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# ABUNDANCE, COMPETITION, PHENOLOGY AND CO-OCCURRENCE OF GRASSLAND SPECIES

*JANA MARTÍNKOVÁ*



SUPERVISOR: RNDR. *PETR ŠMILAUER*, DR.

**Annotation**

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The present study assess the importance of seedling growth characteristics and seedling response to competition for prediction of species abundance and distribution in an oligotrophic dry meadow. Seasonal changes of species cover and phenological phases of grassland species in relation to their ecological and morphological traits were explored. Predictors of species phenological optima using two different methods of describing phenological state of plant populations were found.

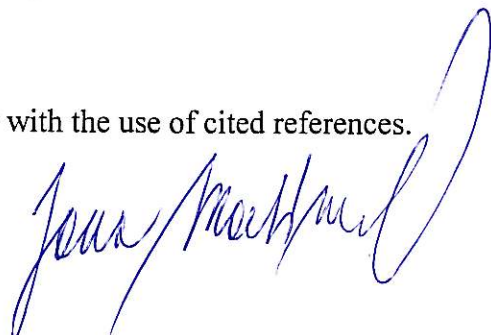
**“The significant problems we face cannot be solved at the  
same level of thinking we were at when  
we created them ...“**

*Albert Einstein*

**To my parents ...**

I hereby declare this thesis worked out by myself only with the use of cited references.

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# Kompetice, abundance, fenologie a distribuce druhů v lučním společenstvu

*Jana Martínková*

*Jihočeská univerzita v Českých Budějovicích, Biologická fakulta,  
Branišovská 31, 370 05 České Budějovice  
Fax +420 38 53 00 366; e-mail: jana.martinkova@tix.bf.jcu.cz*

## **Abundance, kompetice a distribuce druhů v lučním společenstvu *Možnosti predikce na základě skleníkového experimentu***

Abundance druhů je jednou ze základních charakteristik struktury společenstva. Některé druhy jsou početné, jiné vzácné. Co způsobuje rozdíly v této početnosti je podstatnou otázkou rostlinné ekologie (Grime 1979, Grubb 1986, Wilson et al. 1998, Guo et al. 2000).

Některé studie se pokoušejí nalézt vztah mezi početností druhu ve společenstvu a kompetiční schopností druhů, ale závěry těchto prací nejsou jednotné. Některé nalézají přímou souvislost mezi abundancí druhu a kompetiční schopností (Whittaker 1965, Grime 1979, Keddy 1990, Grubb et al. 1997), jiné tento vztah popírají (Taylor & Aarssen 1990, Duralia & Reader 1998). Příbuzným problémem je jak definovat termín „kompetiční schopnost“ (Grime & Hunt 1975, Goldberg 1990).

Popis distribuce druhů ve společenstvu ve vztahu k jiným druhům je cílem mnoha prací (Turkington & Harper 1979, Thorhallsdottir 1990, Gaudet & Keddy 1995). Ve většině z nich je kompetiční schopnost druhu zmiňována jako velmi důležitá vlastnost určující vzájemnou distribuci druhů.

V této studii jsem se pokusila posoudit důležitost růstových charakteristik semenáčků a jejich schopnost tolerovat supresivní efekt susedů (tedy jednu stranu kompetiční schopnosti druhů) pro predikci abundance a distribuce druhů v lučním společenstvu. Mitchley (1990) navrhuje, že interakce mezi semenáčky a dospělými rostlinami jsou důležitými determinanty relativní abundance populací v lučním společenstvu. Na základě tohoto tvrzení jsem se rozhodla pro kompetiční skleníkový experiment se semenáčky a dospělými rostlinami. Modelovým dominantním kompetitorem v tomto experimentu byl druh *Holcus lanatus*, dominantní druh ve zkoumaném lučním společenstvu. Kombinací výsledků

charakteristikami, které ovlivňují distribuci druhů ve společenstvu jsou relativní růstové charakteristiky týkající se převážně kořenového systému.

Z 22 testovaných ekologických a morfologických znaků měly pouze tři signifikantní vztah k měřeným růstovým charakteristikám semenáčků nebo k jejich schopnosti tolerovat kompetitora.

### **Sezónní změny pokryvnosti a zastoupení fenologických fází lučních druhů** *Vztah k ekologickým a morfologickým charakteristikám*

Fenologie je definována jako studium časových sledů událostí během životního cyklu organismu. Otázky vztahující se k tomuto časování jsou důležité v evoluční a rostlinné ekologii, kde upoutávají pozornost po mnoho let (Heinrich 1976, Poole & Rathcke 1979, Cole 1981, Kochmer & Handel 1986, Ollerton & Lack 1992, Stone et al. 1998, Gross et al. 2000). Sezónní načasování životních projevů může být kritické pro reprodukci a přežití rostlinného organismu (Rathcke & Lacey 1985).

Většina fenologických studií se soustřeďuje na studium vybraného společenstva nebo jeho funkční části (Opler et al. 1980, Losvik 1991). Ve fenologických pracích jsou nejčastěji studovanými společenstvy vlhké nebo suché tropické lesy (Frankie et al. 1974, Borchert 1994, Williams et al. 1997). Společenstva v temperátních oblastech jsou spíše opomíjena (Smithramirez & Armesto 1994, Lechowicz 1995). Mnoho otázek týkajících se fenologických změn například v temperátním lučním společenstvu zůstává nezodpovězeno.

Fagerstrom & Agren (1980) se zabývali otázkou, zda diferenciací časů fenologických projevů je výsledkem kompetice mezi semenáčky: Navrhli, že tato diferenciací může být výhodná pro méně kompetičně úspěšný druh a pro kolonizaci prázdných míst jeho semeny.

Většina fenologických studií se zabývá otázkou, zda časy kvetení druhů jsou modifikované kompeticí o opylovače (Gross & Werner 1983, Campbell & Motten 1985, Stone et al. 1998). Tato otázka byla zodpovězena kladně v několika studiích (Pleasants 1980, Gleeson 1981), ale v jiných tato hypotéza podpořena nebyla (Pole & Rathcke 1979, Campbell & Motten 1985). Výhodnost agregovaných časů kvetení byla rovněž diskutována v několika studiích (např. Tompson, 1982, Rathcke 1988).

Přesto můžeme rozdíly v načasování životních cyklů rostlin v rostlinných společenstvech pozorovat. V jednom časovém okamžiku některé druhy kvetou či plodí, zatímco jiné jsou sterilní. Je tedy pravděpodobné, že druhy odlišující se svou dobou kvetení se

Mnoho druhů se pokouší svůj reprodukční cyklus dokončit již před kosením. Několik druhů a mnoho jedinců nikdy nedokončí svůj reprodukční cyklus. K největším změnám v zastoupení jednotlivých fenologických fází dochází v období těsně před kosením.

Mnoho graminoidních druhů začíná s reprodukčním cyklem dříve než ostatní bylinné druhy. Přechod graminoidů od kvetení ke zrání semen je rychlejší než přechod u ostatních bylinných druhů. Některé graminoidní druhy byly nalezeny kvetoucí, nikdy však plodné. Tento stav nebyl pozorován u ostatních bylinných druhů vůbec. Přechod negraminoidních bylinných druhů od kvetení k zralým semenům je pomalejší v jarních měsících, směrem k podzimu se tento přechod urychluje. Žádný graminoidní druh nebyl nalezen v reprodukční fázi v pozdním letě či na podzim.

Druhy s pochvatými bázemi listů, roznášené a opylované větrem kvetou dříve než druhy s řapíky. Existuje průkazný rozdíl mezi graminoidy a bylinami ve fenologickém optimu pro kvetoucí fázi a fázi zralých semen. Tyto výsledky jsou v rozporu s prací Rabinowitz et. al (1981), týkající se préríjních druhů. Autoři žádné rozdíly v časech kvetení mezi větrem a hmyzem opylovanými druhy nenalezli.

Dominantní druhy jsou signifikantně odlišné od nedominantních druhů ve fenologickém optimu kvetení. Dominantní druhy soustředí své reprodukční projevy do středu vegetační sezóny, nedominantní druhy více využívají jejích okrajů.

Některé další charakteristiky druhů mohou mít vliv na pozici fenologických optim lučních druhů. Nicméně predikce těchto optim pro další ekologické skupiny (kromě graminoidů/ostatních bylin a dominantních/nedominantních druhů) je znemožněna příliš jemnou diferenciací druhů v jejich fenologických optimech.

Jedním z mechanismů umožňující koexistenci druhů je diferenciace podmínek prostředí v čase či prostoru (Tilman 1982). Jemná diferenciace druhů ve fenologických optimech může být výhodou při využívání „časového prostoru“. Rozdíly ve fenologických optimech mohou odpovídat časové diferenciaci nik lučních druhů.

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# Abundance, co-occurrence and competition in grassland *Predictive ability of greenhouse experiment*

**Jana Martínková**

*Faculty of Biological Sciences, University of South Bohemia, Branišovská 31,  
370 05 České Budějovice, Czech Republic.  
Fax +420 38 53 00 366; e-mail: jana.martinkova@tix.bf.jcu.cz*

## **Abstract**

I compared experimental results of seedling growth characteristics and competition response of 22 grassland species with their relative abundance and co-occurrence in a field. I identify the best indicators of belowground competition with the dominant competitor *Holcus lanatus* among the seedling growth characteristics. These are the characteristics related to maximization of growth of leaf area or of root length. Further, I assess predictability of seedlings competitive behavior using the plant ecological and morphological traits. I find only a poor relation of measured growth characteristics with the ecological and morphological traits that are evaluated on adult plants.

I assumed that species with a lower response to presence of dominant competitor have a higher abundance in the field than species with a higher response to competition, but this is not confirmed. Therefore, I ask whether the distribution of studied species in the field in respect to *Holcus lanatus* is random or whether their co-occurrence can be related to their performance in the competition experiment. I find that field distribution is not random, but cannot be predicted from the species response to competition in the experiment. Rather, it is related to relative growth rate value of the leaf area and to the relative investment into growth rate of root length.

## **Introduction**

Species abundance is an important feature of community structure. Some species are common whereas others are rare. A fundamental ecological problem of last decades is what causes the variation in species abundance and their distribution in plant communities. This question has been discussed in numerous studies (Grime 1979, Grubb 1986, Crawley 1997, Wilson et al. 1998, Guo et al. 2000).

Many studies deal with the relation between species abundance in a community and various plant traits and strategies both theoretically and using experimental approach (Grubb 1977, Mitchley 1988, Holt et al. 1997, Eriksson and Jakobsson 1998, Reader 1998). But results from these studies are not consistent. Some authors found that the inter-specific competitive abilities explain well the local abundance of species (Whittaker 1965, Grime 1979, Miller and Werner 1987, Keddy 1990, Grubb et al. 1997) while some found no such relation (Rabinowitz et al. 1984, Taylor and Aarssen 1990, Duralia and Reader 1993). Other studies attempted to define a set of plant traits directly related to the competitive ability of



This study addresses following questions:

- Is a lower response of seedlings to competition correlated with higher species abundance in a grassland community?
- Which seedling growth characteristics are correlated with species abundance in the community?
- Which seedling growth characteristics respond to experimentally established belowground competition?
- Is the response of seedlings to competition related to their spatial co-occurrence in grassland community?
- Can be the species response to competition related to their morphological and ecological traits?

## Methods

### Experiment - growth characteristics and competitive response of seedlings

In this experiment, I combined two classical experimental approaches: a comparative study of the seedling growth characteristics (providing data about productivity traits of the studied species) and a competition experiment assessing the growth response of different species to competition. Because I wanted to compare experimental results with field data, a dominant grass species from my field site - *Holcus lanatus* - was used as a model competitor.

I performed the experiment in greenhouse conditions during the spring 1999. Plants of *Holcus* were grown in 440 pots (approximate volume 1.5 l) with sand for 6 weeks to produce enough tillers and relevant amount of belowground biomass to compete (in role of adult plant) with target seedlings. Twelve *Holcus* seedlings were planted in one half of each pot and this half was completely separated from the other half of the pot by a plastic barrier. I covered the empty half of each pot by an opaque foil to prevent algal growth. I used the basic Rorison solution (Hunt et al. 1993) as the nutrient source and I applied it regularly every two weeks. The aboveground biomass of *Holcus* was cut every three weeks to induce production of new tillers. After six weeks, even-aged (two day old) seedlings of all target species (Table 1) were transplanted into the empty portion of the pots. To obtain data on the competitive impact of *Holcus*, I removed the separating barrier in half of the pots. The second group of pots (with the barrier left in place) acted as a control where *Holcus* and the target species entered only into a limited aboveground competition. Five replications were maintained for both treatments

Growth characteristics	Abbreviations
1. Leaf area after 1 <sup>st</sup> harvest without competition	LA <sup>(1)</sup> <sub>control</sub>
2. Leaf area after 1 <sup>st</sup> harvest with competition	LA <sup>(1)</sup> <sub>comp</sub>
3. Leaf area after 2 <sup>nd</sup> harvest without competition	LA <sup>(2)</sup> <sub>control</sub>
4. Leaf area after 2 <sup>nd</sup> harvest with competition	LA <sup>(2)</sup> <sub>comp</sub>
5. Root length after 1 <sup>st</sup> harvest without competition	RL <sup>(1)</sup> <sub>control</sub>
6. Root length after 1 <sup>st</sup> harvest with competition	RL <sup>(1)</sup> <sub>comp</sub>
7. Root length after 2 <sup>nd</sup> harvest without competition	RL <sup>(2)</sup> <sub>control</sub>
8. Root length after 2 <sup>nd</sup> harvest with competition	RL <sup>(2)</sup> <sub>comp</sub>
9. Ratio of root length and leaf area after 1 <sup>st</sup> harvest without competition	RL / LA <sup>(1)</sup> <sub>control</sub>
10. Ratio of root length and leaf area after 1 <sup>st</sup> harvest with competition	RL / LA <sup>(1)</sup> <sub>comp</sub>
11. Ratio of root length and leaf area after 2 <sup>nd</sup> harvest without competition	RL / LA <sup>(2)</sup> <sub>control</sub>
12. Ratio of root length and leaf area after 2 <sup>nd</sup> harvest with competition	RGR LA <sub>control</sub>
13. Relative growth rate of leaf area with competition	RGR LA <sub>comp</sub>
14. Relative growth rate of root length without competition	RGR RL <sub>control</sub>
15. Relative growth rate of root length with competition	RGR RL <sub>comp</sub>
16. Ratio of relative growth rates of root length and leaf area without competition	RGR RL <sub>control</sub> / RGR LA <sub>control</sub>
17. Ratio of relative growth rates of root length and leaf area with competition	RGR RL <sub>comp</sub> / RGR LA <sub>comp</sub>

Responses to competition	Abbreviations
18. Ratio of leaf areas after 1 <sup>st</sup> harvest for seedlings without and with competition	LA <sup>(1)</sup> <sub>control</sub> / LA <sup>(1)</sup> <sub>comp</sub>
19. Ratio of leaf areas after 2 <sup>nd</sup> harvest for seedlings without and with competition	LA <sup>(2)</sup> <sub>control</sub> / LA <sup>(2)</sup> <sub>comp</sub>
20. Ratio of root length after 1 <sup>st</sup> harvest for seedlings without and with competition	RL <sup>(1)</sup> <sub>control</sub> / RL <sup>(1)</sup> <sub>comp</sub>
21. Ratio of root length after 2 <sup>nd</sup> harvest for seedlings without and with competition	RL <sup>(2)</sup> <sub>control</sub> / RL <sup>(2)</sup> <sub>comp</sub>
22. Ratio of RGR of leaf area for seedlings with and without competition	RGR LA <sub>contr</sub> / RGR LA <sub>comp</sub>
23. Ratio of RGR of root length for seedlings with and without competition	RGR RL <sub>contr</sub> / RGR RL <sub>comp</sub>

**Table 2** List of 18 seedling growth characteristics measured / calculated from the greenhouse experiment and 6 responses to competition based on them. Abbreviations used throughout the paper are also given. These abbreviations are based on following components: LA - leaf area, RL - root length, <sup>(1)</sup> - first harvest time, <sup>(2)</sup> - second harvest time, <sub>control</sub> - treatment without competition = separating barrier left, <sub>comp</sub> - treatment with competition = separating barrier removed, RGR - relative growth rate.

## Field study

I recorded the fine-scale pattern of species distribution on a dry oligotrophic meadow at the Zvíkov research site near České Budějovice, Czech Republic (48°59'N, 14°36'E, 500 m a.s.l.) in June 1998.

For this study, I selected part of the field site with a homogenous composition of vegetation cover. Here I placed three parallel, 10 m long transects, positioned one meter apart. I recorded the identity of the uppermost plant species in two centimeters intervals (1500 observations). Only the uppermost species were observed in order to avoid dislocation of species shoots which would bias the measurements at adjacent points.

## Abundance and co-occurrence of species

I calculated abundance and co-occurrence of species from the raw data (counts of individual species) collected on the three transects. The abundance of a species is expressed by relative frequency (Table 1). I calculated the co-occurrence of individual species with

Many of the species traits are polymorphic, i.e. one trait has several states. In these cases, I used fuzzy coding (Ter Braak and Šmilauer 1998) for combination of trait states: every trait state occurring in that species was coded by a number between 0 and 1, so that the sum of those values for one trait was always equal to one, and the fractions had the same size.

### Statistical Analyses

I used STATISTICA 5.0 program for the classical statistical analysis. All the measured growth characteristics were log transformed. The change of the calculated growth characteristics in response to competition was tested using a pair-wise t-test (t-test for dependent samples). Correlation matrices were used to identify significant linear relations between seedling growth characteristics or responses to competition of seedlings and (i.) the species abundance in field, (ii.) the species co-occurrence with *Holcus* in field and (iii.) the target species morphological and ecological traits. I used  $\chi^2$ -test to test for a non-random spatial co-occurrence of the species with *Holcus*.

I used multivariate ordination methods - principal components analysis (PCA) and redundancy analysis (RDA), using software package CANOCO for Windows, version 4 (Ter Braak and Šmilauer, 1998) to illustrate relations between the seedling growth characteristics and their response to competition on one side, and the morphological and ecological traits of the species on the other side. Using the resulting ordination diagrams, I stated new hypotheses for future studies.

Pair-wise T-test compared characteristics		p value	
LA <sup>(1)</sup> <sub>control</sub>	vs.	LA <sup>(1)</sup> <sub>comp</sub>	<i>n.s.</i>
LA <sup>(2)</sup> <sub>control</sub>	vs.	LA <sup>(2)</sup> <sub>comp</sub>	<b>0.0022</b>
RL <sup>(1)</sup> <sub>control</sub>	vs.	RL <sup>(1)</sup> <sub>comp</sub>	<i>n.s.</i>
RL <sup>(2)</sup> <sub>control</sub>	vs.	RL <sup>(2)</sup> <sub>comp</sub>	<b>0.0001</b>
RL / LA <sup>(1)</sup> <sub>control</sub>	vs.	RL / LA <sup>(1)</sup> <sub>comp</sub>	<i>n.s.</i>
RL / LA <sup>(2)</sup> <sub>control</sub>	vs.	RL / LA <sup>(2)</sup> <sub>comp</sub>	<i>n.s.</i>
RGR LA <sub>control</sub>	vs.	RGR LA <sub>comp</sub>	<i>n.s.</i>
RGR RL <sub>control</sub>	vs.	RGR RL <sub>comp</sub>	<i>n.s.</i>
RGR RL <sub>control</sub> / RGR LA <sub>control</sub>	vs.	RGR RL <sub>comp</sub> / RGR LA <sub>comp</sub>	<i>n.s.</i>
LA <sup>(1)</sup> <sub>control</sub> / LA <sup>(1)</sup> <sub>comp</sub>	vs.	LA <sup>(2)</sup> <sub>control</sub> / LA <sup>(2)</sup> <sub>comp</sub>	<b>0.016</b>
RL <sup>(1)</sup> <sub>control</sub> / RL <sup>(1)</sup> <sub>comp</sub>	vs.	RL <sup>(2)</sup> <sub>control</sub> / RL <sup>(2)</sup> <sub>comp</sub>	<b>0.0412</b>

**Table 4** Results of pair-wise T-test (t-test for dependent samples) used to evaluate the response of growth characteristics to experimental competition. Emphasized characteristic names are characteristics significantly response to competition. For explanation of abbreviations of seedling growth characteristics see Table 2.

The two growth characteristics (leaf area and root length) which were significantly affected by the competition treatment are used in Fig. 2 to illustrate differences in response of individual studied species. The species response is expressed as the ratios of average leaf area ( $LA^{(2)}_{\text{control}} / LA^{(2)}_{\text{comp}}$ , on horizontal axis) and average root length ( $RL^{(2)}_{\text{control}} / RL^{(2)}_{\text{comp}}$ , on vertical axis) between the control seedlings and the seedlings entering competition with *Holcus*. The species with values larger than 1.0 lowered their leaf area and/or root length in response to competition.

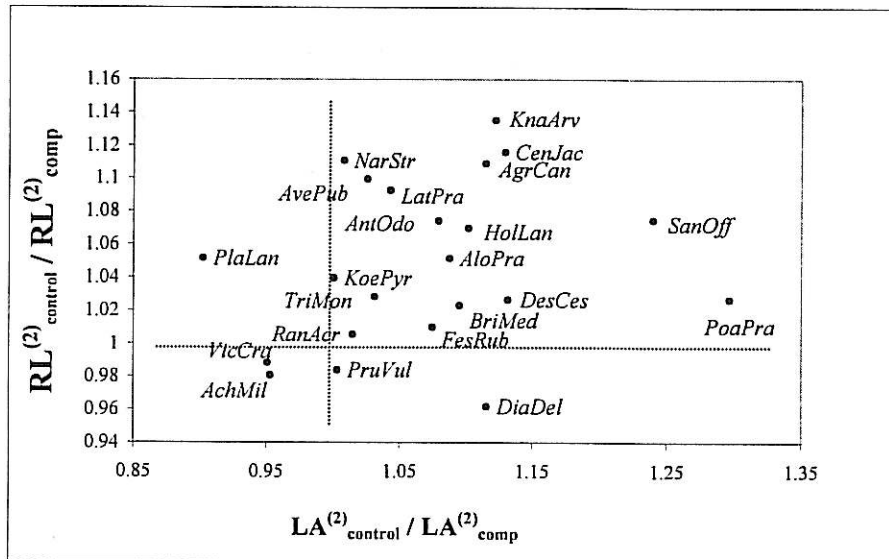


Fig. 2 The response of individual species to experimentally created competition with *Holcus lanatus*. The response is decomposed into two axes, the horizontal one corresponding to response in leaf area and the vertical one to response in root length. Dotted lines correspond to ratios equal to one, therefore species far from the dotted lines in positive direction (with value >1) were more suppressed by the competition. For explanation of species names see Table 1, for seedling characteristics see Table 2.

### Species abundance in the field

I tested the relation between the species responses to competition and their primary growth characteristics on one side (see Table 2) and their relative abundance in the field on the other side. I found that the relative abundance was positively correlated with the ratio between the root length of seedling without competition and those under competition in the first harvest ( $RL^{(1)}_{\text{control}} / RL^{(1)}_{\text{comp}}$ ,  $p=0.039$ ). One primary growth characteristic had a significant positive relationship to the field abundance of the species: root length of seedlings without competition after first harvest ( $RL^{(1)}_{\text{control}}$ ,  $p=0.04$ ). Another three characteristics had a weak relation to the relative abundance of the species in the field: the ratio of root length of seedling under

I also found the ratio of observed and expected frequencies of co-occurrence to have interesting relations to some of the primary growth characteristics: the species occurring more frequently in close neighbourhood of *Holcus* had lower relative growth rate of the leaf area of seedlings without competition ( $\text{RGR LA}_{\text{control}}$ ,  $p < 0.001$ ) and also a higher ratio of the root length' RGR to leaf area' RGR of seedlings without competition ( $\text{RGR RL}_{\text{control}} / \text{RGR LA}_{\text{control}}$ ,  $p < 0.001$ ).

### Morphological and ecological traits

I found the following species traits to be significant ( $\alpha = 0.05$ ) explanatory variables to predict the values of seedling growth characteristics in redundancy analysis (RDA) with a stepwise selection of predictors: maximum species height, presence of heterophylly and the start of the flowering period. The resulting ordination diagram is displayed in Fig. 4.

Positive correlation of early flowering time with minimization of investment into root system is evident. Separation of species along the first ordination axis can be interpreted by their maximum height and many of the seedling growth characteristics are positively correlated with the maximum plant height.

Response of seedlings to the presence of *Holcus* competition expressed by comparing ratio of root length of seedlings without and with competition in first harvest ( $\text{RL}^{(1)}_{\text{control}} / \text{RL}^{(1)}_{\text{comp}}$ ) is positively correlated with the earliest flowering time. ( $\text{LA}^{(2)}_{\text{control}} / \text{LA}^{(2)}_{\text{comp}}$ ) and ( $\text{RL}^{(2)}_{\text{control}} / \text{RL}^{(2)}_{\text{comp}}$ ) are correlated with heterophylly and maximum plant height, and also the ratio of relative growth rate of root length between competition and no-competition treatments ( $\text{RGR RL}_{\text{contr}} / \text{RGR RL}_{\text{comp}}$ ) shows the same pattern.

## Discussion

### Competitive response of grassland species

I measured the competitive response of grassland species to the presence of the most frequent competitor in the field as a characteristic that might indicate the competitive ability of individual species. The response to competition with *Holcus* was quantified using the ratios of leaf area and root length or RGR of leaf area and root length between the seedlings with competition and the control seedlings (Table 2). The best indicators of competition of seedlings with an adult competitor were the growth characteristics related to maximization of growth of either the leaf area or of root length.

competition in natural communities and size-related variables are good indicators of competitive dominance in variety of herbaceous plant communities and my results seem to be consistent with their study. Furthermore, they suggested that biomass may simply integrate or summarize other traits, such as high rates of resource capture above- and belowground. I assumed that leaf area or root length are strongly correlated with plant shoot or root biomass, therefore I expected them to be useful parameters for measuring response to competition. Roush and Radosevich (1985) demonstrated that leaf area ratio (LAR) has a strong relation to species relative competitive ability while the relative growth rate does not, consistently with my results.

It is evident from Fig. 2 that different species responded differently to the competition treatment. One group of species responded by a decrease in the leaf area (*Poa pratensis*, *Festuca rubra*, *Deschampsia caespitosa*), while other one by a change in the root length (*Nardus stricta*, *Knautia arvensis*, *Lathyrus pratensis*), and also the extent of such response varied. Nevertheless, I find no evidence for distinguishing between species with maximum investment into roots or into leaves and also no significant negative correlation (trade-off) between the root length and leaf area of seedlings was found. Grubb et al. (1997) found a relation among root and shoot competition and turfs quality. Their conclusion was that the root competition is more important than shoot competition in enabling some species to be regularly more abundant than others in turf 5-10 cm tall, but that shoot competition is more important in turf ca. 20 cm tall, and paradoxically also more important in a very short turf where species with wide leaves form flat rosettes very close to the ground. Even though I limited ourselves to belowground competition, my results can be in accordance with Grubb et al. (1997): I found differentiation of species reaction to competition, with some responding by change in leaf area and others by change of root length. These two strategies can be preferred in different microhabitats within community, differing for example in turf height and/or in the extent of belowground competition.

The estimation of competitive ability of grassland species by their response to competitive treatment in a greenhouse experiment is a large simplification of this complex issue. I ignored important ecological processes like resource partitioning in space and time or interactions with symbionts and pathogens, which can substantially influence competitive ability, as well as the structural heterogeneity of competing individuals absent in the uniform seedlings. Nevertheless, I believe that even such a simple approach has its value for comparative studies.

### **Species abundance in the field**

I assumed that a species with lower response to competition treatment will be a better competitor, with a higher abundance in field. But I found that the relation between the indicators

Probability of plants gaining or losing space in a mosaic community depends on their neighbors (Thorhallsdottir 1990). Silvertown et al. (1992) propose that spatial distribution must be considered just as important as competition coefficients, density and the frequency of competitors in determining competitive outcome. While the explored distribution of species is not random, I found no relation to experimentally measured responses of seedlings to competition. In relation to this, Epp and Aarssen (1989) suggest that different attributes may be important for relative competitive ability at different stages of grassland community development. As I already suggested, my attempt to use the measured response in competition experiment to express the species competitive ability may be an over-simplification. Nevertheless, like for the results concerning the species abundance in field, the ratio of observed and expected frequencies had interesting relations to some of the primary growth characteristics. Important factors influencing the distribution of species seem to be the growth performance of seedlings (some of the RGR-based characteristics especially related to the root system) and for the relative species abundance the ability to maximize extent of the root system.

### **Morphological and ecological traits**

Further progress in ecology requires a predictive approach that will enable general principles to be deduced that apply beyond the species and conditions of a particular study or site (Gaudet and Keddy 1988). It was suggested that such general principles are best discovered using a comparative approach applied to a large number of species under standardized conditions (Grime 1979). In my analysis, I explored the predictability of seedling growth performance using the ecological characteristics of adult plants.

Fig. 4 demonstrates a positive correlation of early flowering time and maximization of leaf area and minimization of investment into root system. Do the same species flower for long time or only during spring months? Do species with early flowering produce roots in the later months of growing season or is their total root production lower? These are questions for future study.

Separation of species along the first ordination axis of RDA is due to their differences in maximum height and majority of seedling growth characteristic is positively correlated with this trait. Tall structure, extensive lateral spread, build-up of large perennating organs, and the rapid expansion of leaf and root surface are indicative of high relative growth rate (in its original definition, sensu Grime and Hunt, 1975).

From the 22 tested trait states of grassland species, only three had a significant impact on the measured growth characteristics and this frequency corresponds more or less exactly to the  $\alpha$

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# **Phenological pattern of grassland species**

## ***Relation to ecological and morphological traits***

*Jana Martínková*

*Faculty of Biological Sciences, University of South Bohemia, Branišovská 31,  
370 05 České Budějovice, Czech Republic.*

*Fax +420 38 53 00 366; e-mail: jana.martinkova@tix.bf.jcu.cz*

### **Abstract**

I describe, in detail, changes in abundance of phenological phases during vegetative season in an oligotrophic dry meadow, and characterize changes in species composition or ability to record individual species in grassland during vegetative season. Our capability to record species presence or to estimate species cover is probably dependent on their phenological stage. Many grassland species start their reproductive cycle before mowing, but not all species are able to finish their reproductive cycle before it. I found largest changes in phenological composition immediately before the mowing time.

Furthermore, I attempt to find among species' traits the predictors of position of their phenological optima and to compare positioning of phenological optima between graminoids and forbs and between dominant and non-dominant species. Graminoids were found to start their reproductive cycle earlier than forbs. Transition from flowering to fruiting seems to be slower for graminoids than for forbs. Dominant species concentrate their reproductive cycle to the middle of vegetative season, non-dominant species "exploit" the edges of vegetative season. Positions of phenological optima are significantly different between graminoids and forbs.

### **Introduction**

Phenology is defined as a study of seasonal timing of life cycle events. This timing is one of the most important phenomena in plant and evolutionary ecology and has been attracting broad interest for years (Heinrich 1976, Poole and Rathcke 1979, Fagerstrom and Agren 1980, Cole 1981, Kochmer and Handel 1986, Ollerton and Lack, 1992, Fox and Kelly 1993, Stone et al. 1998, Gross et al. 2000). Seasonal timing of life cycle events can be critical for plant reproduction, and therefore for its survival (Rathcke and Lacey 1985).

Phenological studies usually recognize following events of plant life cycle: germination, flowering, fruiting, and death. The pattern of any cycle can be quantitatively defined by parameters like time of occurrence, duration, or synchronization with other individuals. These parameters can contribute to values of higher level parameters, e.g. degree of synchronization among species.

Majority of phenological studies is concerned with description of selected community or its functional part (Heinrich 1976, Opler et al. 1980, Rathcke 1988, Losvik 1991).

O'Neil 1999), while others studies did not (Ollerton and Lack 1992, Gomez 1993, Ollerton and Lack 1998).

Habitat choice by plants (as a result of natural selection) occurs in time as well as in space. Coexistence of species can be a consequence of different habitat choice by species in community (Bazzaz 1991). Coexistence of competitors is apparently associated with some degree of niche differentiation, and 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? Life-history events are timed to coincide with availability of necessary resources for plant growth. Seasonal as well as diurnal flowering phenology represents a form of temporal habitat choice (Bazzaz 1991).

Coexistence of species enabled by difference in phenology was examined (Iwasa et al. 1995, Laurie et al. 1997), but results were inconsistent.

In this study, I look at temporal niche separation from the phenological point of view. I try to find predictors of species phenological optima using two different methods of describing phenological state of plant populations. The characteristics used as predictors are species' morphological and ecological traits, species' average cover, dominance, and their classification into graminoids and forbs. In this way, differences in phenological optima for different ecological groups of species are sought.

This study addresses following questions:

- How the abundance of phenological phases of grassland species changes during vegetative period?
- How are the phenological phases of individual species shifted during vegetative period?
- Are the ecological and morphological characteristics of individual species related to their shift in phenological phases?
- How the number of recorded species fluctuates within a grassland community during vegetative period?
- How the percentual cover of individual species changes during vegetative period?

## **Methods**

### **Study site**

Study site, oligotrophic, traditionally managed meadow, is located near Zvíkov village, 10 km from České Budějovice, Czech Republic (48°59'N, 14°36'E, 500 m a.s.l.). It is

**Phenological phases**

I distinguished 5 phenological phases: sterile plant, plant with buds, flowering plant, plant with immature fruits, and plant with mature fruits (Table 1). Phenological phases were

Species name	Abbreviations	Reg. Tree Analyses	GLM analyses			Multivariate analyses	Dominance	Graminoid
			F	FP	MF			
<i>Allium oleraceum</i>	<i>AliOle</i>	N	Y	N	N	Y	Non-dominant	N
<i>Acetosa pratensis</i>	<i>AcePra</i>	Y	Y	Y	Y	Y	-	N
<i>Acetosa vulgaris</i>	<i>AceVul</i>	Y	Y	Y	Y	Y	-	N
<i>Agrostis tennuis</i>	<i>AgrTen</i>	Y	Y	Y	Y	Y	-	Y
<i>Agropyron repens</i>	<i>AgrRep</i>	Y	Y	N	N	Y	-	Y
<i>Achillea millefolium</i>	<i>AchMil</i>	Y	N	Y	Y	Y	Dominant	N
<i>Alchemilla monticola</i>	<i>AlcMon</i>	N	Y	Y	Y	Y	-	N
<i>Alopecurus pratensis</i>	<i>AloPra</i>	Y	Y	Y	N	Y	-	Y
<i>Anthoxanthum odoratum</i>	<i>AntOdo</i>	N	Y	Y	Y	Y	-	Y
<i>Avenula pubescens</i>	<i>AvePub</i>	N	Y	Y	Y	Y	-	Y
<i>Betonica officinalis</i>	<i>BetOff</i>	Y	Y	Y	Y	Y	Dominant	N
<i>Briza media</i>	<i>BriMed</i>	Y	Y	Y	Y	Y	-	Y
<i>Campanula rotundifolia</i>	<i>CamRot</i>	Y	Y	Y	Y	Y	Non-dominant	N
<i>Cardamine pratensis</i>	<i>CarPra</i>	Y	Y	N	N	Y	Non-dominant	N
<i>Carex</i> spp.	<i>Carex</i>	Y	N	Y	Y	Y	Dominant	Y
<i>Centaurea jacea</i>	<i>CenJac</i>	N	Y	Y	Y	Y	Dominant	N
<i>Cerastium vulgare</i>	<i>CerVul</i>	Y	Y	Y	Y	Y	-	N
<i>Cuscuta europea</i>	<i>CusEur</i>	N	Y	Y	Y	Y	-	N
<i>Dianthus deltooides</i>	<i>DiaDel</i>	Y	Y	Y	Y	Y	-	N
<i>Dactylis glomerata</i>	<i>DacGlo</i>	Y	Y	N	N	Y	-	Y
<i>Festuca ovina</i>	<i>FesOvi</i>	Y	Y	N	N	Y	Non-dominant	Y
<i>Festuca pratensis</i>	<i>FesPra</i>	Y	Y	N	N	Y	-	Y
<i>Festuca rubra</i>	<i>FesRub</i>	Y	Y	N	N	Y	Non-dominant	Y
<i>Fragaria vesca</i>	<i>FraVes</i>	Y	N	Y	Y	Y	-	N
<i>Galium boreale</i>	<i>GalBor</i>	Y	Y	Y	Y	Y	Dominant	N
<i>Galium verum</i>	<i>GalVer</i>	Y	Y	Y	Y	Y	Dominant	N
<i>Helianthemum nummularium</i>	<i>HelNum</i>	N	Y	Y	N	Y	Non-dominant	N
<i>Holcus lanatus</i>	<i>HolLan</i>	Y	Y	N	N	Y	Non-dominant	Y
<i>Knaulia arvensis</i>	<i>KnaArv</i>	Y	Y	Y	Y	Y	-	N
<i>Koeleria pyramidata</i>	<i>KoePyr</i>	N	Y	Y	Y	Y	Non-dominant	Y
<i>Lathyrus pratensis</i>	<i>LatPra</i>	Y	Y	Y	N	Y	Dominant	N
<i>Luzula campestris</i>	<i>LuzCam</i>	Y	N	Y	Y	Y	Dominant	Y
<i>Nardus stricta</i>	<i>NarStri</i>	Y	Y	Y	Y	Y	Dominant	Y
<i>Pilosella officinalis</i>	<i>PilOff</i>	N	Y	Y	Y	Y	Dominant	N
<i>Pimpinella saxifraga</i>	<i>PimSax</i>	Y	Y	Y	Y	Y	-	N
<i>Platago lanceolata</i>	<i>PlaLan</i>	Y	Y	Y	Y	Y	Dominant	N
<i>Platago media</i>	<i>PlaMed</i>	Y	N	N	N	Y	Non-dominant	N
<i>Poa pratensis</i>	<i>PoaPra</i>	Y	Y	Y	Y	Y	Dominant	Y
<i>Potentilla erecta</i>	<i>PotEre</i>	Y	Y	Y	Y	Y	Non-dominant	N
<i>Potentilla reptans</i>	<i>PotRep</i>	N	Y	Y	Y	Y	Non-dominant	N
<i>Prunus spinosa</i>	<i>PruSpi</i>	N	Y	N	N	Y	Dominant	N
<i>Prunella vulgaris</i>	<i>PruVul</i>	N	Y	Y	Y	Y	Non-dominant	N
<i>Quercus juv.</i>	<i>Quercu</i>	N	Y	N	N	Y	Non-dominant	N
<i>Ranunculus acris</i>	<i>RanAcr</i>	Y	N	Y	Y	Y	Non-dominant	N
<i>Sanguisorba officinalis</i>	<i>SaOff</i>	Y	Y	Y	Y	Y	-	N
<i>Sieglingia decumbens</i>	<i>SieDec</i>	Y	Y	Y	Y	Y	-	Y
<i>Silene nutans</i>	<i>SilNut</i>	N	Y	Y	Y	Y	-	N
<i>Tarax</i> spp.	<i>Tarax</i>	N	N	Y	Y	Y	-	N
<i>Thymus pulegioides</i>	<i>ThyPul</i>	Y	Y	Y	Y	Y	Dominant	N
<i>Trifolium medium</i>	<i>TriMed</i>	N	Y	N	N	Y	Non-dominant	N
<i>Trifolium montanum</i>	<i>TriMon</i>	N	Y	Y	Y	Y	-	N
<i>Trisetum flavescens</i>	<i>TriFla</i>	Y	Y	Y	Y	Y	Non-dominant	Y
<i>Veronica chamaedrys</i>	<i>VerCha</i>	Y	N	N	Y	Y	Non-dominant	N
<i>Vicia cracca</i>	<i>VicCra</i>	Y	Y	Y	Y	Y	-	N
<i>Viola canina</i>	<i>VioCan</i>	Y	Y	Y	Y	Y	Non-dominant	N
<i>Viscaria vulgaris</i>	<i>VisVul</i>	N	Y	Y	Y	Y	Non-dominant	N
<b>Total number of species</b>		<b>38</b>	<b>48</b>	<b>43</b>	<b>41</b>	<b>56</b>	<b>dominant 14</b> <b>non-dominant 19</b>	<b>graminoids 18</b> <b>forbs 38</b>

**Table 2** List of species, their use in particular analyses (Y-Yes, N - No) and name abbreviations used in graphs and ordination diagrams. Total number of species used in analyses and presence of species in GLM analyses with phenological forwardness optimum (F), "flowering plant" optimum (FP) and "plant with mature fruits" optimum (MF) is shown, together with species dominance and classification into graminoids and forbs. For details, see Methods.

corresponding to a “phenological peak”), and the optima of individual species were also used as predictors.

Morphological traits	States	Ecological traits	States	Extended traits	States
Leaf type	simple	Dispersal agent	uspecialised	Graminoid status	yes
	compound		wind carried by animals eaten by animals ants explosive mechanism		no
Leaf outline	entire	Dispersule size	value	Dominant species	yes
	lobed toothed crenate				no
Leaf shape I.	pointed rounded	Maximum height	value	Non-dominant species	yes no
Leaf shape II.	> 3 times as long as wide 1-3 times as long as wide length=width			Average cover	value
Leaf base	parallel-sided	Minimum height	value		
	rounded cuneate cordate sagittate				
Leaf petiole	petiolate	Defense on leaves	glabrous hairy soft hairy dense hairy stiff hairs		
	sheathing subsessile sessile				
Heterophylly	yes	Defense on stems	glabrous hairy soft hairy dense hairy stiff hairy		
	no				
Leave area	1.0-1 cm <sup>2</sup>	Pollen vector	insect wind selfed		
	1-10 cm <sup>2</sup>	Shade	light mid none		
	10-100 cm <sup>2</sup>	Soil nutrients	fertile infertile very fertile very infertile		

**Table 3** List of morphological, ecological and extended traits with their status as used in analyses. Adopted from Fitter and Peat (1994).

### Statistical analysis

I used multivariate statistical methods both for exploratory and confirmatory analyses with software package CANOCO for Windows, version 4 (ter Braak & Šmilauer 1998). These analyses were used to summarize:

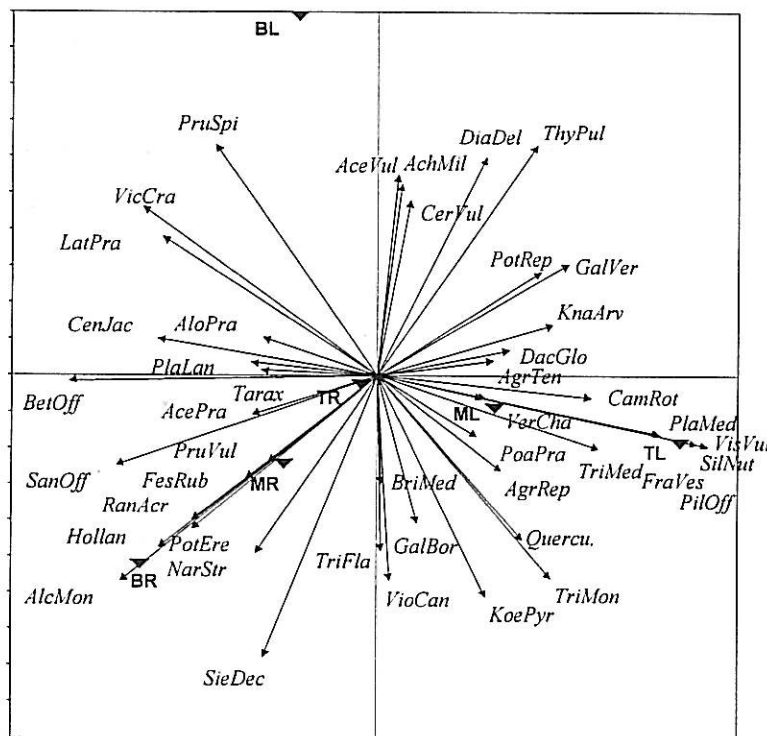
- (i) Difference in species composition among individual plots. Here I used redundancy analysis – RDA. Percentual cover values were log-transformed, standardized and centered by species average. Identification of plots (coded

Monte Carlo permutation tests (999 permutation) were used to assess significance of relations found in multivariate analyses, regression tree cross-validation was used to evaluate optimum complexity of each fitted tree.

## Results

### Percentual cover and number of species

Ordination diagram in Fig. 3 is result of RDA on species percentual cover data with identification of plots as explanatory variables. Effect of time was removed. The difference in vegetation composition was found significant in Monte Carlo permutation test ( $p=0.005$ ). First two ordination axes explain 40% of variability in primary data. Total of 56 species was found in all permanent plots during the whole vegetative season (Table 2). It is evident that species composition of plots ML, TL, TR, MR and BR is different from that in BL plot (with *Vicia cracca*, *Prunus spinosa*, *Thymus pulegioides*, *Dianthus deltoides*), furthermore vegetation of plots ML and TL is different from TR, MR and BL in species composition



(*Silene nutans*, *Fragaria vesca*, *Viscaria vulgaris* in the latter plots) (for abbreviation and location of plots see Fig. 1).

Fig. 3 RDA – ordination diagram displays occurrence of individual species (arrows) on sampled plots (triangles). First two ordination axes are shown. For abbreviation of species names see Table 2, for positioning and labels of plots see Fig. 1

The same diagram in Fig. 3 also shows the “preference” of species for individual plots. Species

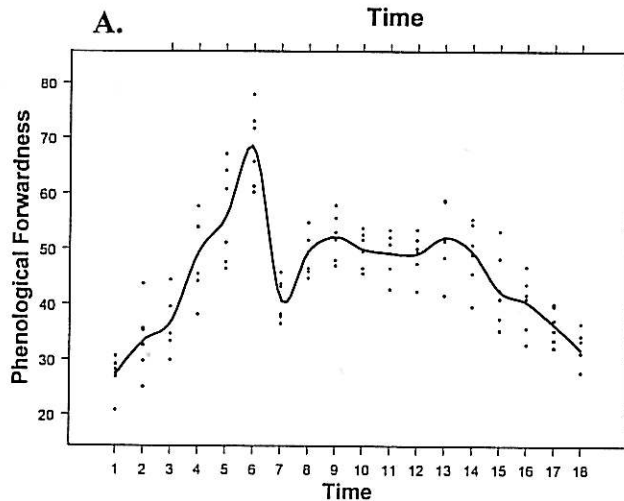
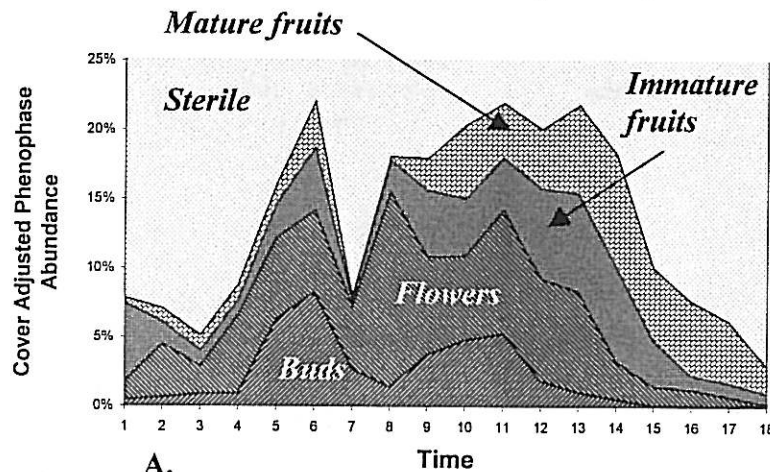
with short arrows are not strictly bound to any one of the plots (*Plantago lanceolata*, *Agrostis tenuis*, *Acetosa pratensis*, *Poa pratensis*, *Taraxacum* sp.) or their total cover is small compared to other species (*Prunella vulgaris*, *Veronica chamaedrys*). Species with longer arrows can be found in only one or two plots (*Thymus pulegioides*, *Alchemilla monticola*,

recorded at the end of May, near to mowing time. Speedy increase of number of species occurs during spring months, but no recovery in number of species after mowing was recorded. Furthermore, the speed of species number decrease is lower than the increase rate.

## Phenological phases

### *Cover-adjusted phenophase abundances*

Cover-adjusted phenophase abundances and phenological forwardness in relation to time are summarized in Fig. 6. Maximal phenological forwardness occurs before mowing time,



**A.**

**B.**

**Fig. 6** Changes in cover adjusted phenophase abundance (A) and phenological forwardness (B) during whole vegetative season. Phenological forwardness for individual plots is shown. Adjusted abundances are shown totally for whole observed part of community.

First two ordination axes explain 19,9 % variability in the primary data. Both ordination axes are significant ( $p=0,005$ ). Longer lines between sampling times mean larger changes in phenological composition. The largest shift in phenophase abundance is between Time 6 and Time 7, i.e. around the mowing time. The second ordination axis seems to separate the times before and after mowing. Larger changes are apparent at the beginning of

but recovery is not recorded afterwards. Maximum values of cover-adjusted phenophase abundances occur before mowing and after moving phenophase abundances reach the same values as before mowing.

The extent of phenological change of the community between observation times is summarized in Fig. 7. This ordination diagram is result of CCA method applied to adjusted phenophase abundance data.

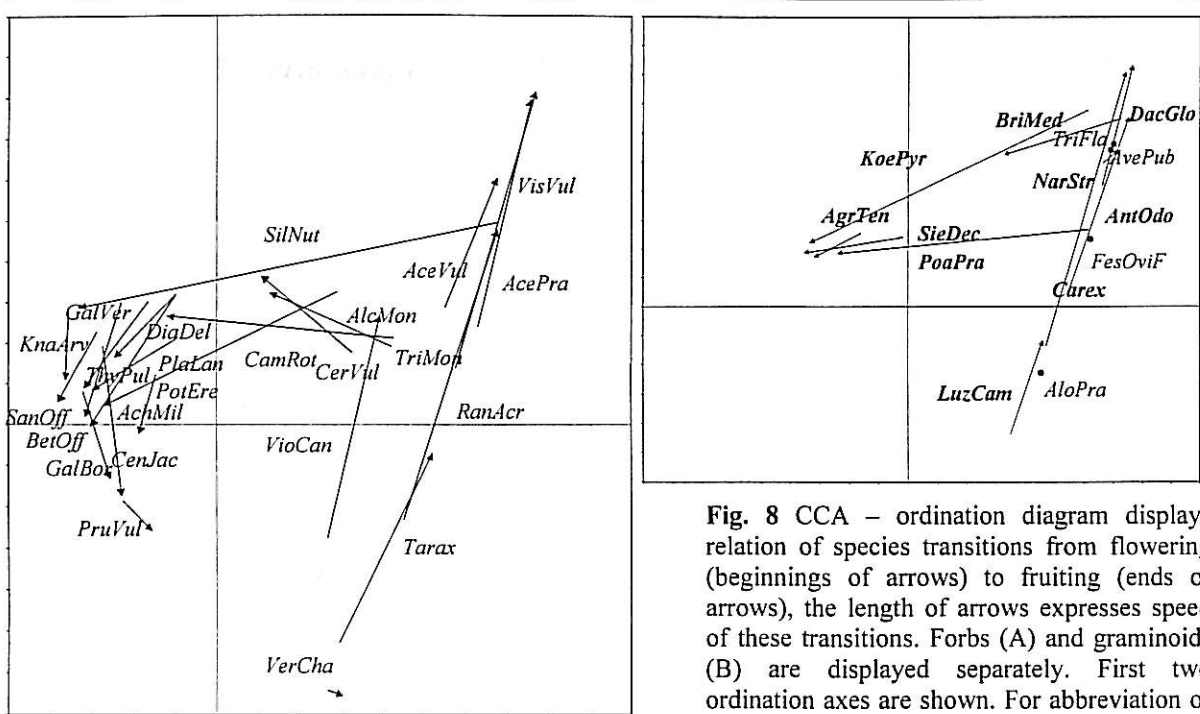


Fig. 8 CCA – ordination diagram displays relation of species transitions from flowering (beginnings of arrows) to fruiting (ends of arrows), the length of arrows expresses speed of these transitions. Forbs (A) and graminoids (B) are displayed separately. First two ordination axes are shown. For abbreviation of species names see Table 2.

Similarity of species in their phenological forwardness is summarized in Fig. 10. This diagram shows distribution of species maxima of phenological forwardness in time. Species with their maximum forwardness in spring months are in the top right quadrant of ordination diagram

(*Luzula campestris*, *Allium oleraceum*, *Veronica chamaedrys*).

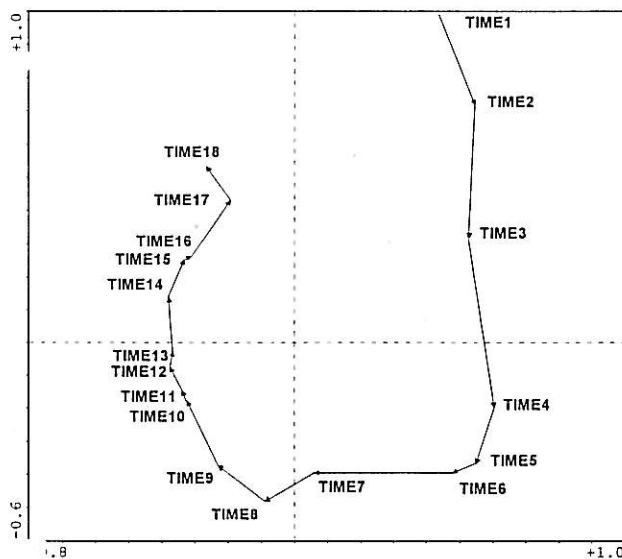


Fig. 9 CCA – ordination diagram displays similarity among observation times in their phenological forwardness. Subsequent observation times are connected by arrows. First two ordination axes are shown. For identification of observation times see Methods - Percentual cover and number of species.

Species with maximum in the last summer months are in the top left quadrant (*Achillea millefolium*, *Knautia arvensis*, *Centaurea jacea*). Clustering of individual species near the plot center indicates the relatively large spread of their phenological forwardness through the whole vegetative season. Outliers in the diagram are species with a poor representation of late phenological phases (plant with mature fruits or immature fruits; *Allium oleraceum*) or with a short period of appearance (recorded only few times; *Prunella vulgaris*, *Festuca pratensis*) or species strictly



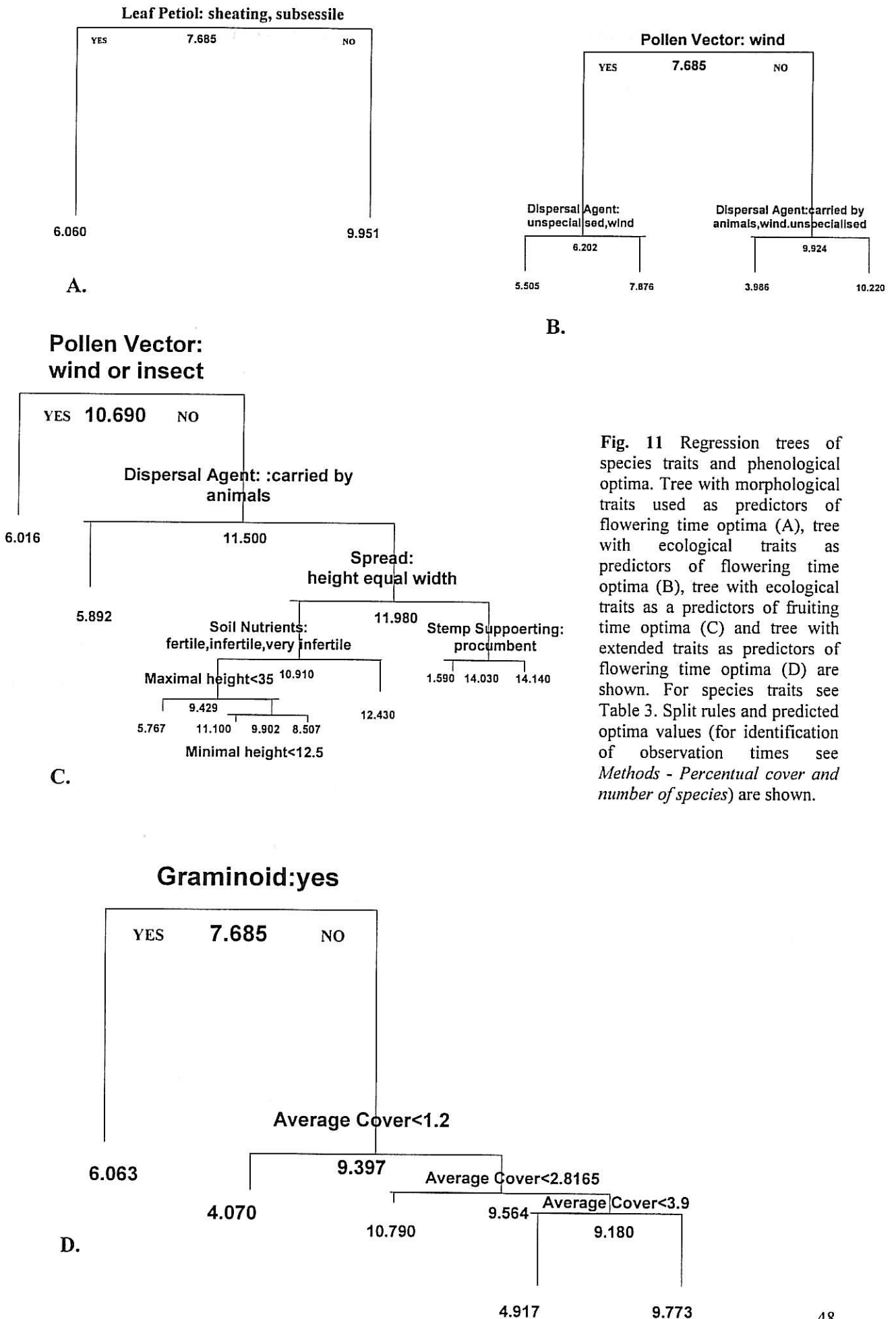
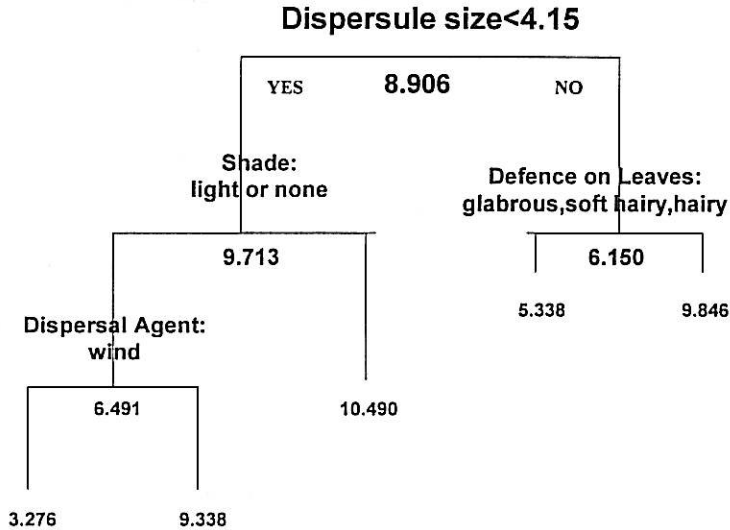
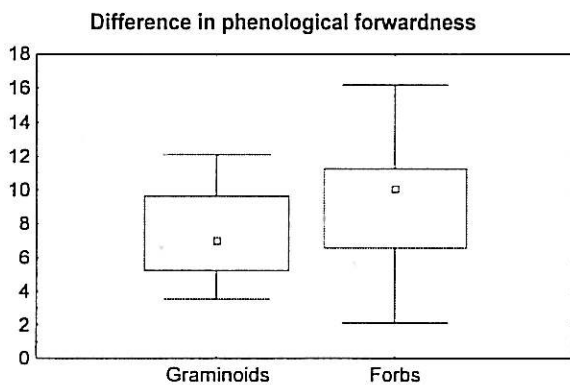


Fig. 11 Regression trees of species traits and phenological optima. Tree with morphological traits used as predictors of flowering time optima (A), tree with ecological traits as predictors of flowering time optima (B), tree with ecological traits as a predictors of fruiting time optima (C) and tree with extended traits as predictors of flowering time optima (D) are shown. For species traits see Table 3. Split rules and predicted optima values (for identification of observation times see *Methods - Percentual cover and number of species*) are shown.



**Fig. 13** Tree with ecological traits as predictors of phenological forwardness is shown. For species traits see Table 3. Split rules, and predicted optimum values (for identification of observation times see *Methods - Percentual cover and number of species*) are shown.

General linear models found significant difference ( $p=0.003$ ) in maxima of phenological forwardness only between graminoids and forbs (Fig. 14). Absolute value of difference between the weighted average of phenological forwardness optima and the optimum of phenological forwardness is negative correlated ( $p=0.02$ ) with the average cover of species (Fig. 15). Non-dominant species (Fig. 2, Table 2) have higher value of this



characteristic ( $p=0,009$ ), dominant species show an inverse pattern, but it is not significant (Fig.16).

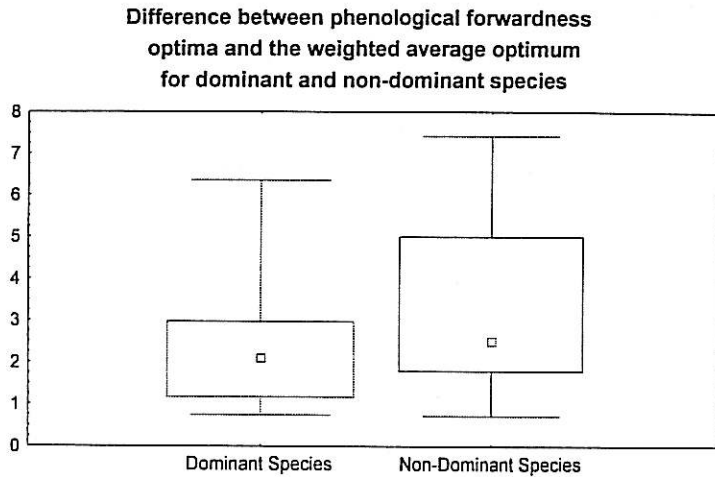
**Fig. 14** Box and whisker plot of differences in phenological forwardness maxima between graminoids and forbs. Median, quartiles and range for individual groups are shown.

## Discussion

I collected the data during one season and on one research site. This must be remembered when thinking about generality and reliability of the achieved results.

### Changes in number of species and percentual cover

Changes in number of species during whole vegetative season were recorded. Maximum number of species was observed at the beginning of May. Decrease of recorded



**Fig. 16** Box and whisker plot comparing absolute values of difference between phenological forwardness optima and the weighted average optimum, between groups of dominant and non-dominant species. Median, quartiles and range for individual groups are shown.

### Changes in phenological composition

Cover-adjusted phenophase abundances describe distribution of individual phenological phases during vegetative season. Total maximal abundance of non-sterile phenophases is up to 25%. Therefore, at most a quarter of total species cover occurs in reproductive cycle at the peak of vegetative season. Phenological forwardness expresses a progress to “fruiting plant” phenophase, which is considered to be most forwarded stage from a phenological point of view. Cover-adjusted phenophase abundances seem to be quite regularly distributed through the main vegetative season (from May to August), except of week of mowing when the most of reproductive organs are removed. Nevertheless, phenological forwardness is at its maximum before mowing, and its recovery was not recorded. This can indicate that many species are close to finishing their reproductive cycle before mowing. Comparing Fig. 6a and Fig. 6b shows that abundance of “plant with mature fruit” phenophase is higher after mowing, but phenological forwardness is larger before mowing. This follows from the difference of these two concepts.

The extent of phenological change of the community between observation times is summarized in Fig. 7 for phenophases abundances and Fig. 9 for forwardness. In both cases, largest changes are recorded immediately before mowing. Higher deceleration of phenological change and larger difference between sampling times after and before mowing is recorded for cover-adjusted phenophase abundances. Abundances are more sensitive to small phenological changes in community, compared with the phenological forwardness.

Phenological difference between graminoids and forbs are evident from Fig. 8a and Fig. 8b. Many graminoids start their reproductive cycle earlier than forbs. Their transition from flowering to fruiting seems to be slower than forbs’ transition. Some graminoid species

### **Coexistence of species**

Mechanisms believed to explain diversity in communities include spatial and temporal environmental variability (Tilman 1982). Although the idea of coexistence due to niche differentiation (differences in habitat selection) is appealing and follows logically from the selection theory, evidence for it in plants has not been forthcoming (Bazzaz 1991). Fine differentiation of species in their phenological optima can be seen as an advantage for “exploitation” of temporal space. This difference in species’ optima may correspond to the difference of species temporal niches. A study on tropical rain forest suggests that equilibrium community may include several distinct groups of species differing in phenology of regeneration (Iwasa et al. 1995). Fine differentiation in species’ phenological optima may contribute to explanation of species coexistence in grassland, but more detailed exploration is needed.

### **Conclusions**

- Our capability to record species or to estimate species cover is probably dependent on species phenological stage
- Many grassland species start their reproductive cycle before mowing, but not all species can finish their reproductive cycle before mowing. Some species and many individuals (mostly graminoids) never finish their reproductive cycle
- Largest changes in phenological composition were recorded immediately before mowing
- Graminoids start their reproductive cycle earlier than forbs. Graminoid’ transition from flowering to fruiting seems to be slower than forbs’ transition, but they finish reproductive cycle earlier than forbs
- Dominant species reach maximum phenological forwardness in the middle of vegetative season, non-dominant species occur more often on edges of vegetative season.
- Phenological optima of species can be partly predicted by their dominance in community and by their classification into graminoid and forb groups, but no such relation was found for the other ecological or morphological groups of species.
- Fine differentiation of species phenological optima can be seen as an advantage for “exploitation” of temporal space during vegetative season.

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