations) and their interactions could account for differences across the studied species of seed germination and seedling emergence timing, which represent differences in adaptation and survival strategies (Leon and Owen 2003). Thus, spatial and temporal variation in seed death rates can have important consequence for plant coexistence (Crawley 1992).
- Comparison of the achieved levels of species traits among native and invasive species revealed some interesting features. All invasive species, except of *Melilotus officinalis*, had very high germination in light - dark treatment. All species of my set of data with transient seed bank are invasive, thus good germination abilities are of great importance once they are to survive in the locality. With respect to the other traits invasive species showed wide range of achieved levels. Such observation is consistent with findings of Williamson and Fitter (1996) that invading species have no particular properties, each of them is invasive for its own reasons. However, some general trends can be revealed. E.g. van Kleunen and Schmid (2003) concluded that life - history characteristics of *Solidago canadensis* including its tall stature, and the production of large numbers of wind - dispersed seeds and perennial rhizomes, have predestinated this species to be a successful invader. Some of these characteristics (large number of small seeds, fast and high germination, transient seed bank) are common also for *Conyza canadensis* and *Tanacetum vulgare*. On the other hand, *Melilotus officinalis* and *Oenothera biennis* figured among slow germinating species and both have the ability to create a long - term seed bank (more than 20 years for *M. officinalis* and even 80 years for *O. biennis*). Both have biennial life cycle, which enables higher reproductive allocation (Hart 1977). It seemed that biennial life cycle combined with long - term seed bank could be advantageous, mainly during occupation of new sites. Findings of Mihulka and Pyšek (2001) revealed that the majority of invasive primrose species are biennials.

6. CONCLUSIONS

- Germination of most studied species significantly differed among the treatments and the habitats. The effect of treatment was not significant in the case of *Conyza canadensis*, *Erysimum durum* and *Trifolium arvense*. The effect of habitat was not significant for *Linaria vulgaris* and *Verbascum lychnitis*.
- The main factors determining species distribution among the studied habitats seemed to be mainly the type of substrate and frequency of disturbances.
- Final analyses indicated that the most frequent species tend to be clonal and have short-term seed bank.

Table 12. Traits and germination attributes of the studied species. Life cycle: **PP** - polycarpic perennial, **SA** - summer annual, **MP** - monocarpic perennial, **Bi** - biennial, **WA** - winter annual. **Invasibility:** invasive status of species (+) invasive, (-) non-invasive; **clonality:** (+) clonal, (-) non-clonal; **seed bank type:** short-term, long-term, transient (Peat and Fitter 1994, Kleyer 1995). For each species four levels of all traits were distinguished: **VH** - very high, **H** - high, **L** - low and **VL** - very low level. Threshold values of each trait were determined ad hoc in order to involve species with similar levels of a particular trait in one group. Abbreviations of species traits: **frequency** - species frequencies from relevés, **s. mass** - seed mass, **s. pool** - average seed production per plant, **recruit.** - percentages of recruited individuals from the field experiment (Desetová 2002), **lag** - time to the beginning of germination, **t(50)** - germination speed (time taken to achieve 50% of final germination), **germ.** - final germination percentages, **L/D** - diurnal light-dark cycle, **D** - continuous darkness.

Threshold values:

frequency (%)	s. mass (mg)	s. pool (N)	recruit. (%)	lag+t(50) L/D (d)	lag+t(50) D (d)	germ. L/D+D(%)
>40 VH	>1 VH	>70 000 VH	>2 VH	>20 VH	>9 VH	>70 VH
40-15 H	1-0.5 H	15-10 000 H	2-1.5 H	20-15 H	9-6 H	70-40 H
15-10 L	0.5-0.1 L	10-2 000 L	1.5-0 L	14-10 L	5-3 L	40-10 L
<10 VL	<1 VL	<2 000 VL	0 VL	<10 VL	≤3 VL	<10 VL

species	spec. frequency	invasibility	clonality	life cycle	seed bank type	seed mass	seed pool	N of recruited individuals	germ. light-dark			germ. dark		
									lag	speed	%	lag	speed	%
<i>PoaComp</i>	VH	-	+	PP	short	L	VL	L	L	VH	L	VL	L	H
<i>ArteVulg</i>	VH	-	+	PP	short	L	H	VH	L	L	VH	VL	L	VH
<i>DaucCaro</i>	H	-	-	MP	long	H	L	L	H	VH	L	VL	L	L
<i>HypePerf</i>	H	-	+	PP	long	L	L	H	L	VH	VH	H	VH	H
<i>TanaVulg</i>	H	+	+	PP	trans.	L	H	H	L	L	VH	L	L	H
<i>TrifArve</i>	H	-	-	WA	short	H	H	L	VL	VL	VL	L	H	L
<i>OenoBien</i>	H	+	-	Bi	long	H	H	L	H	VH	VH	L	L	VL
<i>EchiVulg</i>	L	-	-	Bi	short	VH	L	VH	H	VH	L	VL	VL	VH
<i>ConyCana</i>	L	+	-	SA	trans.	VL	H	L	L	L	VH	VL	VL	VH
<i>MeliOffi</i>	L	+	-	Bi	long	VH	VL	VL	VL	VH	VL	L	H	VL
<i>ErysDuru</i>	L	-	-	Bi	long	L	L	H	L	L	L	VL	VL	L
<i>VerbThap</i>	L	-	-	Bi	long	L	VH	L	H	H	VH	L	H	H
<i>SoliCana</i>	VL	+	+	PP	trans.	VL	L	VL	L	L	VH	VL	H	H
<i>LinaVulg</i>	VL	-	+	PP	long	L	L	L	VH	VH	L	H	H	VL
<i>VerbLych</i>	VL	-	-	Bi	long	VL	VH	L	H	H	VH	VL	L	L

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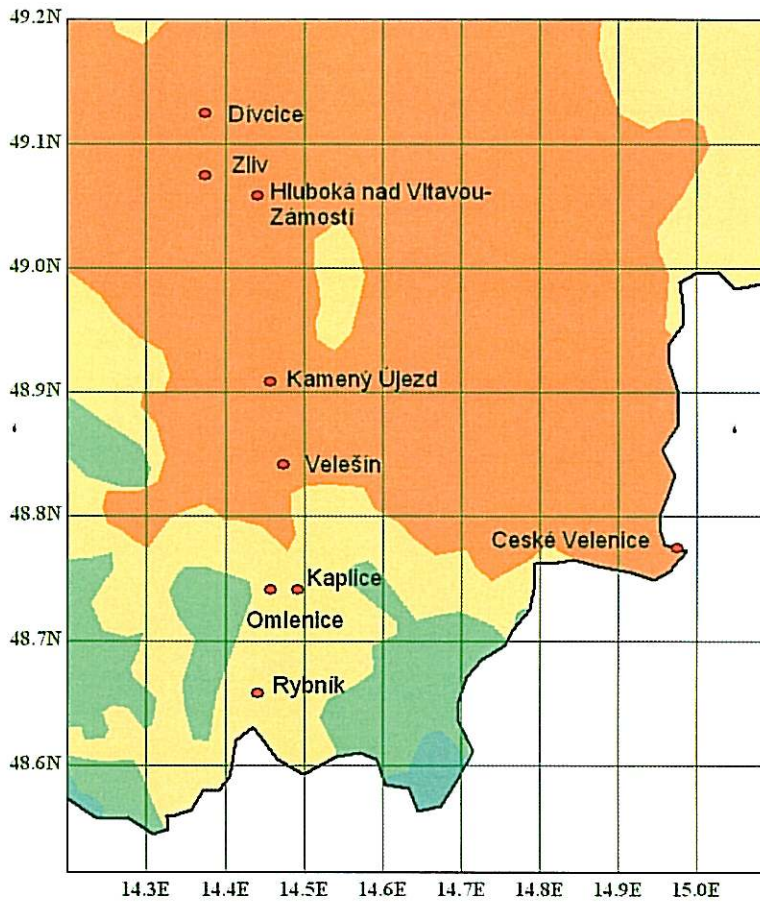
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The pictures of *Oenothera biennis* and *Linaria vulgaris* were obtained at:
<http://wolf.mind.net/SWSBM/HOME/PAGE/GenusIndex.html>

8. APPENDICES

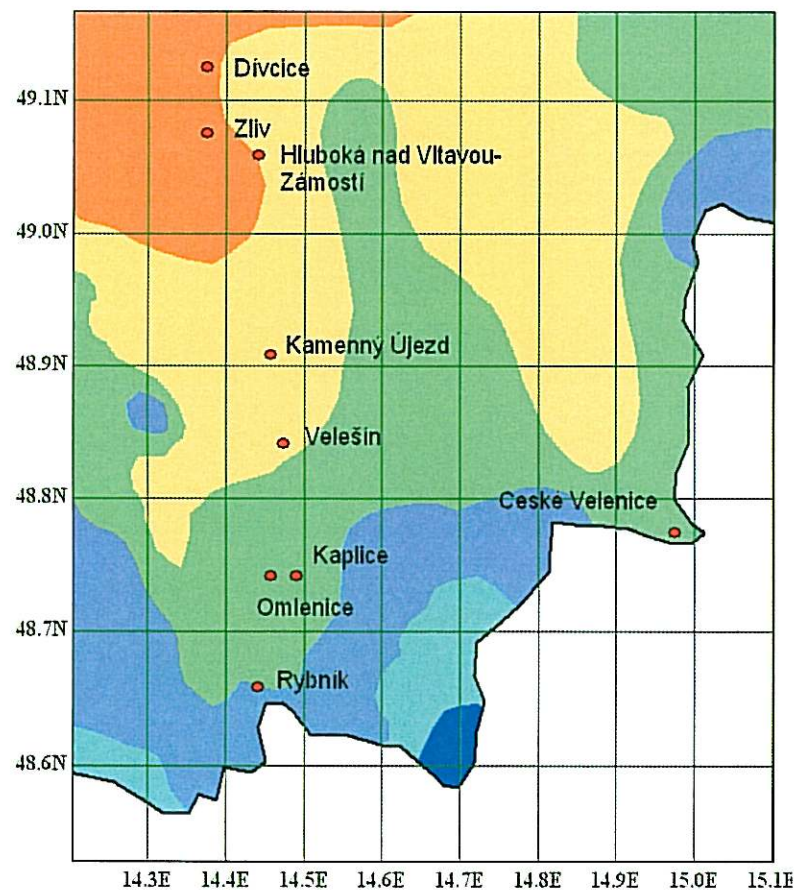


Appendix 1



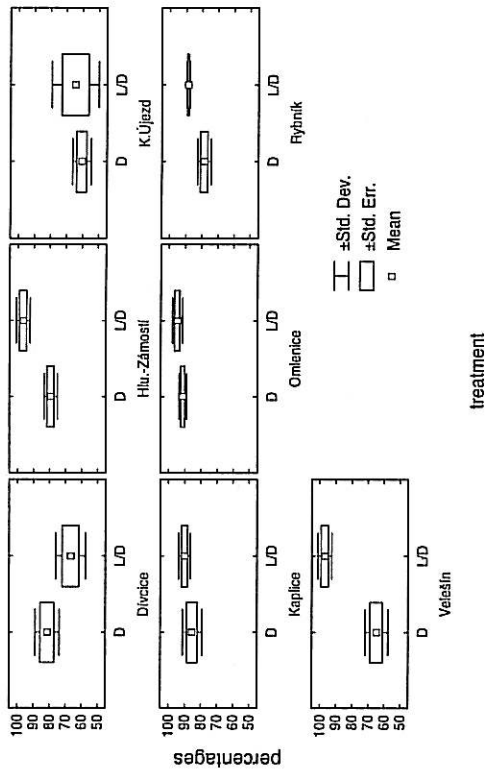
Distribution of the average annual temperatures among the studied localities (obtained from DMAP for Windows).

Distribution of the average annual precipitation among the studied localities (obtained from DMAP for Windows).

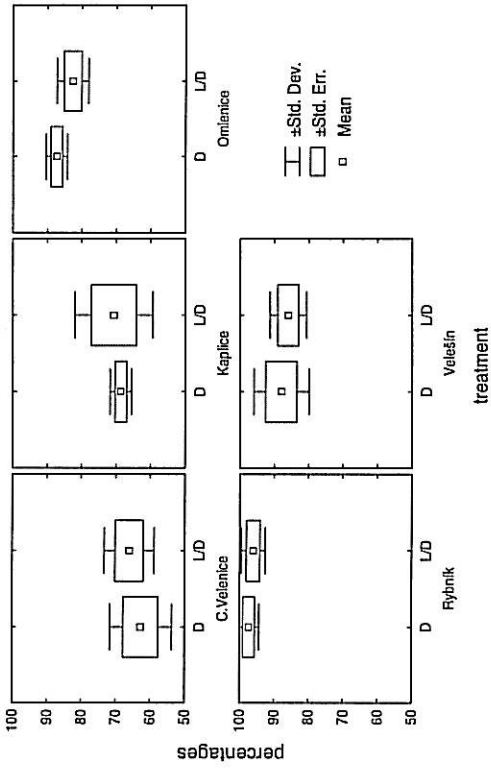


Appendix 2

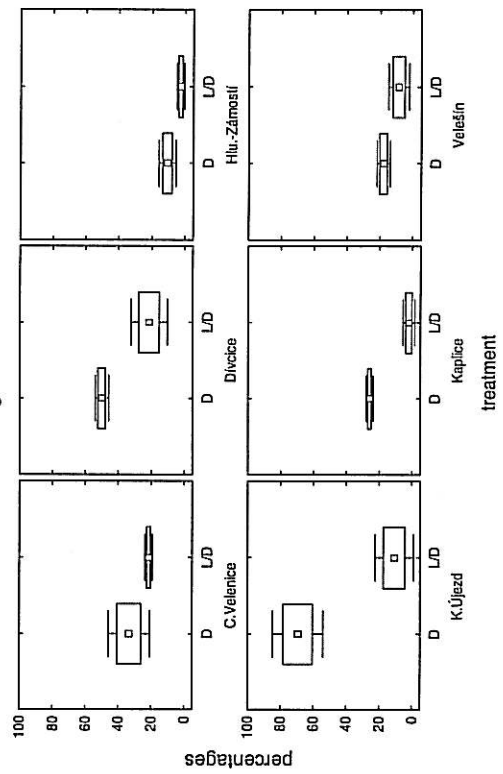
germination of *Artemisia vulgaris*
dark vs. light/dark treatment



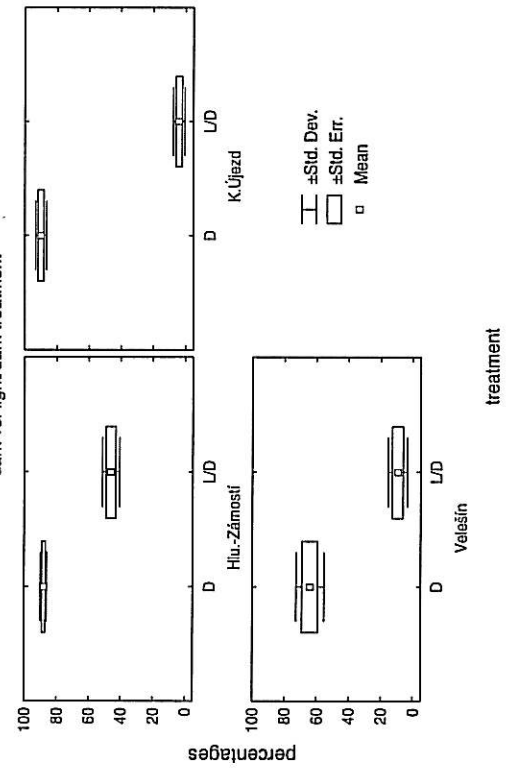
germination of *Conyza canadensis*
dark vs. light/dark treatment



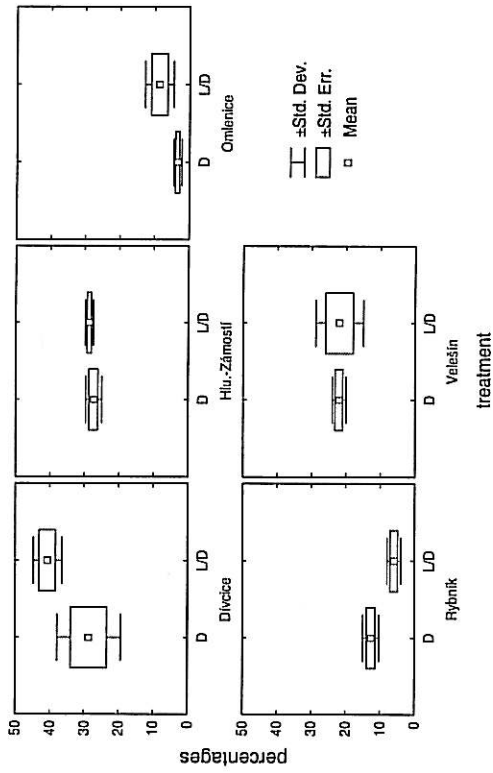
germination of *Daucus carota*
dark vs. light/dark treatment



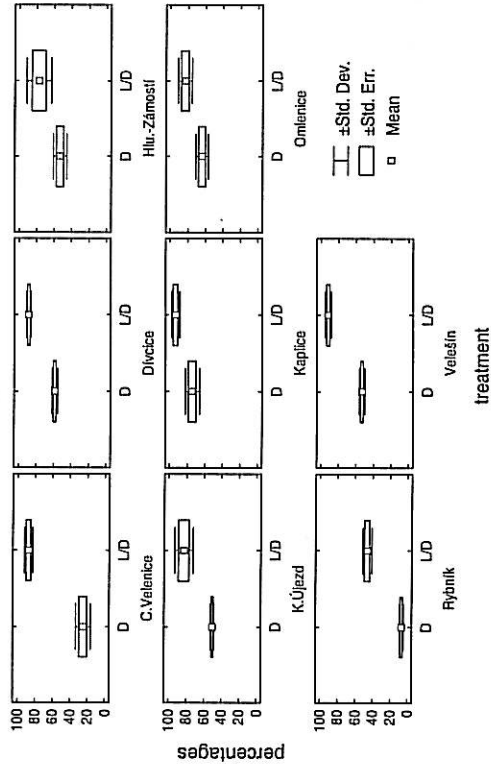
germination of *Echium vulgare*
dark vs. light/dark treatment



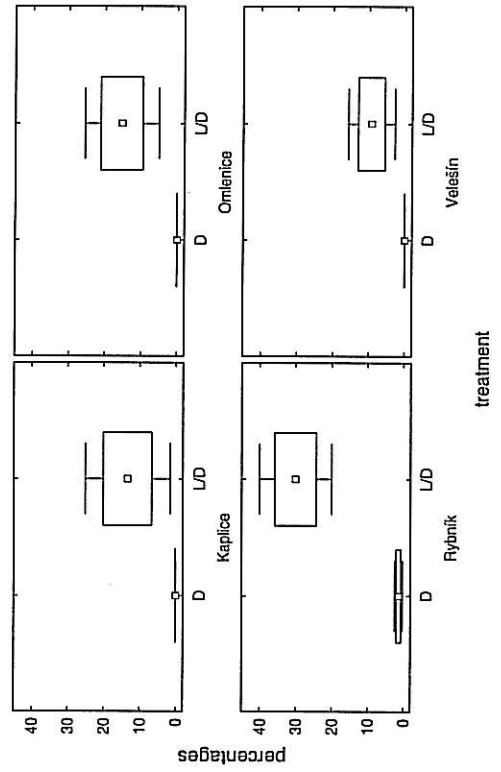
germination of *Erysimum durum*
dark vs. light/dark treatment



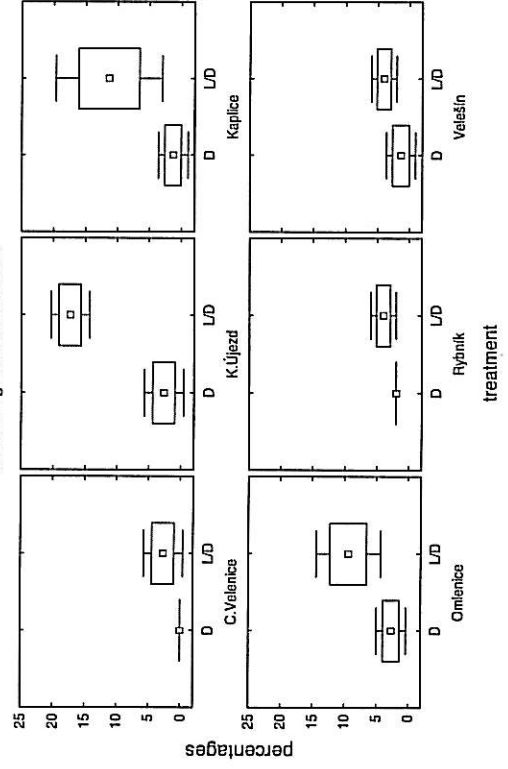
germination of *Hypericum perforatum*
dark vs. light/dark treatment



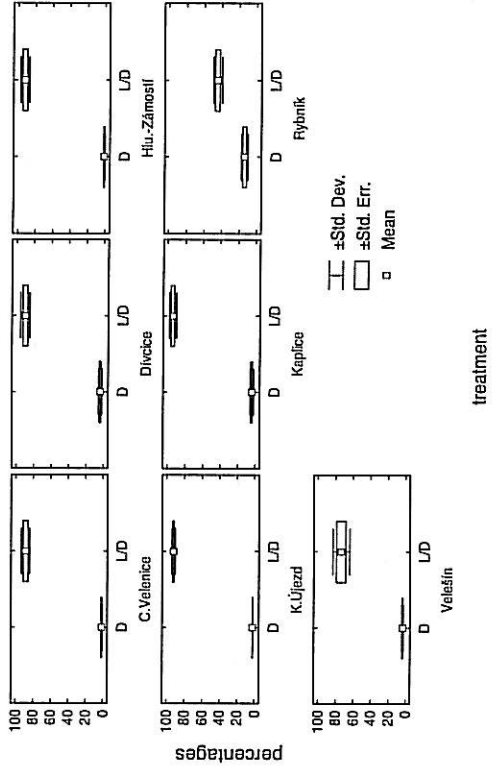
germination of *Linaria vulgaris*
dark vs. light/dark treatment



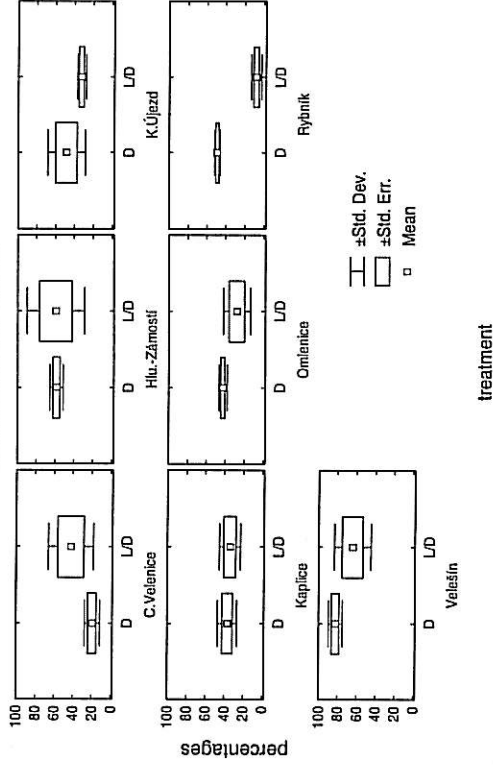
germination of *Meibotus officinalis*
dark vs. light/dark treatment



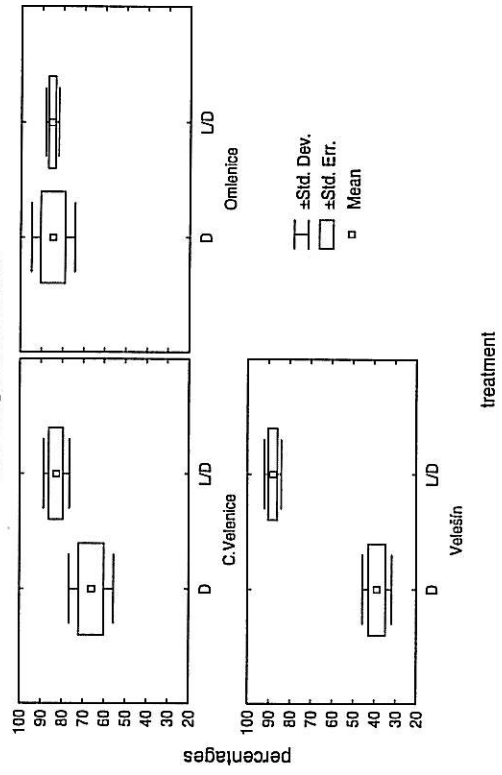
germination of *Oenothera biennis*
dark vs. light/dark treatment



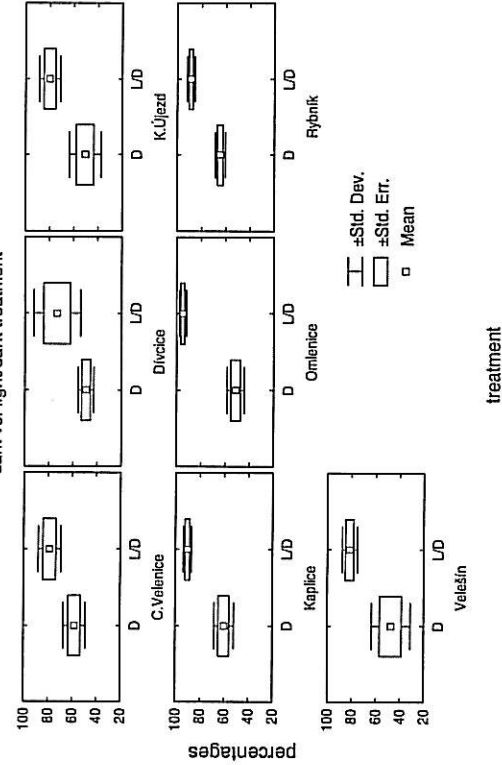
germination of *Poa compressa*
dark vs. light/dark treatment

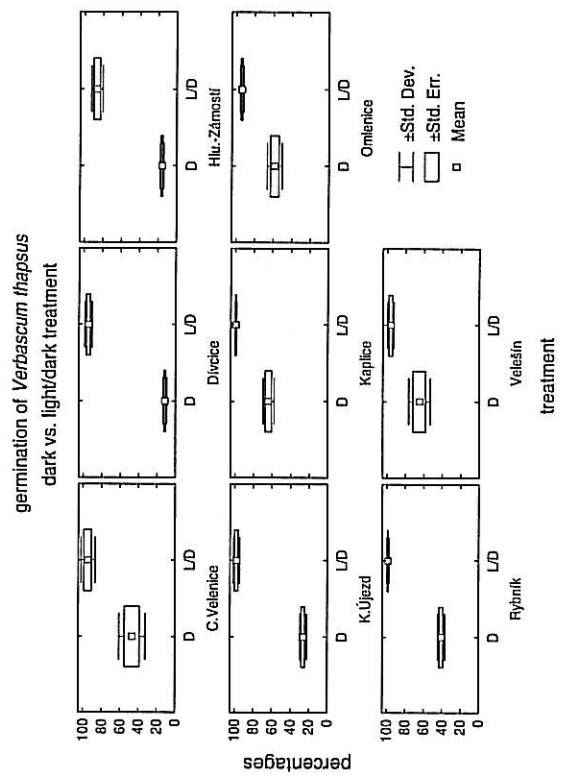
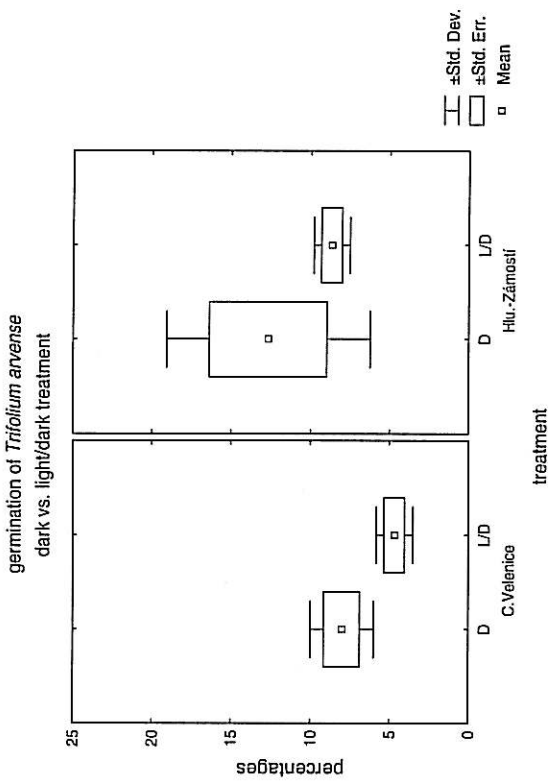
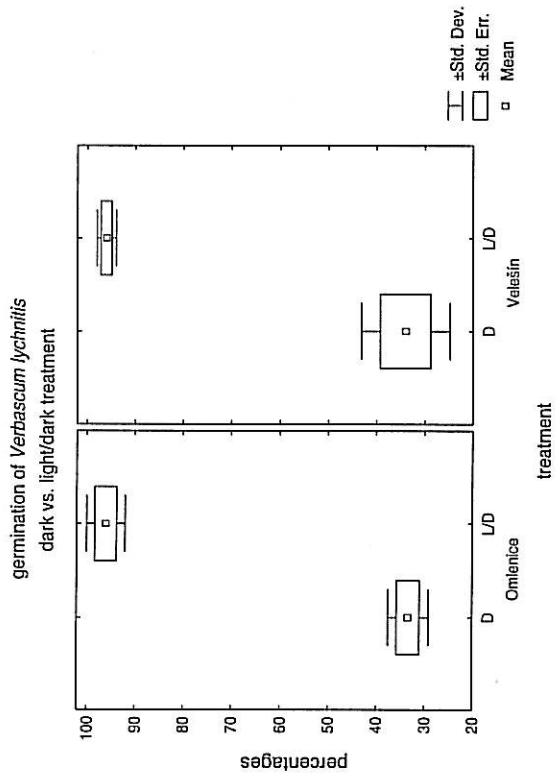


germination of *Solidago canadensis*
dark vs. light/dark treatment



germination of *Tanacetum vulgare*
dark vs. light/dark treatment





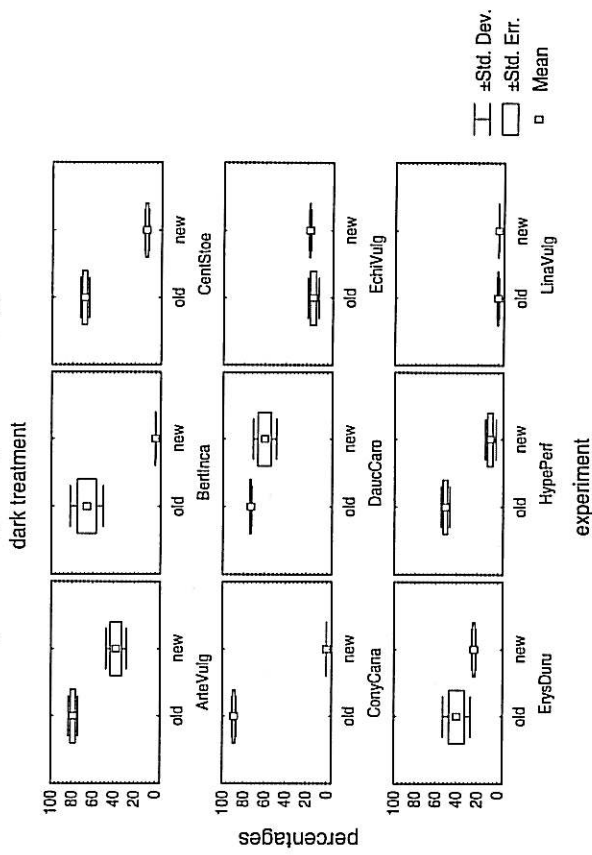
Graphical output of two - way ANOVA with fixed factors "treatment" and "habitat" shows the final germination percentages of each species and studied habitat. Achieved levels of significance of both factors summarises Table 11.

D - dark treatment (germination was monitored for 55 days)

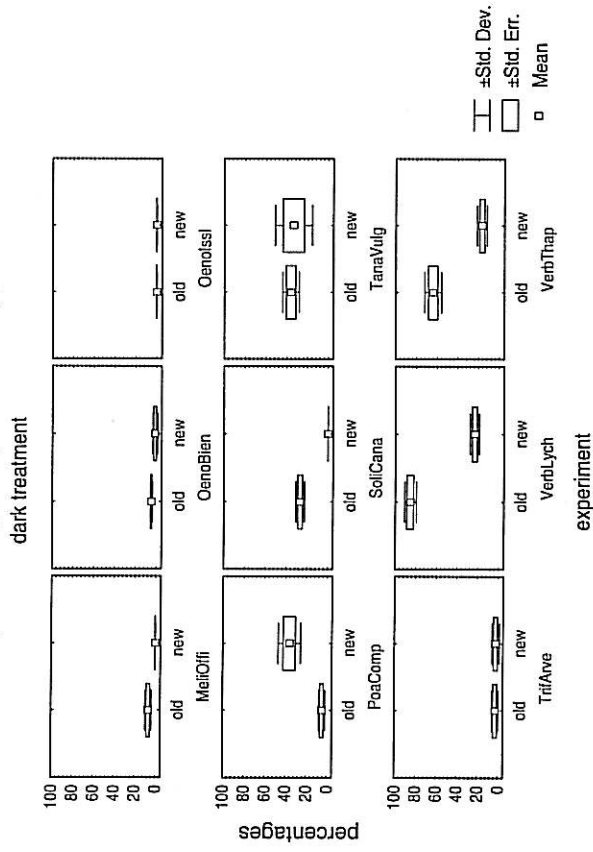
L/D - diurnal light and dark treatment (germination was monitored for 24 days)

Appendix 3

comparison of 2 germ. experiments - Zliv (1)



comparison of 2 germ. experiments - Zliv (2)



Graphical output of two - way ANOVA with fixed factors "species" and "experiment" shows the final germination percentages of all studied species from the reference habitat in Zliv.

old - germination experiment conducted 3 years ago (germination was monitored for 23 days).

new - germination experiment on the same seed set (5 - year old seeds), (germination was monitored for 24 days).

Both experiments ran in the dark.