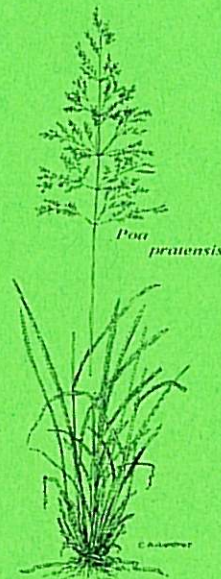


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COMPARATIVE ECOLOGY OF MEADOW GRASSES

Bc. Thesis



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Anotace:

Phenology, response to clipping, habitat preferences and litter decomposition rates were observed at 12 grass species coexisting within locality Ohrazení. Correlations between collected variables were tested.

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Prohlašuji, že jsem tuto bakalářskou diplomovou práci vypracoval sám pouze s použitím citované literatury.

Martin Střelec

V Českých Budějovicích dne 28. května 2001

MOTTO:

Ve stínu květů

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ABSTRACT

I performed observations and experiments on 12 grass species coexisting in an oligotrophic wet meadow Ohrazení close to České Budějovice. In spring 1999 I observed phenology of species. In spring 2000 I tested the effect of clipping on plant growth within manipulative greenhouse experiment. Clipping was done twice. With each clipping (or final harvest) I measured these characteristics: tuft height, number of culms and leaves, shoot biomass, root biomass. I recorded phytosociological samples from meadows and harvested the biomass in order to describe species preference of stand productivity. In winter 2000 / 2001 I carried out field experiment to determine litter decomposition rates. I have tested collected variables and also searched for correlations among them.

Most of grasses peak flowering in May, most likely to avoid dominant *Molinia caerulea* increase in biomass production in early summer. Grasses have significantly different relative growth rate (RGR), but RGR does not always correspond to species abundance in community. Clipping decreased, but also increased or let constant root-shoot ratio of plants. Clipped plants had smaller shoots and produced less biomass during the experiment than control plants. Clipping lowered number of culms, but not number of leaves. *Molinia caerulea* and *Alopecurus pratensis*, species dominant in meadows, occurred in communities with higher productivity, other species preferred rather lower productivity.

Relative growth rate did not correspond to litter decomposition rate. A trade-off was found: early flowering species can not grow much in height because of investing energy into development of flowers. No variable could predict species behaviour in landscape.

1. INTRODUCTION

Grasses is commonly used name for family *Poaceae*. This family contains either annual or perennial species. Grasses very often spread vegetatively producing long rhizomes. The majority of grasses has bisexual flowers (less commonly unisexual, but both types within one inflorescence), i.e. grasses are never dioecious. The whole family is anemogamous and species are very often self-pollinated. Family *Poaceae* splits into few subfamilies (depending on author usually from six to nine), from which the subfamily *Pooideae* is the most common one, in temperate meadows especially. All members of the subfamily are C3 plants (Hendrych 1977, Dostál 1989).

The grass species growing in meadows are mostly perennials. In vegetative phase their stem is very small and so the plumule is close to the ground. It produces leaves that largely exceed above the stem and leaves and sheaths itself in fact form the plant body. In consequence, if grass is grazed, mown or otherwise treated, it is not damaged, because leaf buds remain unaffected. At grasses forming dense tufts axial leaf buds produce additional shoots. This process is called tillering. Another way of lateral spread is forming of additional shoots that grow as underground rhizomes. More shoots usually appear along one rhizome. Performing this strategy the grass does not produce dense tuft, but sod. At some grasses secondary shoots spread across the soil surface.

The vigour of the plant (tuft) declines with age, thus spreading by seeds is also important. Flowering starts by rapid growth of the stem, inflorescence is hidden in leaf sheaths and then it appears outside. After flowering shoot starts to die immediately, just little of it remains alive. Since grasses are often self-pollinated, lack of seeds is very rare.

Grasses form very dense root system. Roots of short grasses reach the depth of maximum 1m, at tall grasses it is up to 2m. In contrary, lateral growth of roots is not very extensive, usually less than 30cm. Most of root biomass (ca. 90%) occupies the layer to 15 cm below soil surface (Archibold 1995).

Meadows are mesophilic plant communities where mainly perennial grasses dominate. In Czech republic the only natural (unaffected by human) meadows occur above the upper forest limits. It is not sure whether some meadows in river floodplains can be also natural. Other types of natural grassland communities occur in dry (e.g. steppes) or wet (several types of wetlands) stands. Beside water supplies they differ also edaphically and microclimatically (Rychnovská et al. 1972) and thus are not count as meadows.

The majority of Central European meadows was man-made. Meadows are regularly mown, because their main purpose is hay production, used mainly to feed cattle. Similar

purpose have pastures, which are short-grass communities. Mowing is disturbance, but grazing is moreover stress factor, including trampling. Unfertilised meadows are usually mown once a year (spring), fertilised twice a year (spring, late summer) (Moravec et al. 1994).

Phytosociologically meadows belong to class *Molinio-Arrhenatheretea*. It contains two orders, *Molinietalia* and *Arrhenatheretalia*. The alliance *Molinion* is subject of my study. This alliance occurs in periodically wet stands, where in wet periods groundwater exceeds above the soil surface. Often occurring species (except *Molinia caerulea*) are *Galium boreale*, *Selinum carvifolia* or *Betonica officinalis*. *Molinion* meadows are in those places, where the potential natural vegetation were most often communities *Quercus robur* – *Padus avium* or *Alnus glutinosa* – *Padus avium*, associations *Ulmo* – *Fraxinetum* or *Molinio* – *Quercetum* (Neuhäuslová et al. 1998). For nature conservation (Petříček et al. 1999) *Molinion* meadows are valuable, because diversity of dicotyledon plants occur there. *Molinion* can be found along altitudinal gradient, but mainly in lowlands. When agriculturally utilised, it used to be mown in late summer to autumn. If management stops, *Molinia* expands, but meadows do not degrade much and can be mown just once a two or three years. *Molinion* is oligotrophic and if overfertilised, the species richness declines.

Grime (1979) describes some basic principles of species coexistence and competition in a meadow. Competition for light is here very strong and very asymmetric, because conditions are very suitable for production and plants can develop their shoot enough. Also because of sufficient light conditions meadow plants are more sensitive to shading. However this does not mean definite advantage only for species capable of fast growing, complementarity between species is also very important. Klika (1955) explains three ways: edaphical (root), height and time (life cycle) complementarity. Because of mowing meadow species have to face disturbance (stress) and probably the most suitable growth forms (sensu Raunkiaer) to do that are "hemicryptophytes", which concerns all grasses.

Grime (1979) describes grasses as stress tolerators and gives explanation. They rely on lateral vegetative spread. In comparison to herbs grasses have lower relative growth rate and consequently longer leaf span. Their biomass production peaks in summer and then plants immediately start to die.

To verify theories about grass features and principles of coexistence various studies were done. Studies concern either single growth characteristics or species behaviour within the community. Negi et al. (1992) observed the phenology in alpine meadow in order to describe phenology at the community level, i.e. growth initiation, seed maturation and dead biomass accumulation of different growth forms. Grasses generally completed their life cycle later than herbs. Veenendaal et al. (1996) observed phenology and seed production of savanna grasses. Short-lived species produced large quantities of seeds,

whereas perennials with long vegetative stolons produced few seeds and their maturation was delayed in comparison to other species. Peak of seed production corresponds with peak of nutrient contents in plant. Lepš & Buriánek (1990) tested whether similar phenology and life history of species implies bigger competition and thus spatial segregation. Spatial segregation was not proved at phenologically similar species, but positive associations among annuals and negative associations among perennials were found. Kubínová & Krahulec (1998) observed invasive *Rumex longifolius*, if his phenology enables him to invade into mountain communities. Life cycle of this species is adapted to short growth period, therefore it can expand into high elevations in the mountains.

Skálová & Krahulec (1992) performed an experiment with *Festuca rubra* and demonstrated that shading of only the plant base results in lower tiller and leaf number and lower height and vitality of plant. Shipley & Peters (1990) tested relations between relative growth rates and root-shoot partitioning of herbaceous species. They rejected Tilman's theory that there is a trade-off between maximum growth rate and partitioning of biomass into non-photosynthetic tissues (Shipley & Peters 1990, Tilman 1991).

Bakker & de Vries (1985) applied different treatments and mowing regimes on abandoned grassland and observed the response of species. Fiala & Zelená (1992) tested changes in underground plant biomass and organic soil matter as a response to different mowing frequencies. Lepš (1999) tested species response to fertilisation, mowing and dominant species removal. He succeeded to predict response to fertilising by plant height, which showed how nutrient status is related to competition for light. Rychnovská et al. (1972) studied differences between dry, mesic and wet grasslands. Mesic meadows are the most productive ones and also have the highest transpiration. Grime & Lloyd (1973) published an atlas where they describe grassland species distribution in landscape in relation to environmental factors (pH, land use, substratum, slope etc.).

Mika (1972) did large measurement of mineral contents at various common agricultural grasses. He found that at twice mown meadows second harvest contains more water (70% of plant weight) than first harvest, also stems have more water than leaves. During senescence relative water content decreases, however the biomass grows, so absolute water content is constant. Ash content varies between 7-10%, second harvest has more than first, because it has more leaves.

Nutrient contents in leaves were also examined in relation to various leaf traits, especially life span (litter decomposition rate) (Berendse 1994, Cornelissen et al. 1997). Berendse (1994) supports an idea that low decomposability of litter is connected with adaptation to nutrient poor environments, because it lowers nutrients losses from plant body. Though, fitness can be increased both by low or high litter decomposition rate. Ryser & Urbas (2000) found a correlation between nutrient availability and leaf life span

just within Central European grasses, but dependent also on disturbance in habitat. Cornelissen & Thompson (1997) proved that graminoids have tougher leaves with higher silicon contents than forbs have. Litter decomposition rate of monocots was predicted by potassium content, but the prediction did not work for dicots.

Grime et al. (1996) found correlation between litter decomposition rate and palatability, either within large scale of species or just within graminoid monocots. Cornelissen (1996) compared litter decomposition rates of many temperate plant species and types. The growth form explained part of the variability in rates. Some leaf attributes (area, biomass) were tested for correlation with relative growth rate. Correlation was found also between relative growth rate and performance of woody species in habitats. Relative growth rate, leaf attributes and allocation can characterise functional groups of woody plants (Cornelissen et al. 1996). Thompson (1994) tested the effect of litter and nitrogen on consecutive generations of *Arabidopsis thaliana*.

In my study I compare several features of grasses coexisting within one locality. I investigated species phenology and describe the process of flowering and its timing within the season. A greenhouse experiment examined species grow response to clipping. The purpose was to quantify the effect of regular shoot removal on tuft formation and biomass production. I observed species performance occurrence in meadows habitats of different productivity in order to know how productive habitats species prefer. I also borrowed the data from an experiment done by Jan Lepš (Lepš 1999) to have description of species response to mowing and fertilising. I established field experiment for measuring species litter decomposition. Finally, I examined correlations between all collected variables in order to find connections among grasses behaviour.

In my study I asked following questions:

- **Is there a difference between timing of life cycle and process of flowering?**
- **What is the effect of clipping on biomass production, partitioning and tuft size and density?**
- **What productivity of habitat do species prefer?**
- **How do species differ in the process of decomposing litter?**
- **Is it possible to predict species behaviour from its growth characteristics?**

2. MATERIALS AND METHODS

2.1 Study sites

Ohrazení

The main study site was an oligotrophic wet meadow "Ohrazení" in the south Bohemia, Czech republic. It is located 10 km southeast from České Budějovice, 48° 57' N, 14° 36' E, 510 m a.s.l. Mean annual precipitation is 620 mm, mean annual temperature is 7.8 °C. It is non-agricultural, species rich meadow of about one hectare area, however quite heterogeneous.

Most of the vegetation belongs phytosociologically to the *Molinion* alliance (association *Molinietum caeruleae*, Moravec et al. 1995), with inserted patches of *Violion caninae*. Dominant species is *Molinia caerulea* (35% cover), other important species are *Nardus stricta* (12%), *Festuca rubra* (6%), *Potentilla erecta* (6%) and *Carex panicea* (4%). The entire locality accounts about 120 vascular and moss species. Traditional management is regular mowing, once or twice a year. The first mowing usually starts at the beginning of July. Meadow has been mown regularly, with a pause between the end of the 1980s and the year 1994. Since this year, some parts of the meadow have had different management regimes (mowing, fertilising, dominant species removal etc.) in various designs carried out within long term research of meadow community (Lepš 1999, Titus & Lepš 2000, Špačková et al. 1998 and others). Manipulated parts of the meadow were not included in my study. Secondary coniferous forest and a field at a short border surround the meadow.

Following parts of the study were performed in this locality:

- complete phenology observation
- observations of the species distribution in the landscape (partially)
- clipping experiment – all tillers were taken from the meadow
- the entire litter decomposition experiment

Lišovský práh

Lišovský práh is a longitudinal ridge between two basins (around towns of České Budějovice and Třeboň). It has a north-south direction and its altitude is in average around 500 m a.s.l., 100 m above the elevation of adjacent basins (400 m a.s.l.). The ridge includes rural landscapes consisting of fields, large agricultural fertilised meadows, productive coniferous forests, few fishponds and oligotrophic wet meadows with low productivity, some of them are protected. The locality Ohrazení is approximately in the middle of the ridge.

Observations of the vegetation mosaic in the landscape were done on the area up to 3 km far from Ohrazení.

Greenhouse

I used a medium-size greenhouse (10 × 20 m) in České Budějovice, belonging to the Faculty of Biological Sciences. The greenhouse has no moisture or temperature regulation. The clipping experiment was performed here.

2.2 Study species

The study concerns members of family *Poaceae* that most commonly occur on the locality Ohrazení. It includes 13 species, but not all of them were used in each experiment. Species used in experiments and observations are listed in Tab.1.

Tab.1 Study species and their inclusion in experiments.

Species	phenology	clipping	litter decomposition
<i>Agrostis canina</i> L.	+	+	+
<i>Alopecurus pratensis</i> L.	+	+	-
<i>Anthoxanthum odoratum</i> L.	+	+	+
<i>Deschampsia cespitosa</i> (L.) P. B.	+	+	+
<i>Festuca ovina</i> L.	+	+	+
<i>Festuca rubra</i> L. s.l.	+	-	-
<i>Helictotrichon pubescens</i> (HUDS.) PILGER	+	+	-
<i>Holcus lanatus</i> L.	+	+	+
<i>Molinia caerulea</i> (L.) MOENCH	+	+	+
<i>Nardus stricta</i> L.	+	+	+
<i>Poa palustris</i> L.	+	-	-
<i>Poa pratensis</i> L.	+	+	+
<i>Sieglingia decumbens</i> (L.) BERNH.	-	+	-

All the species are quite common in Ohrazení and other surrounding meadows, i.e. in oligotrophic or mesotrophic meadows, either permanently or seasonally wet, usually not agriculturally utilised. However, most of the species occur more often in other habitats. E.g. *Alopecurus pratensis* is dominant in river floodplain meadows (alliance *Alopecurion*), *Festuca ovina* grows rather in xerophilous grasslands etc. Some of the grasses are also sown in agricultural productive meadows for hay production or they grow in urban lawns (*Alopecurus pratensis*, *Poa pratensis*, *Holcus lanatus*) (pers.obs., Regal & Šindelářová 1973). Therefore most of these species can also broadly occur in other vegetation types not similar to the locality Ohrazení. The grasses occur only occasionally in nearby forests.

None of the species is protected in Czech republic and doesn't require special attention in the area of south Bohemia (Chán (ed.) 1999).

2.3 Experiments and observations

Phenology

Phenology observations were done in spring 1999 in the locality Ohrazení. I started on 6th May 1999 when the first early species just began to produce culms and the others were still completely sterile. Last samples were taken at the end of June 1999, when flowering of almost all species was finished. I did the observations in 3 – 4 days intervals, from the first half of June after a week or more, because most of species were already fading away. The total of 15 observations was done.

For each species I observed how much percent of the population occurs in each of six phenological phases. These phases were named and defined as following:

- | | |
|------------------|--|
| 1. leaves | sterile plant |
| 2. culms | appearing culms with inflorescence hidden inside |
| 3. inflorescence | inflorescence outside but spikelets still not open |
| 4. flowering | spikelets are open, stamens out |
| 5. fade | fading away, loss of green colour and declines |
| 6. death | dry, dead plant |

Percentage amount of each phase was estimated as percentage cover of individuals / tufts being in that phase in relation to whole population. The percentage was estimated at the nearest 10%, in smaller amounts (up to 20%) by 5%, occurrence of only few individuals was classified as 1%. Unlike standard methods (Balátová-Tuláčková 1987) the estimates were not done in permanent plots, but in the whole locality. Every population was estimated independently from the others, whereas every sample was estimated in comparison to previous sample, i.e. if the value of each phase is bigger or smaller then it was before.

Clipping

This greenhouse experiment was performed in spring 2000. 11 species (details in Tab.1) were grown in pots, their response to clipping was registered and their growth characteristics were measured. All species were taken from the locality Ohrazení in half of March 2000, when all of them were still sterile, but new green leaves were developed after winter. Experiment itself was established by planting tillers into pots on 26th March 2000. Tillers were let to develop, watered equally and regularly. After one month the clipping regime started, as shown in following survey:

- 26.3. tillers measured and planted
- 27.4. 1st measuring and clipping
- 20.5. 2nd measuring and clipping
- 15.6. final measuring and harvest

From each of 11 species, 10 tillers were planted, each one to a separate pot 18 × 18 cm. The used substrate was enriched garden peat soil to avoid nutrient limitations. Tillers of tufted species were all taken from one tuft. Single culm with roots was considered tiller, for tufted species tiller was an entity consisting of few culms kept together and having sufficient root system. Before transplantation measurements of initial height and root length were taken and number of culms and leaves were counted. At the same time five more similar tillers of each species were measured, dried and weighted, and the values were used to determine initial biomass weight of planted tillers using multiple regression.

Pots were placed into trays in fives and were completely randomised. Before the first clipping five tufts of each species were randomly selected and the rest was left as control. Tufts were clipped 2 cm above the surface so that all leaves were almost completely removed. Harvested biomass was dried at 80°C for two days. For each clipping (and final harvest) I measured these set of data for each tuft:

- number of culms
- number of leaves
- tuft height
- shoot dry weight (clipped tufts only)

Within final harvest root and shoot dry weight for all tufts was measured, however, leaves were not counted. For weighing I used laboratory weighting-machine "Precisa" with resolution 0.01 g.

Species distribution in the landscape

Phytosociological relevés were recorded in May and June 2000, when most meadows have a peak of their biomass and the agricultural are just ready for mowing. Relevés were taken from the locality Ohrazení and its close vicinity, usually one relevé from agricultural meadow and about 2 – 3 relevés from non-agricultural (and thus usually more diverse) meadow. The total of 20 relevés was collected during three-week period.

Relevé area was 5 x 5 metres and it was randomly selected, within central zone 5 metres far from meadow boundary to avoid the edge effect. Percentage cover of each vascular plant species (excluding mosses) was visually estimated on the scale with 5% resolution. Values up to 5% were estimated with 1% resolution, few individuals were classified as 0.5% and rare occurrence was classified as 0.1%.

Within each relevé plot of 0.5 x 0.5 metres was randomly selected. The standing biomass from the plot was clipped using scissors and also the litter was collected separately. Both these components were dried at 80°C for two days. The dry weight was considered as a measure of productivity of the meadow. It was also recognised, if the meadow is agriculturally utilised or not.

Litter decomposition

Material for this field experiment was collected in summer 2000 and the decomposition itself lasted from autumn 2000 till spring 2001. The whole experiment was following the standard method of litter-bags (see Tesařová 1987). In the middle of August 2000 standing biomass of eight species (see Tab.1) was harvested from the locality Ohrazení. Key term for accepting a species for experiment was if it is possible to harvest enough biomass from the locality. The biomass was dried at 80°C, exactly dosed into litter-bags, installed into the locality Ohrazení and then sampled according to a following scheme:

- 16.8.2000 biomass harvested
- 15.11.2000 litter-bags installed
- 28.1.2001 1st sample set
- 7.3.2001 2nd sample set
- 18.4.2001 final sample set

Litter-bags were made from nylon netting with mesh size 1.5 mm. This mesh size of gaps allows soil microorganisms (*Bacteria*, *Fungi*, *Protozoa*) and mesofauna (*Collembola*, *Nematoda*) enter the bag, but prevents macrofauna (*Annelida*, *Coleoptera*) take part in the decomposition. Beside that the loss of biomass (especially at narrow-leaved species) is minimised. The nylon netting was fused together with soldering iron. Standard size of a litter-bag was 10 x 7 cm.

For each species 15 doses of biomass were weighted. One dose was on average 1.75 g of dry weight. Exact value was written down and the dose was put into a litter-bag along with tinfoil label. The size of a litter-bag and weight of the dose were chosen on purpose, so that the biomass in the litter-bag is not very dense and thus the conditions for decomposition are close to those in natural conditions. In the locality, litter-bags were put on nylon threads (15 threads, each containing one litter-bag from each species) and fixed to the ground by nail in order to keep them constantly on the surface.

As sample five threads (i.e. five litter-bags of each species) were randomly removed from the locality, dried at 80°C and weighted again with 0.01 g resolution.

2.4 Data analysis

Phenology

Phenology data were plotted as XY or column chart using Microsoft Excel or S-plus. A chart plotted for one species enables to display the sequence of phenological phases within time. A chart summarising one given phase of each species within time enables to compare, how early the species are, and shows the development of whole community.

For simple quantification of how early does the species flower we can use a peak value of one phenophase. It seems it is not very precise to simply use a date of a day, when most of individuals occur in that phenophase. It makes problems if the value remains the same or similar (that was just an estimate) for longer time. Therefore I used weighted mean (1), which somehow reflects the entire process of phenophase peaking.

$$\text{peak}_{p,s} = \frac{d_1v_1 + d_2v_2 + \dots + d_fv_f}{v_1 + v_2 + \dots + v_f} \quad (1)$$

where $d_1 \dots d_f$ day (how late from the beginning)
 $v_1 \dots v_f$ value of phenophase (percent of individuals)
 $\text{peak}_{p,s}$ peak of phase p and species s

To describe the phenology not by using separate phenophases but by regarding the whole life cycle I use one criterion: *index of phenology* (IP). IP=0 for complete sterile plant, IP=1 for dead plant. In between its value is summarised weigh of phenophases as should be clear from formula (2). IP describes current state of phenology (life cycle) in one day. It serves for overall comparison of phenology.

$$\text{IP}_{s,d} = 0.0p_1 + 0.2p_2 + 0.4p_3 + 0.6p_4 + 0.8p_5 + 1.0p_6 \quad (2)$$

where $\text{IP}_{s,d}$ index of phenology of species s in day d
 $p_1 \dots p_6$ percentage of individuals being in phenophase

IP is a non-decreasing function of time. Thus, the earlier is a life cycle of a species, the larger is the area below its IP curve (Fig.1). Therefore the definite integral of IP function can generally quantify, how early the life cycle of the species is. The IP function is simplified as linear joins between plotted points and the integral is count as sum area of trapezoids (Fig.1) on defined interval. To generalise, the integral was divided by length of this interval.

For my study I used weighted mean (1) for phases "inflorescence" and "flowering" as a measure of one phase peaking and IP integral on interval 1. to 29. day as measure of how early the life cycle is.

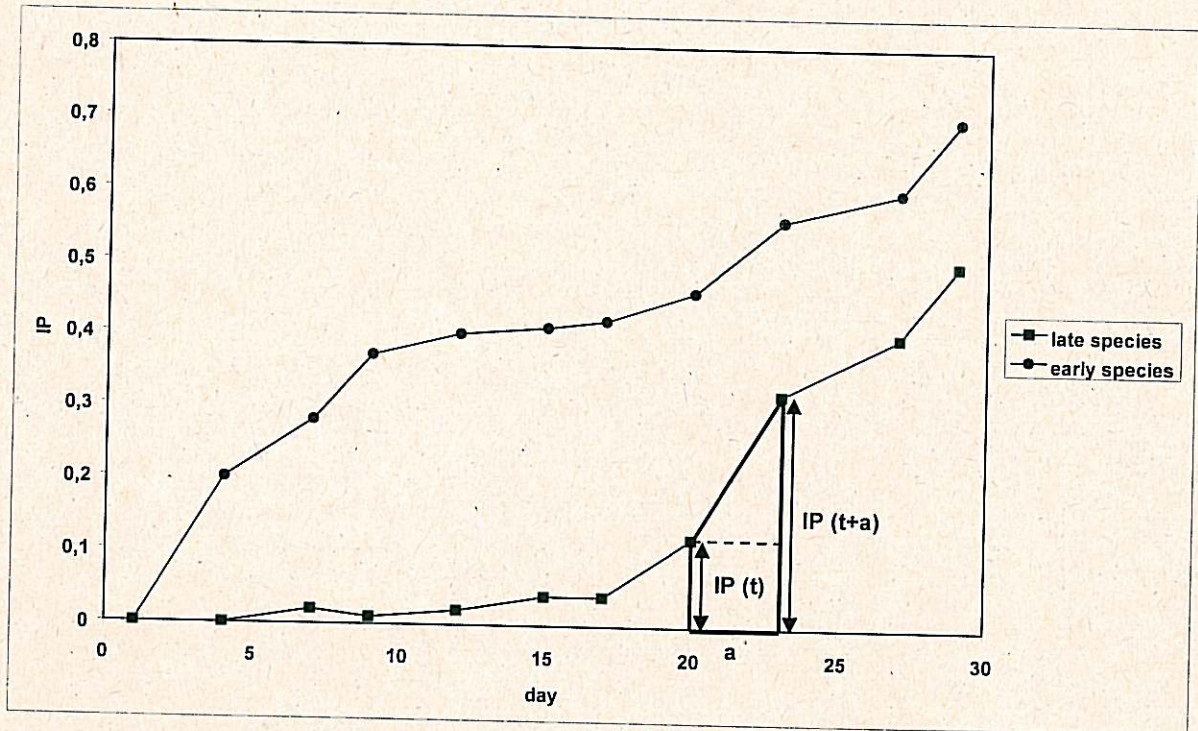


Fig.1 IP function and one trapezoid as basic element for counting the integral.

Clipping

First of all, two growth characteristics were counted for further analyses: RS-ratio and RGR. RS-ratio (root-shoot ratio) was count for each tuft according to formula (3):

$$RS_{s,t} = \frac{\text{root}_f}{\text{shoot}_f} \quad (3)$$

where $RS_{s,t}$ RS-ratio of species s and tuft t
 $\text{root}_f, \text{shoot}_f$ root and shoot final weight of given tuft

Relative growth rate (RGR) was counted only for non-clipped tufts (4).

$$RGR_{s,t} = \frac{\ln(w_f) - \ln(w_0)}{t} \quad (4)$$

where $RGR_{s,t}$ RGR of species s and tuft t
 w_f total final weight of tuft
 w_0 initial weight of tiller (estimated by regression)
 t experiment duration (81 days in this case)

Other measured variables were analysed by ANOVA. It was always two-way ANOVA with fixed effect factors "species" and "clipping". It included variables related to final harvest (and thus describing final state), which are these:

- RS-ratio
- shoot
- final biomass (root + shoot)
- total biomass (total biomass produced during experiment) ⇒
 - non-clipped: total biomass = final biomass
 - clipped: total biomass = final biomass + 1st harvest + 2nd harvest
- total shoot biomass

RGR is defined only for not cut species and therefore it was analysed by one-way ANOVA with factor "species".

Repeated measurements ANOVA with factors "species", "clipping" and "time" (with three levels) was used to analyse variables measured during experiment:

- culms
- height
- leaves (two levels only)

Averages and ratios of all variables were then used as input data for other analyses.

Species distribution in the landscape

Sample data of percentage cover were transferred into a scale 1 to 9 according to following rules (Tab.2):

Tab.2 How to transfer percentage cover to 1 – 9 scale.

Percentage cover upper limit (included)	Value
0.1	1
0.5	2
1	3
5	4
10	5
25	6
50	7
75	8
100	9

This scale provides more detailed resolution in those values of cover in which do grass populations mostly occur. It corresponds to the ordinal transformation of van der Maarel (1979).

Transformed data were used as an input to redundancy analysis (RDA), part of software package CANOCO for Windows (ter Braak & Šmilauer 1998). Also DCA was used to verify, if selected analysis (RDA) is suitable (according to the length of gradient). Dry weights of live biomass and total biomass (live + litter) collected from each sample were used as environmental variables, but only one was selected for the analysis and tested by Monte Carlo permutation test (199 permutations). Results were presented as a triplot. Species scores on 1st canonical axis (identical with environmental variable) were used as a measure of species preference of habitat productivity.

In second RDA analysis, additional binary variable was used to distinguish between agricultural and non-agricultural meadows.

Litter decomposition

For each litter-bag relative decrease of biomass was counted as dividing final dry weight by input dry weight. These relative results were analysed by two-way ANOVA with factors "species" and "time". Time has three levels, because there are three samples the input weight is 100%. Means for each sample and species were also plotted in XY chart. Final proportion of decomposed biomass from input biomass was also used as measure of species litter decomposition rate.

Correlations and predictions

Data from field experiment (Lepš 1999) provide additional information about species behaviour in ecosystem and response to fertilisation and mowing. The goal was to find various correlations between variables. Each variable was counted as an average for each species. Following list shows names of variables and describes them (see corresponding parts of 2.4 Data analysis for details):

phenology:

- integral
- inflorescence
- flowering

clipping:

(Note: There are three variants of one variable for one species: "Y" for clipped, "N" for control, Y/N is ratio of clipped / control. Also variables measured within time were used as ratios 3/1 or 2/1.)

- shoot
- final
- total
- total shoot
- RS
- RGR
- height 3/1
- culms 3/1
- leaves 2/1

landscape distribution, species behaviour:

(Note: All variables are scores on 1st canonical axis that is identical with environmental variable of the same name.)

- live
- total
- mowing
- fertilising

litter decomposition

- litter decomposition rate

Variables related with treatment were considered as dependent. Correlation between dependent and independent variable suggest the possibility of prediction. All of these correlations were *a priori* considered as independent falsifiable hypotheses. Correlation between two independent variables shows the relations and principles in plant growth. From these correlations one was chosen *a priori*: RGR (4) versus litter decomposition rate. The others were *a posteriori* reviewed, whether they are not trivial and are worth interpreting.

Square correlation matrix was counted, using software STATISTICA for Windows. Correlation coefficients were tested at the level of probability $\alpha = 0.05$. Bonferroni correction was not done. Previously selected ones were checked and eventually plotted. Other significant correlations were examined. For species behaviour multiple regression with forward selection was used.

3. RESULTS

3.1. Phenology

Flowering and life cycle

Species differed in changing phenological phases. We can approximately recognise and describe three types of population behaviour, here shown on an example of three species that change between two phenophases:

- whole population remaining in one phase for a long time, phase peak flat (*Poa pratensis*, Fig.2)
- quick passing over one phase (culms) and quick change to next phase, peak far from reaching 100%, remarkable phase overlapping (*Deschampsia cespitosa*, Fig.3)
- continuous change between two phases, clear peak reaching 100%, moderate overlap (*Holcus lanatus*, Fig.4)

(Note: Column charts used only for better display. X-axis is categorised, not scaled.)

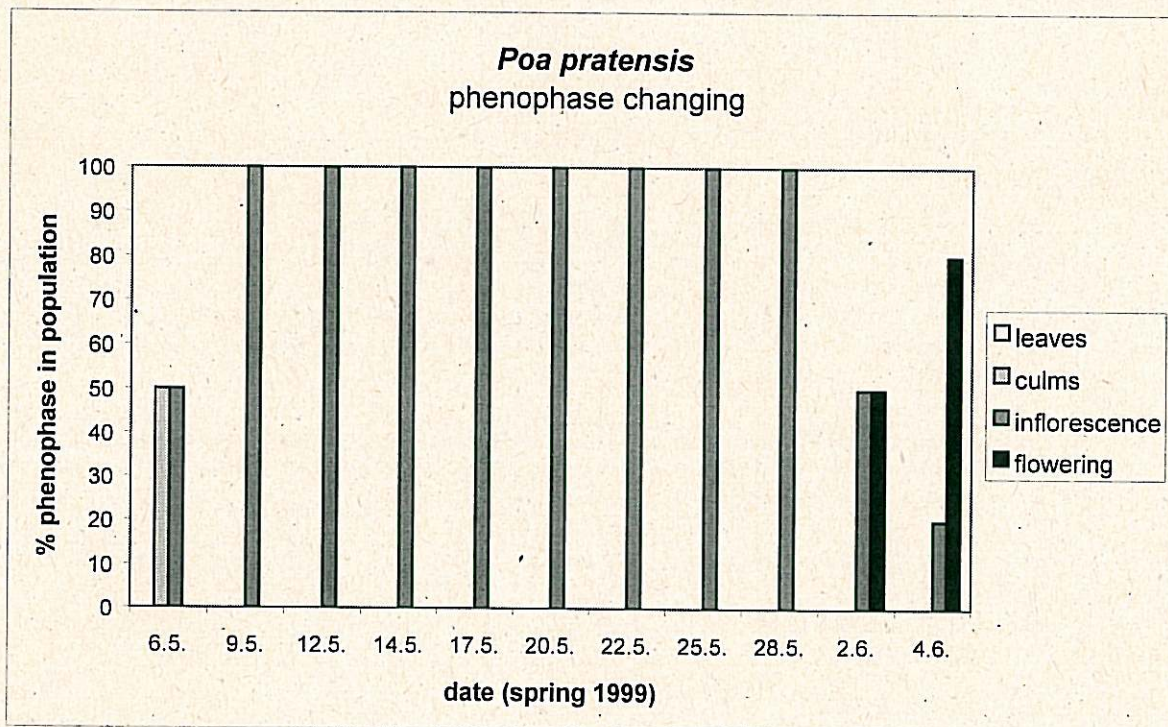


Fig.2 Phenophase changing of *Poa pratensis*, bar chart. One phenophase lasts in population for a long time.

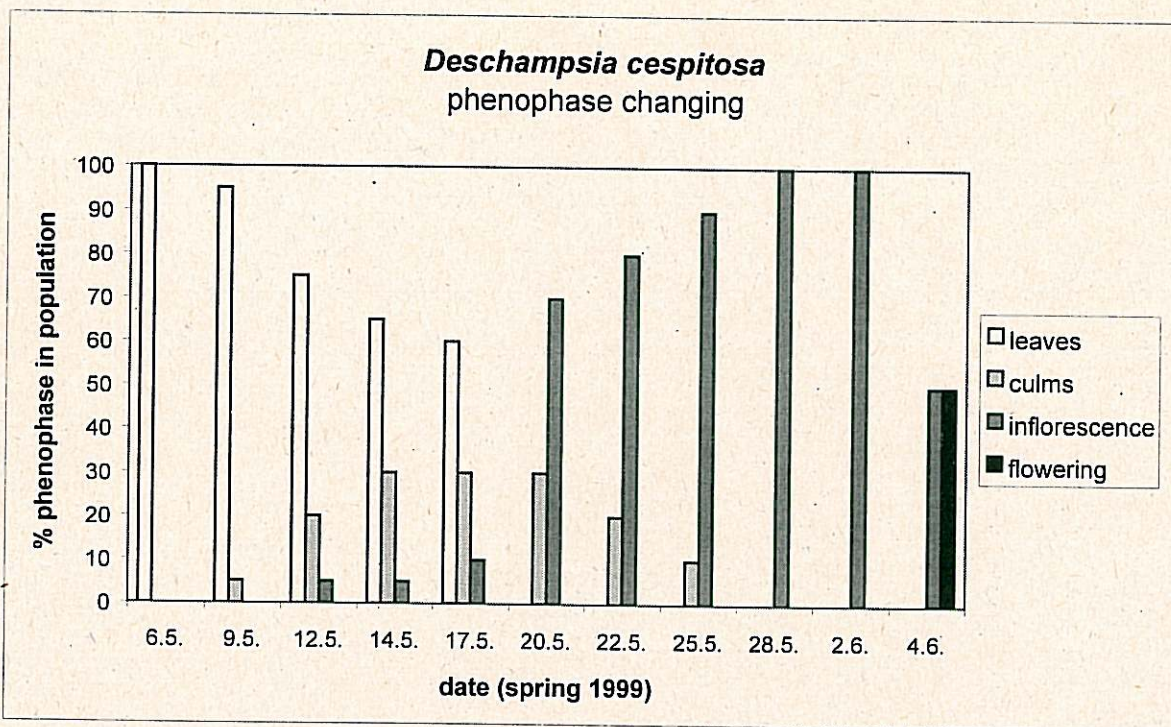


Fig.3 Phenophase changing of *Deschampsia cespitosa*, bar chart. Population quickly passes over one phase .

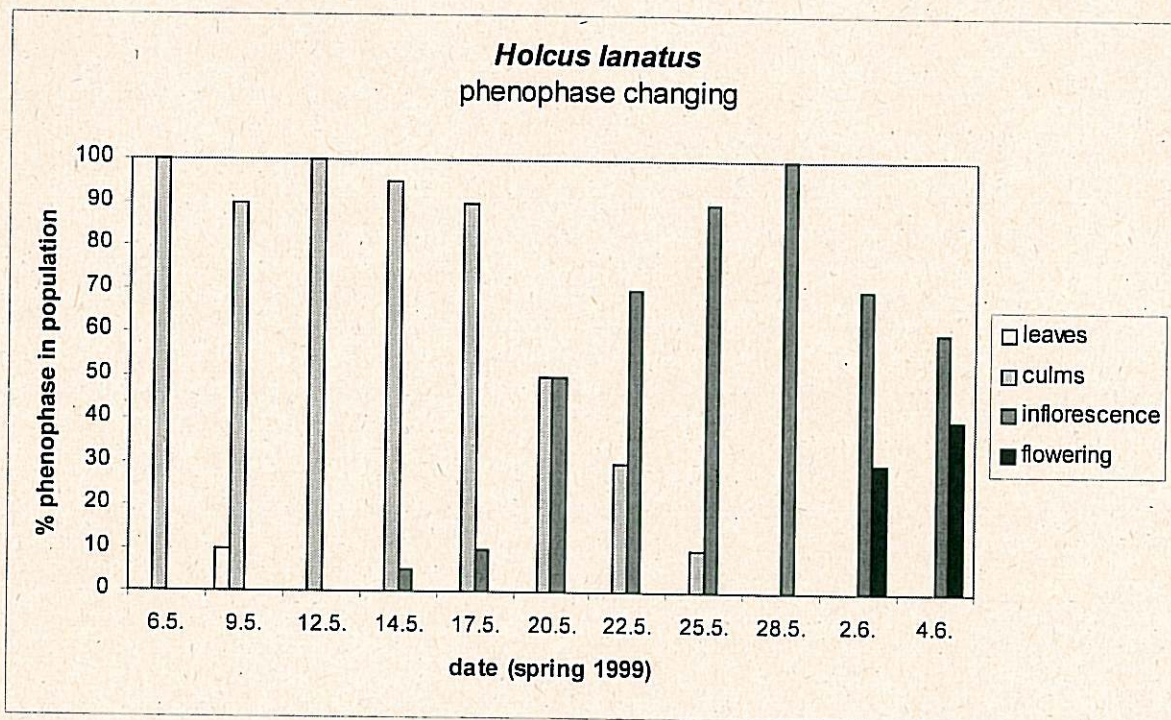


Fig.4 Phenophase changing of *Holcus lanatus*, bar chart. Two phases continuously change with regular overlap.

Species sequence in the community

To review the phenology of the whole community I compared peaking of early phenophases. Fig.5 shows phase "inflorescence" (the very beginning of flowering) of each species we can notice these features:

- two species (*Anthoxanthum odoratum* and *Alopecurus pratensis*) starting to flower obviously earlier than other species – their peaks are visibly separated from others
- quite rapid start of other species (steep curves), peak is reached c. during one week
- earlier start of *Nardus stricta* and *Helictotrichon pubescens* can be distinguished and also later start of *Poa palustris*, but the peaks are not clearly shifted from each other
- very late species almost did not start to flower (*Molinia caerulea*, *Agrostis canina*)
- (*Poa pratensis* was removed off the chart because of its flat peak – compare Fig.2)

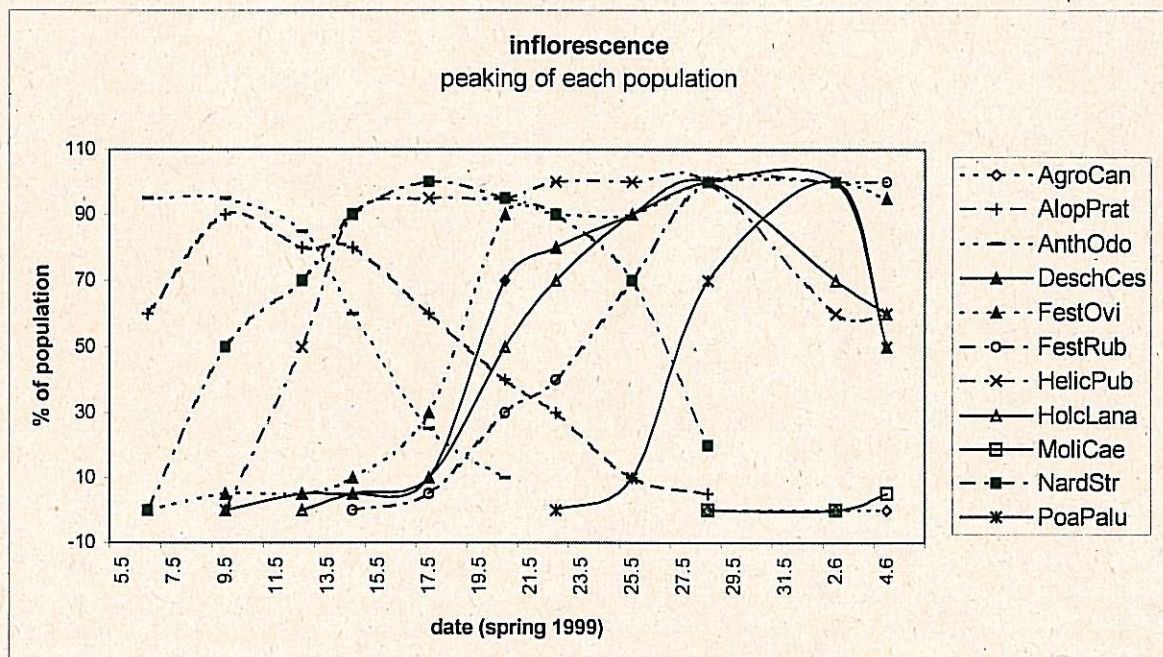


Fig.5 Peaking of phase "inflorescence" in each population, XY chart. Not so many peaks of phase "inflorescence" occur separately, except of those of very early or very late species.

Day of peaking of phases "inflorescence" and "flowering" were also counted as weighted mean (formula (1)). Values are given in Tab.3.

Tab.3 Peaks of phenophase "inflorescence" and "flowering" expressed as a serial number of day after start of observation (i.e. 6.5.2000).

	AnthOdo	AlopPrat	NardStr	PoaPrat	HelicPub	FestOvi
inflorescence	5.5	8.5	13	14	17.5	21
flowering	19	20.5	25	28	28	29
	DeschCes	HolcLana	FestRub	PoaPalu	MoliCae	AgroCan
inflorescence	21.5	23.5	24	26	52	—
flowering	29	31	—	—	—	—

Life cycle time schedule

Index of phenology (IP) was chosen for describing and comparing life cycle of species, since it involves all phenophases (see formula (2)). Differences between phase shifting now become more explicit and also species overall advance in flowering can be seen clearly (Fig.6):

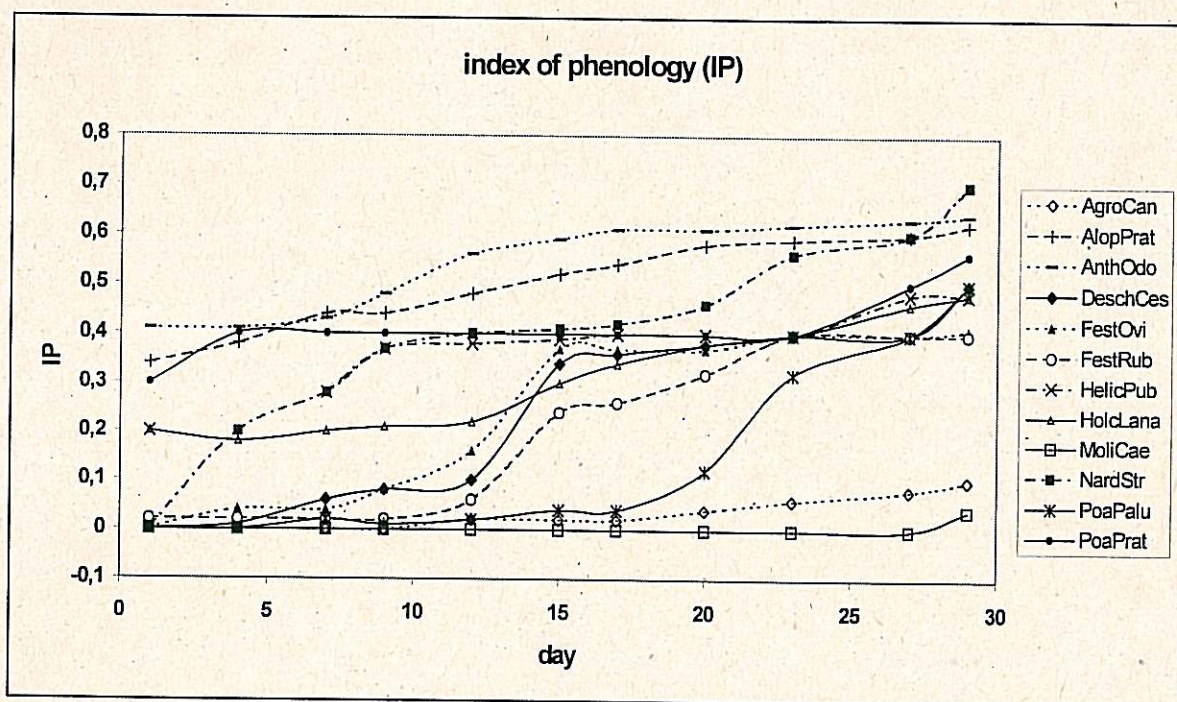


Fig.6 Different advance in species life cycle expressed by index of phenology, XY chart ("day" on X-axis is serial number of day after start of observation).

- *Anthoxanthum odoratum* was obviously ahead of *Alopecurus pratensis* during the whole life cycle (compare Fig.5 dealing only with early stage of flowering)
- at the very beginning *Poa pratensis* and *Holcus lanatus* are also ahead, but then are reached by other species
- in the life cycle of *Festuca ovina*, *Festuca rubra* and *Dechampsia cespitosa* we can see sharp increase, from the global view their life cycle is very similar
- start of life cycle of *Poa palustris* is a bit shifted from others
- *Molinia caerulea* and *Agrostis canina* are extremely late
- generally we can distinguish fast life cycle process (steep curves, e.g. *Nardus stricta*), slow life cycle process (flat curves, e.g. *Poa pratensis*) and rapid steps in development ("steps" in curves, e.g. *Festuca ovina*)
- at early times the advance of species is very diverse, at later times it is more similar (except very late *Molinia caerulea* and *Agrostis canina*)

Exact quantification of life cycle forwardness is the area below IP curves on Fig.6 (for details see 2.4 Data analysis). Succession of species life cycle is following (Tab.4):

Tab.4 Forwardness of life cycle expressed as integral of IP function.

	AnthOdo	AlopPrat	NardStr	PoaPrat	HelicPub	FestOvi
forwardness	0.529	0.488	0.391	0.397	0.330	0.237
	DeschCes	HolcLana	FestRub	PoaPalu	MoliCae	AgroCan
forwardness	0.230	0.294	0.192	0.121	0.0014	0.029

3.2 Clipping

Relative growth rate (RGR)

One-way ANOVA revealed significant differences ($F=15.669$, $p<1 \times 10^{-6}$) in species relative growth rate (RGR) (Fig.7).

- highest RGR has *Agrostis canina* followed by *Poa pratensis*
- *Alopecurus pratensis*, *Anthoxanthum odoratum* and *Holcus lanatus* have almost the same RGR, but the RGR varied among species
- large variability of RGR was in species with low RGR
- the highest RGR was four times bigger than the lowest one

(Note: Lower values of RGR can be biased because of resolution of the weighting machine. Another bias could be caused by regression, which is not so precise method for determining initial weight of plant.)

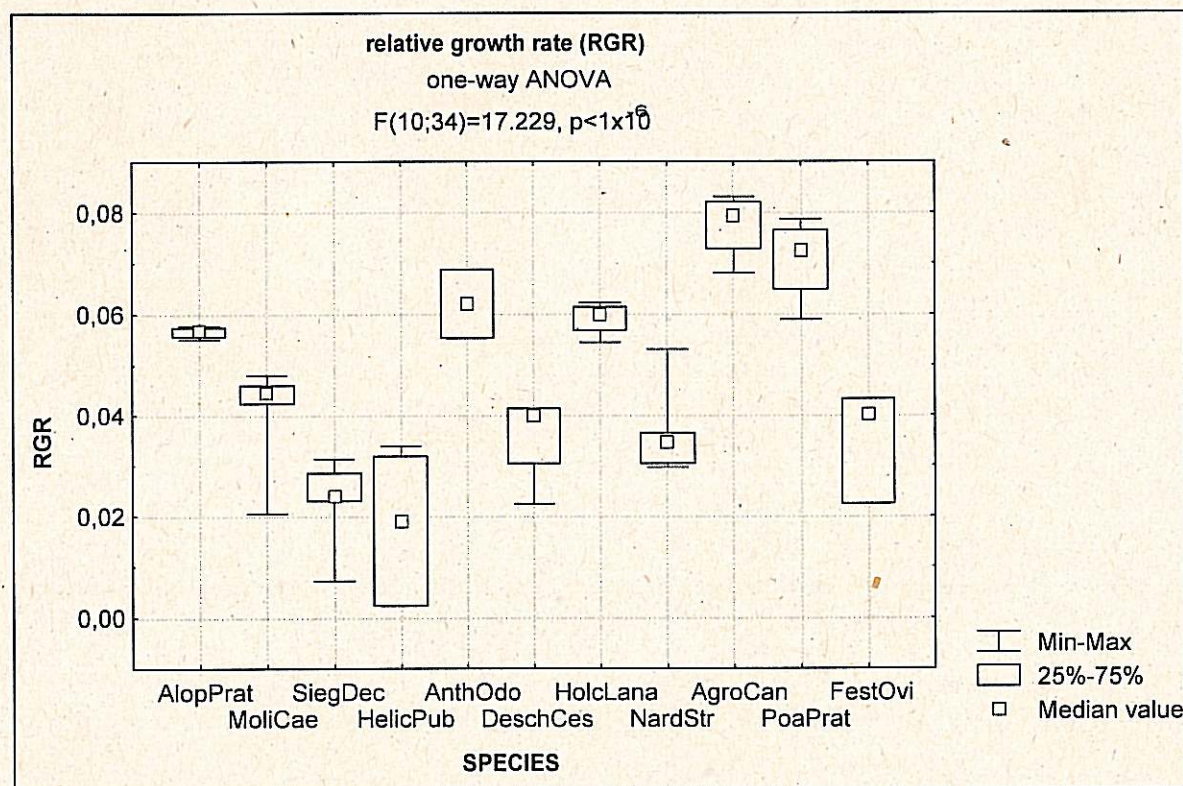


Fig.7 Relative growth rates of species, box & whisker plot.

Effect of clipping on production and distribution of biomass

Two-way ANOVA tested effect of clipping on different species and provides many results about how species develop their biomass and if they distribute it rather to roots or to shoot. The RS-ratio changed – interaction of factors “species” x “clipped” appeared significant ($F(10;68)=2.219$, $p=0.027$). The species differed in changing RS-ratio when clipped i.e. clipping has not unidirectional effect changing RS-ratio. (Details shown in Fig.8):

- Anthoxanthum odoratum, Poa pratensis, Agrostis canina and Alopecurus pratensis decreased RS-ratio
- Holcus lanatus and Festuca ovina increased RS-ratio
- RS-ratio of other species remains almost the same and is usually low
- RS-ratio only rarely reaches or slightly exceeds 1.0 (i.e. roots heavier than shoots)

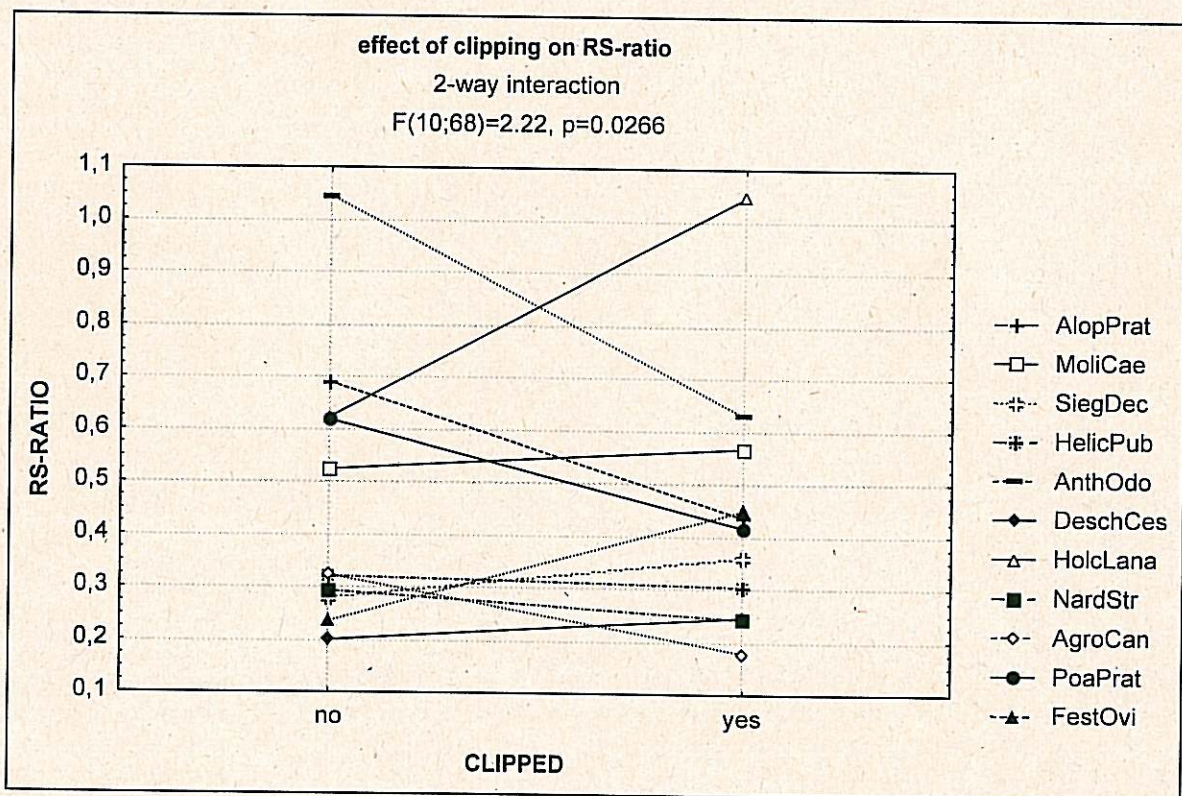


Fig.8 Changing of RS-ratio after clipping, ANOVA, two-way interaction plot. Species either decrease, increase their RS-ratio or leave it constant when clipped.

Species differed in RS-ratio if not clipped (one-way ANOVA, $F(10;34)=3.627$, $p=0.0023$). Clipping did not have effect on RS-ratio if we do not regard species, i.e. it does not change overall average of RS-ratio (two-way ANOVA, main effect “clipping”, $F(1;68)=0.33$, $p=0.57$).

Clipping had additional effect on absolute weight of biomass. Significant interaction "clipped" x "species" ($F(10;68)=3.66$, $p=0.0006$) shows the diversity between species responses, but unlike RS-ratio there is no increase (Fig.9):

- *Alopecurus pratensis*, *Anthoxanthum odoratum* and *Holcus lanatus* have the highest (and almost the same) weight of biomass of non-clipped tufts, but if clipped, the weight decreased dramatically
- another group of species can be seen in the middle of the plot, their biomass and its decrease are very similar
- species with low biomass were very similar and the decrease was very small
- biomass of *Helictotrichon pubescens* increased, but very little (this may be biased, remember the note written at results of RGR)
- in general, difference between species biomass was decreased by clipping

The main effects "clipped" and "species" were significant at $p < 1 \times 10^{-6}$.

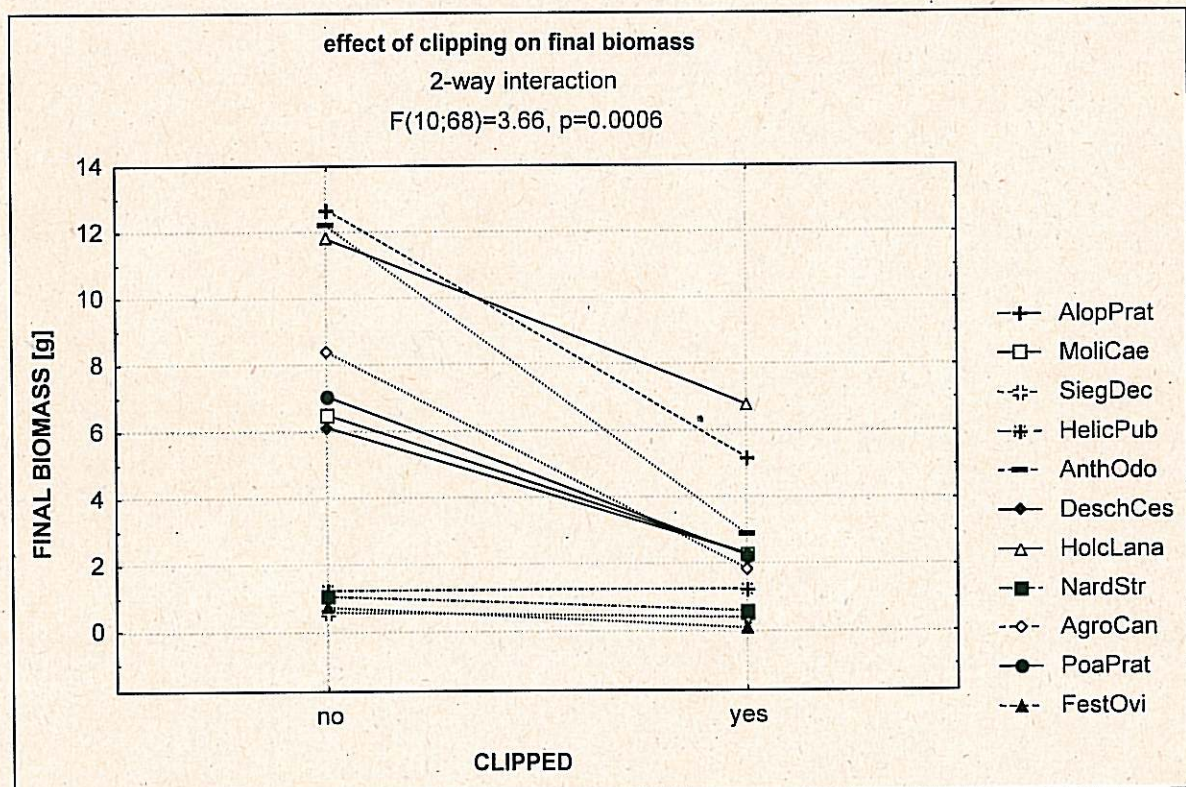


Fig.9 Differences in tuft biomass after clipping, ANOVA, two-way interaction plot. Clipping does not increase biomass weight and decreases the differences between species biomass.

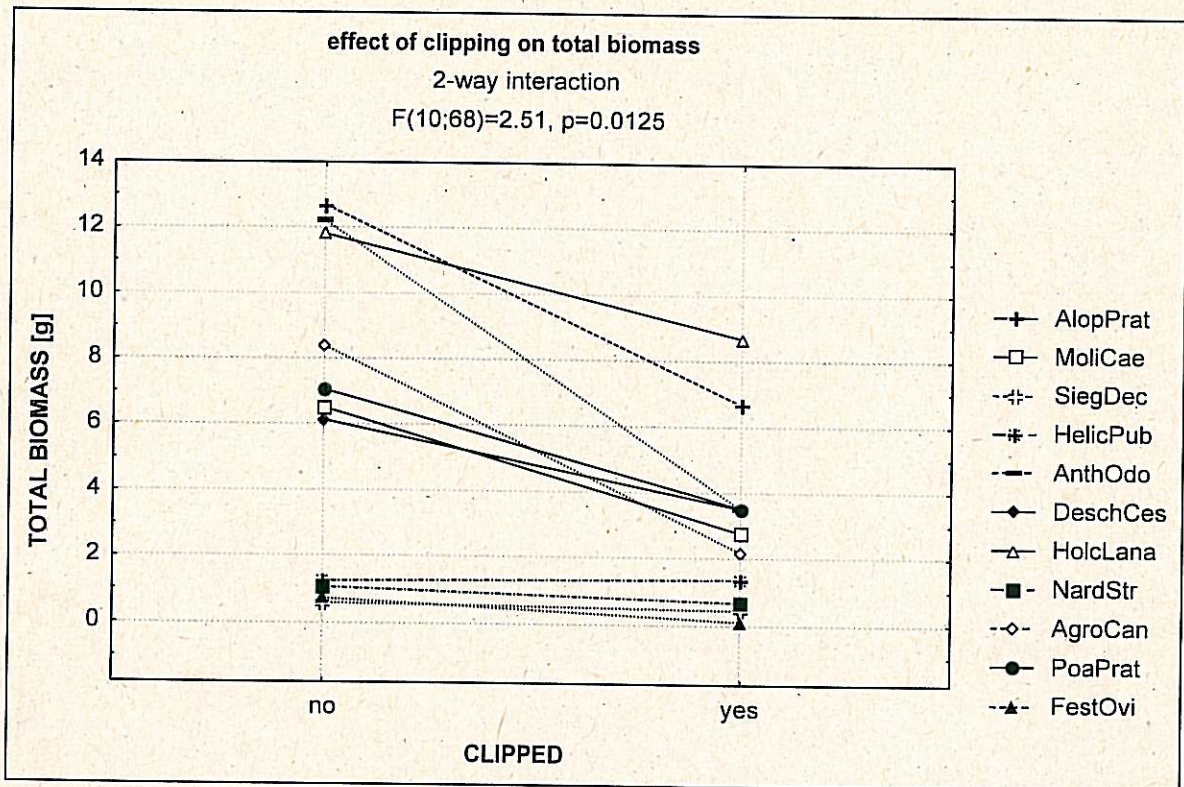


Fig.10 Differences in total produced biomass after clipping, ANOVA, two-way interaction. Clipping also decreased total biomass produced during the whole experiment

Effect of clipping on total biomass produced during the whole experiment was also examined. The results were similar to previous analysis, but the meaning was different. Two-way interaction was significant ($F(10;68)=2.51, p=0.0125$), It means not only final biomass of plant was smaller if plants clipped, but also overall biomass produced during the whole plant development was smaller (Fig.10):

- total biomass of all species declined with clipping, only that of *Helictotrichon pubescens* seemed to increased (compare with previous analysis, Fig.9)
- groups of species with similar response are the same as in previous results, there is no extraordinary behaviour of any species

Effect of clipping on tuft height and density

Analysis show how tuft responds to clipping within time – how it changes its height increases or decreases amount of culms and leaves produced. It provides interesting information about tuft size and density. Repeated measurement ANOVA was performed for number of culms with the three-way interaction between all factors (“species” x “clipped” x “time”) and revealed species do not differ in culm development (Fig.11):

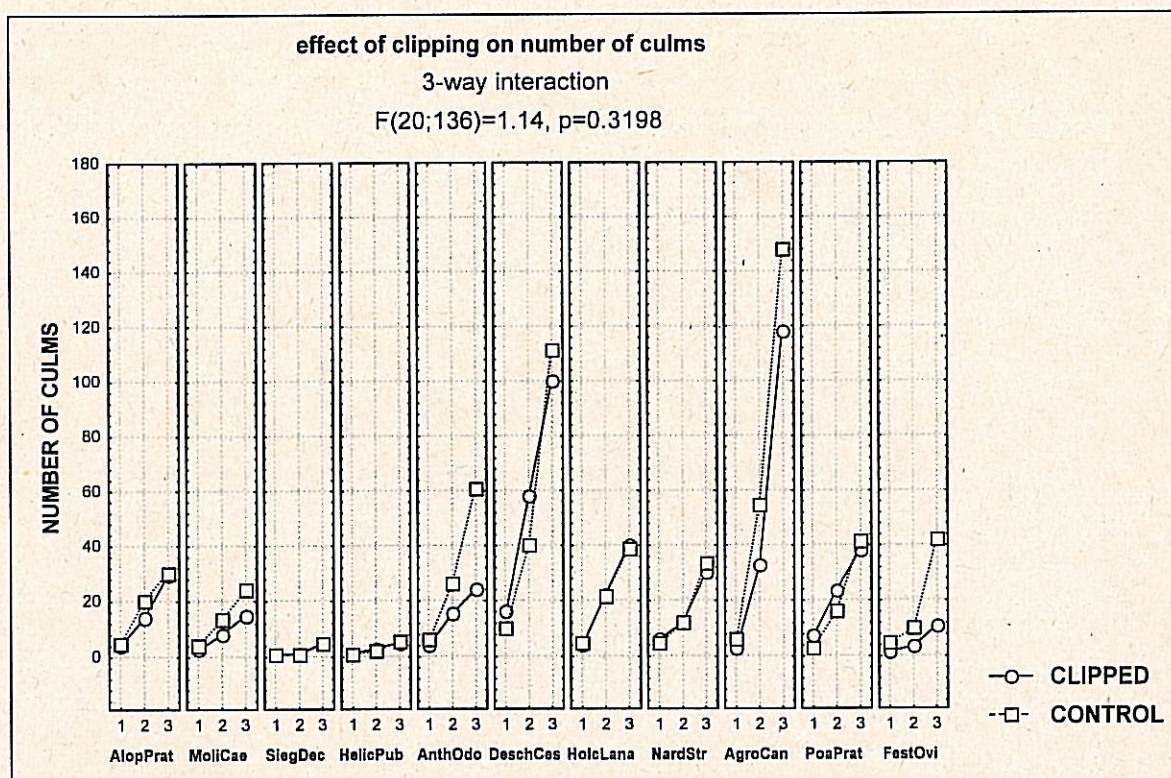


Fig.11 Changes of number of culms after clipping within time, ANOVA, three-way interaction plot. Species do not differ in changing number of culms if clipped.

- clipped and control tufts of most of species almost do not differ in number of culms
- *Anthoxanthum odoratum* and *Festuca ovina* produced less culms if clipped
- *Deschampsia cespitosa* and *Agrostis canina* produce more culms than other species
- clipped tuft of any species did not have more culms compared to control

There were significant interspecific differences in growth dynamics of culms (two-way interaction "species" x "time", $F(20;136)=33.2, p<1 \times 10^{-6}$) and general effect of clipping is that it decreased average number of culms (two-way interaction "clipped" x "time", $F(2;136)=8.2, p=0.000426$).

No effect of clipping on number of leaves was found (three-way interaction, Fig.12):

- most species produce less leaves when clipped
- but *Deschampsia cespitosa* and *Poa pratensis* produce more leaves when clipped
- *Agrostis canina* produces many more leaves than other species, but *Deschampsia cespitosa* produces less (compare with number of culms)

Difference from previous analysis is that average number of leaves was not lower at clipped tufts (two-way interaction "clipped" x "time", $F(1;68)=1.54, p=0.22$).

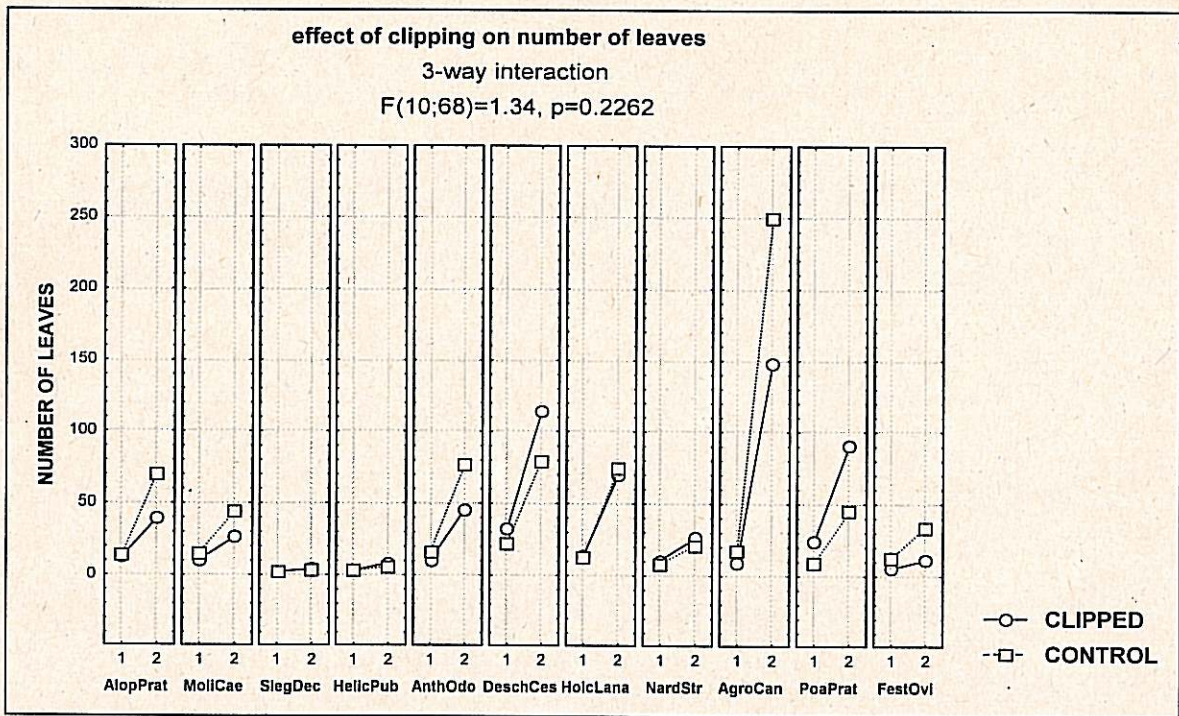


Fig.12 Changes of number of leaves after clipping within time, ANOVA, three-way interaction plot. Species do not differ in changing number of leaves after clipping.

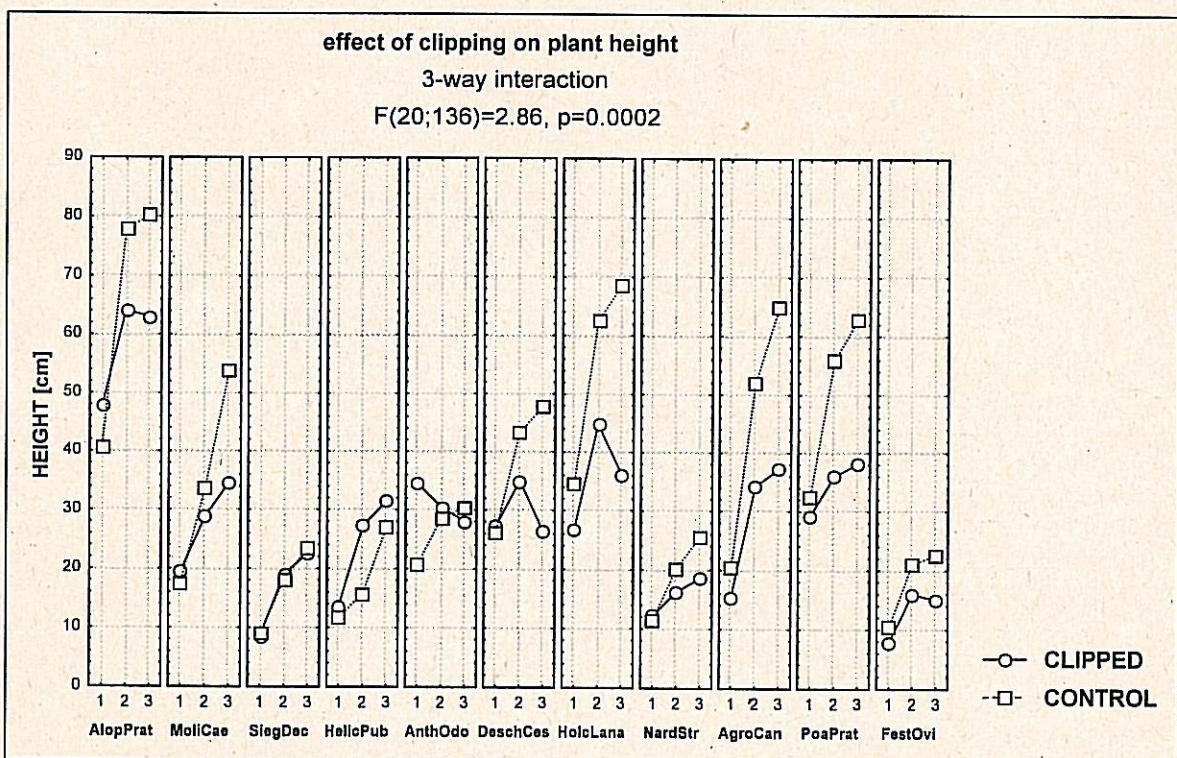


Fig.13 Height after clipping within time, ANOVA, three-way interaction plot. Clipping negatively affected plant height.

Finally, effect of clipping on plant growth was examined by recording development of plant height within time. All effects and interactions were significant. The most important was three-way interaction of increasing plant height with time (Fig.13):

- almost all species did not grow that height after clipping
- only the height of *Helictotichon pubescens* and *Sieglingia decumbens* doesn't change after clipping
- the curve for clipped tufts is still increasing for some species, for others it starts to decrease from second to third measurement

3.3 Species distribution in the landscape

Species occurrence related to productivity of community and land use

Data from phytosociological sampling were analysed by program CANOCO for Windows. DCA analysis showed that the data are more suitable for analysis by RDA (length of gradient on 1st canonical axis 2.158), which also corresponds to the character of data and to the sense of whole analysis (i.e. to examine simple relation to productivity of vegetation).

Environmental variables "alive biomass" and "total biomass" were used each in one separate analysis. Results of Monte Carlo permutation test are summarised in Tab.5:

Tab.5 Significance of RDA with one variable.

	Eigenvalue	explained variability	F-ratio	p-value
alive biomass	0.077	7.7 %	1.505	0.080
total biomass	0.078	7.8 %	1.524	0.080

From this we can understand that both variables can explain the same amount of variability and that their influence is important, although not significant at $\alpha = 0.05$. To display species occurrence in the landscape in relation to the productivity of community, RDA triplot with total biomass (labelled "productivity") as environmental variable is shown (Fig.14):

- only few species are positively correlated with meadow productivity (*Alopecurus pratensis*, *Poa palustris* and *Molinia caerulea*)
- most species were independent on productivity or are a little negatively correlated with the productivity
- some species occur more frequently in meadows with low productivity (mainly *Anthoxanthum odoratum* and *Helictotrichon pubescens*)
- one group of species follows positive direction of second ordination axis, while another group follows the negative one – species from upper part of diagram are those from agricultural or ruderal stands, while the lower part contains species from non-agricultural meadows

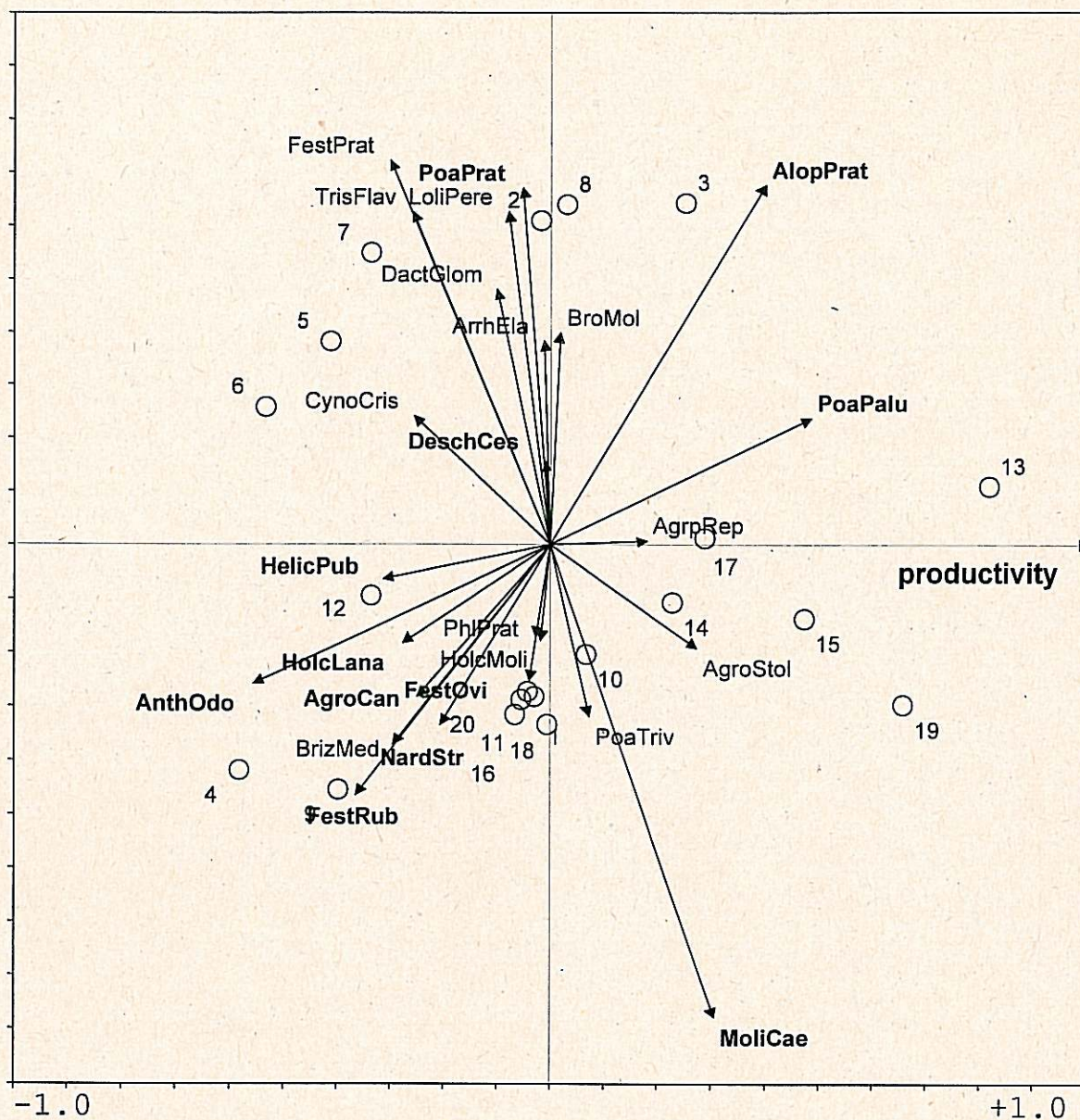


Fig.14 RDA triplot with single environmental variable "productivity". Most species prefer stands with lower productivity.

(Note: Only grass species displayed. Selection was done manually. Study species given in bold.)

Other possible way of describing species distribution was done in other RDA analysis. In addition to previous analysis this one regards also the land use (binary variable "agricultural"). If tested by forward selection, variable "agricultural" was significant at $p=0.005$ and after its inclusion variable "total" was also significant at $p=0.005$. Correlation of these variables with canonical axes and their Eigenvalues are shown in Tab.6:

Tab.6 Results of RDA with two variables.

	Correlation with axis	Eigenvalue of axis	explained variability
agricultural	1 st – 0.9949	0.281	28.1 %
total biomass	2 nd – 0.9791	0.069	6.9 %

Monte Carlo permutation test is highly significant either for 1st canonical axis (F=6.660, p=0.005) or for both (F=4.593, p=0.005). Results from this analysis are again displayed in triplot (Fig.15):

- similar to previous analysis, less species trend to higher values of productivity, more of them prefer average or low values
- *Molinia careulea* occurs just in non-agricultural meadows irrespective of their productivity
- highest negative correlation with productivity can be seen at *Holcus lanatus* and then *Festuca rubra* with *Anthoxanthum odoratum*, while in previous analysis the most negatively correlated species is *Helictotrichon pubescens*

Tab.7 Abbreviations of species names.

AgroCan	<i>Agrostis canina</i>	FestRub	<i>Festuca rubra</i>
AgroStol	<i>Agrostis stolonifera</i>	HelicPub	<i>Helictotrichon pubescens</i>
AgrpRep	<i>Agropyron repens</i>	HolcLana	<i>Holcus lanatus</i>
AlopPrat	<i>Alopecurus pratensis</i>	HolcMoli	<i>Holcus mollis</i>
AnthOdo	<i>Anthoxanthum odoratum</i>	LoliPere	<i>Lolium perenne</i>
ArrhEla	<i>Arrhenatherum elatius</i>	MoliCae	<i>Molinia caerulea</i>
BrizMed	<i>Briza media</i>	NardStr	<i>Nardus stricta</i>
BroMol	<i>Bromus mollis</i>	PhiPrat	<i>Phleum pratense</i>
CynoCris	<i>Cynosurus cristatus</i>	PoaPalu	<i>Poa palustris</i>
DactGlom	<i>Dactylis glomerata</i>	PoaPrat	<i>Poa pratensis</i>
DeschCes	<i>Deschampsia cespitosa</i>	PoaTriv	<i>Poa trivialis</i>
FestOvi	<i>Festuca ovina</i>	TrisFlav	<i>Trisetum flavescens</i>
FestPrat	<i>Festuca pratensis</i>		

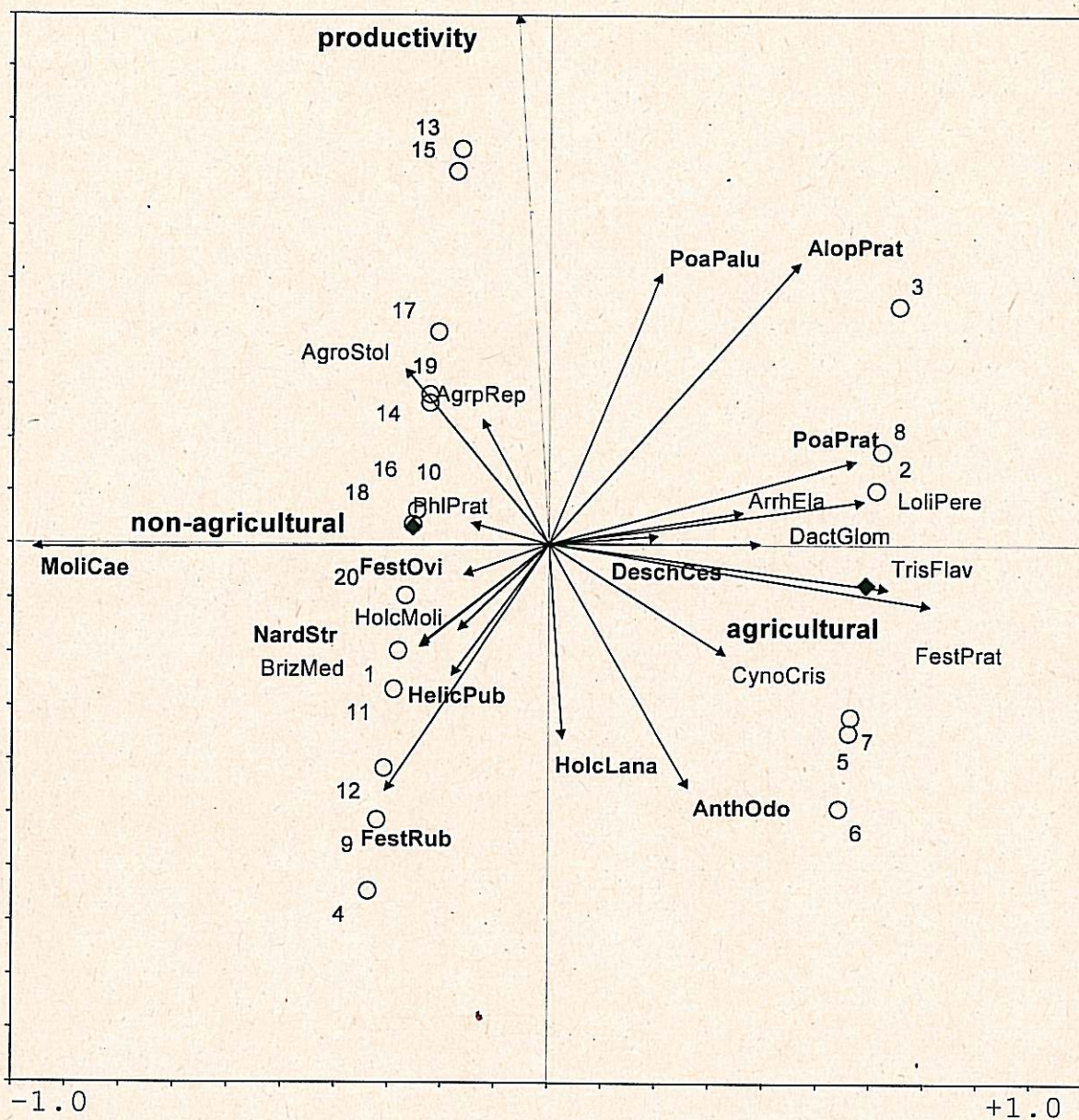


Fig.15 RDA triplot with two environmental variables. Land use significantly explains species distribution and so does productivity.

Quantification of species behaviour

Results from three analyses (RDA) were used to quantify species behaviour as a relation to any environmental variable or as a response to some treatment. Each RDA had only one environmental variable as explanatory variable and therefore species scores on 1st canonical axis are a measure of the behaviour. Jan Lepš provided additional results from analyses examining experimental response to fertilising and mowing (Lepš 1999). Review of species behaviour shows Tab.8:

Tab.8 Species scores on 1st canonical axis from RDA analyses with single environmental variable (productivity, mowing, or fertilising). How do species respond to environmental factors.

	productivity	mowing	fertilising
<i>Agrostis canina</i>	- 0.25	0.10	0.17
<i>Alopecurus pratensis</i>	0.40	-	-
<i>Anthoxanthum odoratum</i> -	- 0.55	0.06	- 0.27
<i>Deschampsia cespitosa</i>	- 0.01	- 0.12	0.20
<i>Festuca ovina</i>	- 0.04	- 0.12	- 0.17
<i>Helictotrichon pubescens</i>	- 0.31	0.07	0.07
<i>Holcus lanatus</i>	- 0.27	0.09	0.01
<i>Molinia caerulea</i>	0.30	- 0.05	0.01
<i>Nardus stricta</i>	- 0.21	0.19	- 0.11
<i>Poa pratensis</i>	- 0.05	0.02	0.22
<i>Sieglingia decumbens</i>	-	- 0.04	- 0.09

3.4 Litter decomposition experiment

Results from two-way ANOVA comparatively show the intensity of litter decomposition among species. Litter decomposition rates did not significantly differ among species (two-way interaction, $F(14;96)=1.19$, $p=0.296$). Fig.16 compares decomposition rates among species. Main effect "species" is however significant ($F(2;96)=43.908$, $p<1\times 10^{-6}$), which means that species differ in initial rate and consequently they differ in amount of undecomposed litter.

- highest decomposition rate has *Festuca ovina*, lowest *Poa pratensis*
- most curves have linear trend
- slope of most curves, but *Deschampsia cespitosa*, *Poa pratensis* were similar

(Note: Initial 100% values are not displayed.)

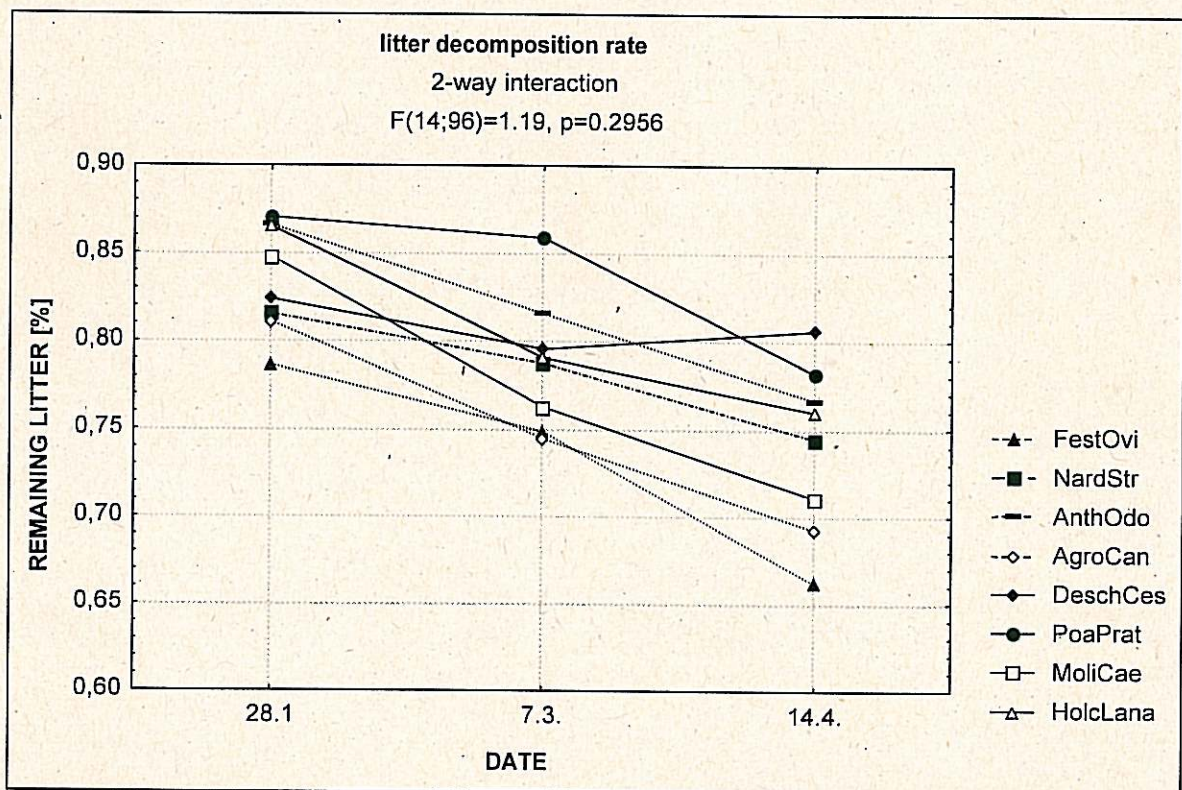


Fig.16 Litter decomposition within time, ANOVA, two-way interaction plot. Differences between litter decomposition rates are not significant

Because the process of decomposition is approximately linear and species do not rapidly change the rate, it is suitable to use values from third measurement as litter

decomposition rate. Final measurements of the differences between decomposed litter are the highest (Fig. 16). Values of rates are listed in Tab.9:

Tab.9 Amount of litter which was not decomposed in the experiment (after four months).

<i>Festuca ovina</i>	<i>Agrostis canina</i>	<i>Molinia caerulea</i>	<i>Nardus stricta</i>
66.2 %	69.3 %	71.1 %	74.5 %
<i>Holcus lanatus</i>	<i>Anthoxanthum odoratum</i>	<i>Poa pratensis</i>	<i>Deschampsia cespitosa</i>
76.0 %	76.6 %	78.2 %	80.6 %

3.5. Correlations and predictions

Square correlation matrix from all variables was built. Each matrix cell contained correlation coefficient and its significance. This helped to review all correlations and to choose those previously selected or to examine others. From large amount of correlations in this chapter are shown only some interesting or important ones and are documented by graph and equation.

Correlations related to tuft size or density

First significant correlation shows how increase of plant height depends on life cycle. Correlation coefficient ($R = -0.81$, $p = 0.002$) describes relation between variables "height 3/1 N" (increase of height from 1st to 3rd measurement at not clipped tufts) and "integral" (integral of IP, means forwardness of life cycle). Graph along with equation is shown in Fig.17:

- very late species increase their height more than three times, whereas early species less then two times
- there are two clusters of values in graph

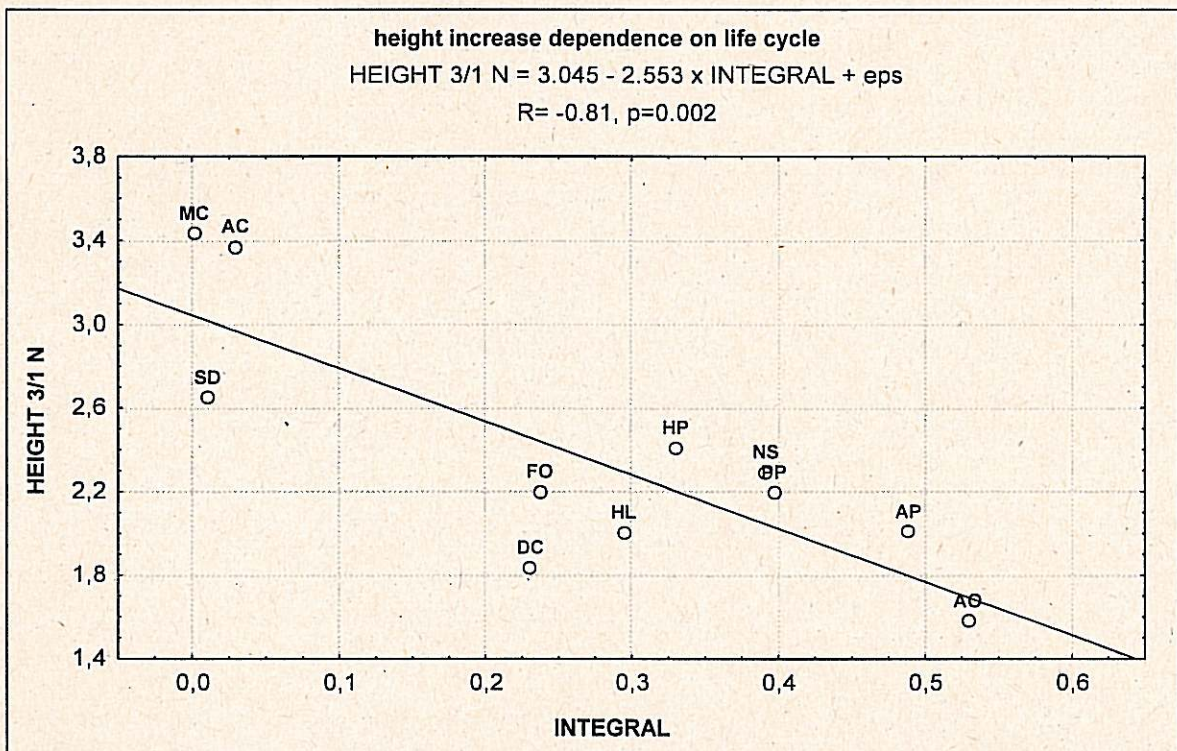


Fig.17 Dependence of height increase on life cycle, linear regression. Species with higher value of integral are early species. Increase of height is higher in phenologically later species.

To add, similar significant correlation was found for variable "height 3/1 Y".

Another correlation shows how tuft density and size correspond to biomass production. First of them, correlation between variables "RGR" and "leaves 2/1 N" ($R=0.78$, $p=0.004$) is shown in Fig.18:

- slow growing species increased number of leaves two times, fast growing five to six times
- *Agrostis canina* highly exceeds average values

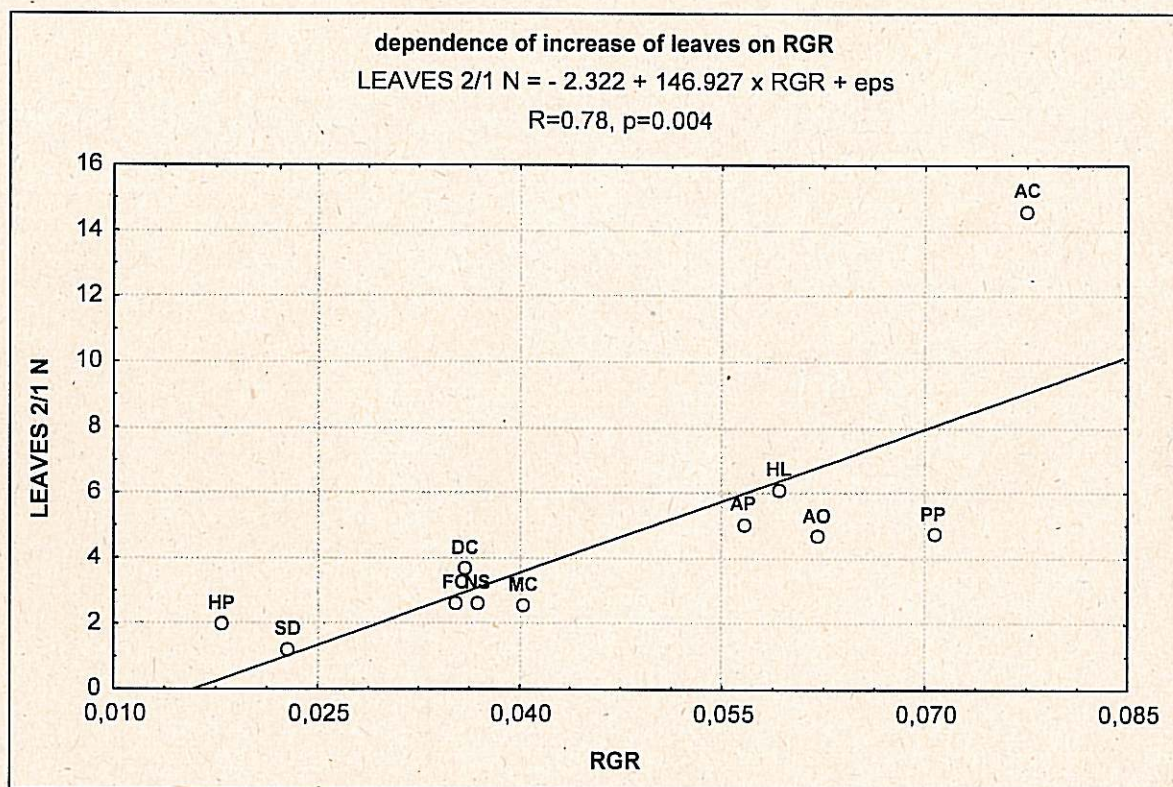


Fig.18 Dependence of changing number of leaves on relative growth rate, linear regression. Fast growing species can increase amount of height three times more than slow growing ones.

Similar to previous analysis, this one is also significant for clipped tufts ("leaves 2/1 Y").

There is also a correlation which quantifies the increase of leaf amount – increase of leaf amount for clipped plants is almost the same as for not clipped tufts ($R=0.97$, $p=1 \times 10^{-3}$), as displayed in Fig.19:

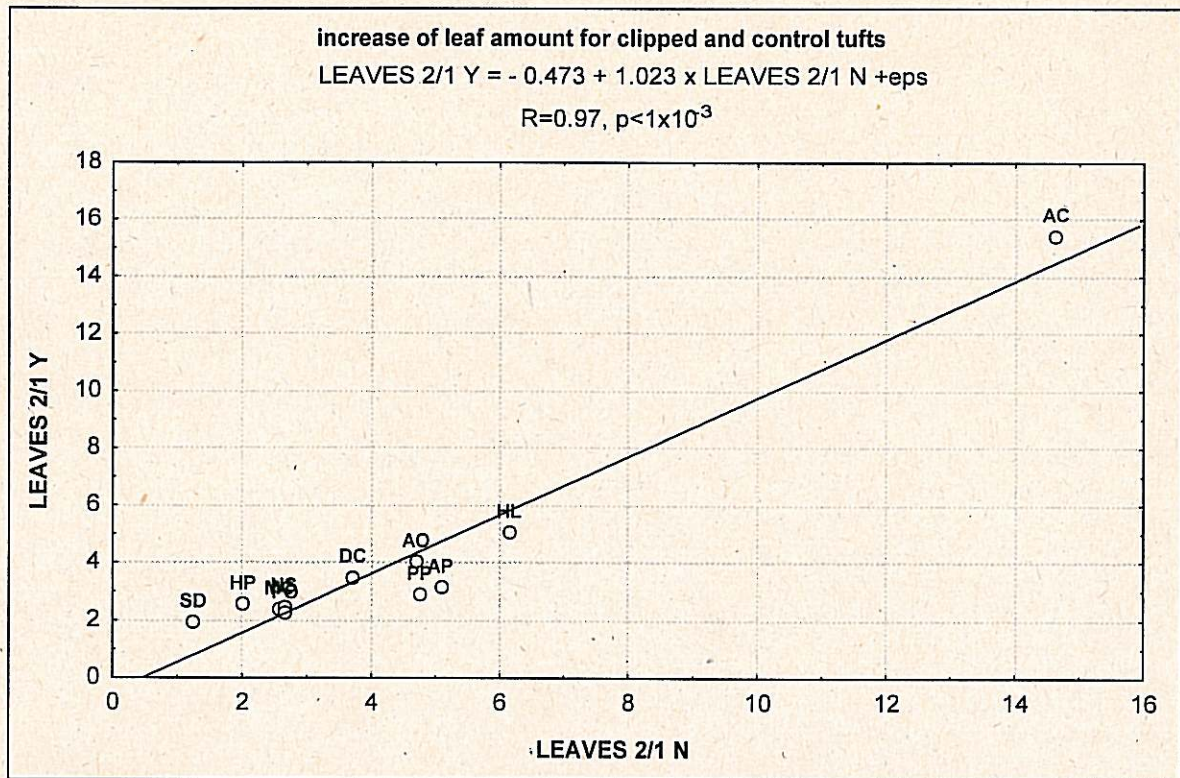


Fig.19 Dependence in changing number of leaves between (clipped tufts on control), linear regression. Increase of amount of leaves is almost the same for clipped and control.

Quantification of biomass

Correlation of shoot biomass (i.e. total shoot produced during whole experiment) for clipped and control tufts ($R=0.84, p=0.008$) was found significant. Variables "total shoot biomass Y" and "total shoot biomass N" are plotted in Fig.20:

- the slope of the curve is about 0.55 and interception is almost exactly zero, so total shoot produced by clipped tuft is one half of shoot biomass of not clipped tuft
- there are three clusters of values
- only some species (*Anthoxanthum odoratum*, *Agrostis canina*) are a little apart from regression line, others are closed

Correlation between variables "shoot Y" and "total shoot biomass Y" ($R=0.98, p=1 \times 10^{-3}$) quantifies, how much of shoot biomass was produced during the whole period is final weight of shoot (Fig.21):

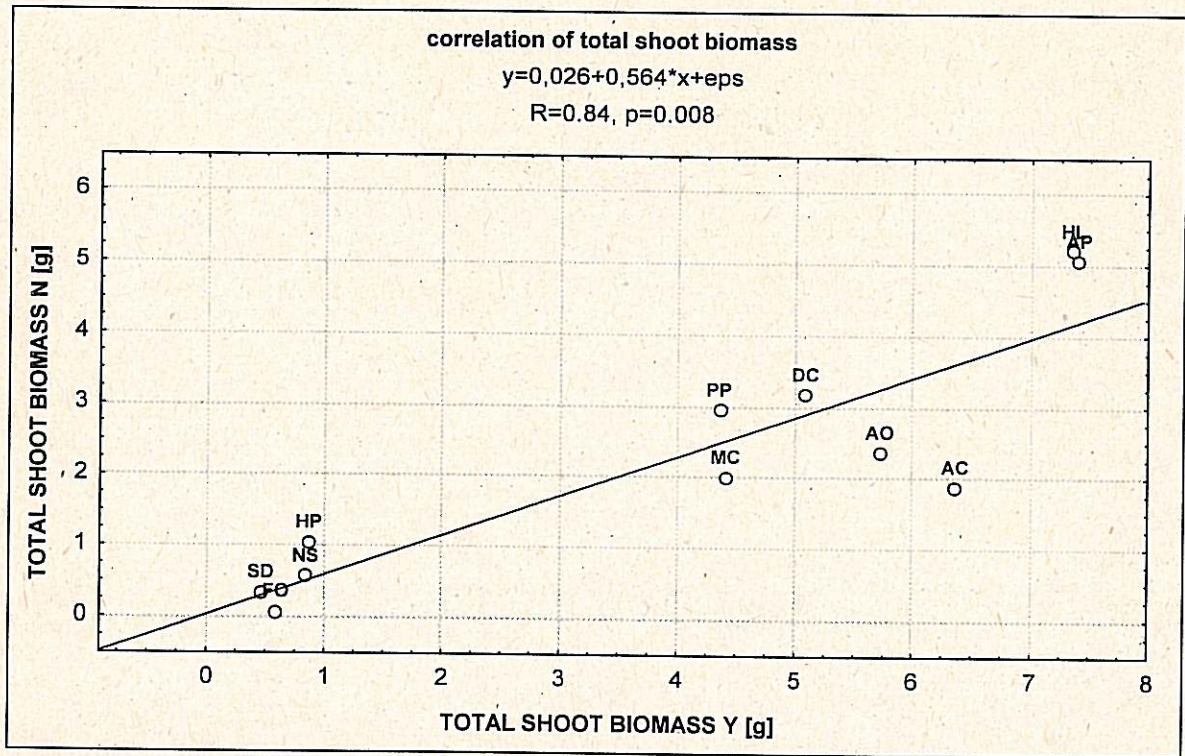


Fig.20 Dependence of total shoot biomass between clipped and control, linear regression. Clipped tuft produces about one half of shoot biomass of control tuft.

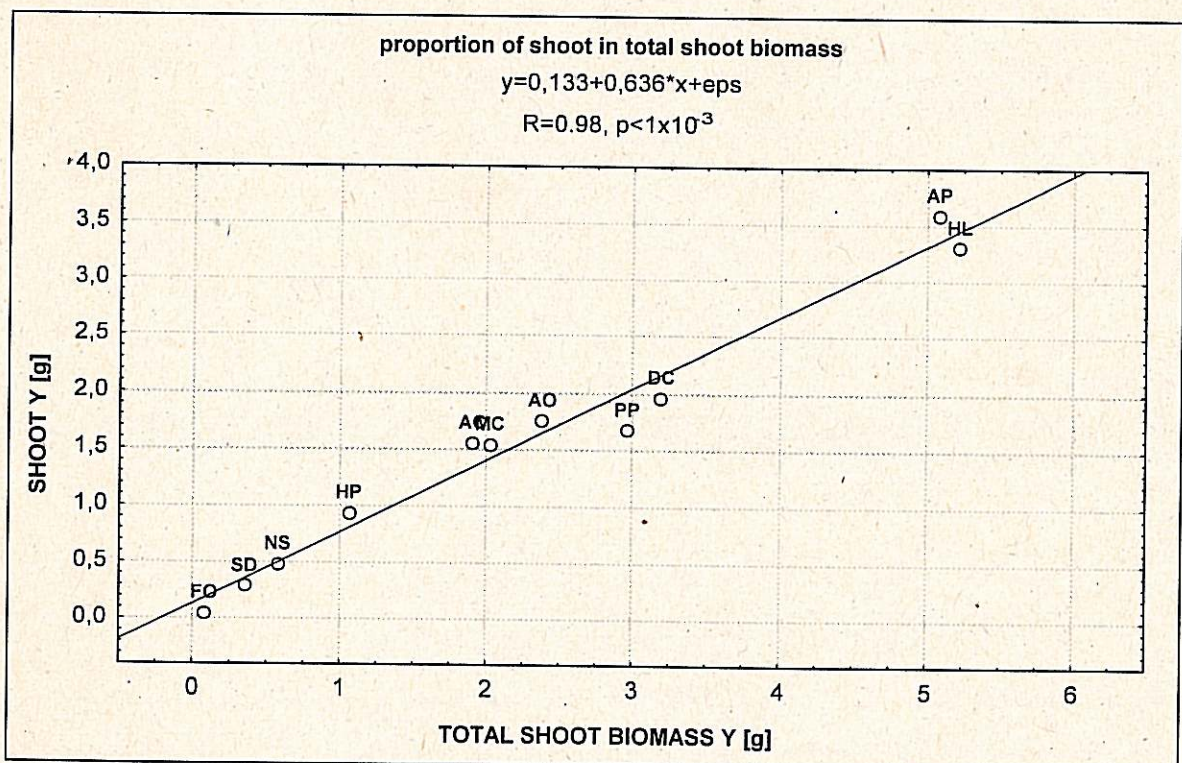


Fig.21 Proportion of final shoot biomass and total shoot biomass at clipped tufts. Shoot of clipped tuft is about 0.6 of total shoot biomass produced by the tuft during experiment.

- the slope of the curve is 0.636, which is the proportion of final shoot in total shoot biomass
- all values are very close to the curve and are equally distributed along it

Correlations related with litter decomposition rate

At the beginning it should be noted that the only one *a priori* selected correlation between "litter decomposition rate" and "RGR" is not significant ($R=0.09$, $p=0.84$). But other two correlations were significant.

First significant correlation is however similar to that one with RGR, because it also somehow concerns biomass production. It is a correlation between "total shoot biomass Y/N" (can be understood as biomass regeneration after clipping) and "litter decomposition rate" ($R=-0.81$, $p=0.014$) and is shown in Fig.22:

- *Festuca ovina* has clearly the lowest biomass production (or decreased biomass after clipping) and has the highest litter decomposition rate
- there are four species with highest and similar values of "total shoot biomass Y/N" and different litter decomposition rate, but from general view they still correspond to the analysis

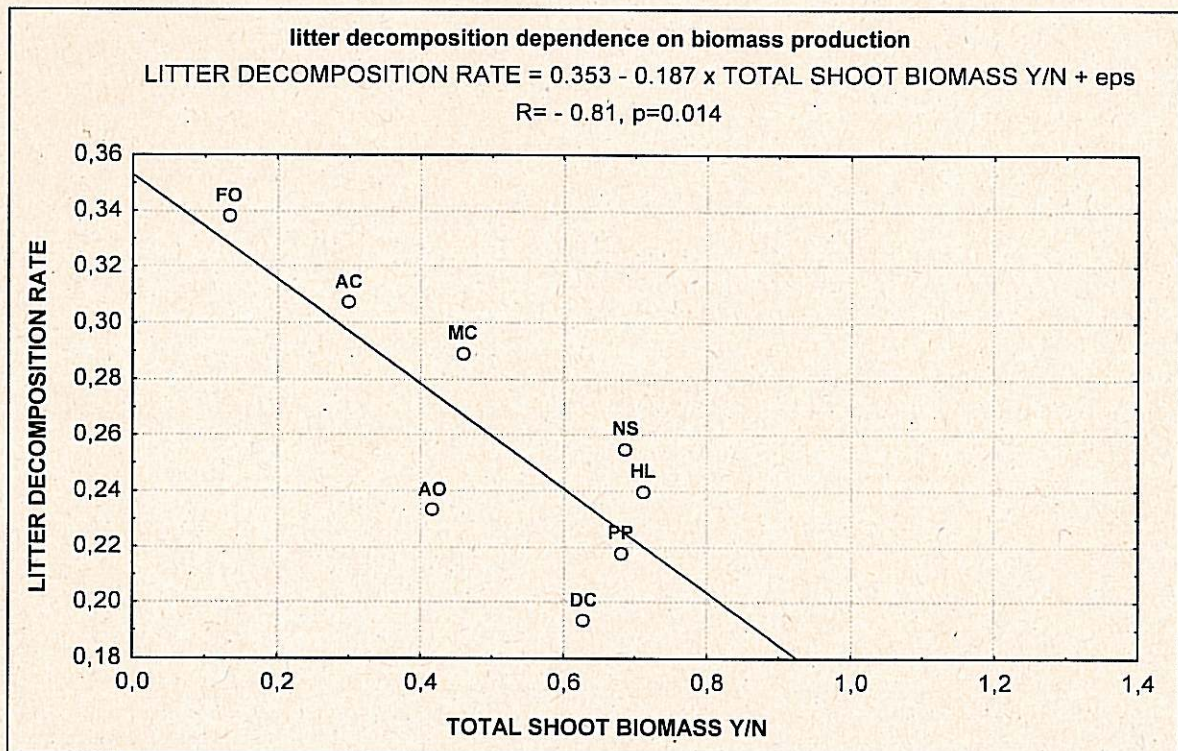


Fig.22 Correlation between litter decomposition rate and total shoot biomass ratio, linear regression. Litter decomposition is faster at species that produce very little shoot biomass after clipping in comparison to control.

Second variable related to litter decomposition rate is "height 3/ Y" (increase of height of clipped tuft). On Fig.23 we can see, how is litter decomposition correlated ($R=0.79$, $p=0.02$) with increase of height after clipping:

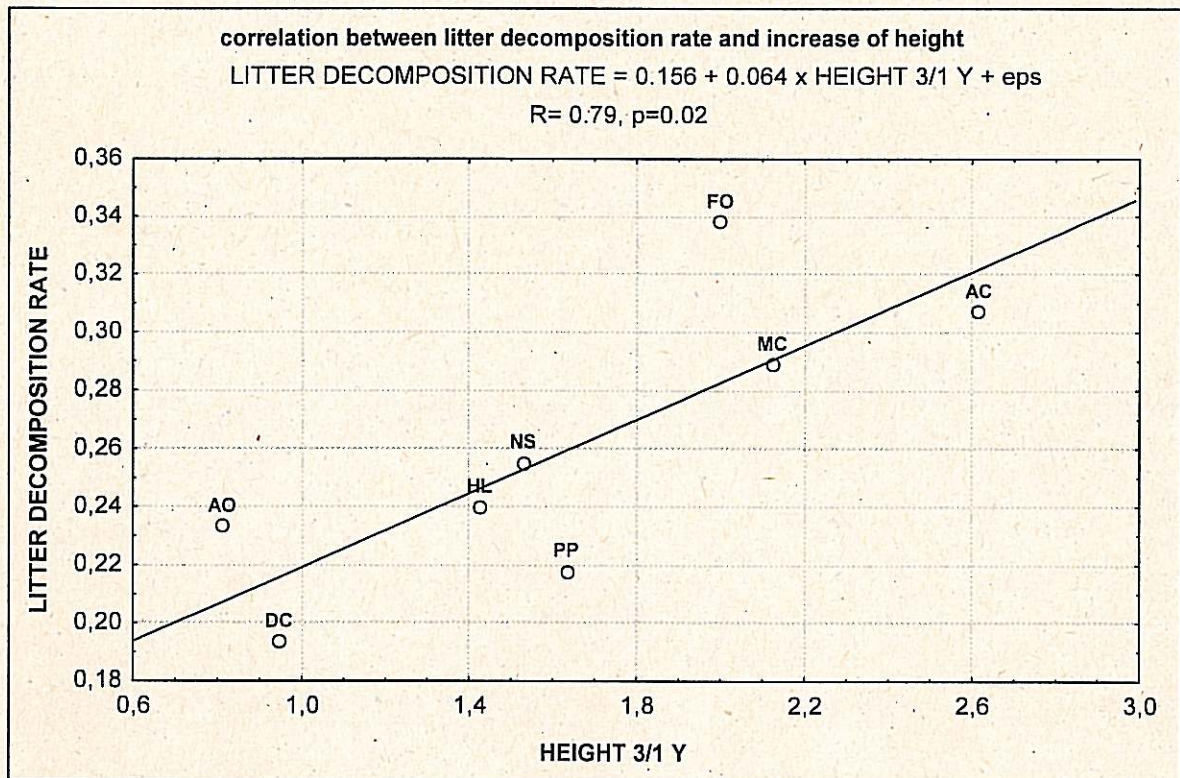


Fig.23 Correlation between litter decomposition rate and increase in height of clipped tuft, linear regression. Species that increased in height if clipped have also high litter decomposition rate.

Predicting species behaviour

Correlations and predictions (as described in chapter 2.4) can be made for evaluating of species behaviour and its preference for meadow productivity and response to fertilising and mowing. Whereas in previous analyses (correlations) it was sometimes difficult to decide, which variable is independent and which is dependent, in this case species behaviour were considered as dependent variables.

Correlation matrix was done similarly to previous analyses (i.e. it displayed both correlation coefficient and p-values), but it was not square matrix, but rectangular matrix (dependent vs. independent variables).

The only result got from this is that none of correlations is significant. In other words, every aspect of species behaviour is statistically independent from each species

characteristics. If species behaviour is not predictable by single parameter, it may be predicted by combination of more variables. Therefore multiple regression with forward selection was done. Some variables were significant in the selection, but the results seem to have no explanatory power (to be discussed). Therefore one regression summary is shown just to document the regression results (Tab.10):

Tab.10 Summary of multiple regression (dependent variable – response to mowing).

$R=0.99994623$ $R_c=0.99989246$ Adjusted $R_c=0.99924724$
 $F(6;1)=1549.7$ $p=0.01944$ Std.Error of estimate: 0.00308

	BETA	St. Err. of BETA	B	St. Err. of B	t(1)	p-level
Interception			- 0.214	0.0064	- 33.662	0.0189
shoot Y/N	2.685	0.0407	2.085	0.0316	65.913	0.0097
leaves 2/1 N	5.442	0.1085	0.152	0.0030	50.142	0.0127
total shoot Y/N	- 2.529	0.0419	- 1.343	0.0223	- 60.294	0.0106
leaves 2/1 Y	- 5.012	0.1116	- 0.127	0.0028	- 44.917	0.0142
height 3/1 N	- 0.161	0.0129	- 0.026	0.0021	- 12.455	0.0510
final biomass Y/N	0.209	0.0285	0.145	0.0198	7.332	0.0863

4. DISCUSSION

Characteristics of grass species were explored in experiments in controlled conditions (greenhouse experiment with clipping, litter decomposition) and also species behaviour in landscape was observed (phenology, landscape distribution) in this study. Correlations between all of these characteristics were examined. Both interesting differences as well as common features were found along.

4.1 Phenology

Two types of differences were found in phenology of species:

1. different rates changing of phenological phases
2. different start and timing of life cycle

One type of variability in changing phenophases is the persistence of phenophase in population and its overlap with other phases. As shown on example of *Deschampsia cespitosa* (Fig.3), some species pass through the phase of culms very quickly, whereas others stay in this phase as long as in others (e.g. *Holcus lanatus*, Fig.4). This feature may be related to the morphology of grass culm and leaf: short and narrow-leaved species form rather short and narrow culms, in which the inflorescence does not persist for a long time. At broad-leaved species the inflorescence remains hidden in tall, big culm. Final effect of this could be, that narrow-leaved species can more quickly start to flower, because their inflorescence appears outside earlier than at broad-leaved species. This hypotheses is supported from the life cycle (Fig.6), where narrow-leaved species (*Festuca rubra*, *Festuca ovina*, *Dechampsia cespitosa*) show sudden increase of IP (exactly because of short phase of culms) in comparison to broad-leaved *Holcus lanatus*.

Another difference is, if the peak of any phase reaches close to 100% or if it is far lower. If we combine this feature together with duration of phenophase, maybe we could distinguish some "strategies" or "types" of grass life cycle, but this would need further detailed investigation.

From Fig.5 we can see, that peaks of one phase are not very separated within time, or if they are, the overlap of species is still very big. Therefore it seems there is no remarkable niche separation in sense separation the peak of flowering of each population. This result a bit corresponds to that of Lepš & Buriánek (1990), that phenological similarity does not lead to niche separation in sense of spatial segregation. To add, there are not many reasons for considering niche separation along time axis within grasses, because they do not compete for pollinators, since they are anemogamic. Also Negi et al. (1992) reports that grasses have almost the same life cycle, but the difference between life cycle of several growth forms (grasses, forbs) is obvious. This may suggest an idea of niche

separation not between species of one growth form (grasses), but between growth forms in general (grasses – forbs).

On the other hand, from the view of the whole life cycle we can clearly distinguish two groups of grass species (see Fig.6):

1. late flowering (summer) *Molinia caerulea*, *Agrostis canina*
2. early flowering (spring) all other species

This result probably corresponds to the theory about maximising growth in summer, when conditions are most suitable for production (Grime 1979). It is exactly the case of *Molinia caerulea* (studied in details by Janeček 2001), that maximises its leaf area in early summer (June to July) and its flowering and seed maturation is therefore delayed to August. Other species flowering in May and senescing in June avoid the maximal growth of *Molinia caerulea*.

One important conclusion should be done from all these results: differences in phenology of grasses should be understood together in terms of flowering and seed maturation, biomass production and also relation to growth forms.

4.2 Growth characteristics and response to clipping

Greenhouse experiment revealed significant difference between species relative growth rates. Highest value of RGR was measured at *Agrostis canina* and *Anthoxanthum odoratum*. Both these species are not dominant neither largely abundant in meadows. It means they do not produce much biomass when growing in meadow community, although values of RGR show, that they have potential ability to do that. From this result we can hypothesise competition weakness of these species.

Other species with quite high RGR are *Poa pratensis*, *Alopecurus pratensis*, *Holcus lanatus* and *Molinia caerulea*. In contrary to already mentioned species these are more abundant and often dominant in communities. RGR of the remaining species roughly corresponds to their abundance in landscape. My results do not support Grime's even Tilman's opinions (Grace 1990). Most species behave according to Grime's theory (Grime 1979), because their RGR quite corresponds to their abundance in landscape, but *Agrostis canina* and *Anthoxanthum odoratum* are definite exceptions.

Maximum value of RGR (0.08 – *Agrostis canina*) is four times bigger than the minimum one (0.02 – *Helictotrichon pubescens*). From formula (4) this example arises, what this ratio explains about ability to produce biomass: if *Helictotrichon pubescens* produces from initial one-gram tiller five grams of biomass, then during the same time and from tiller of the same weight *Agrostis canina* produces 625 grams ($625 = 5^4$) of biomass (exponent corresponds to ratio of RGRs).

Significant interspecific difference was also found in changing RS-ratio after clipping. The principle of changing is not only different decreasing, but also constant value or increasing of RS-ratio. Grime (1979) claims that after clipping (mowing, grazing) the regeneration of removed shoot is connected with decreasing proportion of root biomass. This certainly has to function at species with high regeneration of shoot and corresponding to that our results here show this is not universal strategy of all grasses.

Wet and less diverse habitats decrease their underground biomass after mowing, whereas decrease in seminatural, diverse meadow communities is almost not significant. These results of Fiala & Zelená (1992) are consistent with our results, mainly if we include the fact, that also main effect of clipping was not significant, i.e. the overall proportion of root biomass was not affected by clipping.

RS-ratio is in the interval 0.2 to 1.05 showing shoot weight ranging from the same values as the roots to five times more than roots. This scale remains the same after clipping.

Unlike at RS-ratio, clipping does not cause increase of tuft final biomass – clipped tuft has always less or almost the same biomass than not clipped tuft. Because of this, clipping decreased differences between tuft biomass (Fig.9). It fully corresponds with well-known field experience that mowing equalises initial conditions for species growth, thereby gives more chance to smaller and weak species.

Almost the same quantitative response can be seen in total biomass, although the meaning is very different. We can imagine total biomass as total yield of biomass harvested during given period. Fig.10 clearly says the yield is always bigger or the same, if we harvest the biomass once at the end (not clipped) than if we do it continuously, twice before final harvest (clipped). Moravec et al. (1994) reports, that usually non-fertilised meadows are harvested once a year (late spring) and fertilised meadows twice a year (spring, late summer). Since experimental plants were grown with enough nutrient supplies, a question now arises, why it is favourable to mow meadow twice, when our results show, that bigger yield was gained from one final harvest than from more harvests. To answer, experimental cutting regime was too frequent and it was not applied during the whole vegetation period. Maybe we can conclude that frequent clipping (mowing) lowers total yield of biomass.

Difference in changing culms and leaves growth dynamics as a response to clipping was not determined. Species do not differ in both of these responses, but these responses generally differ from each other: clipping significantly decreases number of culms whereas the effect on number of leaves is not significant (also no species increase number of culms, but some increase number of leaves). Because clipping in fact removes all blades of leaves but bases of culms remain, this result could mean, that not all culms

are regenerated or replaced after clipping and therefore average number of leaves per culm is bigger than it used to be.

Clipping also has significant effect on different changing tuft height. After clipping the tuft starts to growth form almost zero height, therefore it is important, if the curves for case "clipped" in Fig.13 still increase (tuft after second clipping reaches bigger height than after first clipping) or if they start to decrease (tuft does not reach the height it reached after first clipping). This result somehow describes species tolerance (strategy) to shoot removal and based on it we can again guess of species opportunity in competition (mainly for light).

4.3 Distribution of the species in the landscape and preference of habitat productivity

Most of study species prefer rather less productive meadow communities and only few of them are positively correlated with increasing community productivity (Fig.14). From these three study species *Poa palustris* occurred only in one relevé. The other two species *Molinia caerulea* and *Alopecurus pratensis* occurred in most of relevés. They both are dominant species and their negative correlation (along with this different correlation with second ordination axis) confirms they grow in different stands (this feature is also caused by sowing *Alopecurus pratensis* into agricultural meadows). Most negative correlation with productivity was found at *Anthoxanthum odoratum* and *Helictotrichon pubescens*. Species occur in least productive stands and their ability to produce biomass was different from other species (see discussion about RGR).

If we use live biomass or total biomass (live + litter) as explanatory variable of RDA, explained variability is almost the same (ca. 8%, see Tab.5). Therefore it doesn't make difference, which variable we use as a measure of productivity. If we classify relevés according to land-use, this variable is prior selected by forward regression and it explains almost 30% of variability. Variable "productivity" is also significant, independent from land-use and explains 7% of variability. This means species distribution in landscape is mainly (from one third) determined by land-use and then, independently from land-use, by productivity of the stand. On Fig.15 *Molinia caerulea* seems to behave independently from productivity and follows exactly the direction towards non-agricultural meadows. This is caused by the dynamics of biomass productivity of *Molinion* meadows – it has peak of biomass production in August. Landscape distribution was observed in early June, therefore *Molinia caerulea* seems to prefer average values of productivity.

4.4 Litter decomposition

Species do not differ in the process of decomposing litter (non-significant interaction (Fig.16), but they differ in the rate (significant main effect "species"). From that we may generalise that rate of litter decomposition does not change much within time. Therefore we can estimate if any species starts to decompose its litter very rapidly, its litter will probably be during the whole time most decomposed.

Highest litter decomposition rate has *Festuca ovina*, then *Agrostis canina*. *Poa pratensis* decomposes the litter very slowly. Litter of *Festuca ovina* consisted of large amount of very thin leaves, also *Agrostis canina* was very fine structured. It suggests an idea that litter can be decomposed quickly, if the ratio of surface to volume is very high and therefore this large surface enables more effective activity of decompositors.

Another possible factor influencing explanations is proportion of culms and leaves in biomass. Culm has carrying function in plant, thus it needs to be build by tough, dense sclerenchymatic tissues, which predetermines it to be decomposed more difficult than soft leaves. Proportion of culms and leaves in plant is of course given by morphology and structure of the species, but also by previous decomposition. Biomass for field experiment was collected during one single day in mid August, when late species were just fruiting but the early ones had finished their life cycle long ago and some parts of their biomass (leaves) were already more decomposed. It may be confirmed by *Anthoxanthum odoratum* and *Poa pratensis*, biomass of these species consisted mainly of culms.

This review leads to two possible views at litter decomposition: in our case we examine the ability of litter to decompose exactly as it proceeds naturally (biomass is collected in one time as it is in meadow). Then we can guess of competitive impact of litter remaining on meadow until spring (Grime 1979). Though it is not suitable to use these results for interspecific comparison, because input biomass originates from different phase of life cycle and has different content of ash and other substances, as explained by Mika (1980). The second possibility is to harvest biomass of each species in one given phenological phase, i.e each species in different time. This method would be probably more direct for interspecific comparison and especially for comparison with other plant characteristics, which is aim of several studies (Cornelissen 1996, Grime et al. 1996, Cornelissen & Thompson 1997).

4.5 Correlations between observed characteristics

All correlations performed in this study were considered as exploratory analysis of the data set. Consequently, all the pairwise tests were considered separately, and no Bonferroni correction was applied. All the dependencies should be seen in this way and should be subjected to independent testing in future. If two variables tested for correlation

originate each from different observation or treatment, these variables were declared independent and it was acceptable to test the correlation as hypothesis. If variables originate from one treatment (e.g. both from control), it is not reasonable to test the hypothesis and the relation is just for illustration (will be mentioned separately at each conclusion). In next statements I just give advanced interpretations of found correlations.

Fig.17 tells the later the species flowers, the more it increases its height. This result might seem trivial, but can be probably interpreted as very close relation between flowering and growth to height. Note also that flowering was observed in the locality and growth to height was measured within greenhouse experiment. This can be explained as a trade-off: early flowering species cannot invest energy into increasing height but into development of flowers and seeds.

Variables "RGR" and "leaves 2/1 N", plotted in Fig.18, were both measured at control part of experiment and thus are not independent. Correlation shows that ability to produce biomass (RGR) is utilised to multiply number of leaves.

In Fig.19 we can see that species keep their dynamics of leaf production when clipped without difference to control plants. Linear element of equation is close to 1.0, showing that during given period clipped tuft multiplies its number of leaves so many times as does control tuft.

Meaning of Fig.20 and Fig.21 is mainly the quantification of biomass. Equation describing Fig.20 calculates total shoot yield of clipped tuft from the yield of control. It is a bit more than one half of control. Similarly, shoot biomass from final harvest of clipped tuft makes about 65% of total shoot yield (Fig.21). In Fig.20 values of *Anthoxanthum odoratum* and *Agrostis canina* appear remarkably below the regression line. This could mean less resistance to clipping. It should not be forgotten that this applies only provided frequent clipping regime performed during experiment.

Correlation between RGR and litter decomposition rate was not confirmed, in the contrary to Grime (1979). Other two variables were correlated with litter decomposition rate: "total shoot biomass Y/N" and "height 3/1 Y" (Fig.22 and Fig.23). The "total shoot biomass Y/N" can be understood as ability of clipped tuft to produce same shoot biomass as control tuft does. In Fig.22 we can see increasing of this ability implies lower litter decomposition rate. Fig.23 shows the clipped tuft grew more in height in comparison to previous height, the faster its litter decomposes. Explanation of these features (as long as they are not random, because of low number of species) is now difficult and would need further investigation.

There was no significant correlation between any variable resulting from phenology, response to clipping and litter decomposition rate (independent variables) on one side and

responses to environmental factors (scores from multivariate analyses, dependent variables) on the other side. This means we are not able to predict species response from its various characteristics, however the correct answer is we are not able to predict the response from one single parameter (this point was already mentioned in chapter 3. Results). It is obvious that species behaviour in landscape is more complex and depends on more parameters together.

Therefore multiple regression was done, example of regression summary is in Tab.10. From this summary we can see six significant parameters predicting response of eight plant species. Even from such result it has to be clear that to fit six-variable model (however significant) to eight values has no sense. Such a model cannot be extrapolated anyway.

Similar analysis performed by Lepš (1999) provides results, where the only one predictor of response to fertilisation was absolute plant height.

Reasons for our results can be either in small scale of species or in small scale of environmental variable. All our measurements were performed in mesophytic meadows, which should be compared with results of Rychnovská et al (1972) that mesophytic grasslands are a bit more productive than wet grasslands and many more than dry grasslands. Thus, if we involved larger scale of communities in terms of productivity, we would have more diverse response of species and maybe some prediction could appear. But again we can conclude from the work of Rychnovská et al. (1972) that community productivity is closely related with water supplies, soil type and edaphic communities, microclimate etc. It means that involvement of larger scale of productivity brings along involvement of different soil types, variability of water supplies etc., which may bias results, if we think only in terms of productivity.

The final conclusions are: we are not able to predict species behaviour from one parameter and our data are not suitable for predicting from more parameters. Predictions might work if larger scale of species or habitat was involved.

4.6 Conclusions

- **Species life cycle differs in timing, length and changing of phenological phases. Most of species flower in spring, dominant *Molinia caerulea* in summer, when it also largely maximises its biomass.**
- **Species differ in relative growth rate, however, RGR does not even correspond to species biomass within the community.**
- **Species respond to shoot removal by either decreasing, increasing of RS-ratio or keeping it constant. Therefore overall average RS-ratio remains unaffected.**

- Frequent shoot removal decreases either the biomass of shoot or also total biomass produced by tuft during given period. It also decreases interspecific differences in shoot biomass.
- Shoot removal increases number of leaves per one culm, but not absolute number of leaves. Clipped plant can either decrease or increase its height.
- Species distribution in landscape is mainly given by land-use, and, in addition to that and independent from that, by productivity of community.
- Litter decomposition rate does not correlate to relative growth rate, but other correlations were found.
- Early flowering species have to invest energy into development of flowers and seeds and consequently they do not grow much in height.
- It is impossible to predict species behaviour in landscape from only one parameter: more parameters should be used together.
- If any of expected theories failed, it can be that it does not apply within only grasses, but within larger spectra of species, growth forms or even habitats.

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APPENDIXES

Appendix 1

Phytosociological relevés – environmental variables and species percentage cover