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CLONAL GROWTH IN A SPECIES-RICH GRASSLAND: RESULTS OF A 20-YEAR FERTILIZATION EXPERIMENT

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Abstract: We investigated the influence of fertilization on the abundance of species with different clonal growth characteristics using the data from a 20-year fertilization experiment from the Laelatu wooded meadow, in Estonia. The experiment comprised four different fertilization treatments and created a gradient of nitrogen availability. The vegetation composition was recorded every year by measuring the proportions of aboveground biomass for all species. For each species, four parameters of vegetative propagation were measured: speed of ramet vegetative mobility (annual increment of rhizome length), frequency of rhizome branching, placement of branches, and ramet life span. The weighted average of each parameter was calculated for each plot both at the beginning and at the end of the experiment using the relative abundances of the species in the plot as weights. The community changes resulting from the fertilization are reflected in the significant changes of the average values of all studied clonal growth parameters. Increased levels of phosphorus and potassium led to a community with an increased average vegetative mobility and rhizome branching. Both of these traits, however, declined with the increasing availability of nitrogen. The proportion of species with long-living ramets in the community decreased with the increase in the productivity irrespective of the fertilizer used. There was a strong positive correlation between the average ramet life span of the community and the number of species on the plot. We concluded that fertilization increased the ramet turnover rate in this meadow community and reduced species richness. Thus, our results contradict the prediction of a higher ramet turnover rate in species-rich compared to the species-poor grasslands.

Keywords: Clonal plants, Long-term experiment, Nutrients, Ramet life span, Rhizome branching, Species richness, Vegetative mobility

Nomenclature: KUKK (1999)

INTRODUCTION

Several long-term experiments have shown that fertilization reduces species richness both in meadow communities (WILLEMS et al. 1993, MOUNTFORD et al. 1996) and on fallowed arable lands (HANSSON & FOGELFORS 1998). Sometimes also corresponding changes in the life- or growth-form structure of communities have been studied (PONYATOVSKAYA 1978). It has been demonstrated that nutrient addition brings about an increase in above-ground biomass, a decrease in the penetration of light to the soil surface and an increase in the average height of vegetation, which leads to a competitive advantage of tall growth forms over shorter ones (TILMAN 1988). In the Park Grass Experiment the species increasing in abundance following fertilization and liming had a taller growth form (TILMAN 1988), flowered later in the year, and were more outcrossing than common in these communities (DODD et al. 1995). It

has also been shown that clonal growth and the ability to adjust root systems in response to fertilization are adaptively advantageous features (RABOTNOV 1973).

Recently the non-uniform (e.g. clumped) distribution of individuals and populations in space has been emphasized and widely discussed (e.g. VAN DER MAAREL 1988, TILMAN & KAREIVA 1997). On the scale of the individual ramet (sensu HARPER 1977), this has led to the notion that there exists considerable spatio-temporal turnover of ramets (VAN DER MAAREL & SYKES 1993, SYKES et al. 1994, HERBEN et al. 1997), which in turn is largely dependent on the clonal growth form of constituent species (LAW et al. 1994, HERBEN et al. 1995). Meadow communities in the temperate zone consist mainly of clonal species (ABRAHAMSON 1980, CALLAGHAN et al. 1992, VAN DER VALK 1992, PRACH & PYŠEK 1994) and vegetative reproduction prevails (CALLAGHAN & EMANUELSSON 1985, JONASSON 1992). Thus, the dynamics of these communities depends largely on the success of clonal propagation of different species and the consequent task is to discover the community-level regularities in the distribution of species with different clonal growth traits (TAMM et al. 2002).

The mechanical approach to vegetation dynamics requires that simple biologically meaningful and easily measurable characteristics of clonal propagation would be used. We defined the following characteristics of individual ramets, which are important with regard to population and community dynamics (see also KULL 1995, HERBEN 1995):

(1) Ability to spread. This characteristic depends on the combination of two parameters: first, the ability of a ramet to produce new offspring (branching intensity), and second, the distance from a mother ramet to a daughter ramet (ramet vegetative mobility).

(2) Plant unit area (PUA, VAN DER MAAREL 1988, ZOBEL & LIIRA 1997) or patch size. This is the size of the area occupied by one ramet. PUA is evidently related to shoot size. This characteristic was not measured in the current study, but used phenomenologically (see below).

(3) Length of the period during which a genet occupies one patch. There are two ways for a genet to hold a patch. First, when the ramet is perennial and not moving, it may persist within one patch. This can be measured as the life span of (immobile) ramets. Second, a ramet that occupies a particular patch (mother ramet) may produce new (daughter) ramets that persist within the same patch after the death of the mother ramet. This type of patch-holding can be estimated by measuring the amount of short rhizome branches per ramet. Since there were no available data about the size of PUA for different species, we defined a neighbourhood with a radius of < 10 mm as one patch, which is slightly more than has been reported to be the average PUA for Laelatu (ZOBEL & LIIRA 1997). Rhizome branches shorter than 10 mm were defined as ramets that remained within the same patch as the mother ramet (further on in the text referred to as short branches).

Several growth forms have been distinguished on the basis of combinations of clonal growth characteristics (e.g. LOVETT DOUST 1981, KLIMEŠ et al. 1997, JONSDOTTIR & WATSON 1997, TAMM et al. 2002). These typologies are based on the assumption that species can be classified into groups according to their traits of vegetative growth and reproduction. These traits of clonal growth may have a species-specific quantitative range (as several other quantitative accounts, e.g., GRIME & HUNT 1975, ELLENBERG 1974, GRIME et al. 1988, TAMM et al. 2002). Within-species plasticity of the clonal growth parameters has been

extensively studied lately (see reviews by HUTCHINGS & DE KROON 1994, DE KROON & HUTCHINGS 1995). It is obvious that the plasticity of clonal propagation affects ramet placement, however, only a few studies have reported the degrees of plasticity that make plants able to respond to environmental patchiness in natural conditions (cf. STUEFER 1996). Moreover, most studied species seem to lack the ability to plastically change the length of the rhizome (see DE KROON & HUTCHINGS 1995). However, further studies on the species-specificity of plasticity may infer a basis for inclusion of the plasticity parameters into this kind of community analysis.

In this study we investigate whether the balance between species with different clonal propagation traits changes after fertilization and whether this affects the overall ramets' mobility pattern and ramet turnover of the community. We will also relate the clonal growth parameters to the species richness of the community in order to estimate whether the clonal propagation pattern within the community is to some extent related to species coexistence. To address these questions, we use data from a long-term fertilization experiment, carried out at a Laelatu wooded meadow in Estonia, and a set of clonal growth parameters measured for a large number of species from the same community.

METHODS

Study area

Laelatu wooded meadow is located on the western coast of Estonia (58°35′15″ N, 23°33′00″ E) on the West Estonian Lowland. It forms part of the Laelatu-Puhtu Nature Reserve. The area has been used for at least 300 years for hay cutting. The total area of the meadow is 150 ha, of which today ca. 15–20 ha are mown regularly (KUKK & KULL 1997). The area emerged from the sea 1000–2000 years ago (SEPP & ROOMA 1970). The soil is a rendzic leptosol with a pH of 6.7–7.2 (NIINEMETS & KULL, in prep.) and lies on Silurian limestone bedrock covered with calcareous moraine. The humus layer is thin (15–20 cm) and relatively poor in available nutrients (SEPP & ROOMA 1970). The nutrient most limiting for plant growth at this site is phosphorus (NIINEMETS & KULL, in prep.).

The area belongs to the boreo-nemoral zone. The mean temperature for July is 17 °C and for January -5 °C. The annual mean temperature is 6.3 °C in the air and 7.1 °C on the ground. The mean annual precipitation is 500–600 mm, the most rainy seasons are late summer and autumn.

The vegetation of the Laelatu wooded meadow is characterized by a very high species richness and species density. The maximum number of vascular plant species in a 20 × 20 cm plot is 42 and in a 1×1 m plot 76 (KULL & ZOBEL 1991, KUKK & KULL 1997, KUKK, pers. comm.). The vegetation belongs to the *Sesleria caerulea*-association (KRALL & PORK 1970). The tree layer (crown projections) covers on average 30%–50% of the ground surface and consists of *Quercus robur*, *Betula* spp., *Fraxinus excelsior*, *Populus tremula*, etc. (KUKK & KULL 1997). The flora of vascular plants in the Laelatu wooded meadow and adjacent areas comprises 470 species, while 225 species are known specifically from the wooded meadow (KUKK & KULL 1997). The bryoflora of Laelatu consists of 96 species (INGERPUU et al. 1998).

Fertilization experiment

In 1961, a fertilization experiment was set up by K. Pork in the most regularly mown and a uniform, open, relatively dry, old part of Laelatu wooded meadow. Twelve 10 × 30 m permanent plots were marked and randomly assigned to four different treatments (in three replications). Three treatments were fertilized every year during 1961–1981 and one was left as control (C). All three fertilization treatments received 2.6 g m^{-2} phosphorus and 5 g m^{-2} potassium annually. In one treatment (PK) no additional fertilization was applied. Two other treatments received additional fertilization with nitrogen (3.5 g m^{-2}, PKN1, and 10 g m^{-2}, PKN2) annually. P and K fertilizers were introduced in the autumn, N fertilizers were applied in two portions, one in spring and the other after mowing in July. All fertilizers were applied as dry fertilizers. By the end of the experiment the average dry weight of the above-ground parts of plants in different treatments was the following (± standard deviation): C: 129 g m^{-2} ± 11; PK: 258 g m^{-2} ± 53; PKN1: 306 g m^{-2} ± 37; PKN2: 384 g m^{-2} ± 51. The plots were mown every year at the beginning of July and hay was removed.

From each plot an approximately equal amount of above-ground plant parts was collected every summer between 1962 and 1981. The procedure was the following: the plots were traversed along random routes and after every few steps all plants from a randomly located small area (approx. 150 cm^2) were cut close to the ground. This was repeated approximately 20 times, distributing the samples uniformly within the plot. Plot edges were avoided, the buffer zone was approximately 1 meter wide. All small samples were pooled and plant parts were thereafter sorted according to species, dried and weighted. Litter and woody parts of plants were excluded from biomass samples. The relative proportion in weight was calculated for each species and used as an input value for data processing (a summary of the biomass shares of species is given in the Appendix).

Measurement of species characteristics

Clonal fragments (polycormons) of 120 species (those which were most abundant in the plots of the fertilization experiment) were excavated between 1988–1997 (mostly 1995–1996) to measure clonal growth parameters. Due to the continuation of the analysis of vegetation in experimental plots after the cessation of fertilization in 1981, the disturbance to the plots must have been kept to a minimum. Therefore it was impossible to excavate the plants directly from the plots. The plants were mostly excavated from a close proximity to experimental plots, from a homogeneous area of the wooded meadow.

For each species at least 10 clonal fragments were collected. The number of ramets collected this way per species was in most cases between 50 and 100. The age of ramets was estimated, the annual increase of their rhizome parts was measured, and the number of rhizome branches per ramet was counted (see also KULL 1995, TAMM et al. 2002) using scars from dead shoots on rhizomes as well as the size and morphology of internodes and nodes on rhizomes. We also counted the number of short rhizome branches (< 10 mm) per ramet.

Determining the yearly growth of the rhizome is possible due to the differences in the formation of nodes and internodes in different seasons. In spring the internodes of the rhizome are commonly longer and thinner than internodes that have grown later in the year; they may also differ in their colour. In most cases the rhizome is formed within the first year of the

ramet's life. If the ramet is annual, each separate rhizome branch is formed within one year. If the ramet is perennial it mostly does not move horizontally after the first year. Very often there are remains of old leaves or shoots on the rhizome, which shows the place where the shoot has been growing. Such morphological differences allow us to estimate the yearly growth of the rhizome and the ramet age (see also TAMM et al. 2002). To estimate ramet life span, only the age of dead ramets was used. Most species had annual ramets or biennial ramets with very small variability of life span. Only approximately 30% of the herbaceous species had perennial ramets that can reach the age of 15–20 years (TAMM et al. 2002). The branching intensity was calculated as the number of rhizome branches per ramet divided by ramet life span.

All other means of vegetative reproduction beside rhizomes (bulbils, stolons, shoots from root buds) were treated the same way as rhizomes. For *Ophioglossum vulgatum*, the length of the root part from the mother ramet to daughter shoots, sprouting from root buds, was measured and treated as a measure of vegetative mobility.

Annual species and perennial species that do not resprout vegetatively were included in the analyses with their corresponding parameter values (e.g., for annual species: ramet life span = 1 year; branching intensity = 0). Since no large trees and shrubs were growing in the samples taken from the experimental plots, the ramet life span of trees and shrubs was assumed to have median = 2 years and branching intensity to be 0. This corresponds roughly to the life cycle of woody plants in the mown part of the Laelatu wooded meadow community.

Due to the very asymmetric distribution of all measured clonal growth parameters within species it was impossible to transform the variables to fit a normal distribution. Therefore instead of average and variance, the median and quartile range (difference between third quartile and first quartile) were calculated to describe species-specific clonal growth characteristics.

For several species found in the vegetation analyses to have low frequency and small biomass share, clonal fragments were not excavated due to their local rarity. For 24 species it was possible to estimate some of the parameters of clonal growth from the plants available in the herbarium of the Institute of Zoology and Botany of the Estonian Agricultural University. The herbarium plants were measured only if they were collected from communities similar to the studied one. For 39 species out of 166 found in the fertilization experiment, it was not possible to measure all parameters of clonal propagation (mostly the ramet life span was not estimated), or sample size for measurement was very small (< 5). In each experimental plot the sum of the biomass for these species constituted less than 2% of total biomass. The parameters of clonal propagation for these species were treated as missing values and were pairwisely deleted in data processing (the values of used parameters of clonal growth are given in the Appendix).

Data processing

For each species the relative contribution to total dry weight in the fertilization experiment was used as an estimation of species abundance in the statistical analysis. To reduce the effect of between-year variation in species abundances as well as errors in species numbers associated with a non-constant sampling area, we summarized the data of the vegetation

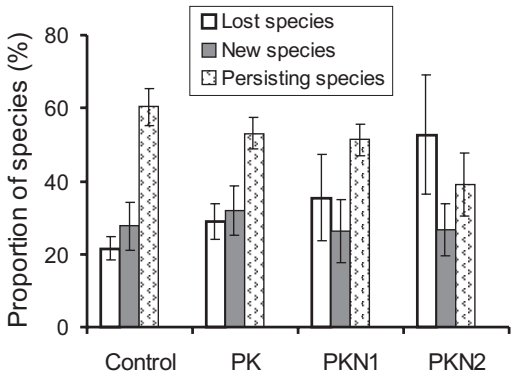

Fig. 1. The proportions of species present in the plots throughout the experiment (persisting species), species that disappeared from the plots in the course of the experiment (lost species), and species that invaded the plots during the experiment (new species). The average of three replicates ± standard deviation is presented. Control – control plots (no fertilization); PK – plots with P and K fertilizers; PKN1 – plots with P, K, and N (3.5 g m^2 y^{-1}) fertilizers; PKN2 – plots with P, K, and N (10 g m^2 y^{-1}) fertilizers.

analyses for the first three years of the experiment (1962–1964) and data for the last three years of the experiment (1979–1981). Thereafter the weight proportions for each species were averaged over three-year periods (beginning and end of the experiment) for each plot.

Based on the species presence or absence in the plot at the beginning and end period of the experiment the following species persistence groups were defined for each experimental plot: (A) species that disappeared from the plot during the experiment (species that were present on the plot at the beginning of the experiment, but not at the end period of the experiment, expressed as a percentage of the number of species that were present on the plot at the beginning of the experiment); (B) the species that invaded the plot during the experiment (species that were present on the plot at the end of the experiment, but not at the beginning of the experiment, expressed as a percentage of the number of species that were present at the end of the experiment); (C) species that persisted in the plot during the experiment (species that were present on the plot both at the beginning and end of the experiment, expressed as a percentage of the total number of species found in the plot during the experiment. We tested whether the number of species belonging to different persistence groups was different in different fertilization treatments by one-way type III SS ANOVA. We applied Tukey HSD tests to estimate the significance of single pairwise differences.

We used one-way type III SS ANOVA to test whether different persistence groups in different treatments contained species that differ in their clonal growth parameters. Species-specific clonal growth parameters were used as input data for ANOVA. The distribution of these parameters within each plot was tested for normality. All variables were also tested for homogeneity of variances and correlations between means and variances. None of the variables violated the assumptions of the ANOVA test.

The effects of fertilization on the proportion of species with different parameters of clonal growth were tested as follows. First, the weighted average of the p^{th} clonal growth parameter (M_p) was calculated for each plot as:

$$M_p = \sum a_i p_i \quad (1)$$

Table 1. Cumulative number of species found in each plot and for each treatment at the beginning and at the end of the experiment (cumulative total of three consecutive years). Treatment abbreviations as in Fig. 1.

Treatment	Plot number	Number of species per plot			Number of species per treatment		
		1962–1964	1979–1981	Plot total	1962–1964	1979–1981	Treatment total
Control	2	79	81	101			
	6	76	93	108	117	117	143
	10	87	89	106			
PK	1	70	63	87			
	7	64	76	94	100	99	123
	9	77	82	101			
PKN1	4	76	47	84			
	8	64	71	88	95	91	115
	11	77	74	98			
PKN2	3	76	36	84			
	5	77	39	86	101	80	116
	12	62	63	84			

where a_i is the weight proportion (from 0 to 1) for species i in the plot and p_i is the median value of a clonal growth parameter r for species i. Second, a type III SS ANOVA with repeated measurements was conducted, with weighted average of the clonal growth parameter (M_p) as dependent variable, fertilization treatment as a fixed factor and period of sampling (beginning vs. end of experiment) as the repeated factor.

Relationships between species number and weighted averages of clonal growth parameters were tested by linear correlation analysis. We used each plot in either studied time period as one case and weighted averages of the clonal growth parameters as well as the number of species found in each plot in this time period as variables (altogether 24 cases and 5 variables). Pearson's r was calculated for each relationship between the species number in a plot and the weighted average of clonal growth parameter.

All statistical tests were applied using the program Statistica 5.0 (STATSOFT 1995).

RESULTS

Trends in species numbers

The proportion of the species that were present in the plots at the end but not at the beginning of the experiment, did not vary in the different fertilization treatments ($F = 0.369$, $P = 0.778$; in all cases here $\text{d.f.}_{\text{effect}} = 3$, $\text{d.f.}_{\text{error}} = 8$, Fig. 1). The proportion of the species that disappeared from the plots in the course of the experiment did vary in the different fertilization treatments ($F = 4.84$, $P < 0.034$). Plots with the PKN2 treatment lost significantly more species than control plots ($P < 0.007$) and plots with the PK treatment ($P < 0.025$). Similarly, the number of the species that were present in a plot throughout the experiment was different in different treatments ($F = 7.00$, $P < 0.013$). The PKN2 treatment included significantly less of such species than the other treatments ($P < 0.032$ for all pairwise

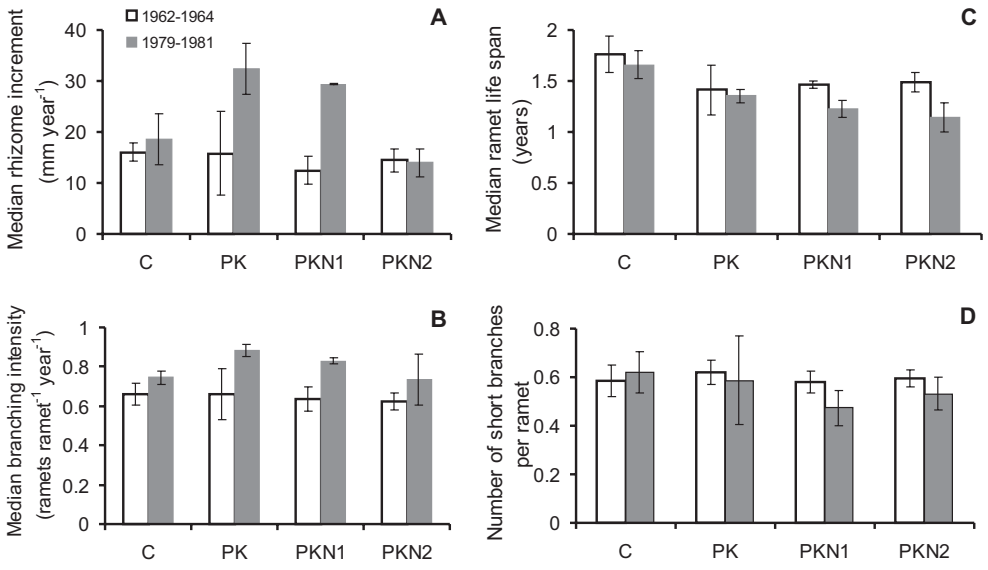

Fig. 2. The weighted average of the median of yearly rhizome increment (A), branching intensity (B), ramet life span (C), and number of short branches per ramet (D) at the beginning (1962–1964) and at the end (1979–1981) of the experiment. The average of three replicates ± standard deviation is presented. Treatment abbreviations as in Fig. 1.

comparisons; Fig. 1). The trends of changes in species numbers corresponded well to the expected decrease in the number of species with the increasing amount of fertilizer (Table 1).

Changes in the weighted averages of clonal growth parameters of the species set in the plot

There were significant differences in the weighted averages of rhizome increment both between different fertilization treatments and between different measurement periods (Table 2). Also, the interaction between the factors time and fertilization was statistically significant. This difference can be attributed to the PK and PKN1 treatments where the biomass share of species with longer rhizome increments increased significantly during the experiment (Fig. 2). No such change was detected for control plots and for plots with the PKN2 fertilization variant.

The main effect of fertilization was not significant for the weighted average of branching intensity, but the main effect of time was. The interaction of the factors time and fertilization was not significant for the weighted average of the median values of branching intensity (Table 2). The species with higher branching intensity increased in biomass during the course of the experiment. However, the weighted average of branching intensity at the end of the experiment was significantly higher than at the beginning of the experiment only in the plots with PK and PKN1 treatments (Fig. 2) and this increase was not big enough to cause the interaction term to be significant.

Table 2. The results of repeated measurements ANOVA. Difference in the weighted averages of the clonal growth parameters of all species between different fertilization treatments (fertilization) and between the beginning and end of the experiment (time – repeated factor). Degrees of freedom for factor effects: fertilization – 3, time – 1, fertilization × time – 3; degrees of freedom of error for all factors – 8.

Trait of clonal growth	Factor	MS effect	MS error	*F*	*P*
Rhizome increment	fertilization	111	12	9.5	**0.01**
	time	476	25	19	**0.002**
	fertilization × time	126	25	5	**0.030**
Branching intensity	fertilization	0.01	0.01	1.3	0.35
	time	0.14	0.00	38.7	**0.000**
	fertilization × time	0.01	0.00	1.7	0.236
Ramet life span	fertilization	0.20	0.02	12.6	**0.002**
	time	0.21	0.02	9.7	**0.014**
	fertilization × time	0.03	0.02	1.2	0.384
Number of short branches per ramet	fertilization	0.01	0.01	0.7	0.572
	time	0.01	0.00	3.3	0.105
	fertilization × time	0.01	0.00	1.5	0.277

The main effects of fertilization and time were significant for the weighted averages of ramet life span (Table 2), while the interaction of time and fertilization was not significant. The latter is because the ramet life span was already initially smaller in fertilized plots although this initial difference was statistically not significant. By the end of the experiment the biomass share of species with longer ramet life span decreased in the plots with a higher amount of fertilizers used (Fig. 2). The strongest impact on weighted average of ramet life span was exerted by the PKN1 and PKN2 treatments, for which the weighted average at the end of the experiment was significantly smaller than the corresponding weighted average for control plots ($P < 0.05$). The difference between the PK, PKN1 and PKN2 treatments at the end of experiment was not significant. The weighted average of ramet life span for the PK treatment was not different from the weighted average for control plots.

Differences in clonal growth parameters between the various persistence groups

Regarding the species that disappeared from the plots during the experiment, the only significant difference between the treatments was revealed by the median of ramet life span ($F = 5.91$, $P < 0.02$, in all cases in this chapter: $d.f._{effect} = 3$, $d.f._{error} = 8$). The species that were lost from plots with the PKN1 and PKN2 fertilization treatments had higher medians of ramet life span compared with species that were lost from the control plots ($P < 0.021$ and $P < 0.004$, respectively).

The only significant difference between treatments in the parameters of clonal growth of the species that invaded the plots during the experiment was the variation (measured by standard deviation of the average) of the median value of rhizome increment ($F = 4.16$, $P < 0.05$). The species that invaded the plots with the PKN1 and PKN2 treatments showed far higher variation of this parameter compared with the species that invaded the control plots

Table 3. Relationships between number of species per plot and weighted averages of clonal growth parameters as tested by linear correlation analysis. Correlation coefficients in boldface are statistically significant at $P < 0.05$, $n = 24$.

Clonal growth parameter	Pearson's r	P
Rhizome increment	0.144	0.503
Branching intensity	-0.038	0.860
Ramet life span	**0.786**	**0.000**
Number of short branches per ramet	0.336	0.108

($P < 0.028$ and $P < 0.036$, respectively). Also, the variation of the median rhizome increment was higher for the PKN1 treatment than for the PK treatment ($P < 0.04$).

The species that were present in the plots throughout the experiment revealed differences between different treatments only in the rhizome increment ($F = 5.78$, $P < 0.02$), which formed two homogeneous groups. One group consists of plots with the PKN1 and PKN2 treatments and the other group consists of control plots and plots with the PK treatment. The groups differed significantly from each other ($P < 0.035$ for all pairwise comparisons), with nitrogen-fertilized treatments containing species with smaller rhizome increments.

The analysis of the patch-holding capacity of species on the basis of species ability to place new ramets in the same patch as old ramets (measured by number of short branches per ramet) revealed that in spite of the lack of change in this parameter when all species were analyzed together, significant differences between different fertilization treatments ($F = 4.46$, $P < 0.013$) occurred when different species groups were treated separately. Species that disappeared from the plots with the PKN2 fertilization treatment had a significantly higher patch-holding capacity than the species that disappeared from the control plots and from plots with the PK treatment ($P < 0.04$ in both cases). Similarly, the species that invaded the plots with the PKN2 treatment had a significantly higher value of this parameter compared with control plots ($P < 0.014$). The species that disappeared from plots with the PK treatment and from plots with the PKN1 treatment displayed significantly lower values of this parameter compared with the species that persisted in or invaded the plots with these treatments ($F = 6.6$, $P < 0.006$).

Relationship between species number and clonal growth parameters

Of the four studied correlations between species number per plot and weighted averages of clonal growth parameters, only one was statistically significant (Table 3). The number of species in a plot was positively correlated with weighted average ramet life span (Fig. 3).

DISCUSSION

Species-specific life-history traits

The four described parameters of clonal growth constitute the main characteristics that are required for describing the life history of clonal species (KULL 1995, TAMM et al. 2002). Differences between communities along these parameters enable the estimation of the impact of vegetative propagation on the changes in community composition (TAMM et al. 2002).

Two of the clonal growth parameters that were estimated in this study (vegetative mobility and branching intensity) are related to the ability of species to spread. The larger the values of

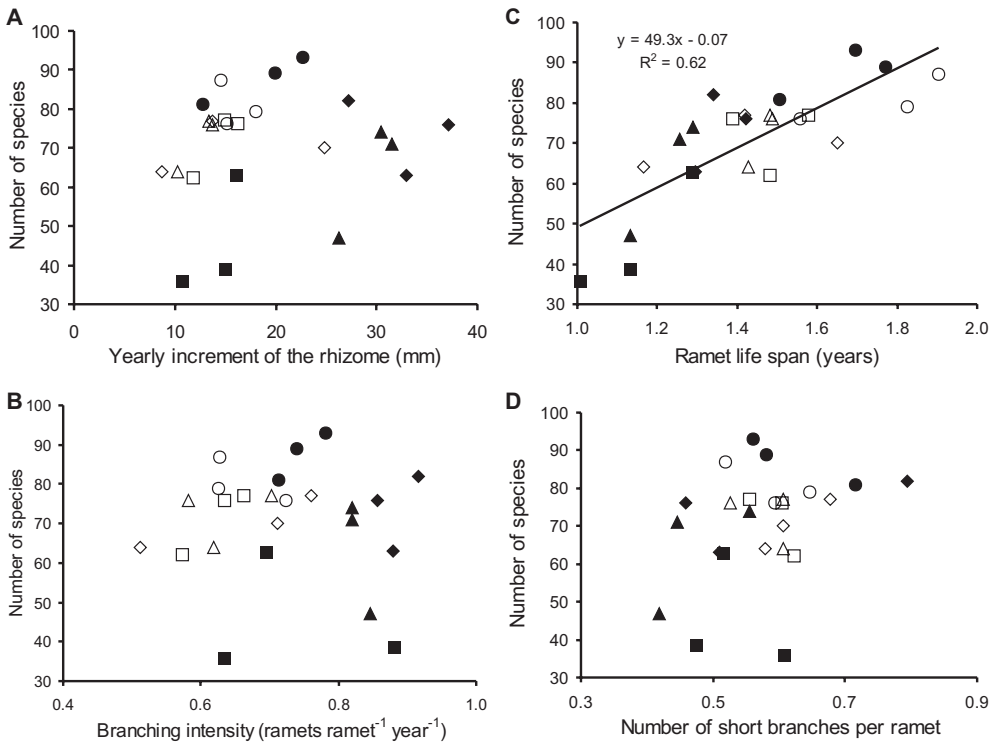

Fig. 3. The relationship between the number of species found in the plot and the corresponding weighted average of the median of yearly increment of the rhizome (A), branching intensity (B), ramet life span (C), and number of short banches per ramet (D). Each point in the figure denotes a separate plot in a single time period. Circles (●) – control plots, diamonds (◆) – PK treatment, triangles (▲) – PKN1 treatment, squares (■) – PKN2 treatment. Open symbols denote the plots at the beginning of the experiment (1962–1964), closed symbols denote the plots at the end of the experiment (1979–1981). The plotted correlation is significant at $P < 0.001$.

these parameters for a species are, the bigger is the ability of the species to gain new space and propagate. Two other parameters (ramet life span and number of short branches) estimate the ability of a genet to keep the space that has been occupied. The patch-holding and vegetative mobility together comprise the major process of community dynamics in perennial herbs.

It is well known that there are species that have the ability for plastic changes in clonal growth in response to changes in environment (see, e.g., the reviews by HUTCHINGS & DE KROON 1994, DE KROON & HUTCHINGS 1995). However, as long as quite similar communities or a restricted area are considered, the parameters may have a species-specific range of variation (KULL & SAMMUL, in prep.). Therefore we treat the values of clonal growth parameters in this study as specific for the Laelatu wooded meadow and realize notion that in some other community these values may not be relevant.

General patterns

It appears that in most cases the species increasing in abundance after fertilization are the species with a bigger ability to spread. These species tend to have longer rhizome branches (i.e., higher vegetative mobility), and higher rhizome branching values (Fig. 2). However, such a response is dependent on the composition of the fertilizers. The increase of more mobile species, most evident in the PK treatment, is reversed by the addition of nitrogen. The response of species with high branching values is similar. This effect is a result of a balance between legumes and grasses, which changes towards a prevalence of grasses in high levels of nitrogen. The abundance of legumes (which are characterized by high mobility and high branching values) increased remarkably in the PK treatment in relation to the control. The most increasing grass species in the PKN2 treatment (e.g., *Dactylis glomerata*, *Festuca rubra*, *Arrhenatherum elatius*) in contrast have a tussock growth form and hence low mobility values. Low mobility is also common for several sedges (e.g., *Carex ornithopoda*) that were very abundant initially, but were first to be excluded by fertilization. Thus, in the treatment that received the highest amount of fertilizers the lost species were replaced by species with similarly low mobility.

Fertilization led to a decrease of the period during which one genet occupies one patch, especially if estimated by the proportion of species with long life-span. For the ability of patch-holding by producing short rhizome branches, the similar tendency (Fig. 2) was statistically not significant (Table 2). The species with long-living individual ramets generally have a low rate of vegetative branching (in terms of ramets per ramet per year), and accordingly in the case of rapid changes in the surroundings, their response is relatively slow.

Evidently, our results depend on the weighting of clonal growth parameters by biomass share of the species in the community. The rationale for this is that communities are not a mere list of species but have specific relationships between the abundances of constituent species. Weighting with biomass makes the results dependent on the fluctuations in the biomass of species. However, in species-rich communities like Laelatu there is no single dominant species whose fluctuations would have an overwhelming effect on the results. Moreover, we averaged three consecutive years to specifically avoid the problem of between-year variation and used biomass share instead of absolute values of biomass. Therefore, the method used is expected to reflect the community structure itself.

Comparison with foraging theory

As shown with theoretical models (SUTHERLAND & STILLMAN 1988, OBORNY 1994), it would be advantageous for clonal plants to reproduce more and move less in spots with higher resource availability. Several studies have shown that higher nutrient levels stimulate the activation of lateral buds and hence increase rhizome branching, while the effect of increasing nutrient levels on rhizome elongation varies among species and is mostly neutral (HUTCHINGS & DE KROON 1994, DE KROON & HUTCHINGS 1995).

Our results demonstrate that when there is an increase in nitrogen availability (i.e. in the sequence of PK-PKN1-PKN2 at the end of the experiment), the species with lower mobility and with lower branching intensity gain in abundance. In contrast, compared to the initial

state, the species with longer rhizome branches dominate in two out of three fertilized treatments and species with more branches increase in all fertilized plots.

The similarity in responses of rhizome increment and branching intensity (Fig. 2) alone suffices to state that one of these parameters behaves similarly to the model of genet-level optimal foraging while the other does not, since the model predicts that it is optimal for plants to increase one trait and decrease the other in response to changes in environment. For our study this would mean that the species with a higher value of one trait and smaller value of the other trait should gain in abundance, but this is not the case. Thus, there appear to be several discrepancies between the theoretically optimal (SUTHERLAND & STILLMAN 1988, OBORNY 1994), the observed intraspecific changes (HUTCHINGS & DE KROON 1994, DE KROON & HUTCHINGS 1995), and the community-level pattern in foraging-related clonal growth parameters (see also review by OBORNY & CAIN 1997).

Relationships between species richness and clonality

The results of the current experiment serve as another example of how fertilization leads to reduced species richness in the community (Table 1). This decrease is caused by increasing the number of species that are lost from the plots with an increasing amount of fertilizers as well as with a decrease of persisting species (Fig. 1). Hence, species richness is controlled by local survival and extinction, while immigration in the plot is not influenced by the fertilization treatment (since the number of species immigrating in the plots was similar in all treatments). This result is in accordance with the studies of the Carousel Model stating that virtually every species can inhabit every patch in the community given enough time (VAN DER MAAREL & SYKES 1993, SYKES et al. 1994), and with studies stressing the importance of competitive interactions in controlling species richness (e.g. GRIME 1973).

It is clear from our results that fertilization increased ramet turnover speed, as it decreased the proportion of species with long-living ramets and mostly (PK and PKN1 in comparison to control) increased rhizome increment and branching intensity. This may have a strong impact on species interactions in meadow communities, since the spatial movement of species is a notable component of small-scale vegetation dynamics (HERBEN et al. 1993, SYKES et al. 1994, HERBEN & HARA 1997) determining which individuals have the potential for interaction, i.e. are located close enough to interact and long enough for interaction to have an effect. However, it is difficult to judge our results in this respect, since there are only a few comparable published data.

The studies of ramet replacement in space and time have shown that there is high ramet turnover in species rich communities (VAN DER MAAREL & SYKES 1993, SYKES et al. 1994), but it has also been shown that low plant mobility does not contradict high species richness (HERBEN et al. 1994, KLIMEŠ 1999). In our case the species richness was related only to the proportion of species with high ramet life span in the community. The latter is in negative correlation with ramet turnover rate. Therefore, and taking into account also the higher abundance of species with higher vegetative mobility in most of the fertilized treatments and the increased average branching intensity with fertilization, our results rather show that species richness may be higher with lower ramet turnover.

CONCLUSIONS

It is important to emphasize that the analysis here concerns the changes in the proportions of species groups in a community. This means that our conclusions are about the changes in the clonal characteristics on the community composition level, and do not claim directly anything about the plasticity effects that may occur in these species.

Our results show that fertilization leads to the increase of ramet turnover speed and to the decrease of species richness. There was no evidence in our data that changes in species composition would create a pattern similar to the negative mobility-branching relationship predicted by the foraging theory. While on the species level the foraging behaviour may be related only to the availability of resources, the specific nature of limiting resource appears to be determining, when changes in species composition are considered.

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APPENDIX

Biomass share and clonal growth characteristics of species (the biomass share is an average of three replicates).

Species	Biomass share of species (%)								Clonal growth parameters (medians)			
	Control		PK		PKN1		PKN2		Ramet lifespan (years)	Rhizome increment (mm year^{-1})	Branching intensity (ramets ramet^{-1} year^{-1})	Number of short branches per ramet
	1962–64	1979–81	1962–64	1979–81	1962–64	1979–81	1962–64	1979–81				
Achillea millefolium	0.01	0.06	0.01	0.22	0.37		0.02	0.03	1	45	2	0.33
Aegopodium podagraria	0.09	0.59	0.07	1.60		2.00		0.11	4	233	0.31	0.00
Agrostis stolonifera	0.39	0.20	0.24	0.09	0.21	0.38	0.34	0.42	1	2	1	0.90
Alchemilla glaucescens	0.11	0.18	0.07	0.22	0.20	0.19	0.12	0.02	5	13	1	0.27
Allium oleraceum		0.05		0.04		0.62	0.03	0.17	2	3.5	1.1	2.17
Allium scorodoprasum		0.36				0.20	0.31	0.21				2.50
Anemone nemorosa	0.01	0.20	0.05	0.01	0.04	0.05	0.03	0.07	1	15	0	0.02
Angelica sylvestris	0.13	0.23	0.11	0.29	0.05	0.25	0.09	0.94	5	5	0	0.04
Antennaria dioica	0.03	0.28	0.05						2	35	1.5	0.00
Anthoxanthum odoratum	0.13	0.47	0.23	1.47	0.35	1.71	0.80	0.08	1	2	0.25	1.31
Anthriscus sylvestris							0.90	0.86			0	
Anthyllis vulneraria	0.46	0.57	0.79	0.04	1.45	0.01	0.04		1	6	1.5	0.91
Arrhenatherum elatius	0.04	0.58	0.02		0.01	1.36	0.26	7.88	1	3	0	1.01
Asperula tinctoria	0.15	0.20	0.11	0.01	0.19	0.02	0.44	0.01	1	18	1	0.50
Betula pubescens	0.03	0.05					0.02		2	0	0	0.00
Brachypodium pinnatum	4.47	5.65	1.37	1.95	2.27	0.54	2.65	0.03	1	4	1	1.28
Briza media	2.07	7.35	1.31	0.77	2.87	0.28	2.69	0.06	1	18	1	0.50
Calamagrostis arundinacea	0.05									10	2	1.38
Calamagrostis epigeios	0.27	1.15	0.17	0.62	0.59	0.24	0.91	0.45	1	6	1	0.46
Campanula cervicaria	0.05		0.01		0.01						0	
Campanula glomerata	0.32	0.98	0.11	0.97	0.25	0.32	0.21	0.01	1	10	1	0.48
Campanula patula				0.00	0.01		0.02		2	7.5	11.5	1.54
Campanula persicifolia	0.10	0.25	0.17	0.19	0.17	0.66	0.16	0.02	1	25	1	0.50
Campanula rotundifolia		0.00							1	24	1.5	0.38
Carex capillaris	0.05	0.01	0.03		0.10							
Carex digitata	0.07		0.03		0.17		0.04		2	34		
Carex ericetorum			0.01						2	13	0.5	0.19
Carex flacca	2.55	2.82	1.50	0.01	1.62	0.02	2.78		2	30	1	0.21
Carex montana		0.19	0.04				0.01		2	13	0	0.36
Carex ornithopoda	0.11	0.98	0.00	0.18	0.10	0.05	0.29	0.01	2	8	1.25	0.80
Carex pallescens	0.01						0.05		2	4	1.5	0.00
Carex panicea	0.90	0.40	0.60	0.01	0.86		0.74		2	14.5	1	0.64
Carex pilulifera	0.01				0.01		0.09		4	12		0.70

Carex pulicaris	0.01	0.02					0.01		2	4	1	0.95
Carex tomentosa	1.91	3.09	0.99	0.14	1.43	0.07	3.44	0.12	1	9	0.5	0.84
Carex vaginata	0.14	0.17	0.06	0.10	0.16	0.00	0.14		2	19	1	0.52
Carex verna	0.08	0.23		0.04	0.01	0.00	0.01	0.01	2	10	0	0.00
Centaurea jacea	7.25	4.97	2.73	2.61	2.87	2.40	1.85	1.81	1	9	1	0.56
Cerastium fontanum					0.01					10		0.65
Cirsium acaule	0.79	2.96	1.29		0.48		0.39		1	13	1	0.31
Clinopodium vulgare		0.10							1	16	1	0.37
Convallaria majalis	1.96	2.40	1.56	0.50	1.05	0.42	0.95	0.21	6	240	0.22	0.00
Crepis paludosa	0.04			0.04	0.06		0.06	0.37	1	9	1	0.64
Crepis praemorsa	0.09	0.32	0.05	0.66	0.11	0.35	0.05	0.15	1	6	1	0.10
Dactylis glomerata	2.06	1.26	1.14	4.52	2.04	6.83	6.25	10.48	1	4.25	0.5	1.03
Dactylorhiza maculata		0.00				0.00						
Danthonia decumbens			0.03							5	1.2	
Deschampsia caespitosa					0.06		0.13	0.30	1	1	1	2.11
Epipactis helleborine				0.02					1	3	1	1.00
Festuca arundinacea	4.30	2.38	1.68	3.21	3.24	3.93	9.57	7.12	1	7	0	0.53
Festuca ovina	0.82	1.12	0.96	0.19	1.65	0.06	1.82	0.01	1	10	1	0.40
Festuca pratensis	0.47	1.03	0.44	5.32	0.24	6.27	0.83	17.92	1	9	1	0.47
Festuca rubra	3.73	4.67	2.42	4.06	4.61	13.18	8.95	16.03	1	5	1	0.32
Filipendula ulmaria	0.01	0.03			0.01		0.02	0.02	1	18	1	0.15
Filipendula vulgaris	0.54	0.13	0.24	0.17	0.16	0.03	0.59	0.13	5	5	0.25	1.00
Fragaria vesca	0.12	0.14		0.01		0.05		0.01	3	186	0.67	0.00
Frangula alnus		0.02							2	0	0	0.00
Fraxinus excelsior		0.01		0.02		0.03		0.00	2	0	0	0.00
Galium boreale	1.17	0.40	0.08	0.32	0.17	0.64	0.33	0.70	1	20	1	0.36
Galium mollugo	1.12	0.28	0.16	0.20	0.18	0.65	0.94	1.96	1	35	1	0.22
Galium verum	0.25		0.17		0.02		0.35		1	25	1	0.35
Gentiana pneumonanthe	0.00									6		1.01
Gentianella uliginosa		0.00							2			
Geranium sanguineum				0.03	0.98	0.10	0.36		1	6	1	0.87
Geum rivale	0.12	0.03	0.06	0.10	0.01	0.14	0.09	0.12	5	15.5	0.71	0.05
Gymnadenia conopsea	0.21	0.15	0.21	0.01	0.11		0.03		1	4		
Gymnadenia odoratissima	0.11		0.04				0.02		1	4		
Helianthemum nummularium	1.71	2.52	1.39	0.12	1.07	0.03	1.49	1	10	0	0.74	
Helictotrichon pratense	10.41	5.91	4.49	1.30	7.73	0.71	8.99	0.20	2	9	0.5	0.86
Helictotrichon pubescens	0.43	0.61	0.11	4.83	0.27	14.16	1.32	12.22	1	15	1	0.25
Hepatica nobilis	0.10	0.35	0.08	0.21	0.13	0.38	0.04	0.16	5	4	0.23	0.98
Heracleum sibiricum				0.46		0.02	0.66	0.23	4	8	1	2.00
Hieracium murorum		0.20		0.03	0.01	0.00						
Hieracium umbellatum	0.01								1	10		0.55
Hypericum maculatum		0.02	0.10						1	45	1	0.03
Hypericum perforatum	0.02	0.05	0.01									
Hypochaeris maculata		0.04	0.03	0.15		0.19		0.02	4	7	0.33	1.25
Inula salicina	0.03	0.12	1.24	0.11	0.28		0.08	0.56	1	22	1	0.30

Knautia arvensis	0.04								1	12	1	0.54
Lathyrus pratensis	2.20	1.75	5.57	27.973.02	18.84	4.82	5.32	1	65	1	0.13	
Lathyrus vernus	3.64	1.66	5.40	0.86	4.40	1.73	1.01		1	6	1	0.82
Leontodon autumnalis			2.06							7		2.00
Leontodon hispidus	5.03	6.73	3.15	0.65	3.86	0.17	1.91		2	6.33	0.5	1.04
Leucanthemum vulgare	1.12	0.69	0.91	0.32	1.24	0.15	0.61	0.00	1	18	1	0.42
Linum catharticum	0.13	0.05	0.05		0.04	0.01	0.01		1	0	0	0.00
Listera ovata	0.10	0.14	0.04	0.23		0.26	0.02	0.07	1	3	1	0.97
Lonicera xylosteum		0.03							2	0	0	0.00
Lotus corniculatus	0.02	0.42		0.32	0.08	0.02	0.01		1	5	1	0.79
Luzula campestris	0.01	0.10	0.01	0.12	0.06	0.04		0.03	2	12		0.38
Luzula multiflora	0.03		0.06				0.09		1	3	0	0.77
Luzula pallidula				0.01		0.04		0.01		4		2.85
Luzula pilosa							2.15		1	4	0	0.58
Maianthemum bifolium								0.02	1	50.5	1	0.39
Malus domestica			0.04						2	0	0	0.00
Malus sylvestris								0.01	2	0	0	0.00
Medicago lupulina	0.31	0.42	5.10	5.13	3.58	0.25	0.98		1	7.5	1	1.05
Melampyrum nemorosum	5.16	19.14	0.02	16.49		4.03	0.01	1	0	0	0.00	
Melica nutans	0.03	0.04		0.01	0.02	0.02	0.01	0.01	1	4	1	0.93
Mentha arvensis	0.04									85		0.00
Molinia caerulea	1.77	1.70	1.66	0.10	1.91	0.02	1.10	0.00	1	3	1	1.01
Myosotis sp.							0.05					
Ophioglossum vulgatum	0.14	0.18	0.04	0.04	0.13	0.01			5	47	0	
Origanum vulgare		0.28							1	20	1	0.45
Paris quadrifolia		0.00				0.05		0.18	1	53	1	0.00
Phleum pratense	0.15		0.22		0.79		0.17		1	8	1	0.87
Pilosella lactucella	0.01											
Pilosella officinarum	0.05	0.13	0.08	0.01	0.04		0.04		2	10	0.5	0.66
Pilosella vaillantii		0.01										
Pimpinella major	0.34	0.03	0.01	0.02		0.05	0.01	0.90	1	7	1	0.64
Pimpinella saxifraga	0.04	0.13	0.05						1	6.75	1	0.86
Pinguicula vulgaris		0.00								8		1.00
Plantago lanceolata	1.88	2.58	1.04	0.57	1.82	0.22	1.23	0.01	3	3	0.63	0.09
Plantago media	1.19	0.85	0.53	0.45	0.90	0.06	0.66		4	5	0	0.21
Poa angustifolia	0.15	1.13	0.09	1.48	0.81	4.62	1.51	3.60	1	14	0.5	0.42
Poa nemoralis						0.00				4		
Poa pratensis	1.07		0.48		1.35		1.80		2	28	0.5	0.55
Poa trivialis	0.01				0.58							
Polygala amarella	0.03	0.09	0.04	0.02		0.00	0.01		1	10	2	1.04
Polygonatum odoratum	0.04		0.06	0.02	0.08	0.05		0.03	1	26	1	0.04
Populus tremula	0.65	0.01		0.07	0.09				2	0	0	0.00
Potentilla erecta	1.07	0.79	0.65	0.03	2.00	0.01	1.12	0.02	3	5.67	0.4	1.18
Potentilla reptans	0.11	0.01					0.03		3	257.5	0.5	0.00
Primula farinosa	0.01	0.02	0.00							4.44		

Primula veris	1.18	0.71	0.41	0.27	0.30	0.74	0.79	0.62	4	5	0.33	1.07
Prunella vulgaris	0.09	0.26	0.08	0.06	0.08	0.00	0.10		1	1	2	1.73
Pyrola rotundifolia	0.07	0.18	0.01	0.03	0.02	0.02	0.11		2	62.5	0.79	0.11
Ranunculus acris	0.14	0.04	0.08	0.04	0.11	0.14	0.21	0.08	1	4	1	1.13
Ranunculus auricomus	0.01		0.01	0.00	0.01		0.02	0.05	3	7.5		1.35
Ranunculus cassubicus					0.01	0.05		0.14	2	3	1	0.71
Ranunculus polyanthemus	0.10	0.40	0.03	0.20	0.05	0.22	0.05	0.26	2	4	1	0.91
Rhamnus catharticus	0.19	0.01		0.00					2	0	0	0.00
Rhinanthus minor		0.11		0.07		0.06			1	0	0	0.00
Rhinanthus serotinus	0.21		0.48		0.32		0.50		1	0	0	0.00
Rosa canina		0.11							2	0	0	0.00
Rosa majalis		0.09							2	0	0	0.00
Rubus caesius	0.17	0.02							1	8	1	0.71
Rubus saxatilis		0.08		0.01		0.15		0.06	1	10	1	0.54
Rumex acetosa				0.04		0.05	0.07	0.18				
Rumex thyrsiflorus			0.01						2	10		0.83
Salix sp.		0.16			0.02				2	0	0	0.00
Saussurea alpina			0.02		0.01					15		
Scorzonera humilis	2.76	1.78	2.03	0.48	1.24	0.31	2.19	0.05	3	18	0.29	0.20
Scrophularia nodosa								0.01		10.5		0.40
Selinum carvifolia		0.00							1	9	1	0.70
Serratula tinctoria	3.76	1.70	1.34	4.09	1.39	1.24	0.94	1.24	4	4	0.38	0.75
Sesleria coerulea	9.99	10.93	7.36	0.32	6.24	0.16	6.06	0.05	2	13	1	0.47
Solidago virgaurea	0.01	0.10		0.02	0.11	0.10	0.02	0.00	2	5	0.29	0.97
Stachys officinalis	0.01									5	1	1.00
Succisa pratensis	0.42	1.25	0.20	0.08	0.56	0.05	0.01	0.03		7	0	0.00
Swida sanguinea	0.09		0.01	0.04	0.06	0.11			2	0	0	0.00
Taraxacum officinale	0.01			0.01		0.02		0.23				
Thalictrum sp.	0.01											
Thymus serpyllum	0.02	0.03								30		
Trifolium montanum	0.30	0.07	0.32	0.68	0.07	0.10	0.01		5	5	0.24	1.29
Trifolium pratense	0.33	1.62	8.60	9.03	3.93	2.93	1.04	0.65	1	5	1	1.89
Trifolium repens			0.05	0.09					2	61.5	1	0.19
Trisetum flavescens	0.27			0.01					1	2		
Trollius europaeus	0.20	0.01	0.17	0.03	0.22	0.48	0.18	1.50	2	3	1	1.29
Veronica chamaedrys	0.10	0.32	0.13	0.75	0.37	2.30	0.23	1.93	1	90	1	0.11
Veronica officinalis		0.02	0.01	0.00			0.05		1	18.5	1.5	1.07
Viburnum opulus	0.07	0.02							2	0	0	0.00
Vicia cracca	0.24	0.21	2.30	3.57	0.49	0.12	0.08	0.12	1	40	2	0.47
Vicia sepium	0.11	0.18	1.02	3.29	0.43	3.85	0.17	0.34	1	70	1	0.25
Viola canina		0.00		0.01				0.01		9		0.78
Viola mirabilis	0.01	0.09	0.02	0.17	0.05	0.21	0.00	0.03	1	13	1	0.00
Viola montana		0.00		0.01		0.00				9		0.78