

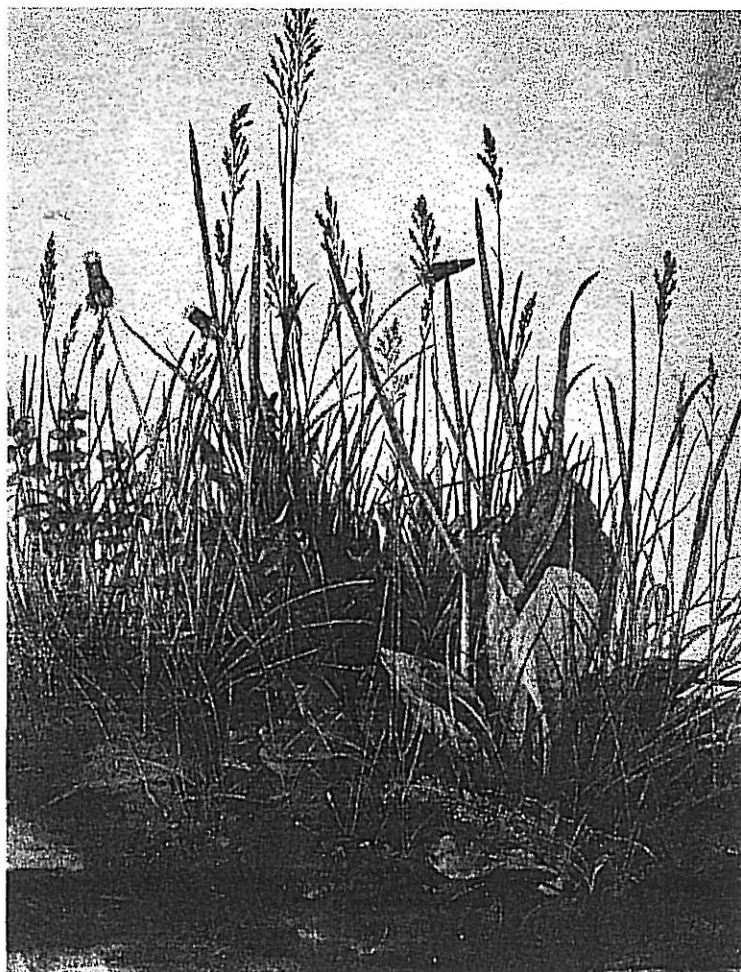
BIOLOGICKÁ FAKULTA JIHOČESKÉ UNIVERZITY V ČESKÝCH BUDĚJOVICÍCH

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Diferenciace nik koexistujících lučních druhů

*Mnohorozměrná analýza
ekologických a morfologických znaků*

JANA MARTÍNKOVÁ



Vedoucí práce: RNDr. PETR ŠMILAUER, Dr.

„ S květinami je to jako s lidmi. Některé potkáváme třeba každý den, a přesto o nich nevíme skoro nic. O jiných víme, jak se jmenují, a pak už třeba jen to, že bydlí v naší ulici. Není to mnoho, ale něco to přece jen je. A potom jsou lidé, které doopravdy známe. Jejich život, záliby a zvyky, jejich osudy a zvláštnosti. Čím je máme raději, tím víc toho chceme o nich vědět a čím víc o nich víme, tím jsou nám bližší. “

Otto Janka, z knihy Naše květiny
autorů Miloše Deyla a Květoslava Híška, vydané v Praze roku 1973



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Prohlašuji, že jsem uvedenou práci vypracovala samostatně, pouze s použitím uvedené literatury.

V Českých Budějovicích, 10. května 1999

Jana Martinková

DIFERENCIACE NIK KOEEXISTUJÍCÍCH LUČNÍCH DRUHŮ

Mnohorozměrná analýza ekologických a morfologických znaků

SHRNUTÍ

Jedním z centrálních problémů současné ekologie je identifikování a vysvětlení procesů, které umožňují existenci druhové diverzity ve společenstvech (Eriksson 1993). Během posledních let bylo vysloveno mnoho hypotéz týkajících se této problematiky (např. Slatkin 1974, Huston 1979, Mahdi et al. 1989, Tilman 1994, Tilman & Downing 1994, Gigon & Leutert 1996, Zobel 1997). Tyto hypotézy obvykle předpokládají, že druhy vyskytující se společně ve stejný okamžik na stejném místě, se musí vyhýbat negativním efektům mezidruhovému kompetice a tak obcházet proces kompetičního vyloučení (Grime 1979; Silvertown & Lovett Doust 1993). Obecně jsou jako možné příčiny umožňující koexistenci druhů uvažovány různé ekologické procesy, např. rozdělení zdrojů mezi potencionální kompetitory či jejich případná diferenciací nik. Frekvenční či hustotní závislost druhů, na hustotě nezávislá mortalita, popřípadě refugia druhů daná jejich agregací rovněž mohou snížit míru vymírání slabšího z uvažovaných kompetitorů (Silvertown & Lovett Doust 1993). Dalším mechanismem umožňujícím koexistenci druhů je pravděpodobně také prostá heterogenita či nestabilita prostředí (Begon 1996).

Mezi nejdůležitější charakteristiky jednotlivých druhů, které pravděpodobně přispívají k diferenciaci nik druhů náleží relativní růstová rychlost nadzemní biomasy (Saverimuttu & Westoby 1996, Grime 1973), charakteristiky týkající se kořenového růstu v čase i prostoru (Parrish & Bazzaz 1976), typy klonálního růstu, životní strategie (Grime 1979) a preference biotopů na různých gradientech prostředí (Ellenberg 1988).

Myšlenkou této práce bylo, že se diference nik lučních druhů odráží v jejich individuálních znacích. Prozkoumání korelačních vztahů mezi morfologickými a ekologickými znaky jednotlivých druhů a kategorizovanými ekologickými proměnnými (Ellenbergovy indikační hodnoty, Grimovy strategie, růstové charakteristiky, typy klonálního růstu) by tedy mohlo, alespoň částečně, objasnit mechanismy jejich koexistence. Cílem práce bylo nalézt nejvhodnější ekologické charakteristiky, které by byly aplikovatelné pro vysvětlení a posouzení míry diference nik lučních druhů.

Studie byla prováděna na 101 běžných lučních druzích nalézajících se na Zvíkovské louce či na Ohrazení. Celkem bylo zahrnuto 25 morfologických a ekologických znaků, jejichž hlavním zdrojem byla BIDS databáze (Peat & Fitter 1994). Jako vysvětlující proměnné tedy byly použity již výše zmíněné kategorizované ekologické charakteristiky: C-S-R strategie, Ellenbergovy hodnoty, klonální typy uvažovaných lučních rostlin (Klimeš et al. 1997) a růstové charakteristiky, získané z vlastního skleníkového experimentu. Výsledky těchto analýz založených převážně na publikovaných datech byly následně porovnány s výsledky analýz dat z reálného lučního společenstva, kde byla zjišťována skutečná koexistence druhů pomocí transektového přístupu.

Ke statistickému zpracování byly použity mnohorozměrné analýzy dat nabízené programem Canoco for Windows, a to jak metody nepřímé lineární analýzy (PCA, parciální PCA), přímé lineární (RDA, parciální RDA), tak nepřímé unimodální (parciální CCA) (ter Braak & Šmilauer 1998, Šmilauer 1992). K posouzení průkaznosti jednotlivých ordinací bylo použito Monte Carlo permutačního testu a k posouzení vlivu vysvětlujících proměnných postupu „forward selection“ s Monte Carlo permutačním testem. Vzhledem k atypickému charakteru dat bylo použito transponovaných primárních datových souborů v analýzách a tzv. „fuzzy coding“ při kódování stavů znaků i ekologických charakteristik.

Výsledky primárních analýz morfologických a ekologických vztahů ukázaly významnou diferenciaci druhů pouze ve znacích charakterizujících rozdíl mezi jednoděložnými a dvouděložnými rostlinami. Analýzy uvažovaných ekologických strategií (Grimovy strategie, Ellenbergovy indikační hodnoty) odhalily jen malou důležitost těchto strategií pro posouzení diference nik lučních druhů. Analýzy

zahrnující C-S-R strategie tedy ukázaly pouze obecné vztahy popsané vlastní definicí C-S-R strategií. Ze zkoumaných růstových charakteristik se ukázala být významnou relativní růstová rychlost nadzemní biomasy, opět pro diferenciaci druhů jen ve znacích odlišujících jednoděložné a dvouděložné rostliny. Naopak analýzy zahrnující klonální typy lučních rostlin diferencují sledované luční druhy daleko více. Klonalita a související znaky kořenového systému se tedy zdají být jedněmi z charakteristik, které pravděpodobně umožňují koexistenci druhů v lučním společenstvu. Výsledky analýz založených na datech z reálného lučního společenstva se shodují s výsledky převážně teoretických analýz, tedy rovněž nenalezly významné rozdíly ve ekologických a morfologických znacích uvažovaných lučních druhů.

Hledání separace nik lučních druhů vzhledem k jejich znakům i ke gradientu fosforu a dusíku ve studii Mahdiho et al. (1989) bylo neúspěšné a autor konstatuje, že separace nik pravděpodobně není hlavním příspěvkem k možné koexistenci druhů, výzkum nezahrnující představu diferenciaci nik k posouzení koexistence druhů by byl pravděpodobně úspěšnější. Jak ukazuje práce Herbena et al. (1995), je perzistence druhů klonálních společenstev jakými louky jsou, založena na struktuře časoprostorové mozaiky, která je dána právě převažující klonální strategií. Dále navrhuje, že koexistence druhů může být umožněna intenzivní dynamikou společenstva na velmi jemném měřítku, která je pravděpodobně spojena s klonální povahou společenstva. Je však otázkou, zda i tato časoprostorová mozaika rovněž, z jiného úhlu pohledu, nepředstavuje určitý způsob diferenciaci nik druhů.

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**Niche differentiation
of coexisting grassland species**
*A multivariate analysis
of ecological and morphological traits*

JANA MARTÍNKOVÁ

supervisor: RNDr. *PETR ŠMILAUER*, Dr.

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NICHE DIFFERENTIATION OF COEXISTING GRASSLAND SPECIES

*A multivariate analysis
of morphological and ecological traits*

ABSTRACT

Differentiation of species niches is one of the possible mechanisms enabling species coexistence. We explored this differentiation for 101 grassland species. The compiled information on 96 ecological traits represented differences in ecological characteristics and we contrasted them with higher level classification of species into ecological groups or gradients, namely Grime's C-S-R classification, Ellenberg's indicator values and types of clonal architecture. Additionally, the growth characteristics of a subset of studied species were determined experimentally.

The usability of ecological traits for explaining real community patterns was tested using fine-scale transect dataset.

Multivariate statistical methods were used both for exploratory and confirmatory analyses of our datasets. We used PCA to identify interesting patterns in the datasets and several constrained ordinations were done using RDA.

The explanatory power of C-S-R strategies, Ellenberg's indicator values, or experimental growth characteristics was negligible, so these gross-scale classifications seem to have a little applicability for the explanation of niche differentiation on the scale of grassland community, except to distinguish between the graminoids and forbs. Clonal architecture exhibits much larger variability among grassland species and shows some interesting patterns in its relation to grassland species' ecological traits.

INTRODUCTION

One of the central problems in ecology is to explain species diversity in communities (Eriksson 1993). Many hypotheses have been formulated with this aim during the last decades (e.g. Slatkin 1974, Huston 1979, Mahdi et al. 1989, Tilman 1994, Tilman & Downing 1994, Gigon & Leutert 1996, Zobel 1997).

Mainstream theory considers role of elementary coexistence or competitive exclusion of species, an ecological phenomenon attracting a broad interest (Hastings 1980, Zobel 1992, Herben et al. 1994, Palmer 1994, Krahulec 1995, Grace 1995, Weiher et al. 1998).

The concept of coexistence is consistent with competition if the competitors partition resources between them and/or occupy different niches. Alternatively, density- or frequency-dependence can prevent competitive exclusion, density-independent mortality affecting a whole community can delay the extinction of inferior competitors, and spatial refuges provided by aggregation can reduce the rate of encounter between competitors. Temporal refuges from competition may be provided by differences in regeneration niche and by storage effect (Silvertown & Lovett Doust 1993).

Factors, which are not included in most standard competition models, allow stable coexistence of trophically equivalent species due to either difference in life-history 'strategy', input of seeds from nearby habitats (spatial mass effect), differences in demographic response to environmental fluctuations (temporal mass effect) and turnover in species composition between different habitat patches (Shmida & Ellner 1984).

Another concept considers equilibrium/nonequilibrium relationship to species coexistence. Conditions allowing coexistence of plant populations fall into two contrasting categories. 1. In constant, uniform environment species can coexist in competitive equilibrium if they differ in niches. A community in competitive equilibrium is one not undergoing compositional or structural change due to competition. If species do not possess some minimum degree of niche divergence then inferior competitors will be excluded from equilibrium community. 2. Biotic events, such as predation, herbivory and diseases, as well as abiotic events, such as fire or windstorm, may stop the process of

exclusion by competition. Coexistence under the influence of such events occurs outside of local competitive equilibrium (Pickett 1980).

Coexistence of competitors is apparently associated with some degree of niche differentiation, but it seems that if we look closely enough, all coexisting species will be found to be different (Begon et al. 1996). How large the niche difference must be to permit species coexistence and what rate of competition permits species coexistence? There are many theoretical studies considering niches overlap (Abrams 1976, Abrams 1980, Parrish & Bazzas 1976, Slobodchikoff & Schulz 1980, Mahdi et al. 1989).

One of the important species traits contributing to differentiation of their niches is relative growth rate. Relative growth rate (RGR) is an influential parameter of ecological performance (Saverimuttu & Westoby 1996, Grime 1973). The rate of dry matter production per unit of dry matter is the most useful comparator of innate growth because it is independent of the scale of organisms (Hunt 1982). Important attributes of plant species in varied environment are differences in maximal RGR (Grime and Hunt 1975). Maximal relative growth rate is one of fundamental axes of the C-S-R scheme of plant strategies or functional types (Grime 1979).

Differential patterns of root growth and clonality of species in time and space can be considered an important means of partitioning soil resources (Parrish & Bazzaz 1976). Thus, differences in rooting habitats and the depth of root penetration of species occurring together can enable coexistence in plant communities. The mode of clonal growth has profound effect on distribution of above-ground parts, as well.

There are many studies that looked at datasets of various autecological and morphological traits in various context (Goldberg & Landa 1991, Leishman & Westoby 1992, Peat & Fitter 1994a, Wardle et al. 1998, Eriksson & Jakobsson 1998). Relations between plant traits and competitive ability as considered e.g. by Gaudet & Keddy 1988, Grace 1990, Rösch et al. 1997.

Recent papers often discuss concept of plant functional types, i.e. generalized groups of plants based on set of various traits with ecological background (Noble 1989, Smith et al. 1997, Diaz et al. 1998).

Nevertheless, concept of species niches differentiation based on relationship between considered species traits and species ecological strategies remains overlooked.

The underlying idea of our analyses was that the niche differentiation in grassland plants is echoed in their various individual traits and exploring of correlative patterns between such traits and categorized ecological strategies (represented by C-S-R, indicator values, RGR and clonality types) can help to reveal mechanisms of their coexistence.

The objective of this study was to find appropriate ecological characteristics which have an applicability for explanation of differentiation of grassland species niches.

METHODS

Primary data set

The main source of primary data for all analyses was the BIDS EcoFlora database (Peat & Fitter, 1994b). The database contains data on 131 ecological characteristics, distributions, mycorrhizal interactions and fungal diseases for 1777 higher plants of the flora of British Isles, together with the bibliography of sources.

Some of the missing values or morphological traits and ecological characteristics, which were not available in the EcoFlora database were supplemented from various floras and other publications (Slavík 1988, Slavík 1990-1997, Dostál 1989, Rothmaler 1994)

For this study, we selected approximately 200 common species occurring at the grasslands at Ohrazení and Zvíkov research sites (both near České Budějovice, Czech Republic). This study is related to other studies done at the Ohrazení and Zvíkov localities concerning the autecology of selected model species, mechanisms of species coexistence in oligotrophic wet meadow community, and mechanisms of species coexistence, related to endomycorrhizal symbiosis and root architecture. Based on species availability in the EcoFlora database and percentage of missing values 101 species were finally selected (see Tab.1, nomenclature according Rothmaler 1994).

96 traits in 25 categories were selected from the approximately 100 of available categories (see Tab.2). We tried to replace missing values of species traits by information from other sources (see above).

Next we excluded traits with a substantial percentage of missing values (more than 3% of species). Remaining missing values (thus no more than 3) were replaced by the average of available values or the most frequent state of species traits. The analyzed traits include leaf area and shape, defence mechanisms on the stems and on the leaves, dispersal agents, ratio of height and width of the plants, presence of heterophyly, presence of polyploidy, data on flowering season, and also more synthetic traits such as life forms or nutrient availability at the places of their occurrence. Next we excluded species with more than 7 missing values (thus more than 10%).

Many of the species traits are polymorphic, i.e. one trait has several states. In some cases we must use fuzzy coding (see, e.g. ter Braak & Šmilauer 1998) for combination of trait' states.

Explanatory data set

Grime's C-S-R classification system was used for the studied species (Grime 1977). Data on C-S-R classification were obtained for 56 species (Grime et al. 1988). But most of the studied species are characterised by a combination of the strategies such as the C-S-R, C-S or S-R strategists. Therefore we used the fuzzy coding for this classification.

Ellenberg' indicator values were used to characterise the position of grassland species on specific environmental gradients (Ellenberg, 1988). From the six Ellenberg's indicator value types, we selected three: position on the gradient of moisture availability, on the gradient of soil acidity and lime content, and on the gradient of availability of nitrogen during the growing season. These Ellenberg' values are on an ordinal scale and full information was obtained for 32 species.

The database of clonal architecture' types of Central European species, as described by Klimeš et al. 1997, contains 2760 species. The data on clonal growth are

based on own experience of the authors and they classify the species into 21 types of clonal growth. Among the 101 species for which the information on the clonal architecture was available, 13 defined types of clonal growth were found. These twelve types were further clumped into 9 clonal type categories (based on Klimeš et al. 1997), see Tab.3 .

To get comparable data on seedling growth characteristics, we have performed an experiment during the spring of 1998. The experiment resulted in data for 27 species, with 8 growth characteristics (see below). We used experimental plan similar to Hunt et al. 1993 with Rorison nutritive solution without variations, sand was used as the germination and growth medium. Standard conditions were modified and adapted to outdoors experimental conditions. The experiment resulted in data for 27 species. From the raw data, the relative growth rates (RGR) (Hunt et al. 1993) of shoot biomass (RGRS) and root biomass (RGRR), of the leaf area (RGRLA) and root length (RGRRL) and ratios of relative growth rate of shoot and root biomass (RGRS/RGRR), of leaf area and root length (RGRLA/RGRRL), and ratio of shoot biomass and leaf area (SBII/LAII*), ratio of root biomass and root length (RBII/RLII*) were calculated (see Tab. 5). Evaluation of root length was made by computer program ROOTARCH (Šmilauer, unpublished,). Evaluation of leaf area was done with the ADOBE PHOTOSHOPTM 4.0 software based on scanned images of seedlings.

* in acronyms means after 3 weeks i.e. second sampling (first sampling was 7 days after germination)

Fine-scale community pattern

Additionally, we have been recording fine-scale species pattern, during the first half of June 1998 at the grassland (dry oligotrophic meadow) at Zvíkov research site nearby České Budějovice, South Bohemia. Three parallel 10 meters long transects were placed 1 meter apart at the grassland. On each 2 centimeters we recorded the plant species, which was the topmost (1500 observations). Totally 40 species were found on the

transects (see Tab.4) but 26 species acted in multivariate analyses because we excluded species which occurred on transect only in one or two samples or species without full information on traits.

STATISTICAL ANALYSIS

Multivariate statistical methods were used both for exploratory and confirmatory analyses of our datasets (ter Braak & Smilauer 1998, Smilauer 1992).

We used PCA - principal components analysis and pPCA – partial PCA, performed on the correlation matrix with transposed data matrix, to identify potential patterns in the primary dataset.

Several constrained ordinations were done using redundancy analysis (RDA) method. The species traits from the EcoFlora database and data collected from various floras acted as primary data (response variables) in all these analyses. In individual analyses, the C-S-R strategy, Ellenberg's indicator values, data from the experiment or the types of clonality were used as the explanatory variables. In direct gradient analyses with C-S-R and clonality types we excluded life forms from the traits data because the parallel part of these classifications similar traits describing preferences for nutrient rich/poor sites were excluded from constrained analysis using Ellenberg' values as explanatory variable.

PCA results revealed mainly the difference in traits between graminoids and forbs. Consequently, the RDA was then run with „graminoid status“ as a covariable, to look for patterns beyond this obvious one.

We used the forward selections with Monte Carlo permutation tests (ter Braak & Šmilauer 1998) to assess the individual hypothesized relations between the ecological traits and the particular set of explanatory variables and also between the ecological traits and specific strategy (explanatory variable) within each ecological characteristic.

To evaluate fine-scale pattern we used partial PCA of primary data (species traits) of selected species (see above) with graminoid status as a covariable. Partial CCA with graminoid status as covariable and species scores on ordination axes from partial PCA as explanatory variables were applied to transposed data matrix of species observations on transects. We use forward selection with Monte Carlo permutation tests to assess significance of the effect of explanatory variables.

RESULTS

Species and traits

In first analysis we used data from BIDS EcoFlora and supplemented data as primary dataset to found basic pattern in species traits. As Fig.1a and 1b show, this PCA found differentiation between graminoid and forb species in their ecological and morphological traits. First two ordination axes explain 17.5% variability in the dataset. The first ordination axis separates species with graminoid and forb traits. The second ordination axis corresponds to gradient of height of plant and of fertility of habitat, which may be related to competitive ability. Primary differentiation of species on the base of their traits in grassland community is probably into group of graminoids and forbs. Next important differentiations seem to be in their competitive ability. Obviously such conclusion depends heavily on the choice of the traits used to characterize individual species.

In partial PCA we used graminoid status as a covariable to find patterns beyond this apparent one. As Fig.2a and Fig.2b show, there is apparent separation of species into two groups. Some interesting patterns are shown. First ordination axis corresponds to competitive ability of species and parallels the second axis of the previous analysis. First ordination axis explains 7.5% of the variability in the primary dataset. Two groups of species (Fig.2a) can be identified by traits (Fig.2b) such as leaf area, ratio of width and

height of plant and ratio of width and height of leaf. The second axis explains 6% of the variability and separates mostly species with small narrow leaves.

Species traits and C-S-R system

In this RDA we used species traits from the EcoFlora database and data collected from various floras as primary data, and the C-S-R strategy system as explanatory variables. The graminoid status was used as a covariable. First two ordination axes explain 13.6 % of variability in primary dataset. The ordination diagram (Fig.3) shows correlation patterns between ecological traits and life strategies. This analysis found patterns corresponding to the common views, with C and R strategists preferring the fertile sites, R strategists are plants with height smaller than width, S strategists „prefer“ infertile stands and the C strategists are tall plants, with large leaves. Nevertheless, the Monte Carlo tests on relation of individual C-S-R components and species traits were all non-significant. This indicates the joint effect of C-S-R space, because test on shared explanatory effect was significant ($\alpha=0.05$).

Ellenberg's indicator values

In RDA with all considered Ellenberg's indicator values, relation was found significant, but the Monte Carlo tests on individual indicator values (N, W and R) were not significant. First two ordination axes explain 7.4 % of variability in primary dataset.

Species traits and growth parameters

In this RDA (Fig.4) the EcoFlora dataset and data collected from various floras were again used as the primary data and the data from the experiment acted as explanatory variables. First two ordination axes explain 22.3 % of variability in primary dataset. On the base of the forward selection of explanatory variables (with Monte Carlo permutation tests, $\alpha=0.05$) we used only the relative growth rate of the above-ground

biomass as the explanatory variable. This analysis found difference between traits of graminoids and forbs, which can be explained on the base of relative growth rate. Increasing RGR is positively correlated with the occurrence of graminoid traits (see Fig.4). Parallel leaf base, wind as a pollen vector and sheathing leaf basis are example characteristics of that pattern. Analysis with graminoid status as a covariable found no significant relation.

Species traits and clonal architecture type

In this RDA (Fig.5), the primary data are the species traits from the EcoFlora database and data collected from various floras again. As explanatory variables, we used four clonal architecture types („*Lycopodium annotinum*“ type, „*Fragaria vesca*“ type, „*Caltha palustris*“ type and „*Rumex obtusifolius*“ type) and non-clonal type, which turned out to be significant in forward selection with partial Monte Carlo permutation tests ($\alpha=0.05$). First two ordination axes explain 38.4 % of variability in primary dataset. The graminoid status was used as a covariable. The ordination diagram shows correlations between species traits and the clonality types. Both „*Caltha palustris*“ and „*Lycopodium annotinum*“ types are positively correlated with occurrence of wind as a pollen vector and early flowering. „*Fragaria vesca*“ type represents plants with decumbent stems, very small leaves (and hence, their height is smaller than width). Self-supporting stems and height of plant bigger than width are positively correlated with occurrence of „*Rumex obtusifolius*“ type. Non-clonal species have their occurrence positively correlated with very fertile sites.

Species traits and fine-scale grassland community pattern

For this problem, we first summarized traits of species occurring on transect using indirect gradient analysis. In partial PCA the EcoFlora dataset and data collected from various floras for transect species were used as the primary data and graminoid status as a covariable. First three ordination axes explain 29.3 % (we refer to three ordination axes,

because the third axis turned out to be significant in next analysis) of variability in primary dataset. Fig.6a,b show the correlation pattern of traits and pattern of co-occurring species. The first ordination axis separates species mostly on the base of morphology of leaves and of plant height.

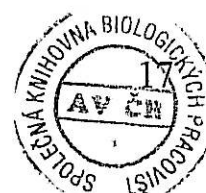
Scores of the species on pPCA ordination axes were used as explanatory variables in partial CCA analysis (Fig.7). The observation from transects was used as primary data. The first and third ordination axes turned out to be significant after forward selection with Monte Carlo permutation test ($\alpha=0.05$). Centroids of species characterize groups of co-occurring species on gradients represented by first and third ordination axes from partial PCA, thus on the „gradient“ of variability of species traits. Differentiation of co-occurring species relating to considered species traits seems to be of very low importance for explanation of species niches differentiation except distinguishing graminoid and forb. This result on real grassland community data is consistent with above-described results

DISCUSSION

The comparative approach is one of the basic tools that provide the empirical basis for scientific discipline, where observed patterns can be matched against theoretical expectations and used to generate hypotheses (Groenendael et al. 1996). We tried to compare common ecological strategies (Grimes', Ellenberg's, RGR pattern, and clonality types) with set of ecological and morphological species traits. This approach can reveal ecomorphological background of mentioned strategies.

Wardle et al. 1998 emphasizes the importance of plant traits in understanding (and predicting) species interactions and effects in communities and ecosystems, and shows that properties considered at whole plant level have the potential to manifest themselves at much larger scales, both spatially and temporally.

Actual species pattern of real grassland is certainly influenced by patch dynamics (temporal and spatial pattern of disturbance and succession at microsites, e.g. Thompson



1978). At present, non-equilibrium coexistence through patch dynamics appears to be a better explanation of plant community organization than does equilibrium niche theory (Pickett 1980). Recent studies suggest that dynamics of specific grassland patch is result of complicated pattern of small and large scale dynamics which are not directly connected (Herben et al. 1993).

Specific structure of grasslands with dominant graminoid species can influence the grassland dynamics. We can consider many of the graminoid grassland species as the “matrix” species. Their ramets forage in the environment for favourable habitats and they are, together with the habitat heterogeneity, the agents of grassland spatial variability. Other species thus might just follow the changes in grassland structure.

In this context the keyhole–key model of coexistence might play an important role, considering observations that, within the same ecosystem, some plant species occupy different microsites. Coexistence of different plant species can thus occur if the diversity of microsites matches the α -diversity of plant species (Gigon & Leutert 1996).

The triangular model proposes that the vegetation that develops in a particular place and at one point of time is the result of an equilibrium established between the intensities of stress, disturbance and competition (Grime 1988). In fact, with respect to these characteristics is the grassland community homogenous. Characteristics of coexisting grassland species are intermediate - most species are characterized by combination of Grime’s strategies as C-S-R/C-R/C-S strategists. Unlike the grassland-like communities, ecological strategies are well-differentiated in plant communities occurring under severe (e.g. high-mountain) conditions (Onipchenko et al. 1998). As Grime 1988 proposed, individual species C-S-R status results in predictable, functionally integrated sets of traits. There are sets of specific traits connected with individual strategies corresponding with common view such as habitat preference of habitats, life forms, ratio of height and width of plants (Fig.1). Grime 1988 figured out evidence that within data sets of restricted geographical and taxonomical scope, some individual traits (e.g. RGR, life span, shoot morphology) may exhibit trends that are sufficiently consistent to allow them to be use as provisional indicators of the primary strategy in established phase. Nevertheless, the Monte Carlo significance tests on individual relations of ecological strategy and species traits were all non-significant. This result is

not surprising, because C-S-R classification is contrasting preferences of habitats of various types (varying in availability of resources, in rate of disturbance and in stress level) and the grassland is relatively homogenous. Nevertheless, range of analysed species represented relatively large variability on gradient of moisture and nutrient availability. This is the reason we considered using this classification in explanation of niche differentiation of grassland species. We agree with Grime 1988 that the triangular model does not challenge the existence of great variability in the characteristics of species and populations, nor does it question the need for studies at these more detailed levels of organizations.

Ellenberg's indicator values represent raw description of species position on environmental gradients. Individual species difference within selected Ellenberg's values is relatively satisfactory (information on grassland species was observed across whole scale), but our results suggest their inability to describe differentiation of species niches on grassland community scale.

It is suggested that the maximum potential relative growth rates of constituent perennial species may be used to provide an index of stability of vegetation with high species density (Grime 1973). Shipley & Peters 1990 proposed that species which allocated part of their biomass to stem tissues had higher relative growth rates than did species without stems. Despite of their results we are consistent with Tilman's model (Tilman 1988) which hypothesized that the maximum RGR of plant is negatively correlated with the ratio of the mass of its non-photosynthetic tissues to that of its photosynthetic tissues. The occurrence of graminoid traits, such as parallel leave base, sheathing leave petiole, wind as a pollen vector, high length of leave and so on are positively correlated with increasing RGR of shoot biomass (Fig.2).

In communities with prevailing non-clonal plants (most forests, for example) the species persistence depends on successful seedling establishment which may be different of spatiotemporal pattern of community. In contrast, in communities of clonal plants (such as grassland), the structure of spatiotemporal mosaic may be critical for species with given growth form and type of clonal growth to persists (Herben et al. 1995). The clonality types show large variability among grassland plants. Clonal growth is observed to originate from either the shoot or the root part of the plant body and it has been

assigned various ecological functions such as reproduction, exploitation and persistence. These functions are rooted in two basic morphological characteristics of clonal growth: the longevity and the length of connection between clonal parts (Groenendael et al. 1996). Clonal plants can display division of labour in resource-acquisition duties, manifested as a local specialization by ramets, which enhances acquisition of each resource from sites of greatest abundance. Recent research is showing that such specialization and resource sharing is a highly efficient strategy for acquiring resources and that it can result in considerably greater growth when resources are heterogeneously distributed than when the same quantity of resources is distributed homogeneously (Hutchings & Wijesinghe 1997). Wardle et al. 1998 shows that different plant species apparently adapted to similar habitats can have vastly differing effects on soil biological properties, presumably because plant species differ considerably in terms of release of rhizosphere compounds, efficiency of nutrient acquisition and root litter quality. As our results show (Fig.5), variability of ecomorphological traits of grassland species can be explained on the base of their clonal architecture type. Most of them (5 of 6) are significantly correlated with considered species traits. Based on our results and proposed role of clonality in patch dynamics, the clonality types (and set of clonality-related traits) can be crucial for species coexistence. When investigating processes enabling species coexistence (not only in "differentiation of niches" point of view), we must focus on the traits with resolution similar to that used for defining this system of clonality types and start looking on the survival of individual ramets, lifetime of rhizomes and roots, branching patterns of clonal units and so on.

In a limestone grassland community study of Mahdi et al. 1989, the separation of species in niche space and on a resource-ratio gradient of nitrogen and phosphorus was unsuccessful. However, it is argued that separation in niche space is unlikely to make major contribution to coexistence in community, and that investigation of models which permit coexistence in the absence of niche differentiation could be more fruitful.

As Herben et al. 1995 show, attempts to explain the mechanism of species coexistence in the grassland should take into account high dynamics on the fine scale. Our results with assumption that niche differentiation is echoed in various individual species traits show essential differences in traits which can be explained by ecological

strategies, especially between graminoids and forbs. Differences which were found between species are probably insufficient to explain differentiation of species niches on the grassland community scale except characteristics relating to clonal architecture types. These results of our exploratory study of niche differentiation in grassland community should be followed by some manipulative and removal experiments on specific groups co-occurring species to test them. Next, this study shows some interesting patterns of species traits and characteristics and results can be inspiring for above-mentioned experiments or for other exploratory analyses on gross or fine scale.

The testing on constrained analyses did not take phylogenetic relatedness into account, except at the high level (grasses vs. dicotyledoneous forbs). This might potentially influence our conclusions, because two or more species might share a particular trait value only because their common ancestor possessed it and it was not modified by evolution since their divergence. This implies that there might be a „nuissance cross-correlation“ between our sampling units, i.e. individual grassland plant species. There are several approaches attempting to deal with that issue (see e.g. Pagel 1992, Harvey & Pagel 1995), but other authors (see Westoby et al. 1996, for example) suggested that these methods might over-estimate correlation between traits that is related to phylogeny and, therefore, underestimate correlations associated with ecological factors. In our dataset, the practical problem of non-balance in frequency of species from higher taxonomical units (like families or genera) prevented us from attempting to correct for phylogenetic relatedness.

CONCLUSIONS

- Considered ecological strategies (Grime's strategies, Ellenberg' indicator values and growth characteristics) seem to have little importance for explaining differentiation of grassland species niches.
- Analysis of C-S-R classification system shows pattern corresponding to common view only and growth parameter analysis shows differences between traits of graminoid and forbs.
- Clonality types exhibits much larger variability among grassland species than other considered ecological strategies. Clonality and relating characteristics seem to be one of the ecological strategies which probably contribute to enabling species coexistence in plant community.

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Last but not least I thank my parents for patience and support.

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TABLES AND FIGURES

Fig. 2a

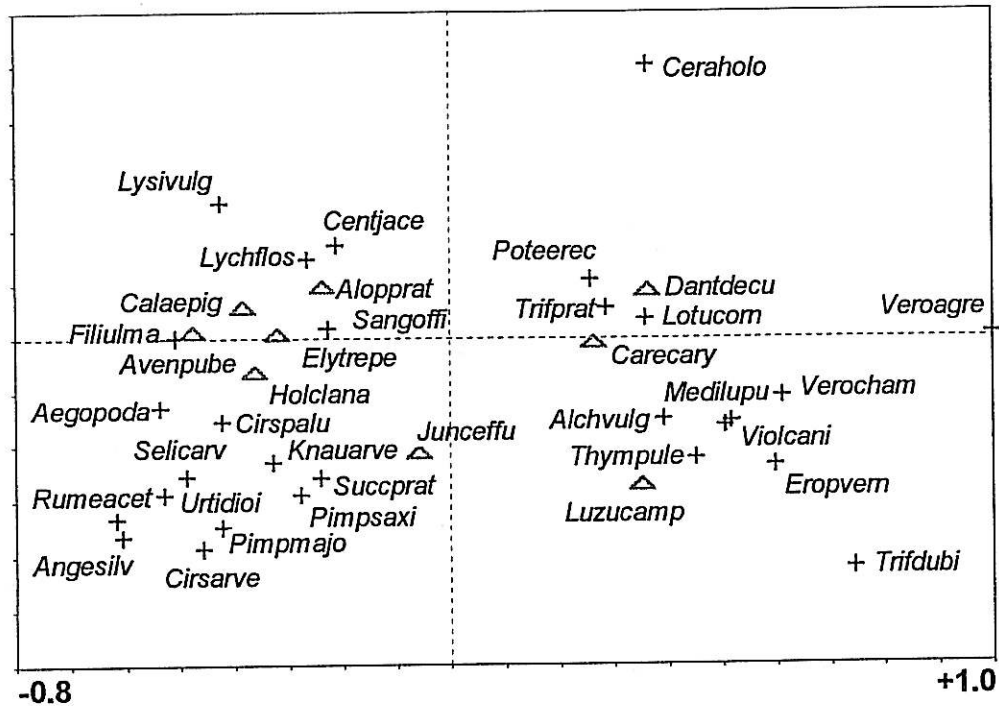


Fig. 2b

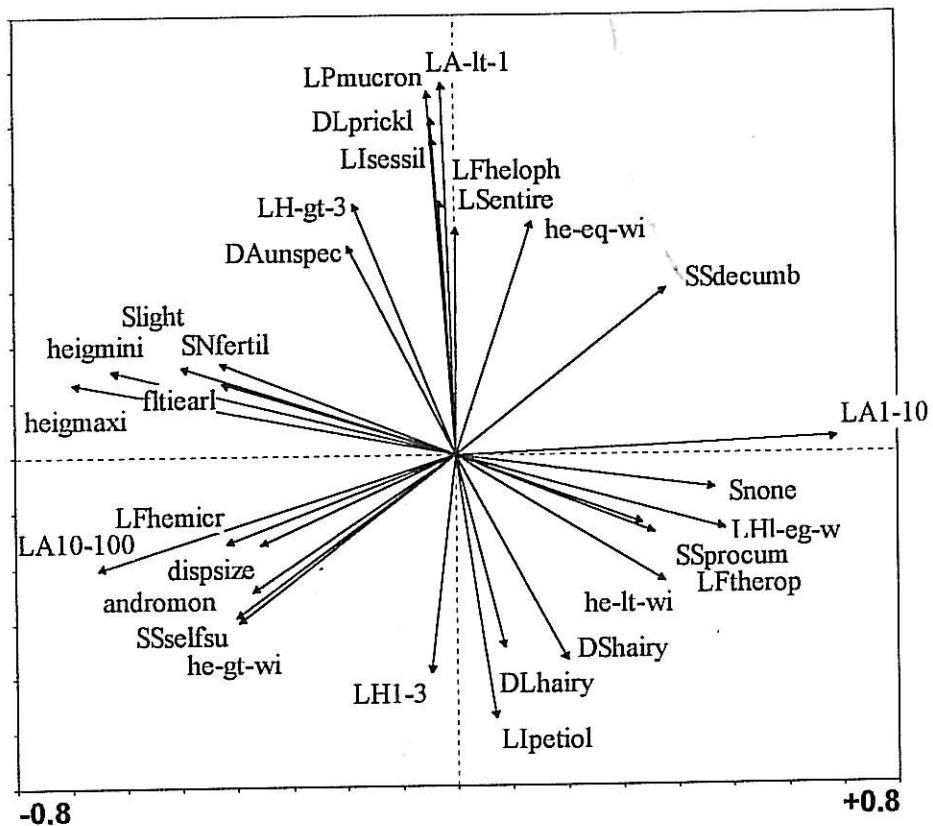


Fig.2a,b. Partial PCA ordination diagrams (first and second ordination axes are shown) displaying relation of species (graminoids are displayed as triangles, forbs as crosses) (Fig.2a) in primary data set and correlation pattern of their ecological and morphological traits (Fig.2b) with graminoid status as a covariable. Abbreviations of species names represent first four letters from either names of species (see species list Tab.1), for abbreviation of species traits see Tab.2.

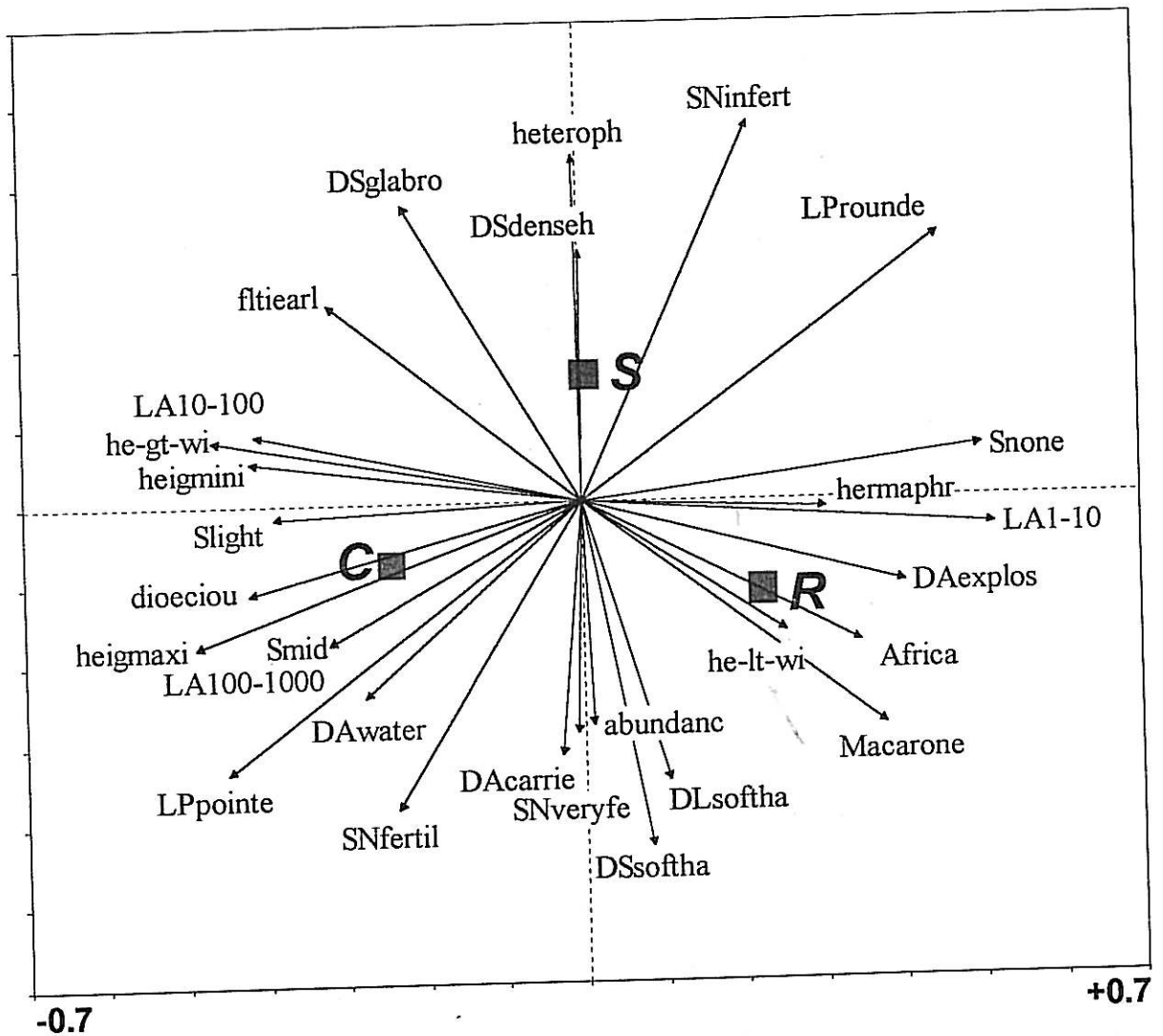


Fig.3. RDA ordination diagram (first and second ordination axes are shown) displaying relation of patterns of species traits (arrows) and components of Grime's CSR system (squares). Species traits fitted well by first two ordination axes are shown, for abbreviation of species traits see Tab.2.

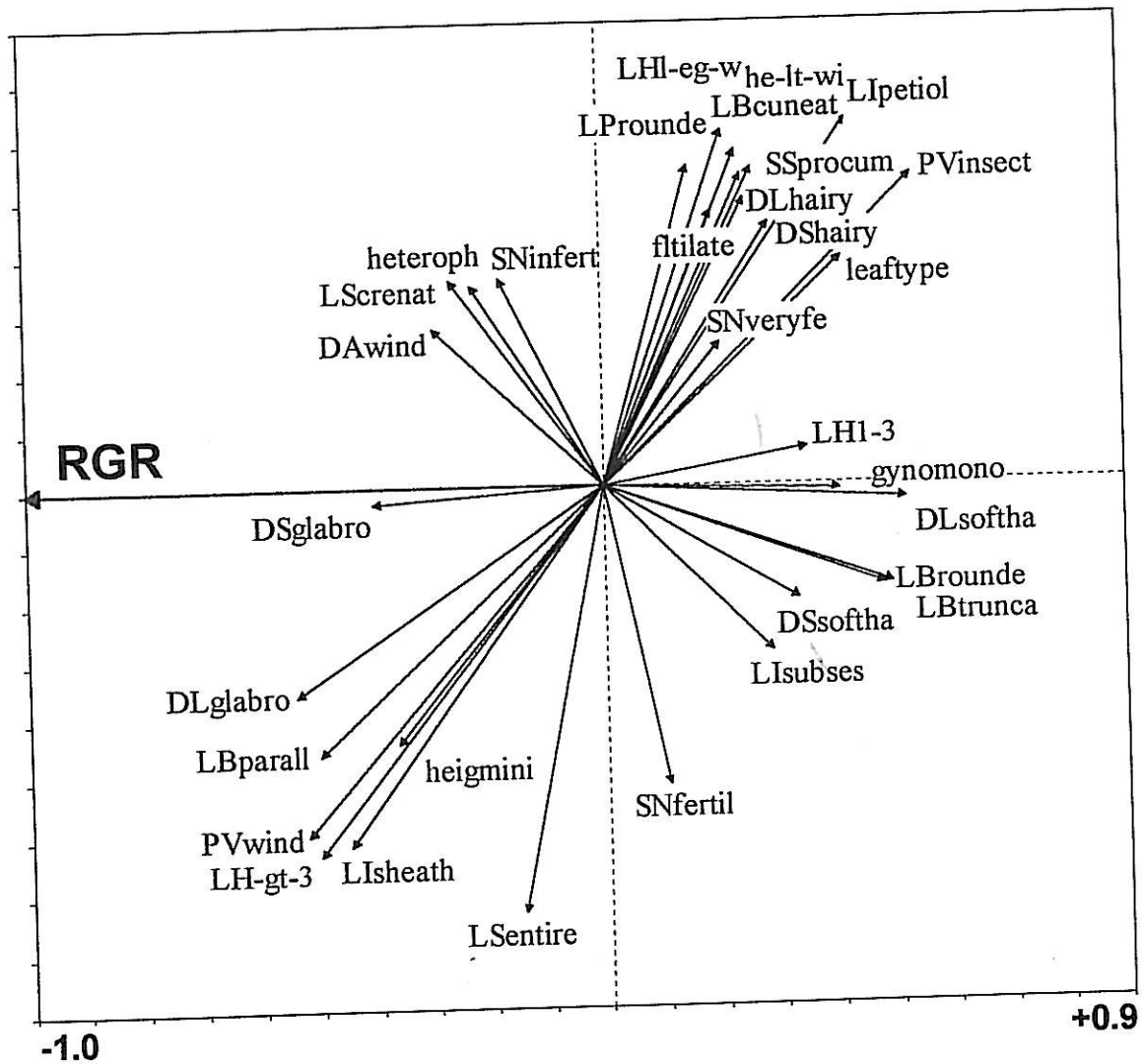


Fig.4. RDA ordination diagram (first and second ordination axes are shown) displaying relation of species traits (arrows) to relative growth rate of shoot biomass (RGR). Species traits fitted well by first two ordination axes are shown, for abbreviation of species traits see Tab.2.

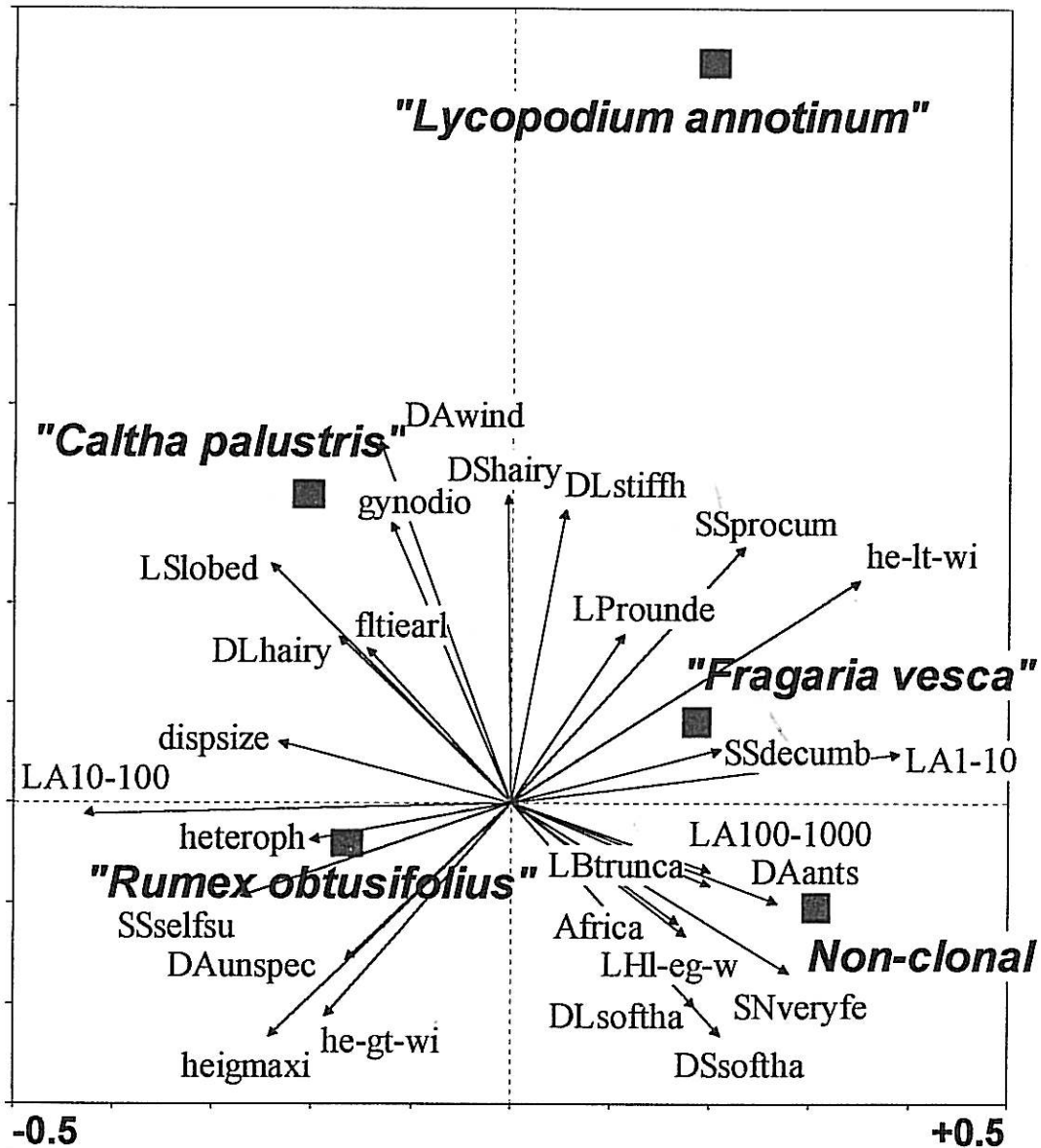


Fig.5. RDA ordination diagram displaying relation of species traits (arrows) and clonal architecture types (squares). Species traits fitted well by first two ordination axes are shown, for abbreviation of species traits see Tab.2.

Fig. 6a

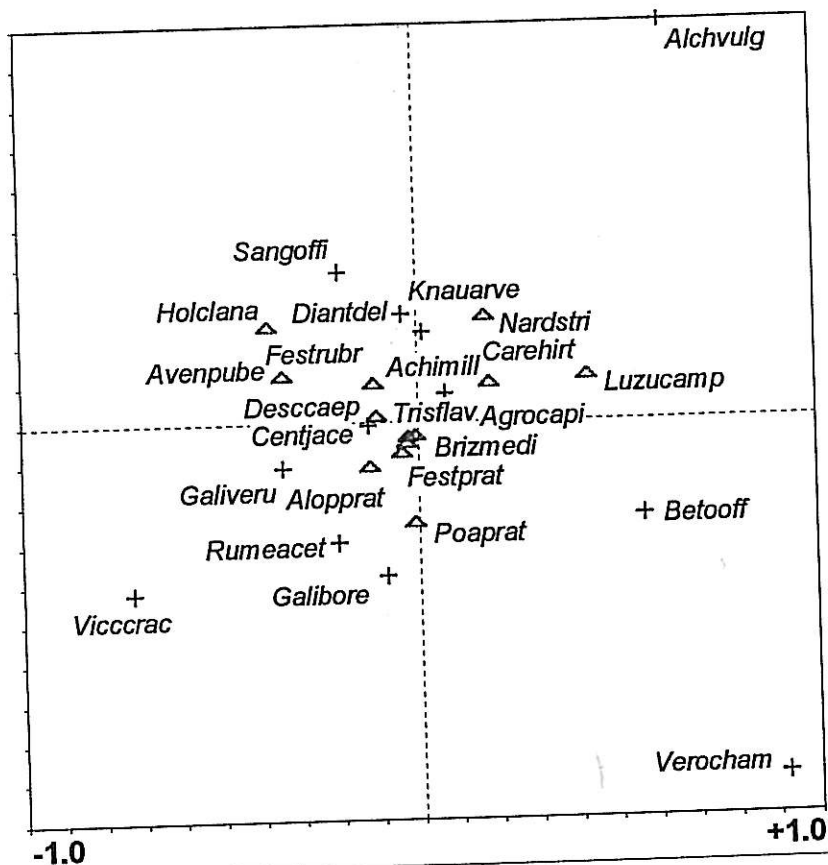


Fig. 6b

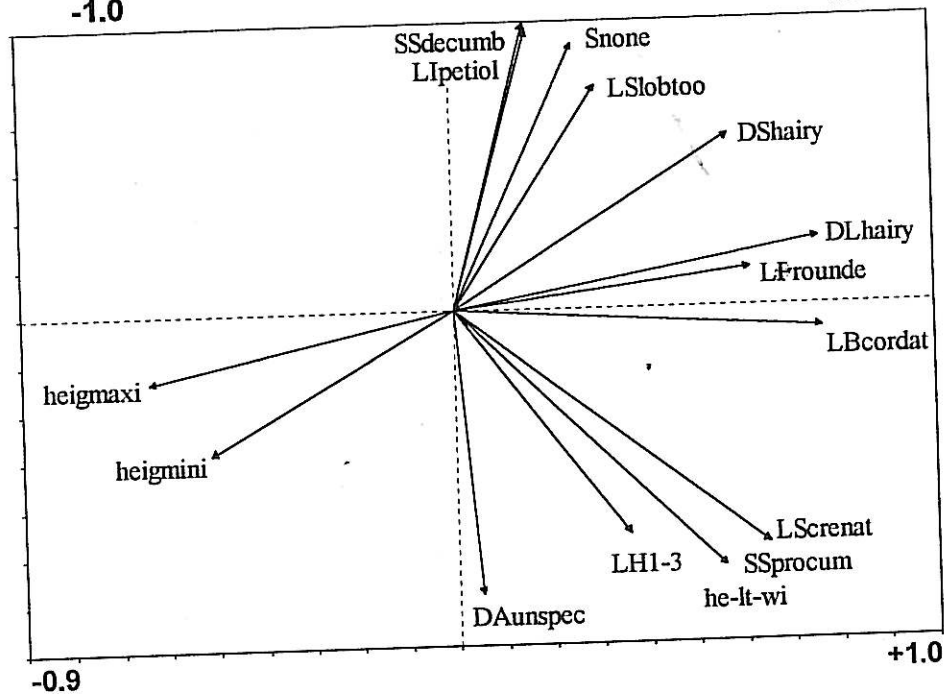


Fig.6a,b. Partial PCA ordination diagrams (first and third ordination axes are shown) displaying relation of species from transects (graminoids are displayed as triangles, forbs as crosses) (Fig.6a) in primary data set and correlation pattern of their ecological and morphological traits (Fig.6b) with graminoid status as a covariable. Abbreviations of species names represent first four letters from either names of species (see species list Tab.4), for abbreviation of species traits see Tab.2.

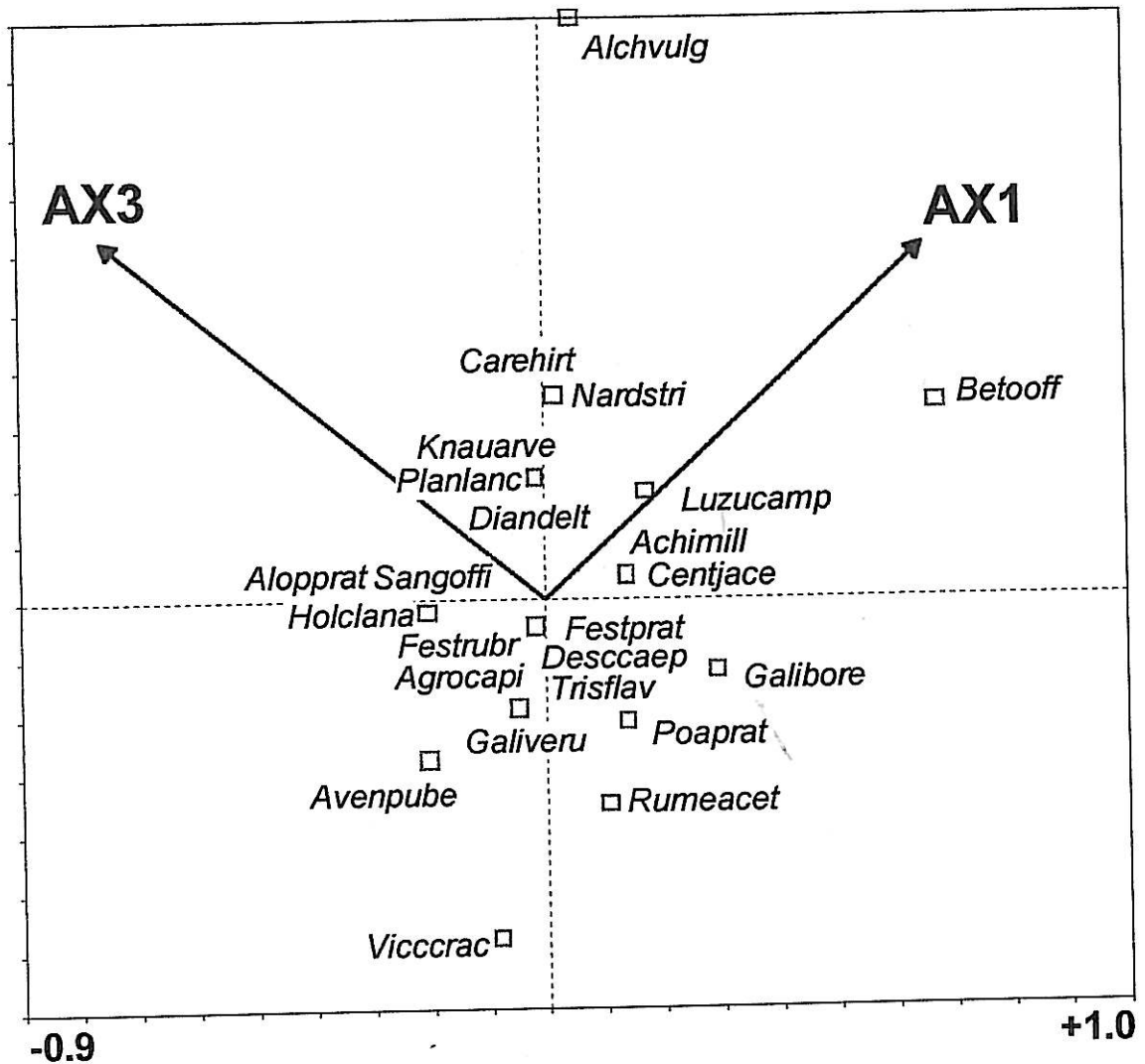


Fig.7. Partial CCA ordination diagram (first and second ordination axes are shown) displaying relation of species from transects (squares) in observation transect data set and explanatory variables (axes from partial PCA representing score of species - see Fig. 6a,b) with graminoid status as a covariable. Abbreviations of species names represent first four letters from either names of species (see species list Tab.4), for abbreviation of species traits see Tab.2.

Tab. 1. Species list - letters in parenthesis mean use of species in RDAs:
G – Grime's CSR strategies, **E** – Ellenberg's values, **R** – growth characteristics,
L – clonality types

<i>Aegopodium podagraria</i> (E,L)	<i>Knautia arvensis</i> (L)
<i>Agrostis canina</i> (G,E,L)	<i>Lathyrus pratensis</i> (G,E,R,L)
<i>Agrostis capilaris</i> (G,E,R,L)	<i>Leontodon autumnalis</i> (G,L)
<i>Achillea millefolium</i> (G,R,L)	<i>Leontodon hispidus</i> (G,R,L)
<i>Ajuga reptans</i> (L)	<i>Leucanthemum vulgare</i> (G,L)
<i>Alchemilla vulgaris</i> (L)	<i>Lotus corniculatus</i> (G,E,R,L)
<i>Alopecurus pratensis</i> (G,E,R,L)	<i>Luzula campestris</i> (E,L)
<i>Angelica silvestris</i> (G,L)	<i>Luzula multiflora</i> (E,L)
<i>Avenula pubescens</i> (L)	<i>Lychnis flos-cuculi</i> (R,L)
<i>Betonica officinalis</i> (L)	<i>Lysimachia nummularia</i> (L)
<i>Briza media</i> (G,R,L)	<i>Lysimachia vulgaris</i> (L)
<i>Calamagrostis epigeios</i> (L)	<i>Medicago lupulina</i> (G,R,L)
<i>Campanula patula</i> (E,L)	<i>Mentha arvensis</i> (L)
<i>Campanula rotundifolia</i> (G,R,L)	<i>Molinia caerulea</i> (G,L)
<i>Cardamine pratensis</i> (G,L)	<i>Myosotis arvensis</i> (G,L)
<i>Carex caryophylla</i> (G,L)	<i>Myosotis silvatica</i> (L)
<i>Carex echinata</i> (E,L)	<i>Nardus stricta</i> (G,L)
<i>Carex hartmanii</i> (L)	<i>Pimpinella major</i> (E,L)
<i>Carex hirta</i> (L)	<i>Pimpinella saxifraga</i> (G,L)
<i>Carex leporina</i> (E,L)	<i>Plantago lanceolata</i> (G,R,L)
<i>Carex nigra</i> (G,E,L)	<i>Plantago media</i> (E,R,L)
<i>Carex pallescens</i> (E,L)	<i>Poa pratensis</i> (G,R,L)
<i>Carex panicea</i> (G,L)	<i>Potentilla erecta</i> (G,L)
<i>Carex pilulifera</i> (G,E,L)	<i>Prunella vulgaris</i> (G,R,L)
<i>Carex pulicaris</i> (L)	<i>Ranunculus acris</i> (G,L)
<i>Centaurea jacea</i> (G,L)	<i>Ranunculus auricomus</i> (E,L)
<i>Cerastium holosteoides</i> (L)	<i>Ranunculus bulbosus</i> (G,E,L)
<i>Cirsium arvense</i> (G,E,R,L)	<i>Ranunculus repens</i> (G,L)
<i>Cirsium palustre</i> (G,E,L)	<i>Rumex acetosa</i> (G,L)
<i>Clinopodium vulgare</i> (L)	<i>Rumex acetosella</i> (E,L)
<i>Cynosurus cristatus</i> (G,L)	<i>Sanguisorba minor</i> (G,E,L)
<i>Dactylis glomerata</i> (G,R,L)	<i>Sanguisorba officinalis</i> (L)
<i>Danthonia decumbens</i> (L)	<i>Saxifraga granulata</i> (L)
<i>Deschampsia caespitosa</i> (R,L)	<i>Scirpus silvaticus</i> (E,L)
<i>Diantus deltooides</i> (E,R,L)	<i>Scorzonera humilis</i> (E,L)
<i>Elytrigia repens</i> (L)	<i>Selinum carvifolia</i> (L)
<i>Erophila verna</i> (L)	<i>Succisa pratensis</i> (G,L)
<i>Festuca ovina</i> (G,R,L)	<i>Taraxacum sp.</i> (G,L)
<i>Festuca pratensis</i> (G,L)	<i>Thymus pulegioides</i> (L)
<i>Festuca rubra</i> (G,R,L)	<i>Trifolium dubium</i> (G,E,R,L)
<i>Filipendula ulmaria</i> (G,L)	<i>Trifolium pratense</i> (G,R,L)
<i>Fragaria vesca</i> (G,R,L)	<i>Trifolium repens</i> (G,L)
<i>Galium boreale</i> (L)	<i>Trisetum flavescens</i> (G,R,L)
<i>Galium molugo</i> (L)	<i>Urtica dioica</i> (G,E,L)
<i>Galium palustre</i> (G,L)	<i>Valeriana dioica</i> (L)
<i>Galium uliginosum</i> (L)	<i>Veronica agrestis</i> (E,L)
<i>Galium verum</i> (E,L)	<i>Veronica chamaedrys</i> (G,L)
<i>Hieracium pilosella</i> (G,L)	<i>Vicia craca</i> (G,R,L)
<i>Holcus lanatus</i> (G,E,R,L)	<i>Viola canina</i> (E,L)
<i>Juncus effusus</i> (G,E,R,L)	

Tab. 2. Traits list

(traits categories and species traits with their abbreviations in ordination diagrams)

I. Dieliny

1. andromon	andromonoecious
2. androdio	androdioecious
3. gynomono	gynomonoecious
4. gynodio	gynodioecious
5. dioeciou	dioecious
6. monoecio	monoecious
7. hermaphr	hermaphrodite

II. Dispersal agent

8. DAunspec	unspecialised
9. DAants	ants
10. DAwind	wind
11. DAwater	water
12. DACarrie	carried by mammals
13. DAEatema	eaten by mammals
14. DAexplos	explosive mechanism

III. Dispersule size – length of longest axis (mm)

15. dispsize	<i>value</i>
--------------	--------------

IV. Height of plant – typical value (cm)

16. heigmaxi	<i>value</i>
17. heigmini	<i>value</i>

V. Leaf type

18. leaftype	compound=1/simple=0
--------------	---------------------

VI. Leaf shape - margins

19. LScrenat	crenate
20. LSentire	entire
21. LSlobed	lobed
22. LSlobtoo	lobed and toothed
23. LStoothe	toothed

VII. Leaf shape - apex

24. LPpointe	pointed
25. LProunde	rounded
26. LPmucron	mucronate

III. Leaf shape

- | | |
|--------------|---------------------------|
| 27. LH-gt-3 | >3times as long as wide |
| 28. LH1-3 | 1-3 times as long as wide |
| 29. LH1-eg-w | length equal width |

IX. Leaf petiole

- | | |
|--------------|------------|
| 30. LIpetiol | petiolate |
| 31. LIsubses | subsessile |
| 32. LISheath | sheathing |
| 33. LISessil | sessile |
| 34. LIclaspi | clasping |

X. Life form

- | | |
|--------------|-----------------|
| 35. LFhemicr | hemicryptophyte |
| 36. LFgeophy | geophyte |
| 37. LFheloph | helophyte |
| 38. LFthreop | therophyte |
| 39. LFchamae | chamaephyte |

XI. Defense on leaves

- | | |
|--------------|-----------------|
| 40. DLglabro | glabrous |
| 41. DLglandh | glandular hairs |
| 42. DLgland | glandular |
| 43. DLhairy | hairy |
| 44. DLprickl | prickles |
| 45. DLsoftha | soft hairs |
| 46. DLspines | spines |
| 47. DLstiffh | stiff hairs |

XII. Defense on stems

- | | |
|--------------|-----------------|
| 48. DSglabro | glabrous |
| 49. DSdenseh | dense hairs |
| 50. DSsoftha | soft hairs |
| 51. DSstiffh | stiff hairs |
| 52. DSglandh | glandular hairs |
| 53. DShairy | hairy |
| 54. DSspines | spines |
| 55. DSthickc | thick cuticule |

XIII. Pollen vector

- | | |
|--------------|--------|
| 56. PVwind | wind |
| 57. PVinsect | insect |
| 58. PVselfed | selfed |

XIV. Leaf base

59. LBcordat	cordate
60. LBCuneat	cuneate
61. LBtrunca	truncate
62. LBparall	parallel
63. LBrounde	rounded
64. LBSagitt	sagittate

XV. Shade preferences

65. Snone	none
66. Slight	light
67. Sdeep	deep
68. Smid	mid

XVI. Soil nutrients

69. SNveryfe	very fertile
70. SNfertil	fertile
71. SNinfert	infertile
72. SNveryin	very infertile

XVII. Growth form: spread

73. he-eq-wi	height = width
74. he-lt-wi	height < width
75. he-gt-wi	height > width

XVIII. Stem supporting

76. SSselfsu	self supporting
77. SSdecumb	decumbent
78. SSprocum	procumbent
79. SStendri	tendrils

XIX. Typical abundance where naturally occurring

80. abundanc	frequent=1/rare=0
--------------	-------------------

XX. Chromosomal number

81. chromnum	<i>value</i>
--------------	--------------

XXI. Polyploidy

82. polyploid	yes=1/no=0
---------------	------------

XXII. Flowering time

83. fltiearl	the earliest month of flowering
84. fltilate	the latest month of flowering

XXIII. Heterophyly

85. heteroph yes=1/no=0

XXIV. Leaf area

86. LA<1-1 < 1 mm²
87. LA1-10 1-10 mm²
88. LA10-100 10-100 mm²
89. LA100-1000 100-1000 mm²

XXV. Biogeography: Continents where native

90. Europe Europe
91. Africa Africa
92. Asia Asia
93. Macarone Macaronesia
94. N-Americ North America
95. S-Americ South America
96. Australi Australasia

Tab. 3. Clonal architecture types

(see Klimeš et al. 1997) Letter A in parenthesis means presence of type in our dataset. Names of types, which we used, are bolded.

Type 1:	"<i>Trifolium pratense</i>" type (A)
Type 2:	" <i>Alliaria petiolata</i> " type (A) "<i>Rumex acetosella</i>" type (A)
Type 3:	" <i>Ranunculus ficaria</i> " type
Type 4:	"<i>Lycopodium annotinum</i>" type (A)
Type 5:	" <i>Festuca ovina</i> " type (A) "<i>Rumex obtusifolius</i>" type (A) " <i>Rumex alpinus</i> " type (A) " <i>Dactylis glomerata</i> " type (A) " <i>Aegopodium podagraria</i> " type (A)
Type 6:	"<i>Fragaria vesca</i>" type (A)
Type 7:	" <i>Caltha palustris</i> " type (A) " <i>Asperula odorata</i> " type (A) " <i>Calystegia sepium</i> " type
Type 8:	" <i>Lycopus europeus</i> " type " <i>Corydalis cava</i> " type " <i>Corydalis solida</i> " type
Type 9:	" <i>Galanthus nivalis</i> " type " <i>Ornithogalum gussonei</i> " type " <i>Tulipa sylvestris</i> " type "<i>Dentaria bulbifera</i>" type (A)

Tab. 4. Species list from small-scale transects

(letter A in parenthesis means use of species in pPCA and pCCA in transect analyses)

<i>Agrostis capilaris</i> (A)	<i>Holcus lanatus</i> (A)
<i>Achillea millefolium</i> (A)	<i>Knautia arvensis</i> (A)
<i>Alchemilla vulgaris</i> (A)	<i>Koeleria pyramidata</i>
<i>Alopecurus pratensis</i> (A)	<i>Lathyrus pratensis</i>
<i>Antoxantum odoratum</i>	<i>Luzula campestris</i> (A)
<i>Avenula pubescens</i>	<i>Nardus stricta</i> (A)
<i>Betonica officinalis</i> (A)	<i>Pimpinella saxifraga</i>
<i>Briza media</i> (A)	<i>Plantago lanceolata</i> (A)
<i>Cardamine pratensis</i>	<i>Poa pratensis</i> (A)
<i>Carex hirta</i> (A)	<i>Prunella vulgaris</i>
<i>Centaurea jacea</i> (A)	<i>Ranunculus acris</i>
<i>Cerastium arvense</i>	<i>Rumex acetosella</i> (A)
<i>Cirsium palustre</i>	<i>Sanguisorba officinalis</i> (A)
<i>Dactylis glomerata</i>	<i>Stellaria graminea</i>
<i>Deschamsia caespitosa</i> (A)	<i>Taraxacum</i> sp.
<i>Dianthus deltoides</i> (A)	<i>Trifolium montanum</i>
<i>Festuca pratensis</i> (A)	<i>Trisetum flavescens</i> (A)
<i>Festuca rubra</i> (A)	<i>Veronica chamaedrys</i> (A)
<i>Galium boreale</i> (A)	<i>Vicia cracca</i> (A)
<i>Galium verum</i> (A)	<i>Viola canina</i>

	RGRR	RGRS	RGRLA	RGRRL	RGRS/RGRR	RGRLA/RGRRL	SBI/LAI*	RBI/RLII*
<i>Achillea millefolium</i>	0,0876	0,106	0,0974	0,0945	1,21	0,7034	0,012	0,0026
<i>Agrostis capillaris</i>	0,1185	0,1441	0,1468	0,0865	1,216	0,5014	0,0131	0,0024
<i>Alpecurus pratensis</i>	0,0964	0,117	0,1068	0,0818	1,2137	0,5119	0,0185	0,0042
<i>Briza media</i>	0,0896	0,1072	0,1314	0,1402	1,1964	0,5284	0,0207	0,0047
<i>Campanula rotundifolia</i>	0,1095	0,1353	0,1634	0,1015	1,2356	0,6886	0,0106	0,0016
<i>Cirsium arvense</i>	0,1174	0,1005	0,1305	0,1488	0,856	1,0174	0,0128	0,0052
<i>Dactylis glomerata</i>	0,1026	0,1355	0,1021	0,0712	1,3207	0,5923	0,0135	0,0035
<i>Deschampsia caespitosa</i>	0,0682	0,1168	0,1622	0,0966	1,7126	0,3978	0,0145	0,0028
<i>Dianthus deltoides</i>	0,0728	0,1249	0,1431	0,1079	1,7157	0,7944	0,0168	0,0027
<i>Festuca ovina</i>	0,1093	0,0993	0,1393	0,143	0,9085	0,3159	0,02	0,0032
<i>Festuca rubra</i>	0,0884	0,1034	0,1018	0,114	1,1697	0,8929	0,0202	0,003
<i>Fragaria vesca</i>	0,0892	0,0836	0,106	0,1525	0,9372	0,4386	0,0166	0,0021
<i>Holcus lanatus</i>	0,0824	0,1233	0,1229	0,0609	1,4964	0,6338	0,0116	0,0018
<i>Juncus effusus</i>	0,0455	0,1386	0,1227	0,0661	3,0462	0,5446	0,0159	0,0024
<i>Lychnis flos-cuculi</i>	0,0196	0,0987	0,1246	0,104	5,0357	0,5656	0,0161	0,0023
<i>Lotus corniculatus</i>	0,1101	0,0846	0,1039	0,1288	0,7684	0,5329	0,016	0,0023
<i>Leontodon hispidus</i>	0,1462	0,1086	0,1502	0,207	0,7428	0,6332	0,0155	0,0028
<i>Lathyrus pratensis</i>	0,1215	0,1182	0,1546	0,1831	0,9728	0,8443	0,0187	0,0146
<i>Medicago lupulina</i>	0,0421	0,1002	0,1038	0,1161	2,38	0,012	0,0192	0,0066
<i>Plantago lanceolata</i>	0,0972	0,1186	0,1158	0,0915	1,2202	0,7646	0,017	0,0031
<i>Plantago media</i>	0,0918	0,0543	0,0859	0,104	0,5915	0,6595	0,0136	0,0045
<i>Poa pratensis</i>	0,1143	0,128	0,1544	0,1118	1,1199	0,406	0,013	0,0022
<i>Prunella vulgaris</i>	0,0899	0,0398	0,0697	0,1013	0,4427	0,2519	0,0197	0,0026
<i>Trifolium dubium</i>	0,0925	0,0709	0,0682	0,0986	0,7665	0,4255	0,0189	0,0034
<i>Trifolium pratense</i>	0,0832	0,0814	0,086	0,1016	0,9784	0,787	0,0174	0,0049
<i>Trisetum flavescens</i>	0,0956	0,1254	0,1363	0,1285	1,3117	0,2938	0,0158	0,0019
<i>Vicia cracca</i>	0,0549	0,0571	0,0426	0,0562	1,0401	1,335	0,0289	0,0258

Tab. 5. Calculated growth characteristics : these results of growth experiment were used as explanatory variable in RDAs. Abbreviations mean: Relative growth rates of shoot biomass - RGRS and root biomass - RGRRL, of the leaf area - RGRLA and root length - RGRRL, ratios of relative growth rate of shoot and root biomass - RGRS/RGRR, of leaf area and root length - RGRLA/RGRRL, and ratio of shoot biomass and leaf area SBI/LAI*, ratio of root biomass and root length - RBI/RLII*. * in acronyms means after 3 weeks i.e. second sampling (first sampling was 7 days after germination)

